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Post-establishment changes in habitat selection by an invasive species: beavers in the Patagonian steppe

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Abstract Changes in habitat use over the course of a biological invasion may influence the fraction of the landscape that is ultimately affected by the invader. However, this intermediate stage of invasion has been less studied than the initial or final stages. Here, we investigated the recent invasion by an ecosystem engineer, the American Beaver (*Castor canadensis*), in an area of the Patagonian steppe. We utilized repeated high resolution satellite images to identify beaver ponds, and used them to study changes in beaver abundance and habitat use over time. The number of beaver ponds increased 85 % between 2005 and 2014. During this period, beavers changed their habitat selection pattern, presumably as a response to increased density. Beavers established on small watercourses in canyons first, but as more canyons became occupied over time, beavers moved to less preferred watercourses in plains and U-shaped valleys. Potential new beaver colonies established close to existing beaver ponds, suggesting proximity to a beaver pond is an important determinant of beaver colonization. Identifying habitat preferred by beavers in the steppe, could help to increase early detection of the invader at the invasion front. Our work highlights the importance of the use of high resolution remote sensing technologies to better understand and control biological invasions.

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Introduction

Much of the theory on ecological invasions has addressed the determinants of the speed of invasion (Hastings et al. 2005; Kot et al. 1996; Skellam 1951). These studies have focused on the invasion front, defined as the points in space where population density has reached a threshold level. But perhaps as important as the rate of movement of the invasion front are changes in the distribution and abundance of the invader behind the front, after the invader has become established. Demographic or behavioral responses behind the front may reflect density dependent feedback, and may shed light on the ultimate abundance toward which the established invader population may tend, as well as the ultimate fraction of the landscape that will be affected (Dwyer and Morris 2006; Ehrlén and Morris 2015; Pachepsky and Levine 2011).

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Resources competition is one way in which density dependence can limit abundance and distribution of organisms. For instance, Pimm et al. (1985) found that blue-throated hummingbirds (*Lampornis clemenciae*) preferred high sucrose feeders rather than low sucrose feeders at low densities, but this preference vanished as density increased. Changes in habitat selection patterns with increasing density have been found for mice, ants and fish, and have given rise to mechanistic theories of density dependent habitat selection (Fretwell and Lucas 1969; Rosenzweig 1981). Biological invasions are good models to study density dependent habitat selection, although this has been rarely tested in animal invasions or reintroductions (Armstrong et al. 2005; Nummi and Saari 2003). At the initial stages of the invasion we might see individuals selecting optimal patches, but as optimal patches fill and resource availability changes, we expect to see a weakening in habitat selection.

Twenty American beavers (*Castor canadensis*) were introduced to southern Argentina in 1946 (Pietrek and Fasola 2014). Since then, they have spread throughout the archipelago of Tierra del Fuego and mainland Chile, where they were first detected in the early 1990s (Skewes et al. 2006). Beavers change the structure and composition of the *Nothofagus* riparian forests (Anderson et al. 2006a; Martínez Pastur et al. 2006), affect native fish and aquatic macroinvertebrate assemblages (Anderson and Rosemond 2007; Moorman et al. 2009), and impact food webs of Subantarctic streams (Anderson and Rosemond 2010). More importantly, beavers create entirely new habitats in the forests of Tierra del Fuego allowing the establishment of other invasive species (Anderson et al. 2006b). Thus understanding the post-invasion changes in habitat use by beavers is important for gauging their impacts on native species and ecosystems. In Tierra del Fuego, beavers first established in the forests in which they were introduced, but by the 1990s beavers began to establish in the adjacent steppe where very little research has been conducted to date (Lizarralde 1993; Skewes et al. 2006; Wallem et al. 2007).

Factors affecting beaver settlement and dam building in North America include vegetation cover, stream gradient, bank slope and hydrological order among others variables (Barnes and Mallik 1997; Dieter and McCabe 1989; Suzuki and McComb 1998). However, most of these studies have looked at native populations with a long settlement history. But near carrying capacity, beaver colonies could be settling in suboptimal sites that other beavers left unutilized. For instance, John et al. (2010) found reintroduced European beavers (*Castor fiber*) were more likely to settle in areas with steeper gradients, smaller watersheds, and closer to roads 12 years after their initial release. Recent spread of beavers in the Patagonian steppe sets up a unique scenario to test this hypothesis.

