Biol Invasions
DOI 10.1007/s10530-016-1135-0

ORIGINAL PAPER

A synergistic trio of invasive mammals? Facilitative interactions among beavers, muskrats, and mink at the southern end of the Americas

Ramiro D. Crego · Jaime E. Jiménez · Ricardo Rozzi

Received: 18 September 2015 / Accepted: 25 March 2016

Abstract With ecosystems increasingly having co-occurring invasive species, it is becoming more important to understand invasive species interactions. At the southern end of the Americas, American beavers (*Castor canadensis*), muskrats (*Ondatra zibethicus*), and American mink (*Neovison vison*), were independently introduced. We used generalized linear models to investigate how muskrat presence related to beaver-modified habitats on Navarino Island, Chile. We also investigated the trophic interactions of the mink with muskrats and beavers by studying mink diet. Additionally, we proposed a conceptual species interaction framework involving these invasive species on the new terrestrial community. Our results indicated a positive association between muskrat presence and beaver-modified habitats. Model average coefficients indicated that muskrats preferred beaver-modified freshwater ecosystems, compared to not dammed naturally flowing streams. In addition, mammals and fish represented the main prey items for mink. Although fish were mink's dominant prey in marine coastal habitats, muskrats represented >50 % of the biomass of mink diet in inland environments. We propose that beavers affect river flow and native vegetation, changing forests into wetlands with abundant grasses and rush vegetation. Thus, beavers facilitate the existence of muskrats, which in turn sustain inland mink populations. The latter have major impacts on the native biota, especially on native birds and small rodents. The facilitative interactions among beavers, muskrats, and mink that we explored in this study, together with other non-native species, suggest that an invasive

---

Electronic supplementary material The online version of this article (doi:10.1007/s10530-016-1135-0) contains supplementary material, which is available to authorized users.

R. D. Crego (✉) · J. E. Jiménez · R. Rozzi
Department of Biological Sciences, University of North Texas, 1511W Sycamore, Denton, TX, USA
e-mail: ramirocrego84@gmail.com

J. E. Jiménez · R. Rozzi
Department of Philosophy and Religion, University of North Texas, 1155 Union Circle, Denton, TX, USA

R. D. Crego · J. E. Jiménez · R. Rozzi
Instituto de Ecología and Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Casilla 653, Santiago, Chile

J. E. Jiménez · R. Rozzi
Universidad de Magallanes, Manuel Bulnes 1855, Punta Arenas, Chile

R. D. Crego · J. E. Jiménez · R. Rozzi
Sub-Antarctic Biocultural Conservation Program, University of North Texas, 1155 Union Circle, Denton, TX, USA

meltdown process may exist; however further research is needed to confirm this hypothesis. Finally, we propose a community-level management to conserve the biological integrity of native ecosystems.

Keywords Cape Horn · Ecosystem changes · Invasive meltdown · Invasive species interactions · Sub-Antarctic Magellanic forests

Introduction

The movement of species around the globe mediated by humans has been so persistent that currently almost all ecosystems, even in remote places, include multiple invasive species (Hobbs et al. 2006). While most studies focus on the relationships of single invasive species with native ones, it is becoming more important to understand the interactions among invasive species that coexist in the same colonized habitats (Kuebbing et al. 2013). These interactions have crucial implications for management and ecological restoration of affected ecosystems (Zavaleta et al. 2001).

Interactions between invasive species can be neutral, negative (antagonistic), or positive (facilitative) with different implications for the net ecological impact (Kuebbing and Nuñez 2014; Jackson 2015). In neutral interactions, invasive species do not affect each other and their ecological impacts remain independent, whereas in antagonistic interactions invasive species affect each other through competition, predation, or parasitism, resulting in a net impact that is less than the sum of their independent effects (Kuebbing and Nuñez 2014; Jackson 2015). In contrast, facilitative interactions tend to increase the net negative impacts of coexisting invaders. These impacts can be additive, the sum of their independent effects, or synergistic. Synergistic interactions are known as "invasional meltdown," a complex community-level process in which one invasive species increases the likelihood of survival and/or the magnitude of impacts of other invasive species that are greater than the sum of their independent effects (Simberloff and Von Holle 1999; Simberloff 2006).

Two recent meta-analyses have shown that interactions between co-occurring invasive plants or animals are mostly neutral or antagonistic (Kuebbing and Nuñez 2014; Jackson 2015). Nevertheless, an increasing number of studies are documenting facilitative additive interactions (Johnson et al. 2009; Tella et al. 2016) and synergistic interactions among invasive species with broad ecological impacts (Heimpel et al. 2010; Green et al. 2011; Nuñez et al. 2013; Hayward et al. 2015). As Jackson (2015) points out, more research is needed to examine the complex interactions among multiple invaders, especially for invasive animals in terrestrial ecosystems, including a broader taxonomic and geographic spectrum to overcome a bias toward studies of arthropods and aquatic ecosystems in the USA. In this context, the mosaic of forest and wetland ecosystems at the southern end of the Americas provides an ideal case.

Several non-native species have established in the Magellanic Sub-Antarctic ecoregion of South America, one of the less directly human-impacted regions of the world (Rozzi et al. 2006). Today, non-native mammalian species outnumber natives (Anderson et al. 2006a; Valenzuela et al. 2014). Three out of the 12 documented non-native mammals in this region are considered the most invasive and harmful: the American beaver (*Castor canadensis*), the muskrat (*Ondatra zibethicus*), and the American mink (*Neovison vison*) (Anderson et al. 2006b). These three species, which naturally interact in their native range in North America and Canada (Viljugrein et al. 2001; Shier and Boyce 2009; Mott et al. 2013), create an assemblage that has a large impact on biodiversity (e.g. Schüttler et al. 2008, 2009) and the structure and function of Magellanic Sub-Antarctic ecosystems (e.g. Anderson et al. 2006b; Anderson and Rosemond 2007).

The beaver is one of the best known and studied invasive species in the Magellanic Sub-Antarctic ecoregion. Since the introduction of beavers in 1946 to Tierra del Fuego Island (Jaksic et al. 2002), they quickly colonized nearly every environment. Given their nature as ecosystem engineers, their dam and den building and foraging activities have altered stream nutrient cycles and stream food webs (Anderson and Rosemond 2007; Ulloa et al. 2012), and changed large areas from closed southern beech (*Nothofagus* spp.) forests to grass- and rush-dominated meadows (Anderson et al. 2006b; Martínez Pastur et al. 2006). These habitat alterations are extensive in spatial scale and long-lasting with likely permanent changes from forest to meadows (Martínez Pastur et al. 2006).

Beaver ponds are frequently used in North America by muskrats (Mott et al. 2013); another species capable of altering invertebrate and plant abundance and nutrient flow in aquatic habitats (Connors et al. 2000; de Szalay and Cassidy 2001). Muskrats were introduced to Tierra del Fuego simultaneously with beavers (Jaksic et al. 2002; Deferrari 2007); however, there are no studies on their potential impact on stream banks and wetlands. Additionally, the mink was introduced to Tierra del Fuego during the 1940s, becoming abundant along the Beagle Channel by the end of the 1990s (Lizarralde and Escobar 2000). Shortly after, they crossed the channel reaching Navarino Island, in southern Chile (Rozzi and Sherriffs 2003). Mink are natural predators of muskrats (Eagle and Whitman 1987) and correlated population fluctuations in this predator–prey interaction have been documented in Canada (Viljugrein et al. 2001; Shier and Boyce 2009). On Navarino Island, muskrats represent a substantial portion of mink's diet, especially during winter (Schüttler et al. 2008; Ibarra et al. 2009) when other food sources diminish in abundance. As Navarino Island was free of native terrestrial mammalian predators, mink negatively affect native avian (Schüttler et al. 2009; Maley et al. 2011; Jiménez et al. 2014) and likely rodent populations (Crego et al. 2014).

