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Artículo

HABITAT USE BY INVASIVE NORTH AMERICAN BEAVER DURING INTERMEDIATE AND LONG-TERM COLONIZATION PERIODS IN SOUTHERN PATAGONIA

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ABSTRACT. Since their introduction to southern Patagonia in 1946, North American beavers (*Castor canadensis*) have become a major impact to streams and forests. Scientists and managers now call for their eradication, requiring research to orient actions. John et al. (2010) showed that predicting beaver presence, which is crucial to plan eradication efforts, varies throughout colonization time (initial = unpredictable occupation of random sites; intermediate = predictable occupation of optimal sites; long-term = unpredictable occupation of sub-optimal locations). Beaver presence/absence and habitat variables (geomorphology, soil, and vegetation) were measured in the field and from satellite images in sites colonized at intermediate (Brunswick Peninsula ~1994) and long-term (Navarino Island ~1960) periods to predict this species' habitat use. Habitat suitability models were constructed using generalized linear models with those variables significantly different between sites with and without beaver. As hypothesized, a significant explanatory habitat model could not be developed for long-term occupation sites. However, beaver presence was predictable at intermediate colonization sites, and the best significant model included only river sinuosity and explained 74% of data variability. The model suggested that beavers used areas with greater river sinuosity, which could be measured from satellite images. Since remotely-sensed information requires less field effort, this approach could be useful in southern Patagonia's remote areas, where access is difficult. Additionally, these findings highlight the overall difficulty of planning a large-scale beaver eradication program and predicting beaver habitat use across a gradient of habitat types and colonization stages.

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RESUMEN. Uso del habitat por el castor norteamericano invasor durante etapas de colonización intermedia y de largo plazo en la Patagonia austral. Desde su introducción en la Patagonia austral en 1946, el castor norteamericano (*Castor canadensis*) ha provocado graves impactos en ríos y bosques nativos. Científicos y tomadores de decisiones recomiendan su erradicación, requiriendo investigación para orientar acciones. John et al. (2010) mostraron que la predicción de presencia de castores, fundamental para planificar una erradicación, varía a través del tiempo (colonización inicial = ocupación de sitios al azar e impredecible; intermedia = ocupación predecible de sitios óptimos; antigua = ocupación impredecible de sitios sub-óptimos). Evaluamos presencia/ausencia de castores y variables de hábitat (geomorfología, suelo, vegetación) in situ y mediante imágenes satelitales en ríos de colonización intermedia (Península Brunswick ~1994) y antigua (Isla Navarino ~1960) para predecir el uso de hábitat de la especie. Construimos modelos de hábitat adecuado usando modelos lineales generalizados con las variables significativamente diferentes entre sitios con y sin castores. Como hipotetizamos, no fue posible obtener un modelo de hábitat para sitios de ocupación antigua. Sin embargo, la presencia de castores fue predecible en sitios de colonización intermedia y el mejor modelo incluyó solo la variable sinuosidad del rio y explicó un 74% de la variabilidad. Este modelo sugiere que los castores usan sitios con alta sinuosidad, variable que puede ser registrada en forma remota. La información obtenida desde sensores remotos requiere menores esfuerzos de trabajo en terreno, una aproximación que sería útil en áreas alejadas de la Patagonia austral donde el acceso a sitios colonizados por castor es dificultoso. Adicionalmente, estos resultados remarcan la complejidad de diseñar un programa de erradicación del castor a gran escala y la de predecir su ocupación en un gradiente de hábitats y etapas de colonización.

Key words: *Castor canadensis*. Decision-making tools. Exotic species. Habitat suitability models. Management.

Palabras clave: *Castor canadensis*. Especies exóticas. Herramientas para toma de decisiones. Manejo. Modelos de hábitat adecuado.

INTRODUCTION

Invasive exotic species are recognized as one of the world's most pressing threats to native biodiversity, ecosystem function and human socio-economic systems (Mack et al., 2000). At the same time, the study of invasion biology has answered fundamental questions about ecology and evolution (Simberloff, 2003). Yet, understanding the spatial dynamics of populations is important not only for theoretical ecology, but is also germane for application in the management and conservation of biodiversity and ecosystems (Greaves et al., 2006). In the case of biological invasions, such research becomes a tool to predict the population's presence/absence and density, and can be applied to budget time and effort to detect, control, eradicate or mitigate the invasion (Simberloff, 2009; Vicente et al., 2013).