Another important factor that may influence the probability of beaver settlement is the proximity of established colonies. At a small scale beavers can expand their home range by impounding new areas nearby, but at a larger scale new ponds can provide insight into the dispersal distances of beavers. A study on beaver dispersal in New York State found that 88 % of the dispersers moved to a location within 5 km from their native colonies (Sun et al. 2000). What we do not know is what dispersal distances are in newly invaded regions, and whether those distances change post-establishment.

Our objectives in this paper were: (1) to quantify the increase in the number of ponds and the area impacted by beavers over time in an invaded area of the Patagonian steppe; (2) to identify what landscape features invasive beavers select at different stages of the invasion; and (3) to understand how the proximity of neighboring colonies affects the likelihood that a site will become colonized.

Methods

Study area

We selected a 500 km^2 area of mixed steppe in northern Tierra del Fuego, Argentina, based on high resolution satellite image availability (Fig. 1). Annual rainfall ranges from 200 to 300 mm. Altitude varies from sea level close to the Atlantic, to 300 m to the west of the study area. Shrub cover is dominated by the woody plant *mata negra* (*Chilliotrichum diffusum*) used by beavers for food and dam construction and ranges from 0 to 60 % shrub cover. Geomorphology has been shaped by glacial, marine, and glaciofluvial processes that established the canyons and valleys where the major watercourses flow (Rabassa et al. 2000).

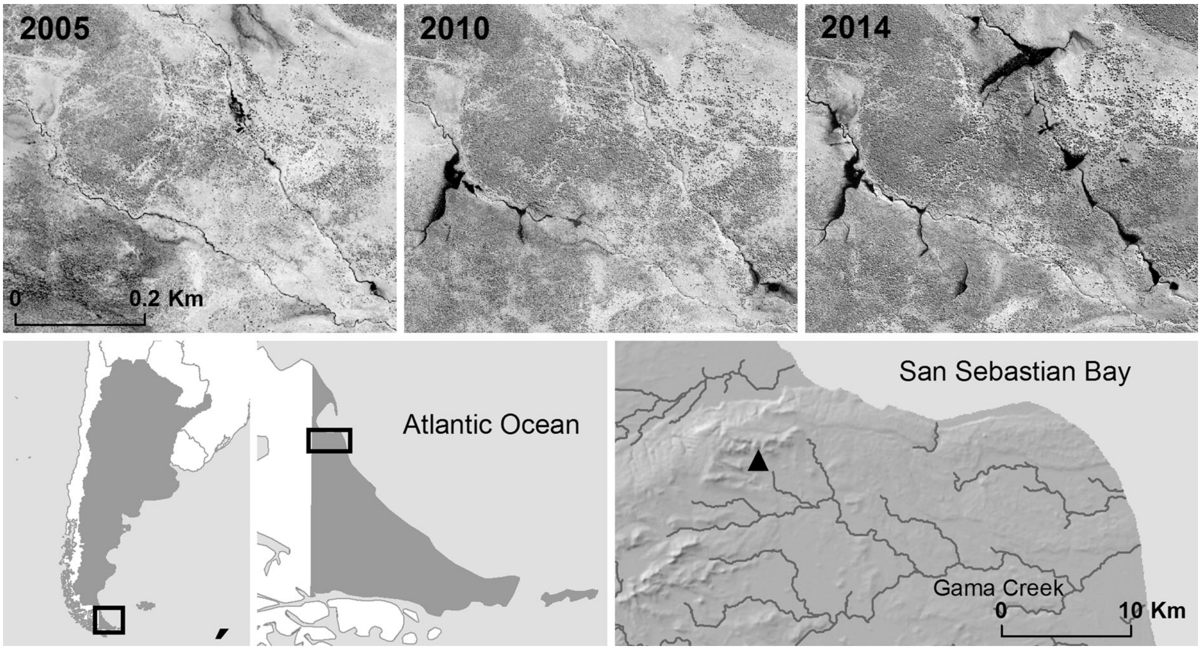

Fig. 1 *Bottom row* detail of the study area (far right), the *triangle* indicates location of the top row images. *Top row* high resolution satellite images. No ponds are distinguished in 2005, but new ponds are formed in 2010 and 2014

The study area is part of one of the largest private ranches in Argentina, *Estancia Sara* (53°25′59″S, 68°10′59″W), which is mainly dedicated to sheep farming and oil and gas extraction. Beaver ponds were first detected here in the early 1990s (Carlos Mann, pers. comm., Lizarralde 1993) and beaver hunting and dam destruction is only occasional and restricted to nuisance beavers. From 2011 to 2015 we have been conducting demographic studies on beavers in this ranch and the area has been prospected by air and land repeatedly. One major water course, Gamma Creek, flows through our study area to the Atlantic and is fed by several smaller streams that depend primarily on local precipitation which is mainly concentrated in autumn–winter.