Although facilitation effects between beavers and muskrats (Silva and Saavedra 2008) and muskrats and mink (Schüttler et al. 2008) have been suggested, no study has investigated the association among these three mammalian species and the community-level effects of their interactions. In this study, we investigated beaver, muskrat, and mink interactions in forest-dominated areas of northern Navarino Island, Chile. We asked three questions. First, does the muskrat presence depend on beaver-modified habitats? Second, is there a current strong trophic relationship between mink and muskrats and/or mink and beavers in the marine coast and in inland habitats? And third, based upon this and on previously published studies on Navarino Island, are these three species interacting in an "invasive meltdown" process, incurring a larger negative impact on the native and non-native terrestrial community as compared to each species' impact independently?

Low variations in water levels found in standing waters, such as ponds (lentic waters), and aquatic vegetation make habitats suitable for muskrats (Artimo 1960). However, on Navarino Island, streams are steep mountain rivers with narrow river beds and high water velocities (lotic or running waters) (Contador et al. 2015). Given that beaver transform riparian forests into meadows resulting in a transformation from a lotic aquatic system into a lentic one with abundant grass and rush vegetation (Anderson et al. 2006b), we predict that muskrats will be present in beaver-modified habitats and will be absent in non-modified lotic streams. In addition, given the known predator–prey interaction between mink and muskrats, we expect that muskrats will be well-represented in mink diet in inland rivers and ponds, as a more sea-dominated diet would be expected nearer the marine shoreline (Gomez et al. 2010). As beavers do not represent natural prey of mink (Schüttler et al. 2008) no predation on beaver will be expected. Overall, we propose the existence of facilitative interactions between beavers and muskrats, which otherwise would not be present in the study region, and between muskrats and mink, since muskrats could provide a substantial component of the diet for mink population inhabiting inland environments. By forming a synergistic sympatric trio, these three invasive species will have a greater impact on the Magellanic Sub-Antarctic biota and ecosystems.

Materials and methods

Study area

This study was conducted on the northern slope of Navarino Island (68°W, 55°S, ca. 2500 km^2), in the southern end of South America. Navarino Island is part of the Cape Horn Biosphere Reserve (Fig. 1), which protects the southernmost ecosystems of the Sub-Antarctic Magellanic forest ecoregion (Rozzi et al. 2012). The forests are dominated by *Nothofagus betuloides*, *N. pumilio*, *N. antarctica* and *Drimys winteri*, which are embedded in the Magellanic moorland complex, comprised of a matrix of peatlands and meadows (Rozzi et al. 2006). The rugged topography presents a mountain landscape, with maximum altitudes $\leq$1000 m.a.s.l. The climate is oceanic and cold, with a mean annual temperature of 6 ± 5 °C. Precipitation is uniform with an annual average of 467.3 mm (Rozzi and Jiménez 2014).

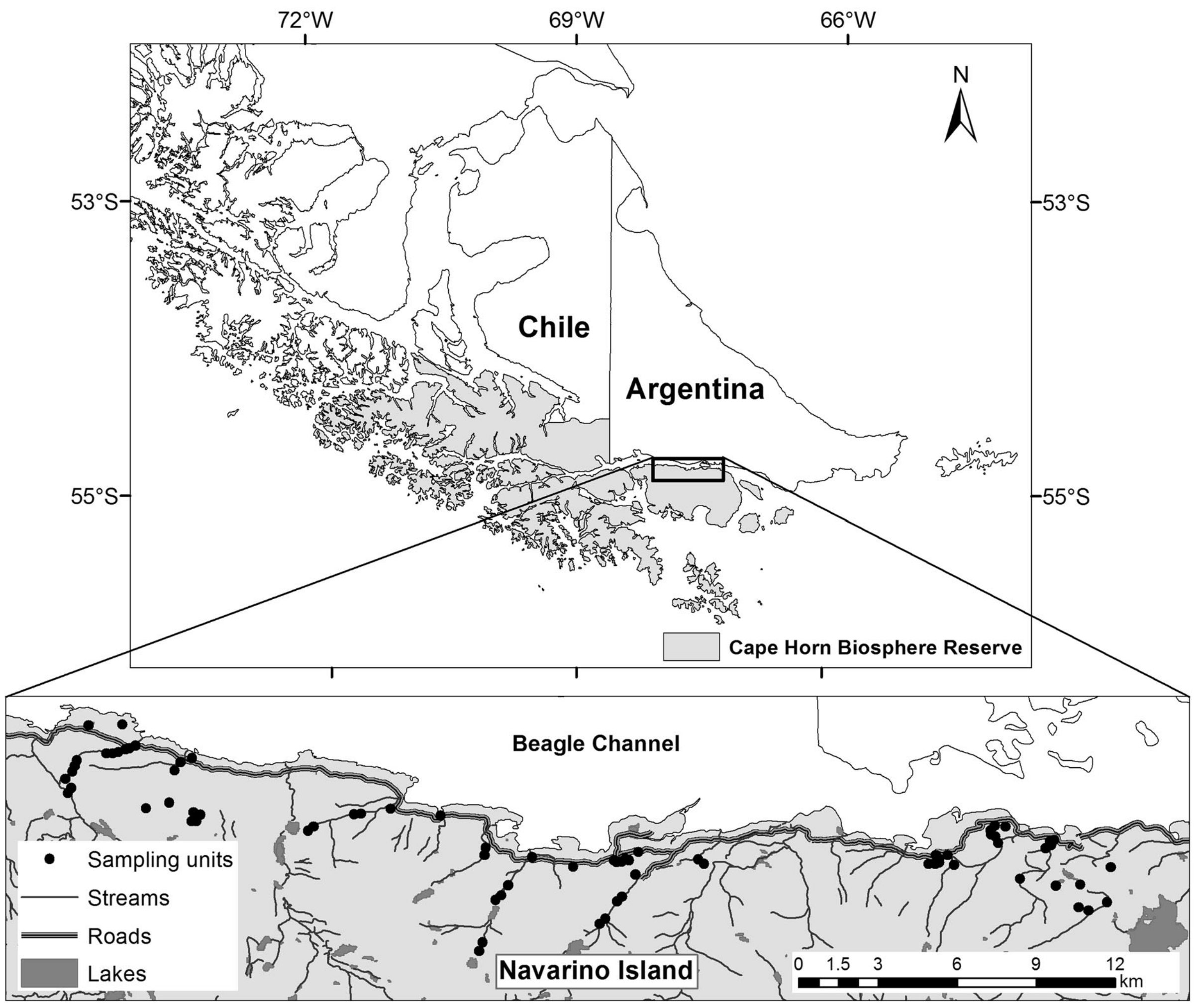


Fig. 1 Location of 75 sampling units used to survey presence or absence of muskrats in streams and beaver ponds along the northern slope of Navarino Island, within the Cape Horn Biosphere Reserve, southern Chile

American beaver—muskrat interaction

Data collection

In 2014 and 2015, from February to April (austral late summer-early fall), we documented the presence/absence of muskrats by sampling their tracks, scats, and burrows along 75,200-m transects >100 m apart (Engeman and Whisson 2005) in an area of approximately 70 km^2. Transects were run parallel along the banks of streams and beaver ponds non-randomly, as they were surveyed while developing another research project to study mink with camera traps (Crego et al. unpublished data). However, while walking through the diverse habitats between random points where cameras were deployed, we decided the starting point of transects where a stream or a beaver pond was crossed (Fig. 1). We sampled 14 different streams ensuring starting points of transects were >100 m apart from starting or ending point of other transects. We avoided placing two transects in the same beaver pond. Transects were walked following the coast of streams or ponds by two observers, one on each side of the stream, or walking together along the shore on beaver ponds. For transects located alongside a beaver pond, we searched for fresh tree cuts or tracks to determine recent beaver activity. The 75 transects were classified into four types of aquatic systems: 15

were active beaver dams with a lentic pond system, 21 inactive beaver dams with a lentic pond system, 18 inactive beaver dams with a lotic system (i.e., old beaver dams with recovered stream flow), and 21 lotic streams with no beaver activity.