Southern Patagonia (Chile and Argentina) inadvertently has become a natural laboratory for theoretical and applied studies in invasion biology (Valenzuela et al., 2014). Yet, there is a clear gap in linking research with decision-making and management tools (Anderson and Valenzuela, 2014; but see also Fasola and Valenzuela, 2014). In this context, strengthening the nexus between the knowledge of a species' ecology and the decision making process for its control includes developing models of habitat suitability. Such models provide important information on the conditions necessary for a species to inhabit a location, which also aids to control or manage those that become harmful or nuisance (Hester and Cacho, 2012).

The North American beaver (*Castor canadensis*) was introduced to Tierra del Fuego Island in 1946 for its fur and to date has colonized most of the archipelago and the southern tip of the mainland (Anderson et al., 2009). Its ability to impact extensive aquatic and riparian ecosystems, as well as human and economic systems, led Chile and Argentina to sign a binational agreement in 2008 to restore the ecosystems affected by beavers through eradication of this species. In particular, proponents seek to stop the northward expansion of this invasion on the mainland (Anderson et al., 2011; Malmierca et al., 2011). Therefore, to control beavers it is important to study such factors as habitat selection in different stages of its colonization.

Previously, a beaver habitat suitability index (HSI) was developed for this area (Soto et al., 2006) to help managers predict the colonization of *C. canadensis* on the mainland. The HSI used Allen's (1983) proposition, based on beaver habitat in their native range, and included food availability and physical characteristics of the watershed as key variables affecting beaver distribution. However, such indices require field validation, taking into account local conditions and other variables, such as time since the invasion. For example, while site quality may remain more or less stable, previous research in Europe has shown that site selection by beavers during the colonization process follows a three-step pattern over time since first arrival (John et al., 2010). In the initial stage of colonization, beavers randomly spread in a watershed, and it is impossible to predict their selection of a specific location. During intermediate periods, the most suitable sites are colonized, based on the availability of food, building materials for their dams and lodges, and proper waterways (i.e., the values used in the HSI). Therefore, site selection models should be more accurate during this period. When the occupation becomes long-term, carrying capacity reaches a limit; beavers will select suboptimal locations, making it again more difficult to predict occupied sites, since the animal's biological requirements do not match the optimal standards (John et al., 2010).

In this context, the present study developed habitat suitability models in different colonization stages for the introduced North American beaver in southern Patagonia based on empirical data in its invasive range. It was also of interest to build the models with two data types that demand different amounts of time and resources to obtain: (a) field-measured habitat variables, and (b) remotely sensed habitat variables determined from satellite images and Geographic Information Systems (GIS). An emphasis was placed on GIS tools as a way to potentially reduce the field efforts, logistics and cost, and to reach remote areas where direct measurements may not be practical, especially considering that southern Patagonia frequently experiences extreme weather conditions and extensive areas have no access infrastructure. We hypothesized that habitat use by beavers in southern Patagonia would follow John et al.'s (2010) proposal, and therefore habitat variables would be useful to predict beaver occupation only in rivers experiencing an intermediate colonization stage.

MATERIALS AND METHODS

Study area and sites

The Magellanic sub-Antarctic forest ecoregion was identified by Conservation International as one of the last 37 "wilderness areas" on the planet due to low human density and large extensions of intact native vegetation (Mittermeier et al., 2003). Yet, it experiences all facets of global environmental change and is particularly threatened by numerous invasive species, including the beaver (Valenzuela et al., 2014). The vegetation in the area is made up of mixed forests with *Nothofagus betuloides* and *N. pumilio* and a mosaic of non-forested habitats, including peat bogs (*Sphagnum* spp.), shrublands, steppe grasslands and high Andean ecosystems. The two study areas were selected to represent distinct phases of beaver colonization in southern Patagonia: (a) the Brunswick Peninsula (Brunswick) and (b) Navarino Island (Navarino; **Fig. 1**).