Extraction of covariates

Beavers are the quintessential ecological engineers, building dams that are easily discerned in high resolution images by their morphology (Meentemeyer and Butler 1995). This is particularly true in semiarid shrubby environments where tree interference is absent. Beavers can also dig bank holes in river slopes of high order rivers (Breck et al. 2001), not impounding water, but this is rare in stream systems (Barnes and Mallik 1997; Collen and Gibson 2001) such as our study area where beavers frequently build dams. For this study we used satellite images to determine beaver ponds location and extent over time. The images used were from October 2003 (Quickbird panchromatic, 60 cm), August 2005 (Quickbird multispectral, 60 cm), March 2010 (Geoeye panchromatic, 50 cm), and March 2014 (Worldview panchromatic, 50 cm). Images were already georeferenced, and since no major alignments errors were identified, no correction was needed. Upon visual inspection of the images (scale 1:3000), ponds were identified and a polygon hand-drawn to delineate each one using ArcGIS 10.2.2 (ESRI 2014). From this dataset we estimated the number of ponds per year and their total area. As images from 2003 covered only half of the study area, we separately analyzed the increase of the number of ponds for half of the study area between 2003 and 2014 and for the entire study area between 2005 and 2014. Likewise, we only used years 2005, 2010, and 2014 for the analysis of habitat selection and establishment of potential new colonies.

Topographic features determine water movement along the landscape, and can consequently affect beaver dispersion and establishment in the Patagonian steppe. We used a 30 m digital elevation model (DEM) from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER-GDEM V2) (Tachikawa et al. 2011) to derive a set of covariates which could affect pond establishment. A 30 m pixel size was considered appropriate for this study, given that it approximately matches the mean size of beaver ponds (~ 850 m^2). Due to the lack of a detailed hydrologic map of the study area, we used the DEM to develop a stream dataset based on the accumulation of up-stream cells using Spatial Analyst hydrology tools in ArcGIS (ESRI 2014). All cells with an accumulated flow of at least 100 units were classified as streams. As we did not have an actual measurement of stream flow we used catchment area as a proxy to flow and likelihood of flooding which are arguably important features for pond establishment. Catchment area of each pixel in the stream network was defined as the up-stream area draining through that particular pixel, and was determined using the flow accumulation raster. Stream gradient was estimated for each cell in the stream network as mean percent change in elevation for a 120 m long section, 60 m upstream and 60 m downstream of the corresponding cell.

We considered available habitat to be all stream cells, including areas occupied by ponds. For that, we converted the hand digitized polygons to pixels matching the 30 by 30 m cells of the DEM used to create the stream network. All pixels in contact with a polygon identified as a pond in a particular year were considered used.

To describe the topographic position of each cell in the stream network (i.e. the relative position of each cell relative to its surroundings) we calculated landforms as suggested by Weiss (2001). Of the ten available landform types, we removed all cells with land form types with <3 % representation in the stream network and where use was a rare event, leaving only 4 classes: (1) Canyons and deeply incised streams (17 %), (2) U-shaped valleys (36 %), (3) Plains (30 %), and (4) Open slopes (9 %), these landforms accounted for 92 % of the available pixels in the study area.

Vegetation cover is a key attribute affecting ecosystem functioning, from water movement to the availability of resources beavers need to feed and build dams. To estimate woody cover in the vicinity of ponds, we used the panchromatic satellite images from 2014. Using a combination of texture analysis (3 by 3 window variance) and ISODATA unsupervised classification (Ge et al. 2006); we created a land cover map with two classes: woody or non-woody. From this map we estimated percent woody cover at an aggregated scale of 1 m. For each pixel of available habitat woody cover was estimated as the mean woody plant cover of a 60 m radius circular buffer around each cell. Sixty meters is along the longest distances from ponds beavers are known to forage (Fryxell 1992; Muller-Schwarze 2011). Correlation among covariates was generally low, except for vegetation cover and elevation (0.59) and therefore all variables were kept for the analyses.