The high altitudinal gradient of the region is important in shaping the fresh-aquatic system and determining streams water flow, with steeper streams found at higher altitudes (Contador et al. 2015). To account for the potential effect of altitude and water flow on muskrat presence we recorded the mean altitude between the starting and ending point of each transect using a GPS unit. In addition, muskrats arrived to Navarino Island likely on the north coast crossing the Beagle Channel from Tierra del Fuego (Jaksic et al. 2002). To account for a possible effect on distance from the Beagle Channel on muskrat presence, we calculated the shortest distance to the sea shoreline from the center point of each transect using ArcGIS 10 (ESRI, Redlands, California, USA). Finally, we categorized riparian habitat by the predominant vegetation observed at each transect either as forest or meadow. Forest was primarily composed of mature evergreen (*N. betuloides*, *D. winteri*) or deciduous (*N. pumilio, N. antarctica)* tree species, while meadows were dominated by *Sphagnum spp.* mosses and the rush *Marsippospermum grandi*, native and non-native grasses, and sometimes *N. antarctica*, the only tree species adapted to flooded zones (Rozzi et al. 2006).

Statistical analysis

We fit generalized linear models (GLMs) with binomial distributions and logit functions to study how muskrat presence was related to the four predefined aquatic system types, altitude, distance from marine shoreline, and habitat type (forest or meadow). We first examined correlations among variables based on a cluster analysis using package *Hmisc* in R programming language (R Development Core Team 2013). Altitude and shortest distance to marine shoreline were highly correlated (*rho* = 0.76). Therefore, we decided to discard shortest distance to sea shoreline and used altitude given the importance of the high altitudinal gradient of the region determining streams water flow and the importance of water flow on muskrat establishment (Artimo 1960). Data in the full model presented a good fit (c-hat = 1.06); thus, there was no need to account for overdispersion (Crawley 2002). To select the most parsimonious models, we used Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). We performed model average within models of $\Delta AIC_c < 2$ to calculate parameter estimates, unconditional standard errors, and 95 % confidence intervals (CI) for each explanatory variable (Burnham and Anderson 2002). We used the package *AICcmodavg* in R programming language for model selection analysis (R Development Core Team 2013).

American mink trophic interaction

Data collection

We analyzed the trophic relationship of minks with beavers and muskrats by examining 202 mink scats collected between February 2014 and April 2015 at 24 sites. Collection sites were >1 km apart to ensure that scats represented different individuals.

We washed each sample with warm water, sieved it through a 0.3 mm mesh, and dried it on a stove. We identified undigested remains using a binocular microscope to the lowest taxonomic level possible and classified items into seven categories: mammals, birds, fish, insects, crustaceans, mollusks, and seeds. For prey identification, we used different techniques: arthropods were identified by local entomologists; small mammalian hairs, bones, and teeth were compared with voucher specimens, photographs, and guides (Chehébar and Martín 1980; Pearson 1995); barbules of bird feathers were compared with keys (Rau and Martínez 2004) and local references; and fish scales and bones, as well as seeds, were compared to local references. We excluded plant material and crustaceans <5 mm in length as they were considered as secondary prey, incidental intake, or adhesion after defecation (Valenzuela et al. 2013). Each scat was weighted to the nearest 0.1 g and the percentage volume of each prey category was estimated to the nearest 5 % (Schüttler et al. 2008).

Statistical analysis

To compare with previous studies in Navarino Island, we followed Schüttler et al.'s (2008) analyses. We calculated two indices that quantified relative importance of each prey group on mink's diet: the relative frequency of occurrence (RFO) expressed as a percentage (number of occurrences of a prey category divided by the number of occurrences of all prey categories) and the percentage of biomass (BIO) (dry mass of prey item multiplied by its empirically-determined coefficients of digestibility divided by the total corrected mass of scats). The coefficient of digestibility represents the ratio between the biomass of prey consumed and the dry mass of undigested remains in scats, enabling more accurate estimations of real prey intake of different size and digestibility (Brzezinski and Marzec 2003). We used the following correction factors obtained from the literature: mammals (17.3), birds (17.2), eggs (687.5), fish (30.8), crustaceans and mollusks (14.8) (from Brzeziński and Marzec 2003), insects (5.0) and seeds (14.0) (from Lockie 1961).

We differentiated scats found along the marine coast ($n = 92$; <100 m from the marine shoreline) from those found on inland rivers and ponds located in forests and meadows ($n = 110$; >100 m from the marine shoreline). We tested for differences in diet composition between habitats using Chi squared tests with Yates' continuity and Bonferroni corrections, and Fisher's exact tests when expected values were <5.

Conceptual framework of community interactions

To describe a proposed scenario of direct pairwise interactions in the recently-formed terrestrial community, we conducted a literature review of peer-reviewed studies on Navarino Island regarding the effects of the three invasive mammal species. Then, following Simberloff and Von Holle (1999) definitions of species interactions in an invasive meltdown framework, we defined four types of interactions: "+/+": individuals of two species benefited from the presence of one another; "+/0": individuals of the first species benefited from the presence of the other, whereas individuals of the second species were not known to be affected by the presence of the first; "+/−": individuals of the first species benefited by the presence of the second, whereas individuals of the second were negatively affected by the first (Simberloff and Von Holle 1999); and we added, "0/0": no effects of one species on the other. Beaver effects on aquatic invertebrates were not included given that for the scope of this analysis the interactions are complex and numerous, and also depend on the species, where some are benefited and others are affected (see Anderson and Rosemond 2007; Ulloa et al. 2012).

Results

American beaver—muskrat interaction

We detected muskrat signs in 41 % of transects. Muskrat activity signs were found 39 % in forest habitat and 61 % in meadows; 97 % were in beaver-modified habitats. Based on AICc, we found two best-supported models that best explained the presence of muskrats (Table 1). Together these models accounted for 76 % of model weight, and included the three co-variables: altitude, habitat type, and type of aquatic system. On the base of the averaged model, the probability of finding muskrats showed a decreasing trend with altitude (Fig. 2), however 95 % CI included zero (Table 2). Similarly, meadows presented higher probability of muskrat presence than forests; nevertheless 95 % CI of the parameter included zero and this variable was present only in one of the two best-supported models (Table 2). The most influential factor on the probability of muskrat presence was the type of aquatic system, being higher for inactive and active beaver ponds, lower for beaver-modified habitats where the river flow was recovered, and almost nonexistent in lotic streams with no beaver intervention (Fig. 2). The lotic streams parameter estimate and 95 % CI presented negative values in relation to active beaver dams, whereas the lotic inactive beaver dams parameter estimate was negative, but with 95 % CI including zero (Table 2).

American mink trophic interaction

Mink feces analysis showed that overall, mammals represent the main prey item (relative frequency of occurrence [RFO] = 27.21 %; percentage of biomass [BIO] = 41.91 %), followed by fish (RFO = 23.54 %; BIO = 36.11 %), and birds (RFO = 20.18 %; BIO = 12.94 %; Fig. 3). Relative frequency of occurrence of mammals, fish, and birds were not significantly different ($\chi^2 = 1.04$, $df = 2$, $p = 0.59$), but mammals and fish biomass represented a significantly higher intake than birds ($\chi^2 = 15.301$, $df = 1$, $p < 0.0001$; $\chi^2 = 10.95$, $df = 1$, $p < 0.0009$, respectively). Insects and seeds were frequent (13.14 and

Table 1 Model selection results to investigate muskrat presence on Navarino Island, Chile

Model	K	AICc	ΔAICc	AICc W	Cum W
Aquatic system + altitude	5	85.16	0.00	0.54	0.54
Aquatic system + habitat + altitude	6	86.85	1.70	0.23	0.76
Aquatic system	4	87.59	2.44	0.16	0.92
Aquatic system + habitat	5	89.07	3.91	0.08	1.00
Habitat + altitude	3	99.20	14.04	0.00	1.00
Habitat	2	100.40	15.25	0.00	1.00
Altitude	2	102.12	16.96	0.00	1.00
Null model	1	103.76	18.61	0.00	1.00

K number of estimated parameters, *AICc* Akaike's information Criterion corrected for small samples, *ΔAICc* differences in AICc, *ΔAICc W* akaike weight, *Cum W* cumulative Akaike weight