On Navarino, the first report of this invasive species in rivers near the town of Puerto Williams was in the early 1960's (Sielfeld and Venegas, 1980). On Brunswick, the earliest confirmed dates in the Parrillar Lake area are 1994 (Wallem et al., 2007) and 1996 (Graells et al., 2015). Therefore, these sites were considered to have long-term and intermediate colonization, respectively. Three rivers with beaver presence were selected at each colonization study area to obtain an adequate number of transects to test the hypotheses while considering the site logistics and accessibility. The rivers at each site were similar in terms of beaver colonization stage and surrounding habitat, a mosaic of peat bog, forest and shrublands. The long-term colonization rivers were Guanaco, Ukika and Róbalo on the north coast of Navarino Island, along the southern shores of the Beagle Channel (mean annual precipitation and temperature are 467 mm and 6 °C, respectively). The intermediate-colonization rivers were Turbas, Hermoso, and Biterlich, all in or near the limits of the Parrillar Lake National Reserve on Brunswick Peninsula, which constitutes the extreme tip of the

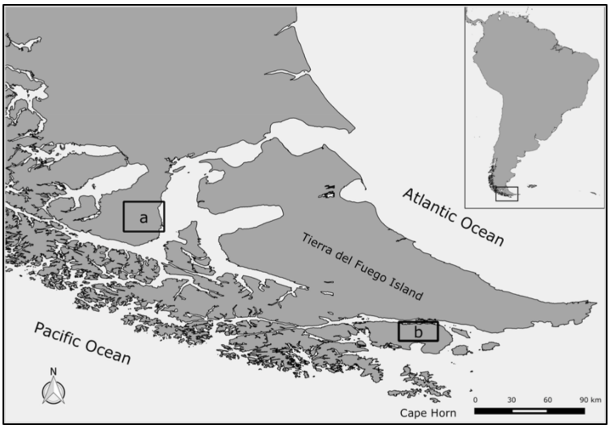

Fig. 1. Study area in (a) Brunswick Peninsula (Brunswick) and (b) Navarino Island (Navarino), southern Chile, where presence/absence of invasive North American beaver (*Castor canadensis*) was examined. Habitat variables were measured in the field and from satellite images (**Table 1**) along three rivers (Ukika, Guanaco, Róbalo) on Navarino, and three rivers (Hermoso, Turbas, Bitterlich) on Brunswick to generate beaver habitat suitability models as predictive tools to guide management and control efforts.

South American mainland (mean annual precipitation and temperature are 400-600 mm and 7 °C, respectively; Pisano, 1973).

Habitat characterization and use

We determined presence/absence of beavers and a suite of habitat variables reported in the literature as important for beaver site use based on the species' biology (**Table 1**). We set 250 m sampling transects consecutively along the stream, starting at the mouth of each study river.

Field measurements: In each sampling transect, beaver presence/absence, soil type, tree diameter at breast height (DBH) and herb and shrub cover were directly measured in the field during the austral autumn (March-May) of 2011 on Navarino, and during the austral autumn of 2012 and 2013 in Brunswick. Presence/absence of *C. canadensis* was determined through signs (e.g., dams, lodges, scent mounds, gnawed trees). Additionally, herbaceous and shrub vegetation cover were categorized and determined with the Braun-Blanquet (1948) method (B-B) in a 10 x 25 m plot placed next to the center of each transect. The B-B categories were considered together as groups, not by species, to characterize the existing cover and also to indicate soil moisture and drainage classes. Soil was classified into four categories according to draining capacity: 1-very poor (i.e., peat); 2-poor; 3-moderate; 4-good/excessive (sandy texture, gravel) using the U.S. Department of Agriculture method (USDA, 2014). The DBH was measured for each tree present within the plot.

Remotely Sensed Measurements: We overlaid the 250 m transects on high-resolution images with QGIS (v.2.4.0), centered with a georeferenced field point, to evaluate additional geomorphologic and vegetation variables (**Table 1**). A sinuosity index was calculated as the ratio of river length between beginning and end points of each transect to the linear distance between them.

Percent of woody vegetation cover was calculated applying radial buffer areas of 100 and 200 m (Howard and Larson, 1985) from the central point of each transect and using the buffer and grid tools. We also calculated river slope (°) and width (m) for each transect using QGIS.

Data analysis

The density of beaver sites in each watershed was calculated as the number of active beaver dams per river kilometer. The variables used to construct a predictive habitat suitability model were selected based on those that were significantly different between transects with and without beavers. The differences were assessed using ANOVA and Kruskal-Wallis tests for parametric (stream slope, sinuosity, width, forest cover at 100 and 200 m from the river and DBH) and non-parametric (soil type, herb and shrub cover) habitat variables, respectively. Significant differences were considered at $P < 0.05$.