Data analysis

Resource selection functions

We used resource selection functions (RSF) to study the variables affecting pond establishment by beavers (Boyce and McDonald 1999; Manly et al. 2002). Resource selection functions describe the relative probability of use of habitat features by animals and have been widely used in ecology (Johnson et al. 2006; Keating and Cherry 2004; Lele and Keim 2006; Northrup et al. 2013). We followed a used-availability design in which all suitable parts of the landscape are assumed to be available to the individuals but some units are preferred over others. Beavers can travel long distances (we have recorded a 19 km dispersal event in this area using radio-telemetry) (see Leege 1968; Sun et al. 2000; VanDeelen and Pletscher 1996), so they are likely to be able to sample all suitable units in the landscape. We decided to take all pixels occupied by watercourses in our study area as the landscape available to beavers.

As this is a non-equilibrium population, where new ponds form every year, and we wanted to understand what habitat features beavers select over time, we made availability time specific. Thus, used units at time t were not available for colonization at time t + 1. Likewise, we defined used units at time t to be only newly occupied pixels. We set 2005 as our first year and all beaver ponds identified in 2005 defined our first used units.

To build the dataset for our analysis we sampled without replacement 5 % of the available landscape for each year and added all the used units for the corresponding year. To avoid unit overlap we removed units contained in both the available and used sample from the used sample as suggested by Manly et al. (2002). We also discarded repeated units among the available sample at different years for the analysis. In the final dataset across all years, the available sample represented 13 % of all available pixels. Used units were only 4 % of the units in the study area and ranged from 365 to 467 pixels per year.

We ran 16 logistic regression models to elucidate what variables predict beaver pond establishment (Manly et al. 2002). The dependent variable was use (1 = used, 0 = non-used) of landscape units as previously defined. The simplest model contained all landscape variables (catchment area, elevation, landform, stream gradient, vegetation cover) and a year effect. Two more complex models included either an interaction of catchment area with stream gradient or catchment area with vegetation cover and were included based on biological grounds. Areas with little vegetation cover may not provide enough material for dam construction at high flows which can be caused by high catchment areas or steeper gradients. All other models were variants of the first three that included an interaction of year with each predictor variable for the simplest model, and an additional three way interaction with year for the other two.

We ranked models using Akaike Information Criteria (AIC) (Burnham and Anderson 2002). For the best model we estimated a RSF using the exponential function:

$$P(y = 1|x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p) \qquad (1)$$

where the betas represent the coefficients of the logistic regression and the x's represent the landscape variables under study. Equation 1 allowed us to estimate relative likelihoods of use, and variances of the estimators were calculated using a Taylor's series approximation as suggested by Manly et al. (2002).

We assessed goodness of fit of our RSF function using k-fold validation (Boyce et al. 2002; Johnson et al. 2006). We used Huberty's rule of thumb to determine the optimal training to testing ratio (Fielding and Bell 1997) and we determined a testing ratio of 20 % based on the number of model parameters. We divided the data into fifths, estimated the parameters of logistic models using 4/5 of the data and used the remaining group as the testing dataset. We repeated this analysis five times, each time computing the Spearman's rank correlation between the area adjusted frequency of cross validated points within individual bins and the bin rank. Area adjusted frequencies were simply the frequencies of cross validated points divided by the frequency of the RSF values within the bin across the study area. Predictions were divided in ten equal sized bins and rare bins occurring at the tail of the RSF scores were merged for the analysis.

Effect of proximity to existing colonies on establishment of potential new colonies

We were interested in making inferences about dispersal patterns in beavers based on establishment of new ponds over time. New ponds can result from expansion of preexisting beaver colonies or from the founding of new colonies. For this analysis we considered all ponds mapped between 2005 and 2014 using high resolution images. Based on the minimal distance we found between neighboring colonies in the field (Pietrek in prep.) and in the scientific literature (Bergerud and Miller 1977), we defined a potential new colony to be a pond or set of ponds at time t + 1 that is separated at least 200 m from the closest pond at time t. Potential new colonies were only added to the dataset if they were closer to another beaver pond than to the edge of the satellite image, as the occurrence of other ponds outside of the image could affect the probability of establishment of a potential new colony. We placed a 60 m buffer around the center of a new colony, and we extracted the same landscape covariates used in previous analysis. For continuous variables we assigned the mean value over all the pixels included in buffers, and for landforms we assigned the habitat that overlapped more than 50 % of the pixels. The final set of landscape variables included catchment area, elevation, landform, stream gradient and vegetation cover.