All candidate models and the null model are presented. The explanatory variables are aquatic system (active beaver dam with pond lentic system, inactive beaver dams with a pond lentic system, inactive beaver dams with a lotic system, lotic stream with no beaver), habitat type (forest or meadow), and altitude

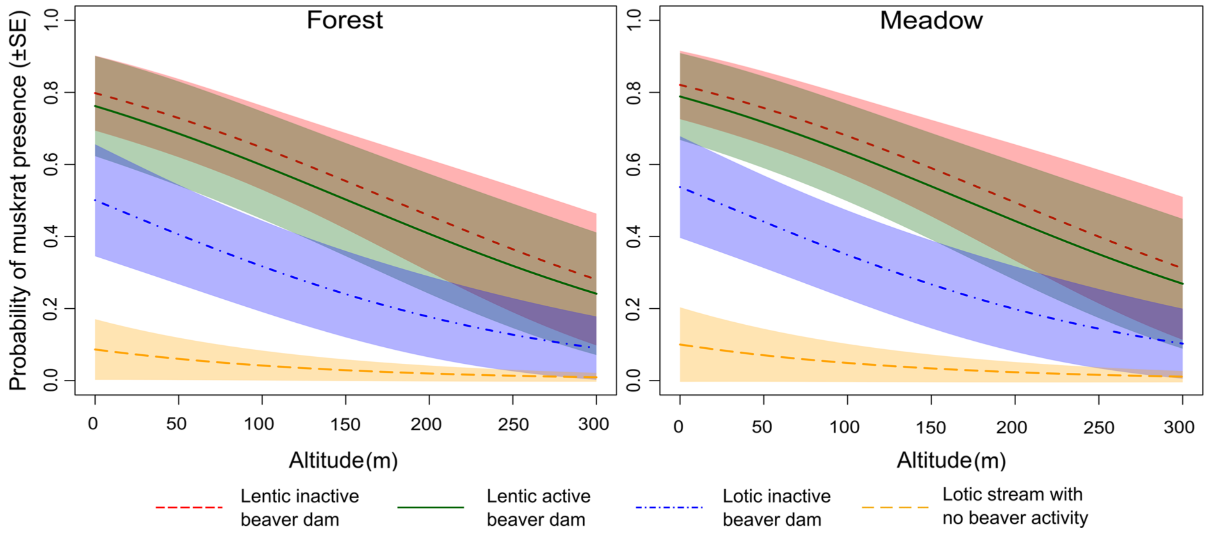


Fig. 2 Predicted muskrat presence (±1 SE) based on average model of best-supported models on the northern slope on Navarino Island, Chile (February–April 2014 and 2015), for meadow and forest habitats in relation to altitude for four different aquatic systems: inactive beaver dams with a pond lentic system (*red*), active beaver dams with a pond lentic system (*green*), inactive beaver dams with a lotic system (i.e. old beaver dams with recovered stream flow; *blue*), and lotic streams with no beaver activity (*orange*)

10.09 %), but represented a small amount of the biomass intake (2.43 and 3.38 %, respectively; Fig. 3). Within mammals, muskrats were the most frequent prey, representing 25.57 % of the biomass consumed. In contrast, beavers were almost completely absent in the mink's diet (RFO = 0.3 %; BIO = 0.09 %).

We found a significant difference between mink's diet in marine vs inland habitats (RFO: Fisher's exact test, $p < 0.0001$; BIO: Fisher's exact test, $p < 0.0001$). While fish represented 70.34 % of the biomass intake by mink in marine habitats, mammalian biomass was 69.65 % in inland habitats. Diet within marine habitat concentrated specifically on seashore fishes of the family Nototheniidae (RFO = 36.25 %; BIO = 67.75 %; Online Resource 1). Muskrats were nearly absent in scats collected along

Table 2 Model averaged coefficients, unconditional standard errors (± SE), and 95 % confidence intervals for the best-supported models (ΔAICc < 2) relating muskrat presence in aquatic systems, habitat types, and altitude on Navarino Island

Variable	Parameter estimate	±SE	95 % CI	
Aquatic system-lentic inactive beaver dam	0.21	0.74	−1.25	1.66
Aquatic system-lotic inactive beaver dam	−1.17	0.78	−2.71	0.37
Aquatic system-lotic stream no beaver	−3.53	1.20	−5.89	−1.18
Altitude	−0.01	0.00	−0.02	0.00
Habitat-meadow	0.49	0.61	−0.69	1.68

Variables of aquatic system were compared to the base factor, lentic active beaver dam; whereas habitat type meadow was compared to the base factor forest

the marine coast (RFO = 0.62 %; BIO = 0.14 %); however, they represented not only the most important mammalian prey (75.62 % of mammal prey biomass), but also the most important mink prey item in inland habitats (RFO = 20.95 %; BIO = 52.67 %; Fig. 3).

Conceptual framework of community interactions

We found and evaluated 9 published research articles on the effects of beaver, muskrat, or mink on other biota conducted on Navarino Island that complement this study (Table 3). Based on the data from these sources combined with those of our study, we propose an interaction network among the three invasive core species, as well as with other species or group of species that are part of the new terrestrial community assemblage (Table 3; Fig. 4). Our study suggests that beavers directly benefit (0/+) muskrats by creating new habitat. Mink benefit from the presence of muskrats in a predator/prey interaction (+/−), as muskrats are affected by this predation pressure. Beavers have no direct effect (0/0) on mink; however, mink benefit indirectly through the habitat provided for the muskrat.

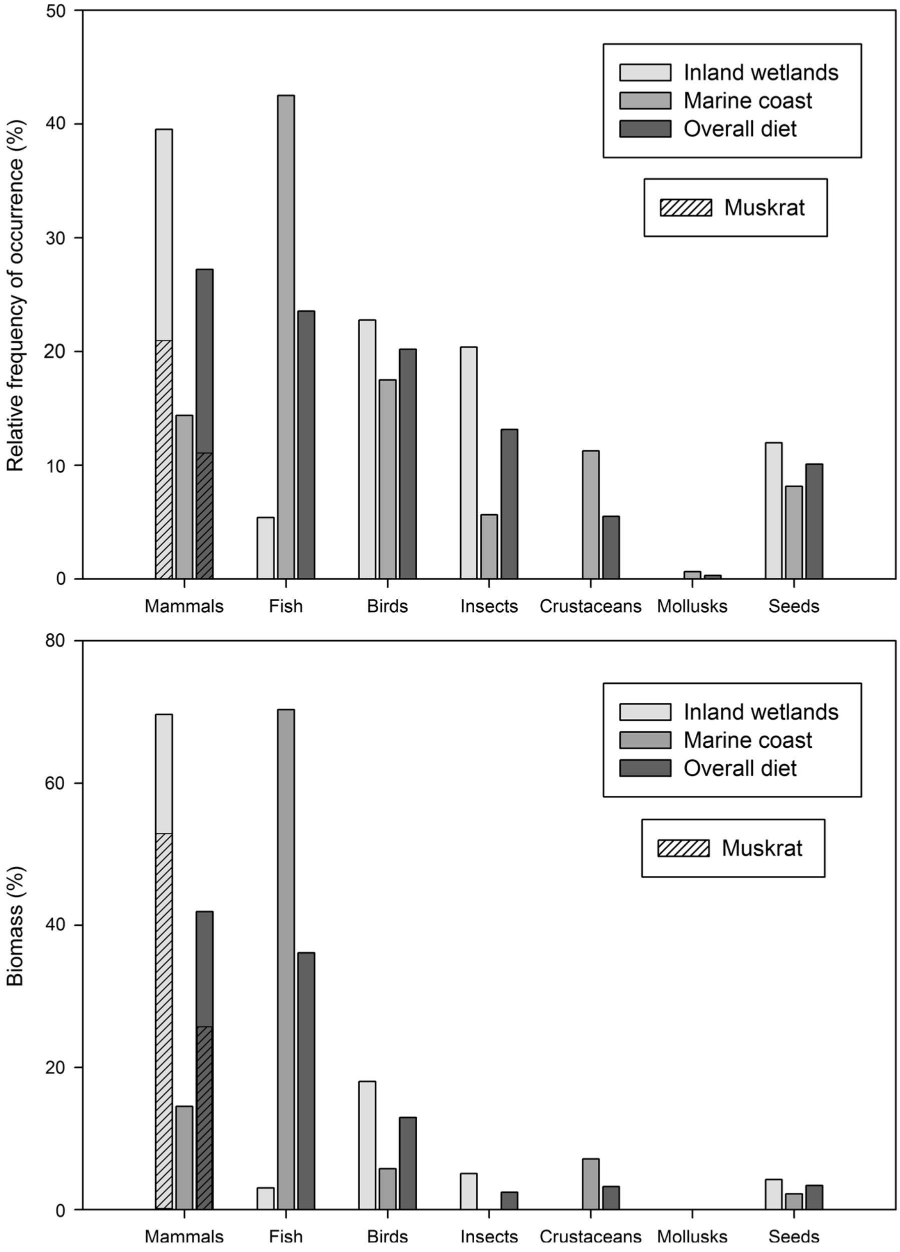
By examining direct interactions with the rest of the community, we can conclude that beavers negatively affect southern beech forests (+/−), whereas they have neutral effects (0/0) on invasive trout species [brook trout (*Salvelinus fontinalis*), and rainbow trout (*Oncorhynchus mykiss*)]. Beavers positively affect (0/+) a native fish species (*Galaxias maculatus*), and exotic grasses by creating suitable habitat. Beavers also appear to favor Magellanic Woodpeckers (*Campephilus magellanicus*) (0/+) by temporarily increasing foraging opportunities; however, this benefit diminishes over time through habitat loss. Additionally, mink potentially benefit by the presence of trout (+/−), as it comprises a small portion of mink's diet; however, trout negatively affect the native fish, *G. maculatus* (+/−). Moreover, mink negatively affect (+/−) several native vertebrate species including, geese, ducks, forest birds, and two species of small rodents by preying upon them.