All variables that showed significant differences in *C. canadensis* habitat occupation were integrated into the habitat suitability models using Generalized Linear Models (GLM; Nelder and Wedderburn, 1972). The response variable was presence/absence (binary) of beaver signs in each transect. The GLMs used the Bernoulli binomial error distribution family with a canonical logit link function. We tested the global model, which included all variables that differed between sites with and without beavers, for both Navarino and Brunswick. If the global model fit the data, then we tested all models arising from the possible combinations of explanatory variables. Akaike's Information Criterion (AIC) for small sample sizes was used for model selection (Akaike, 1974; Burnham and Anderson, 2002); models that differed by less than 2 AIC units of difference with the best model obtained were considered significant.

Table 1

Habitat variables previously reported to influence beaver habitat selection in southern Patagonia and North America. Shown are the variables measured in the field or remotely from satellite images (**Table 3**), and their source literature: (1) Howard and Larson (1985), (2) John et al. (2010), (3) Soto et al. (2006), (4) Wallem et al. (2007), (5) Allen (1983)

Habitat variable	Unit	Data type	Positive effect on beaver occupation	Source
Geomorphological variables				
River slope	°	remote	Low slopes	1, 2, 3
Sinuosity	m linear/m river	remote	High sinuosity	2, 3
River width	m2	remote	Smaller width	1, 2
Soil variables				
Soil type	drainage class	field	Poor drainage	1, 2
Vegetation variables				
Tree size (DBH)a	cm	field	Optimal handling size	1, 3
Woody veg cover 100 m	%	remote	Greater cover	1, 2, 3, 4
Woody veg cover 200 m	%	remote	Greater cover	
Canopy cover	%	field	Greater cover	1, 2, 4, 5
Herbaceous cover	B-B classb	field	Greater cover	3
Shrub cover	B-B classb	field	Greater cover	3

[a] DBH: Diameter at Breast Height
[b] B-B: Braun-Blanquet scale (Braun-Blanquet, 1948)

All statistical analyses were performed using R 2.9.1 software (R Development Core Team, 2008).

RESULTS

Habitat characterization and use

A total of 26.7 km of rivers were examined on Navarino and 17.4 km on Brunswick. *Castor canadensis* was present in all surveyed rivers and in 21 of 78 and 9 of 56 transects, respectively. Densities of beaver-inhabited sites fluctuated between 0.6 and 0.89 km^{-1} on Navarino (average 0.78 km^{-1}) and between 0.2 and 0.72 km^{-1} (average 0.52 km^{-1}) on Brunswick (**Table 2**).

On Navarino, DBH, river slope, river width, % forest cover at 200 m, herbaceous cover and shrub cover were not significantly different between beaver occupied and unoccupied transects. However, sinuosity was greater and % forest cover at 100 m was lower at sites with beavers (**Table 3A**). Also, soil type was significantly different between sites with and without beavers (**Table 3A**). Similarly, at Brunswick, no significant differences were detected for DBH, river slope, river width and riparian vegetation cover between transects with and without beavers, and sinuosity was again significantly greater in sites with beavers (**Table 3B**). Soil type was different between beaver-occupied and unoccupied sites as well (**Table 3B**). In most beaver-occupied sites, both on Brunswick and Navarino, soil type was of B-B category 1 and 2 (moist, low drainage soil), and only in Navarino two of the beaver-occupied sites were B-B category 4 (good drainage, sandy-gravel texture).

Predictive habitat suitability models for *C. canadensis*

Based on the selection of significant habitat traits, the explanatory variables used to build the habitat suitability models for both long-term and intermediate colonization sites were sinuosity, soil type and percent forest cover within 100 m of the river. Even though these variables were important for occupation probability (i.e., ANOVA results), and the data fit the global model (includes all variables), in the case of long-term invasion on Navarino, this general model only explained 13.9% of the total vari-

Table 2

Results from surveys to detect the presence of *C. canadensis* along three watersheds (study sites) on Navarino Island and three watersheds on the Brunswick peninsula, Southern Chile. Density of beaver-use was calculated as the number of active beaver dams per river kilometer.