We used a control-case design (Hosmer and Lemeshow 2005) in which 60 m radius buffers around the centers of potential new colonies were the sampling units and were matched to an equal sized sample of randomly located areas that did not contain beaver ponds. We built logistic regression models with all 30 possible combinations of variables and ranked models using AIC corrected for small sample size (AICc). As the number of potential new colonies was small, we combined potential colonies from 2010 and 2014 in the analysis. We added the variable Euclidean distance from ponds formed at time t + 1 to the nearest pond at time t to the best model, and estimated the probability of a potential new colony establishment as a function of distance to the nearest pond. All analyses were performed using R version 3.1.

Results

The number of beaver ponds and the area covered by ponds increased over time in our study area (Fig. 2). Analysis of the area that included an image from 2003 showed a rapid increase from 2003 to 2005, followed by a more or less linearly increase from 2005 to 2014. Overall, the number of ponds increased 85 % from 2005 (N = 117) to 2014 (N = 217) in our study area.

The full model that included all variables, a two-way interaction between landform and year, and a three-way interaction between vegetation cover, catchment area and year was ranked first among competing models (Table 1). All other models ranked at least 14 AIC units below the best model. The interaction between landform and year was selected twice among the five best ranked models. This

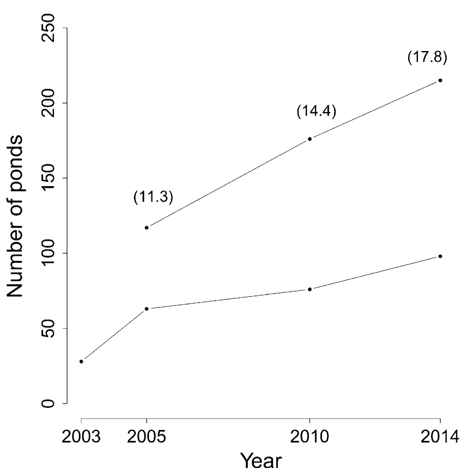

Fig. 2 Increase in the number of beaver ponds for our entire study area (*top*) and for a subset of our study area (*bottom*). *Numbers* in parenthesis indicate the area in hectares flooded by beaver ponds

suggests that habitat selection of beavers changed over time. We fit logistic models for each year to better analyze the interaction between vegetation cover and catchment area. Beavers preferred areas with low vegetation cover when watercourses were small, but at high catchment area, the probability of pond establishment increased as vegetation cover increased in 2005 (Fig. 3). We found little or no difference in the probability of pond establishment at low catchment area with different levels of vegetation cover for 2010 and 2014. Smaller watercourses probably are easier to manage for beavers and vegetation cover is not as needed to build ponds as higher water flows may demand.

To understand how beavers used the landscape we calculated a relative likelihood of landform use using a RSF fitted with the parameters of the best ranked model. Based on proximity, similar geomorphology and use by beavers we merged open slopes and plains into one category called plains. Beavers used canyons more frequently at the first years of our study, but the likelihood of canyon use decreased with time (Fig. 4). Conversely, beavers increased use of both plains and U-shaped valleys in 2010 and 2014, although watercourses in U-shaped valleys were preferred over those in plains.

We tested predictive performance of the best RSF. Correlations between area adjusted-frequencies and bin ranks were high and ranged between 0.82 and 0.93. A Spearman's rank correlation for mean frequency values by bins was also high (0.93) confirming the model predicted used locations well.

Twenty-six potential new colonies were founded in 2010 and 2014. The small sample size of colony foundation events unfortunately prevented us from asking if dispersal distances changed over time. Distances to the closest pond at t−1 ranged from 258 to 3246 m (Fig. 5a). The median distance to the nearest colony was 618 m and the mean was 864 m. Incorporation of distance to nearest pre-existing pond improved the best ranked logistic regression model by 7 AIC units (Table 2). The best ranked model included catchment area, elevation, stream gradient and distance. We used the best ranked model to estimate the probability of establishment of potential new colonies as a function of the distance to the closest pre-existing pond (Fig. 5b). The probability of new colonies declined slowly with distance, consistent with the high dispersal distances observed for beavers.