Discussion

The fur industry catalyzed the introduction of three of the most invasive and harmful species to the Cape Horn Biosphere Reserve and Tierra del Fuego: the beaver, the muskrat, and the mink (Anderson et al. 2006a). These three species form a natural assemblage in their native ranges at temperate and subpolar latitudes in North America. Our results suggest that this same assemblage is now successfully established at subpolar latitudes of South America, synergistically interacting to invade and change the terrestrial community of the once "pristine" sub-Antarctic Magellanic forests.

Conforming to our first hypothesis, muskrats are more likely to be found in beaver-modified habitats, where conditions are more suitable than in naturally-occurring fast flowing streams, where muskrats are almost completely absent. Beaver ponds appear to facilitate muskrat's establishment by creating suitable habitat. The probability of muskrat presence was equally high for lentic beaver ponds, whether or not beavers were present. Thus, the association between the muskrat and the presence of beaver appears to be facultative after beaver have modified the hydrological system. The effect of beaver on the river bed is long lasting in time; however, when the river recovers its flow dynamic, the probability to find muskrats becomes lower than in lentic ponds, but still important,

Fig. 3 Diet of the American mink on Navarino Island (February 2014 to April 2015) expressed as relative frequency of occurrence (RFO) and biomass (BIO) in inland habitats (rivers and ponds located in forests and meadows), marine coast, and overall diet. RFO and BIO of muskrat in mink diet is highlighted



likely due to the remaining abundant vegetation in the river bed. In this study, we did not assess large lakes that are common to Navarino, especially on the southern part of the island, because lakes are not abundant on the northern slope of Navarino and because our goal was to compare rivers with and without beaver impact. Moreover, the literature indicates that muskrats cannot establish viable populations on oligotrophic lakes due to the lack of vegetation productivity needed for their own survival (Artimo 1960). Further research should address this; however, it is important to note that during the course of our study, besides observing many beavers and beaver dens on lakes, no muskrat nor muskrat track, scat, or burrow were observed.

At a regional scale, a distribution analysis of muskrats and beavers shows that both species occur on the same major islands in the archipelagoes of the

Table 3 Types and nature of direct interactions based on literature and present study among the three invasive species, American beaver, muskrat, and American mink and with other non-native species [Exotic grasses, brook trout, and rainbow trout] and native species [Trees of the genus *Nothofagus*, Magellanic woodpecker, several species of Anseriform and Passeriform birds, two species of rodents (*Abrothrix xanthorhinus* and *Oligoryzomys longicaudatus*), and one species of native fish (*Galaxias maculatus*)] in the new terrestrial community of Navarino Island, Chile

Species	Interaction type	Nature of interaction	Source
American beaver—*Nothofagus spp.*	+/−	Foraging, soil modification	(Anderson et al. 2006b)
American beaver—exotic grasses	+/+	Foraging, soil modification	(Anderson et al. 2006b)
American beaver—Magellanic Woodpecker	0/+	Increase of foraging opportunities	(Soto et al. 2012)
American beaver—muskrat	0/+	Creation of suitable habitat	This study
American beaver—American mink	0/0	Neutral effects	(Schüttler et al. 2008; Ibarra et al. 2009; This study)
American beaver—trout	0/0	Neutral effects	(Moorman et al. 2009)
American beaver—native fish	0/+	Creation of suitable habitat	(Moorman et al. 2009)
American mink—Muskrat	+/−	Predator/prey	(Schüttler et al. 2008; Ibarra et al. 2009; This study)
American mink—anseriformes	+/−	Predator/prey	(Schüttler et al. 2008, 2009; Ibarra et al. 2009; This study)
American mink—passeriformes	+/−	Predator/prey	(Schüttler et al. 2008; Ibarra et al. 2009; Maley et al. 2011; Crego et al. 2014; This study)
American mink—Magellanic Woodpecker	+/−	Predator/prey	(Jiménez et al. 2014; This study)
American mink—small rodents	+/−	Predator/prey	(Schüttler et al. 2008; Ibarra et al. 2009; Crego et al. 2014; This study)
American mink—trout	+/−	Predator/prey	(Schüttler et al. 2008; Ibarra et al. 2009; This study)

Cape Horn and Tierra del Fuego region (Deferrari 2007; Valenzuela et al. 2014; Crego et al. 2015). Moreover, muskrat expansion history from its initial point of release in Tierra del Fuego followed beaver expansion (Jaksic et al. 2002). For instance, estimates suggest beavers and muskrats crossed the Beagle Channel to Navarino Island around 1962 (Jaksic et al. 2002). Even if other factors may explain this biogeographical pattern, the sympatric distribution provides another strong evidence for the facilitative interactions between beavers and muskrats at the southern end of the Americas.

In line with our second hypothesis, our results show a strong trophic interaction between mink and muskrats in inland habitats, with muskrats representing >50 % of its total biomass intake. In contrast, similarly to results from previous studies on Navarino (Schüttler et al. 2008; Ibarra et al. 2009) and in its native range (Dunstone 1993), mink did not prey on beavers, and beaver consumption may be only opportunistic.