Study Site	Linear kms. examined	Number Active Beaver Dams	Density (Number/Km)
Navarino Island			
Guanaco	10.2	9	0.89
Róbalo	8.3	5	0.60
Ukika	8.3	7	0.84
TOTAL	26.7	21	0.79
Brunswick Peninsula			
Biterlich	4.9	1	0.20
Hermoso	6.9	4	0.58
Turbas	5.6	4	0.72
TOTAL	17.4	9	0.52

ance, i.e., the model had low predictive power (**Table 4**). Additionally, these data showed over-dispersion, meaning that, even when the average data value fits the global model, the distribution of data values is not adequate to be used to predict the probability of beaver presence. Therefore, since all possible models had less predictive power than the general model, the analysis was not continued. In rivers with intermediate colonization on Brunswick, the global model also fit the data, explaining 85.3% of the variance and there was no over-dispersion of data. Then, all possible habitat suitability models for beaver presence were compared. The model that best explained (i.e., lowest AICc) beaver presence included only river sinuosity, accounting for 73.6% of the variance. The probability of beaver presence in intermediate colonization sites (e.g., Brunswick), was higher in rivers with greater sinuosity than those less winding (linear predictor of logistic equation = -19.59 [±6.16] + 12.86 [±4.17] * sinuosity index). In particular, there was an important increase for sinuosity values between 1 and 1.6, reaching 90% of presence probability at 1.7 of sinuosity (**Fig. 2**).

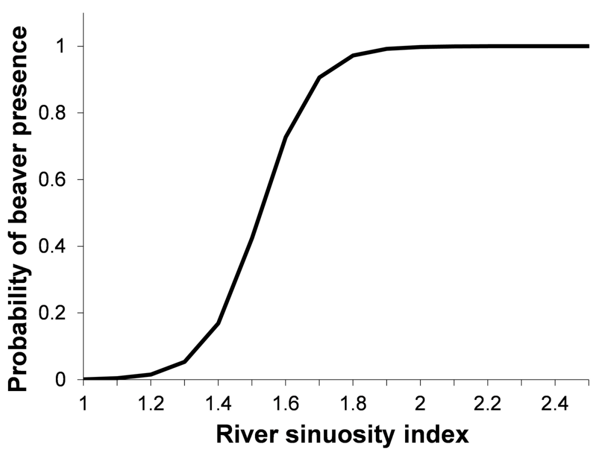

Fig. 2. The probability of presence of the invasive North American beaver (*Castor canadensis*) in the Brunswick Peninsula, southern Chile, was found to be predictable as a function of river sinuosity, with a greater than 50% chance of occupation occurring at sites with a sinuosity index higher than 1.51.

DISCUSSION

Modeling biological invasions

This study was developed to test a basic ecological question, but also aids in refining tools to predict beaver presence for the planning and design of management strategies. Our results offer a useful model of invasive beaver habitat suitability in southern Patagonia with empirical data obtained both, in the field and from

Table 3

Differences between mean (±SD) values for habitat variables measured along river transects with and without North American beaver (*Castor canadensis*) on Navarino Island (A) and Brunswick Peninsula (B), southern Chile, evaluated using one-way ANOVAs and Kruskal-Wallis tests; *denotes significant differences (P < 0.05).

Habitat variables	Unit	w/out beavers (mean ± SD)	with beavers mean ± SD)			
(A) Navarino Island					**ANOVA**	
Geomorphology				F	df	P
Slope	º	2.3 ± 1.4	2.4 ±1.6	0.14	1	0.71
Sinuosity	m/m	1.3 ± 0.2	1.5 ± 0.3	4.71	1	0.03*
River width	m	5.1 ± 3.6	6.6 ± 6.2	1.81	1	0.18
Vegetation						
DBH	cm	13.6 ± 12.5	12.3 ±19.2	0.12	1	0.73
Forest cover 100 m	%	54.4 ± 34.4	35.5 ± 26.1	5.23	1	0.03*
Forest cover 200 m	%	58.4 ± 27.1	47.1 ± 19.9	3.02	1	0.09
					Kruskal-Wallis	
Geomorphology			N	H	df	P
Soil type	Drainage categories		78	9.81	3	0.02*
Vegetation						
Herbaceous cover	B-B Scale		78	3.02	5	0.70
Shrub cover	B-B Scale		78	5.38	4	0.25
(B) Brunswick Peninsula					**ANOVA**	
Geomorphology				F	df	P
Slope	º	1.3 ± 1.5	0.54 ± 0.9	1.97	1	0.17
Sinuosity	m/m	1.2 ± 0.1	1.77 ± 0.3	110.7	1	0.00*
River width	m	4.7 ± 4.0	6.28 ± 5.2	0.95	1	0.34
Vegetation						
DBH	cm	38.2 ± 16.6	24.3 ±10.2	1.34	1	0.26
Forest cover 100 m	%	48.3 ± 35.1	43.00 ± 25.0	5.23	1	0.67
Forest cover 200 m	%	43.7 ± 29.3	38.27 ± 23.5	3.02	1	0.63
					Kruskal-Wallis	
Topography			N	H	df	P
Soil type	Drainage categories		56	7.8	2	0.02*
Vegetation						
Herbaceous cover	B-B Scale		56	7.86	4	0.10
Shrub cover	B-B Scale		56	1.52	3	0.68