Table 1 Five best ranked logistic models to study resource selection by beavers

Model	K	AIC	ΔAIC	AIC wt	Cum weight
CA+CO+ELEV+SG+LA+YR+CA*CO*YR+YR*LA	16	4879.81	0	1	1
CA+CO+ELEV+SG+LA+YR+CA*CO*YR+YR*SG	14	4894.65	14.84	0	1
CA+CO+ELEV+SG+LA+YR+CA*CO*YR	13	4897.28	17.46	0	1
CA+CO+ELEV+S+LA+YR+CA*CO*YR+YR*ELEV	14	4899.28	19.47	0	1
CA+CO+ELEV+SG+LA+YR+SG*CO*YR+YR*LA	16	4914.71	34.9	0	1

CA catchment area, *CO* vegetation cover, *ELEV* elevation, *LA* landform, *SG* stream gradient, *YR* year

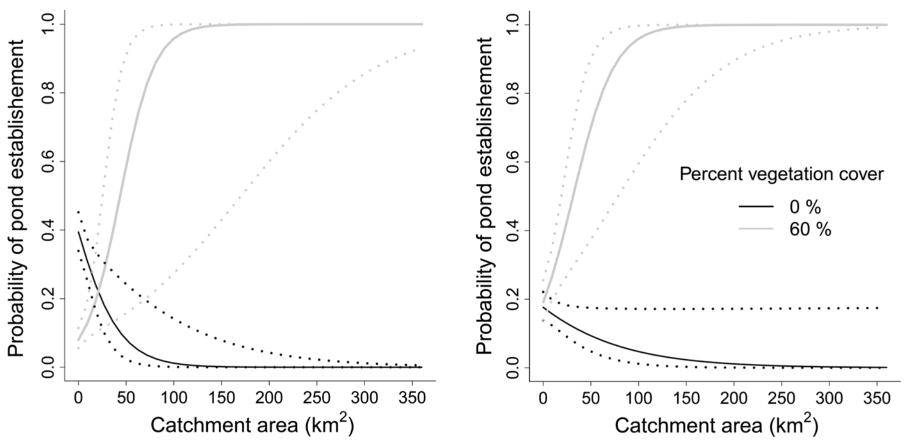

Fig. 3 Interaction between catchment area and vegetation cover for 2005 (*left*) and 2014 (*right*). *Solid lines* indicate the probability of pond establishment at different levels of vegetation cover, *dotted lines* indicate 95 % confidence intervals

Discussion

High resolution imagery provides information about both population increase and habitat selection of beavers in our study area. By studying both processes simultaneously, we were able to assess how changes in population density affected patterns of habitat selection. Beavers settled on watercourses in canyons in the beginning of our study and used other habitats that were initially less preferred as the number of beaver ponds in the study area increased. Images can also shed light on the dispersal capabilities of an invader in a recently colonized landscape. As we now discuss, understanding both density dependent habitat selection and dispersal can be of critical importance for controlling invasions in general and for beaver management in Patagonia in particular.

Although the time scale of the study was relatively short (11 years) we could easily discern an increase in the number of beaver ponds and in the area affected over time. This increase was particularly high in the first years of our study, suggesting high rates of population growth. In a study conducted during a period of beaver population expansion between 1940 and 1986 in Minnesota, Johnston and Naiman (1990) found that 75 % of the ponds were established in the first 20 years. Moreover, they found this increase to be linearly related to the increase in the number of colonies, confirming that the number of ponds is likely a good indirect measure of abundance.