Mink are generalist predators, preying on a wide range of items along its range in Patagonia (e.g., Previtali et al. 1998). However, only in the Cape Horn Biosphere Reserve and Tierra del Fuego region mink and muskrats are sympatric. In coincidence with the findings by Gomez et al. (2010) and Valenzuela et al. (2013) on Tierra del Fuego, our results on Navarino Island showed that minks specialize on terrestrial mammals when inhabiting inland habitats, whereas mink specializes on marine fish when inhabiting the marine coast. We could not analyse mink diet seasonally because we could not determine the exact time in which the scats were dropped. However, previous studies demonstrated that muskrats are particularly important in mink's

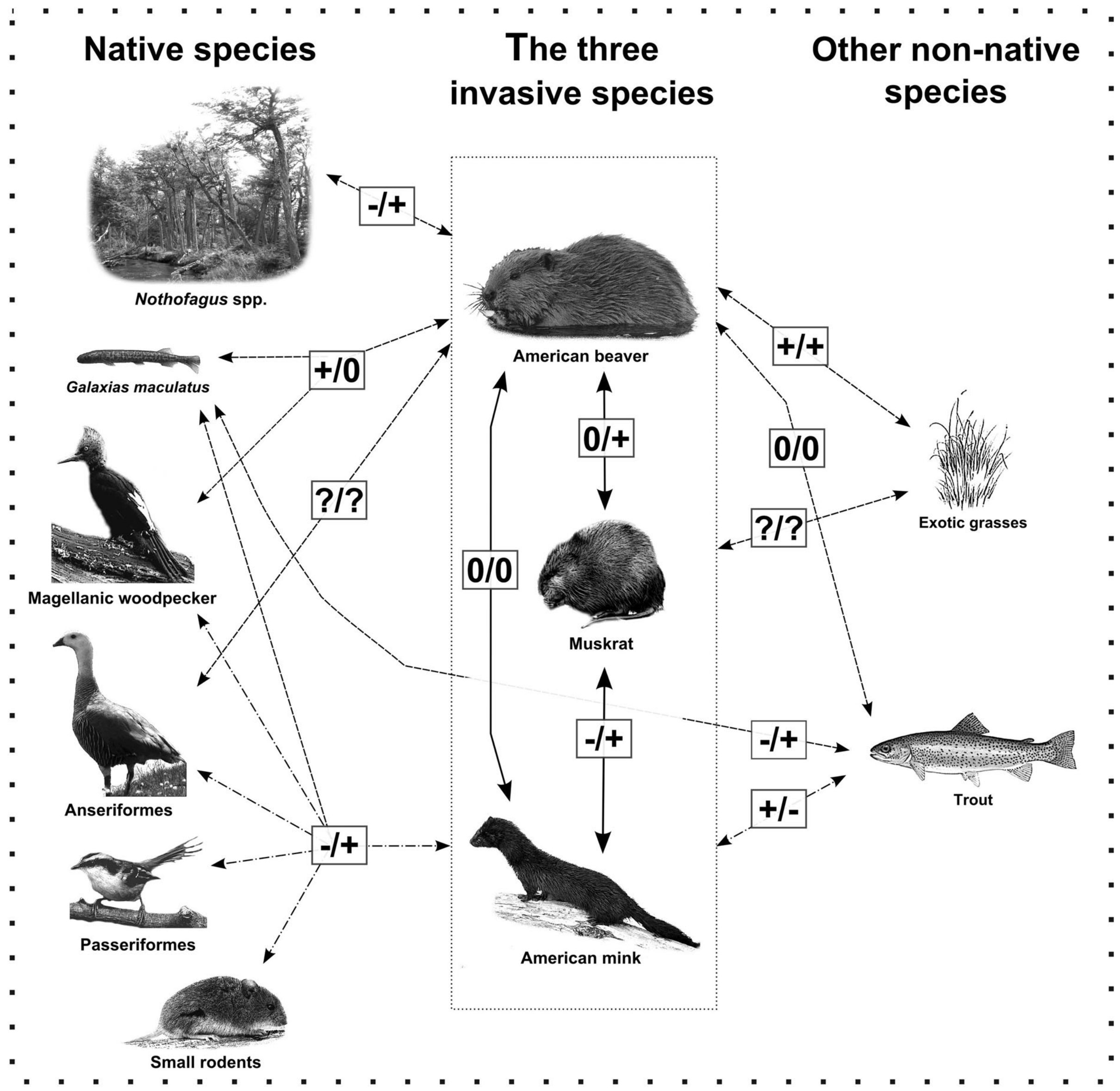


Fig. 4 Proposed representation of direct interactions of American beaver, muskrat, and American mink, among them, with native species, and with other non-native species on Navarino Island, Chile. Interactions are defined based on Simberloff and Von Holle (1999): "+/+": individuals of two species benefit from the presence of the other; "+/0": individuals of first species benefit from the presence of the other, while individuals of the second species are not known to be affected by the presence of the first; "+/−": individuals of the first species benefit by the presence of the second, whereas individuals of the second are negatively affected by the first; "0/0": no effects of one species on the other. *Continuous-line arrows* represent interactions documented by this study, *dashed-line arrows* represent interactions documented by other studies, and *dashed-line-point arrows* represent interactions documented by both, others and this study. See text for a discussion on strength of interactions and indirect effects

diet during winter, when the availability of other prey items decreased (Schüttler et al. 2008; Ibarra et al. 2009). Therefore, muskrats, together with sea food, may play an important role in allowing mink to survive winters and reproduce the following springs.

One of our most interesting results regarding the relevance of muskrats in the mink's diet is its drastic increase in our study as compared to previous studies. We report that muskrat biomass represents 25.6 % of overall mink diet as compared to 13.9 % reported by Schüttler et al. (2008); we report that 32 % of scats contain muskrat in inland habitats compared to 19 % as reported by Ibarra et al. (2009). We speculate on two different hypotheses that could explain this. First, an increase in muskrat depredation could result from a decrease in native rodent and bird abundances (Crego et al. 2014), which constituted important prey in previous years shortly after the arrival of minks to Navarino Island (Schüttler et al. 2008; Ibarra et al. 2009). This is also in accordance with studies in Canada, where muskrat increased in mink's diet as other prey items decreased (Shier and Boyce 2009). Moreover, mink inhabiting the marine coast now rely more heavily on marine fish, which may also be a response to lower abundances of native rodents and birds in marine coastal habitats (Crego et al. 2014). A second hypothesis is that prey species developed antipredator behaviors over time. This may occur for birds (Macdonald and Harrington 2003), but we know it did not occur for native rodents (Crego et al. unpublished data).

Conceptual framework of community interactions

Results from this study suggest that on Navarino Island beaver activity favours the establishment of muskrats, which in turn acts as the main prey for the mink population inhabiting inland habitats, which also affects native species through predation (Fig. 4). At a broader community level, previous research has shown that beavers and mink also affect other non-native and native species of the terrestrial island community, with muskrat effects thus far being unknown.

Beaver activities, such as foraging and dam building, have a large impact on native forests, as native *Nothofagus* trees cannot survive in flooded soils. The riparian vegetation community is then replaced by a meadow dominated by exotic grasses and rushes (Anderson et al. 2006b). Helped by livestock that forage freely in meadows, beavers facilitate exotic grasses establishment in these new habitats, resulting in ten exotic plant species inhabiting beaver meadows, in contrast to only one species found in naturally-forested riparian areas (Anderson et al. 2006b). Cows and horses, which are non-native species, also likely have large impacts on the community structure; however further research is needed to understand this process. Similar community-wide beaver effects on forest ecosystems were described in Tierra del Fuego (e.g. Lizarralde et al. 2004; Martínez Pastur et al. 2006).

Beaver dams favor the native fish *G. maculatus* by increasing its abundance; whereas, they do not have significant effects on the abundance of invasive trout (Moorman et al. 2009). Nevertheless, the abundance of *G. maculatus* is reduced in beaver ponds by the presence of invasive trout (Moorman et al. 2009). Therefore, positive beaver effects on *G. maculatus* might be compensated by the invasive trout.

Previous research also suggests that beavers improve feeding opportunities for the Magellanic Woodpecker (Soto et al. 2012). The abundance of wood-boring insects may increase in senescent trees with flooded roots; however, this is a short term process, and feeding resources disappear sometime after trees perish (Soto et al. 2012). Sielfeld et al. (1980) suggested that beaver ponds favor several aquatic avian species, claiming that such species present higher abundances in beaver meadows than non-altered habitat, as described for native habitat (Edwards and Otis 1999). Nevertheless, these authors did not present evidence to support this claim. Similarly to their observations, we have repeatedly observed Yellow-billed Teal (*Anas flavirostris*) using beaver ponds. However, further research should be conducted to determine these potentially positive interactions. Moreover, positive interactions between beavers and other aquatic species may be offset by increasing mink depredation on them.