satellite images. These data also provide new information on beaver site densities and habitat use for the mainland. Our findings generally agreed with the hypotheses that emanated from John et al.'s (2010) study, which suggested that it is difficult to predict beaver occupation in areas with long-term colonization, but at intermediate occupation stages, this species' presence can be modeled based on "optimal habitat" variables. Specifically, we found that on Navarino Island (long-term colonization), a predictive model of beaver presence could not be developed, but on the Brunswick Peninsula (intermediate colonization), habitat variables were useful to generate a predictive explanatory model.

The lower predictive power of the GLMs on Navarino could have two plausible explanations. On the one hand, there may be other habitat

Table 4

Habitat suitability models tested to predict the presence of North American beaver (*Castor canadensis*) in the Brunswick Peninsula and in Navarino Island. Shown is the model that best explains (i.e., lower AICc) beaver presence or Best model, the global (all explanatory variables) and the null (no explanatory variables) models for Brunswick peninsula. For each model, the variance explanation (VAR%), the likelihood log values (LogLik), the number of parameters involved (k), the Akaike Information Criterion for small sample size (AICc) and its value differences (ΔAICc) are shown.

Model	Explanatory Variables	VAR%	LogLik	k	AICc	ΔAICc
NAVARINO						
Global	Sinuosity + Soil type + Vegetation 100 m	13.9	38.572	7	92.74	-
BRUNSWICK						
Best Model	Sinuosity	73.6	13.039	2	17.27	0
2nd model	Sinuosity + Soil type	79.7	10.651	5	19.49	2.2
Global	Sinuosity + Soil type + Vegetation 100 m	85.3	8.135	6	21.85	4.6
Null	Intercept	-	49.375	1	51.45	34.2

factors that we did not measure and that may be needed to predict beaver habitat use (e.g., catchment area; Pietrek and González-Roglich, 2015) in long-term colonization sites. However, since long-term colonization stages include intermediate ones, the results from Brunswick suggest that the variables used to generate the models were significant and predictive. Thus, apparently the beavers on Navarino are not "selecting" the habitat, even though the data fit the global model and the variables show some degree of significance (i.e., ANOVA and Kruskal-Wallis results). On the other hand, the beavers would seem to be using habitats at random or occupying suboptimal locations, as predicted by John et al. (2010). But, as the intermediate colonization stage already occurred in this area, some of the beaver sites where already selected at that moment (using the variables for intermediate stage). Therefore, the global model fit to the empirical data pool obtained, which included situations of intermediate colonization (i.e., habitat occupation), but only explained a small amount of the variability because also suboptimal random sites were included. Alternately, it is also worth considering whether the lower predictive power of the model for the long-occupied areas (Navarino), unlike the more recently colonized sites on Brunswick, might be due to differences in beaver population size and density. As suggested by Pulliam (1988), the notion that population density will be highest at the sites most optimal for a species (an assumption of our approach), might not be applicable in a densely populated area. Highest densities might accrue in suboptimal sites, or "sinks" (Pulliam, 1988), to which individuals are driven by behavioral aspects of the species in question.

On Brunswick (intermediate colonization), our results suggest that river sinuosity was the most important determinant in estimating the probability of beaver presence. Overall, beaver presence was higher in river sections with greater sinuosity, which tends to increase with decreasing elevation (Timár, 2003; Cardenas, 2009) and which also leads to slower water flow that favors beaver dam construction (Howard and Larson, 1985). Given its importance, this specific variable might be pursued further to determine its relationship with flow measurements, which were not available for this study. Other studies have considered catchment area and stream order (only remote imagery; Pietrek and González-Roglich, 2015), but our objectives were to test beaver habitat variables both, in the field along with remote sensing tools.