Aerial photographs have been used to identify beaver ponds (Cunningham et al. 2006; Johnston and Naiman 1990; Meentemeyer and Butler 1995; Naiman et al. 1988), but high resolution satellite images offer new possibilities. They can be used over extended areas in remote locations and, unlike photographs, their quality is relatively constant over space and time (Gergel et al. 2010). High resolution images for our

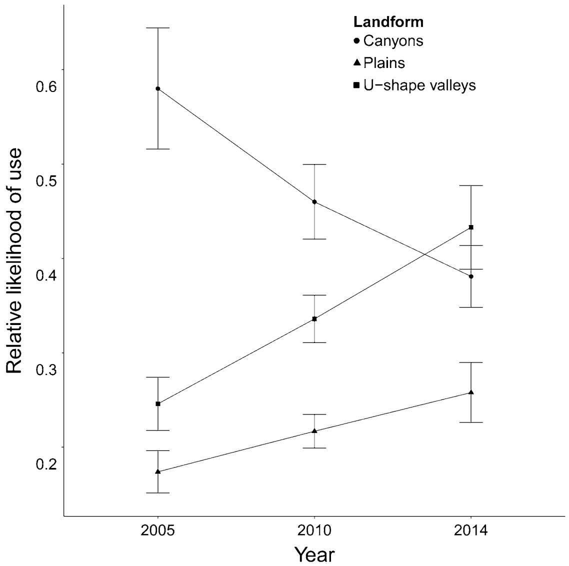

Fig. 4 Relative likelihood of landform use (±SD) for 2005, 2010 and 2014. Relative likelihoods were calculated using a RSF where covariates were set at the median values

study area are only available from 2003 and later, which prevented us from studying the first years of the invasion. However, the high increase in the number of ponds since 2003 suggests beaver settlement in the area is recent. First records of beaver ponds in Estancia Sara go back to the early 1990s but beaver remains were found in systematic searches by cetacean biologists in San Sebastian Bay (Fig. 1) in the early 1980s (N. Goodall Pers. Comm). Lags between invaders' first detection and population spread are frequent in biological invasions (Crooks 2005; Sakai et al. 2001) and can be a consequence of exponential growth starting from low population numbers.

Beavers first selected canyons to establish their ponds. Streams located in canyons often occurred close to headwaters and are not very deep nor wide, facilitating dam construction (Barnes and Mallik 1997). Johnston and Naiman (1987) proposed that deeply incised streams can also facilitate access to resources from the pond and escape from predators compared to broad riparian valleys. In a study we are

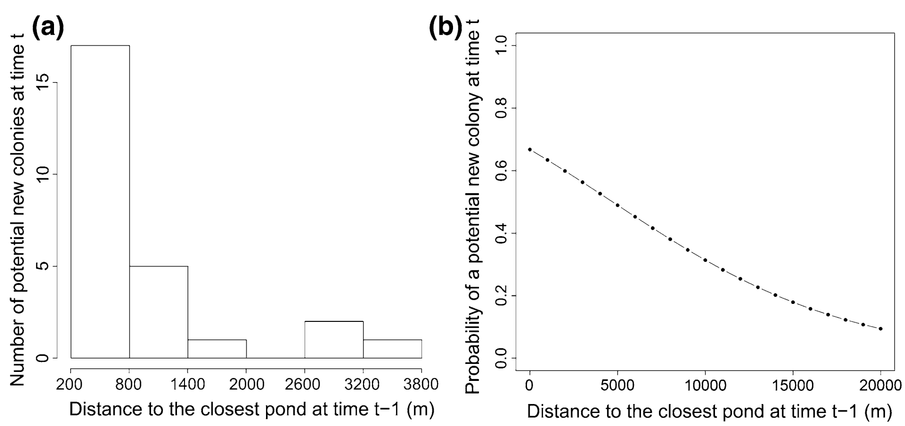

Fig. 5 **a** Distribution of the distances of potential new colonies to the closest pond at time t−1. **b** Probability of establishment of potential new colonies as a function of the distance to the closest pond. Probabilities were calculated from the best ranked logistic model that incorporated distance

Table 2 Logistic models to study the establishment of potential new colonies

Model	K	AIC	ΔAIC	AIC wt	Cum weight
CA + ELEV + SG	4	60.52	0	0.28	0.28
CA + SG	3	61.3	0.78	0.19	0.47
CA + CO + ELEV + SG	5	62.3	1.91	0.11	0.57

Models with AIC < 2 are presented

CA catchment area, *COV* vegetation cover, *ELEV* elevation, *SG* stream gradient conducting in this area, we found colony densities along some of these canyons to be 1.5 colonies per km of stream length, among the highest densities ever recorded for beavers (Muller-Schwarze 2011). Use of canyons declined over time, and beavers increased the use of watercourses in plains and U-shaped valleys in recent years. Streams located in canyons represented 17 % of the pixels in our study area while watercourses on plains and U-shaped valleys comprised 75 % of the total landscape. Our study highlights the importance of geomorphology for beaver settlement in the steppe in agreement with other studies (Coronato et al. 2003; Hartman 1996; Johnston and Naiman 1987; Suzuki and McComb 1998).