It has been well documented in various regions of the world that the establishment of mink in new areas produce significant negative impacts on other native species (Macdonald and Harrington 2003). This is particularly relevant for Navarino Island where mink depredates on native species of small rodents and birds that evolved in the absence of terrestrial mammal predators. Hence, these vertebrates are potentially naïve to mink predation risk. High predation rates on native species documented in this and other studies (Schüttler et al. 2008, 2009; Ibarra et al. 2009; Maley et al. 2011; Jiménez et al. 2014) may have important consequences on population dynamics (Crego et al. 2014), even though more long term studies are needed to evaluate mink impact.

Overall, beaver impacts do not appear to depend on synergistic interactions with other invasive species. However, they favor the establishment of muskrats. Muskrats then subsidize the diet of inland mink populations that would allow for their survival during winters when other prey items are less abundant. Therefore, the creation of suitable habitat by beavers is a key facilitative process regarding the synergistic interactions among the three species, because muskrats will be less abundant or even absent without beavers in the system, affecting also mink population, especially in inland habitats during winters. Our data are indicative of facilitative synergistic interactions, however, to prove that an invasional meltdown exists on Navarino Island our current evidence in not sufficient. To demonstrate the possibility of an invasional meltdown in the Cape Horn Biosphere Reserve, future research will be needed to incorporate population growth, spread, and impact of the three invasive mammals.

Management implications

Species interactions among invasive species have important implications for management and ecosystem restoration (Zavaleta et al. 2001). Holistic approaches may be more effective in conserving native biodiversity than single-species management approach, avoiding unexpected consequences on other species that are intended to be protected (Ruscoe et al. 2011; Glen et al. 2013). Perhaps more importantly, considering community level interactions in management may be more beneficial for preserving native biological integrity (Angermeier and Karr 1994). In our specific case, based on the evidence and our proposed interaction network (Fig. 4), a combination of the control of beaver population and habitat restoration to recover river flow together with the control of mink population, would provide more effective results to preserve the integrity of sub-Antarctic Magellanic forest ecosystems. Forest regeneration in beaver dams is limited; thus, recovering river-flow dynamics and tree cover needs human action (Martínez Pastur et al. 2006). Such river flow restoration would benefit not only the benthic ecosystem structure and function (Anderson et al. 2009), but also would reduce suitable habitat for muskrats. This should trigger a reduction of muskrat population, which in turn would also affect inland mink populations, especially during winter when food shortage occurs.

A release of the predatory pressure on native fauna should be expected after the reduction in mink abundance. However, the reduction of muskrat populations might instead provoke an increase in the predatory pressure of mink on native birds and mammal populations. Therefore, mink trapping efforts are critically necessary, especially on coastal marine habitats. This habitat provides alternative food sources, and may act as a source for mink that could later disperse toward inland habitats. On the other hand, trapping mink without control of beaver and muskrat population will release predatory pressure on muskrats, potentially trigging a muskrat population outbreak. In sum, we propose a community-level management and population monitoring approach in contrast to a single-species one, to more effectively protect the biological integrity of the ecosystems in the Cape Horn Biosphere Reserve.

Concluding remark

The interactions among beavers, muskrats, and mink that we explored in this study involving other native and non-native species suggest a potential invasive meltdown process. The presence of muskrat due to beaver habitat modification, may be critical for mink survival in inland habitats, resulting in a critical pillar that supports the synergistic relationship among the beaver, the muskrat, and the mink. However, the lack of demographic data and experimental studies limit our current capacity to demonstrate this invational meltdown. For the Cape Horn Biosphere Reserve action plan, we encourage the inclusion of further experimental research and long-term studies to evaluate changes in the population dynamics and ecological impacts of these invasive species. We expect that our study will also encourage future research to allow a better understanding of the interactions among invasive species in similar systems of both the northern and southern hemispheres, to further test the hypothesis of invasional meltdown and its implications for the conservation of impacted ecosystems.

Acknowledgments We thank Matías Barceló, Nicolás Carro, Gabriel Gómez, Simón Castillo, Ana Piñeiro, Fernando Saldivia, Rocio Jara, Omar Barroso, and Javier Rendoll for all their hard field work help. We appreciate the valuable support of Nicolas Soto and Cristian Soto to this project. We also thank Amy Wynia and two anonymous reviewers for their valuable comments that significantly improved this manuscript. Tamara Contador and the Omora Foundation provided support to this project, with access to the Wankara Laboratory facilities and insect identification. This study was financed by the Toulouse Graduate School Program at the University of North Texas (UNT), the Rufford Foundation, the Conservation Research and Education Opportunities International (CREOi), and the Institute of Ecology and Biodiversity of Chile (IEB; grants ICM P05-002 and Basal-CONICYT PFB-23). This study is a contribution of the Sub-Antarctic Biocultural Conservation Program, jointly coordinated by UNT in the US, and by IEB and the Universidad de Magallanes in Chile.

References

Anderson CB, Rosemond AD (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. Oecologia 154:141–153

Anderson CB, Rozzi R, Torres-Mura JC, McGehee SM, Sherriffs MF, Schüttler E, Rosemond AD (2006a) Exotic vertebrate fauna in the remote and pristine Sub-Antarctic Cape Horn Archipelago, Chile. Biodivers Conserv 15:3295–3313

Anderson CB, Griffith CR, Rosemond AD, Rozzi R, Dollenz O (2006b) The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile: do exotic beavers engineer differently in Sub-Antarctic ecosystems? Biol Conserv 128:467–474

Anderson CB, Pastur GM, Lencinas MV, Wallem PK, Moorman MC, Rosemond AD (2009) Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration. Mamm Rev 39:33–52

Angermeier PL, Karr JR (1994) Biological integrity versus biological diversity as policy directives. Bioscience 44:690–697

Artimo A (1960) The dispersal and acclimatization of the muskrat, *Ondatra zibethicus* (L.), in Finland. Pap Game Res 21:1–101

Brzeziński M, Marzec M (2003) Correction factors used for estimating prey biomass in the diet of American mink *Mustela vison*. Acta Theriol 48:247–254

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York

Chehébar C, Martín S (1980) Guía para el reconocimiento microscópico de los pelos de los mamíferos de la Patagonia. Acta Vertebr 16:247–291

Connors LM, Groffman PM, Ostfeld RS (2000) Muskrat (*Ondatra zibethicus*) disturbance to vegetation and potential net nitrogen mineralization and nitrification rates in a freshwater tidal marsh. Am Midl Nat 143:53–63

Contador T, Kennedy JH, Rozzi R, Villarroel JO (2015) Sharp altitudinal gradients in Magellanic Sub-Antarctic streams: patterns along a fluvial system in the Cape Horn biosphere reserve (55°S). Polar Biol 38:1853–1866

Crawley M (2002) Statistical computing: an introduction to data analysis using S-Plus. Wiley, New York

Crego RD, Jiménez JE, Soto C, Barroso O, Rozzi R (2014) Tendencias poblacionales del visón norteamericano invasor (*Neovison vison*) y sus principales presas nativas desde su arribo a isla Navarino, Chile. Boletín de la Red Latinoamericana para el Estudio de Especies Invasoras 4:4–18

Crego RD, Jimenez JE, Rozzi R (2015) Expansión de la invasión del Visón Norteamericano (*Neovison vison*) en la Reserva de la Biosfera de Cabo de Hornos, Chile. Anales del Instituto de la Patagonia 43:157–162

de Szalay FA, Cassidy W (2001) Effects of muskrat (*Ondatra zibethicus*) lodge construction on invertebrate communities in a Great Lakes coastal wetland. Am Midl Nat 146:300–310

Deferrari G (2007) Biología y ecomorfología de la rata almizclera en Tierra del Fuego. Tesis Doctoral, Universidad Nacional de La Plata

Dunstone N (1993) The Mink. T and A D Poyser Ltd., London

Eagle TC, Whitman JS (1987) Mink. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, pp 615–624

Edwards NT, Otis DL (1999) Avian communities and habitat relationships in South Carolina piedmont beaver ponds. Am Midl Nat 141:158–171