Furthermore, we found that on average, the Brunswick Peninsula rivers had lower density of active beaver dams than the rivers on Navarino Island, which had similar or lower densities than other streams on the Fuegian Archipelago with a similar colonization history (**Table 5**; Lizarralde, 1993; Skewes et al., 2006). Besides representing an earlier colonization stage and despite having similar geomorphology and vegetation to the archipelago, the Brunswick watersheds also have a different predator assemblage. For example, foxes (*Lycalopex griseus*, *L. culpaeus*, Johnson and Franklin, 1994; Rodríguez et al., 2010) and cougars (*Puma concolor*, Rau and Jimenez, 2002) could influence patterns of habitat use and behavior of beavers. Similarly, beavers can occasionally be preyed upon by invasive mink (Valenzuela et al., 2013a) and both species use similar environments (Valenzuela et al., 2013b). Though further research on this issue is necessary, our results should be used taking into account the potential trophic relationships at each site.

Managing invasive species

In southern Patagonia, invasive exotic species represent a growing challenge for environmental scientists and managers (Anderson and Valenzuela, 2014; Valenzuela et al., 2014). Ecological research provides baseline information that can be applied to conservation issues. For example, habitat suitability models allow a better understanding of the habitat's influence on the distribution of a species. Such tools become particularly necessary when efficient and effective strategies are required for management of harmful organisms, such as invasive exotics species (e.g., Davis et al., 2012). Anderson et al. (2011) identified a lack of applied research into habitat selection models in the context of southern Patagonia's efforts to control beavers. As such, the present study helps link basic ecological research and decision-making on the control of invasive species in southern Patagonia to optimize resources on multiple dimensions (e.g., financial, man hours, species-response time).

The design of effective eradication and control programs for invasive exotic species ought to include the identification of high priority areas where the species capturing efforts must be concentrated (Simberloff, 2009). We recommend that managers take into account the model presented here to improve success in controlling the beaver population at intermediate colonized sites or to stop its spread, or both. Management strategies in the Brunswick Peninsula should be focused in areas with high probability of beaver presence (i.e., rivers with greater sinuosity). A similar criteria could apply to define areas that are currently free of beavers, but with higher probability to be occupied, to guard them from invasion. Further studies ought to test the model proposed, not only in intermediate stages of invasions, but also in regions under early- or even pre-colonization. Such a strategy would allow decision-makers in the region to minimize time and costs needed for the management of this invasive species. Additionally, most of the successful eradication programs elsewhere include the definition

Table 5

The density of active North American beaver (*Castor canadensis*) dams (number dams km-1) on Navarino Island and the Brunswick Peninsula, southern Chile. These values were compared with previous work from a range of habitat types in the Fuegian Archipelago (Chile and Argentina). Shown are the results from this study (**Table 2**) and the source literature: (a) The present study; (b) Lizarralde (1993); (c) Skewes et al. (2006).

Locations	Habitat	Mean density (beaver sites km^{-1})
Navarino Island (average)	Forest and peatland mosaic	0.78[a]
Brunswick Peninsula (average)	Forest and peatland mosaic	0.52[a]
Tierra del Fuego Island	Forest	2.0 – 4.7[b]
Tierra del Fuego Island	Peatland	5.8[b]
Tierra del Fuego Island (mid)	Forest	0.6[c]
Tierra del Fuego Island (south)	Forest and peatland mosaic	1.9[c]
Navarino Island	Forest and peatland mosaic	1.1[c]

of management unit areas and control points between them (Genovesi and Monaco, 2013). Our results could also help in finding those sites with low probability of beaver settling and which can serve as control points. Concurrently, these data highlight the difficulty of eradicating beavers. While this modeling exercise suggests that efforts can be oriented in certain colonization stages (intermediate), in others (long-term and potentially early occupation) the ability to anticipate beaver presence may remain uncertain. The results from our study re-enforce the need to design eradication programs based on effective management units and simultaneously maintain alternative strategies (e.g., Sanguinetti et al., 2014) oriented towards permanent control in certain areas.

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