High rates of population growth combined with reduced availability of preferred habitat can cause organisms to shift their habitat selection over time. Such density-dependent habitat selection has been very well studied in rodents (Halama and Dueser 1994; Messier et al. 1990; Morris 1989), and RSFs have been increasingly used to study density dependent habitat selection (McLoughlin et al. 2010; van Beest et al. 2014). John et al. (2010) studying the expansion of a reintroduced population of the European Beaver did also observed changes in habitat selection over time. Still, those changes were related to vegetation features rather than geomorphology as we show in this study.

Here we argue that high resolution data on the spread of invasions can not only help us to better understand density dependent habitat selection, but shed light on the mechanisms affecting invasion success. Rapid behavioral and population responses to increased density can promote invader persistence (Duckworth and Badyaev 2007; Human and Gordon 1999; Sol et al. 2013). As beavers fill up watercourses in canyons (as suggested by very high densities and RSFs), they begin to use other, less preferred habitats. For beavers, streams in plains often have higher flows as they collect water from headwaters, making dam construction and water management more difficult. Yet once most canyon sites were occupied, beavers in the landscape we studied demonstrated the behavioral flexibility to use streams in plains. We do not know however whether their demography is poorer in such sites, which might eventually slow the rate of population increase.

For small streams, we did not expect to see differences in pond establishment as a function of vegetation cover, as mud can suffice as a building material to manage running water. Interactions between shrub vegetation cover and catchment area showed that areas with less vegetation cover in smaller watercourses were preferred over those with higher vegetation cover in 2005. Shrubs usually grow in drier areas on river banks and the absence of woody vegetation can be ascribed to the presence of meadows that are easier to flood and to excavate for dam construction material. Contrary to what many beaver biologists may believe, we think woody material is mainly used to build dams and its importance as forage may be less relevant for individuals in the steppe than previously thought (Beier and Barrett 1987; Hartman 1996; Suzuki and McComb 1998). Models that included an interaction of vegetation cover with stream gradient ranked poorly. This is probably a consequence of relatively low gradients in the steppe. We believe as we move closer to the Andes higher water flows and gradients will make stream gradient a more important variable for beaver habitat selection (Coronato et al. 2003).

Distance to the nearest pre-existing pond was an important predictor of establishment of potential new colonies. This is not surprising as other studies in the native range found juveniles dispersed close to their natal colonies (Sun et al. 2000; VanDeelen and Pletscher 1996). The mean distance of a potential new colony to the nearest pond was 864 m, substantially less than the mean distance other studies on beaver dispersal have recorded. If we use the distribution in Fig. 5a to represent dispersal distances, we are assuming that dispersers came from the nearest colony, which is not necessarily true. Beavers can disperse much longer distances, and measuring long-distance dispersal events requires a larger study area. For instance, using telemetry we detected a 19 km dispersal event of a juvenile residing in the study area (A. Pietrek, pers. obs.). Such events are likely to become more frequent as habitats fill up.

Most population models assume the speed of the invasion is governed by constant dispersal and a density independent growth rate at the wave front (see Hastings et al. 2005 for a review), but few have investigated how declining vital rates and an increase in dispersal distance behind the front affects the speed of the invasion. Dwyer and Morris (2006) found that an increase in the dispersal distance as result of resource depletion can lead to fluctuating rates of spread. Consequences of this can be profound and may turn our attention to the areas behind the invasion front to better manage the invasion. At a more practical level, our research may provide a guideline to better target search efforts and beaver detection in the continental steppe. Although there may be some differences between steppe habitats on the mainland (where beavers are now invading) and on the island of Tierra del Fuego (where we conducted our study), our results suggest that geomorphological features are important in beaver habitat selection. Patagonia still harbors remote areas hardly accessible by road, and use of high resolution satellite images can be an important tool to more efficiently detect beaver activity. Furthermore, at the initial stages of the invasion stronger habitat selection can increase chances of detecting the invader if the preferred habitat is identified.

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