Engeman RM, Whisson DA (2005) A visual method for indexing muskrat populations. Int Biodeterior Biodegradation 52:101–106

Glen AS, Atkinson R, Campbell KJ et al (2013) Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? Biol Invasions 15:2589–2603

Gomez JJ, Gozzi AC, Macdonald DW et al (2010) Interactions of exotic and native carnivores in an ecotone, the coast of the Beagle Channel, Argentina. Polar Biol 33:1371–1378

Green PT, O'Dowd DJ, Abbott KL et al (2011) Invasional meltdown: invader–invader mutualism facilitates a secondary invasion. Ecology 92:1758–1768

Hayward J, Horton TR, Nuñez MA (2015) Ectomycorrhizal fungal communities coinvading with Pinaceae host plants in Argentina: Gringos bajo el bosque. New Phytol. doi:10.1111/nph.13453

Heimpel GE, Frelich LE, Landis DA et al (2010) European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. Biol Invasions 12:2913–2931

Hobbs RJ, Arico S, Aronson J et al (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob Ecol Biogeogr 15:1–7

Ibarra JT, Fasola L, Macdonald DW, Rozzi R, Bonacic C (2009) Invasive American mink *Mustela vison* in wetlands of the Cape Horn Biosphere Reserve, southern Chile: what are they eating? Oryx 43:87–90

Jackson MC (2015) Interactions among multiple invasive animals. Ecology 96:2035–2041

Jaksic FM, Iriarte JA, Jiménez JE, Martínez DR (2002) Invaders without frontiers: cross-border invasions of exotic mammals. Biol Invasions 4:157–173

Jiménez JE, Crego RD, Soto GE et al (2014) Potential impact of the alien American mink (*Neovison vison*) on Magellanic woodpeckers (*Campephilus magellanicus*) in Navarino Island, southern Chile. Biol Invasions 16:961–966

Johnson PTJ, Olden JD, Solomon CT, Vander Zanden MJ (2009) Interactions among invaders: community and ecosystem effects of multiple invasive species in an experimental aquatic system. Oecologia 159:161–170

Kuebbing SE, Nuñez MA (2014) Negative, neutral, and positive interactions among nonnative plants: patterns, processes and management implications. Glob Chang Biol 21:926–934

Kuebbing SE, Nuñez MA, Simberloff D (2013) Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. Biol Conserv 160:121–129

Lizarralde MS, Escobar JM (2000) Mamíferos exóticos en la Tierra del Fuego. Ciencia Hoy 10:52–63

Lizarralde MS, Escobar J, Deferrari G (2004) Invader species in Argentina: a review about the beaver (*Castor canadensis*) population situation on Tierra del Fuego ecosystem. Interciencia 29:532–536

Lockie JD (1961) The food of the pine marten *Martes martes* in West Ross Shire, Scotland. Proc Zool Soc London 136:187–195

Macdonald D, Harrington L (2003) The American mink: the triumph and tragedy of adaptation out of context. New Zeal J Zool 30:421–441

Maley BM, Anderson CB, Stodola K, Rosemond AD (2011) Identifying native and exotic predators of ground-nesting songbirds in Subantarctic forests in Southern Chile. An Inst Patagon 39:51–57

Martínez Pastur G, Lencinas M, Escobar J et al (2006) Understorey succession in *Nothofagus* forests in Tierra del Fuego (Argentina) affected by *Castor canadensis*. Appl Veg Sci 9:143–154

Moorman M, Eggleston D, Anderson CB, Mansilla A, Szejner P (2009) Implications of beaver *Castor canadensis* and trout introductions on native fish in the Cape Horn Biosphere Reserve, Chile. Trans Am Fish Soc 138:306–313

Mott CL, Nielsen CK, Bloomquist CK (2013) Within-lodge interactions between two ecosystem engineers, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*). Behaviour 150:1325–1344

Nuñez MA, Hayward J, Horton TR et al (2013) Exotic mammals disperse exotic fungi that promote invasion by exotic trees. PLoS ONE 8:e66832. doi:10.1371/journal.pone.0066832

Pearson OP (1995) Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, Southern Argentina. Mastozoología Neotrop 2:99–148

Previtali A, Cassini MH, Macdonald DW (1998) Habitat use and diet of the American mink (*Mustela vison*) in Argentinian Patagonia. J Zool 246:482–486

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rau J, Martínez DR (2004) Identificación de los órdenes de aves chilenas a través de la microestructura de sus plumas. In: Muñoz A, Rau J, Valenzuela J (eds) Aves rapaces de Chile. CEA Ediciones, Valdivia

Rozzi R, Jiménez JE (2014) Magellanic sub-Antarctic ornithology: first decade of bird studies at the Omora Ethnobotanical Park, Cape Horn Biosphere Reserve, Chile. University of North Texas press, Universidad de Magallanes, Denton, Punta Arenas

Rozzi R, Sherriffs MF (2003) El visón (*Mustela vison* Schreber, Carnivora: Mustelidae), un nuevo mamífero exótico para la Isla Navarino. An Inst Patagon 31:97–104

Rozzi R, Massardo F, Anderson CB, Heidinger K, Silander JA (2006) Ten principles for biocultural conservation at the southern tip of the Americas: the approach of the Omora Ethnobotanical Park. Ecol Soc 11:43–70

Rozzi R, Armesto JJ, Gutiérrez JR et al (2012) Integrating ecology and environmental ethics: earth stewardship in the southern end of the Americas. Bioscience 62:226–236

Ruscoe WA, Ramsey DSL, Pech RP et al (2011) Unexpected consequences of control: competitive versus predator release in a four-species assemblage of invasive mammals. Ecol Lett 14:1035–1042

Schüttler E, Cárcamo J, Rozzi R (2008) Diet of the American mink *Mustela vison* and its potential impact on the native fauna of Navarino Island, Cape Horn Biosphere Reserve, Chile. Rev Chil Hist Nat 81:585–598

Schüttler E, Klenke R, McGehee S, Rozzi R, Jax K (2009) Vulnerability of ground-nesting waterbirds to predation by invasive American mink in the Cape Horn Biosphere Reserve, Chile. Biol Conserv 142:1450–1460

Shier C, Boyce M (2009) Mink prey diversity correlates with mink-muskrat dynamics. J Mammal 90:897–905

Sielfeld WK, Venegas C, Vanegas CC (1980) Poblamiento e impacto ambiental de *Castor canadensis* Kuhl, en Isla Navarino, Chile. Anales del Instituto de la Patagonia 11:247–257

Silva C, Saavedra B (2008) Knowing for controlling: ecological effects of invasive vertebrates in Tierra del Fuego. Rev Chil Hist Nat 81:123–136

Simberloff D (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecol Lett 9:912–919

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Soto GE, Vergara PM, Lizama ME et al (2012) Do beavers improve the habitat quality for magellanic woodpeckers? Bosque 33:271–274

Tella JL, Lambertucci SA, Speziale KL, Hiraldo F (2016) Large-scale impacts of multiple co-occurring invaders on monkey puzzle forest regeneration, native seed predators and their ecological interactions. Glob Ecol Conserv 6:1–15

Ulloa E, Anderson CB, Ardón M, Murcia S, Valenzuela AEJ (2012) Organic matter characterization and decomposition dynamics in sub Antarctic streams impacted by invasive beavers. Lat Am J Aquat Res 40:881–892

Valenzuela AEJ, Raya Rey A, Fasola L et al (2013) Trophic ecology of a top predator colonizing the southern extreme of South America: feeding habits of invasive American mink (*Neovison vison*) in Tierra del Fuego. Mamm Biol 78:104–110

Valenzuela AEJ, Anderson CB, Fasola L, Cabello JL (2014) Linking invasive exotic vertebrates and their ecosystem impacts in Tierra del Fuego to test theory and determine action. Acta Oecol 54:110–118

Viljugrein H, Lingjærde OC, Stenseth NC, Boyce MS (2001) Spatio-temporal patterns of mink and muskrat in Canada during a quarter century. J Anim Ecol 70:671–682

Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends Ecol Evol 16:454–459