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ORIGINAL PAPER

How effective are buffer zones in managing invasive beavers in Patagonia? A simulation study

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Abstract In an age of invasions, it is critical to design and test management strategies to more efficiently control foreign species. Spatially explicit individual based models (SEIBMs) are a powerful tool to explore different management scenarios to control invaders, but we rarely have enough data to parameterize these models, particularly for relatively long-lived species. Here we take advantage of our previous work estimating demographic rates of invasive beavers in Patagonia, and develop an SEIBM to model the spread of beavers in Patagonia. We used our SEIBM both to estimate dispersal distances by fitting their observed rate of spread and to test how placing a buffer zone (a longitudinal strip of land perpendicular to the direction of spread within which a fraction of beavers are culled) beyond the invasion front would work as a control strategy. Specifically, we explored six different scenarios with two different culling rates and two buffer zone widths. We found that beavers in Patagonia must disperse long distances on average to account for the observed rate of spread, and thus our model predicts that a 100 km buffer zone will be needed to slow (but likely not halt) the spread of beavers. Interestingly, culling a higher proportion of beavers within a 100 km buffer zone (90 vs. 60%) did not improve buffer zone performance. Our study shows that wide buffer zones can slow (but likely not halt) continental spread of beavers in Patagonia and potentially pave the way for beaver eradication.

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Introduction

Introduction of foreign species continues to be one of the most pressing threats to biodiversity, and its impact is intensifying as global trade and transportation increase (Mack et al. 2000; Wilcove et al. 1998). When invaders pose a threat to native species or ecosystems, a central question is how to eradicate or control the invasion in the face of uncertainty and limited economic resources (Manchester and Bullock 2000; Simberloff 2009). Eradication of the invader may be the best option, but in the real world, costs of eradication can be prohibitive. Often, managers face a tough decision: is it possible to stop the invasion and limit the damage to the areas already invaded, or is eradication the only option that will limit further damage?

One potential strategy, similar to one that was proposed to control the spread of rabies in foxes (Murray et al. 1986) and raccoons (Russell et al. 2005), is to place a “buffer zone” or “cordon sanitaire” just beyond the invasion front. In epidemiology, a cordon sanitaire usually refers to a buffer area of a certain width that separates the unaffected at-risk population from the infected population and in which a fraction of the vector population is either removed and/or vaccinated. This approach has been successful in wildlife disease cases to control fox rabies in Europe (Freuling et al. 2013) and to avoid declines of Ethiopian wolves during rabies outbreaks (Haydon et al. 2006), and had variable results in controlling the spread of tuberculosis from badgers to cattle in Ireland and Britain (Sleeman et al. 2008) and from possums to cattle in New Zealand (Pech et al. 2010). However, much less attention has been paid to the use of buffer zones as a strategy to slow the spread of invaders. For instance, a buffer zone strategy was proposed to stop the spread of American mink in Scotland but was never implemented (Harrington et al. 2008). More recently, White et al. (2014) studied how to manage the spread of invasive grey squirrels on red squirrels strongholds separated by a buffer area where a fraction of the invader was removed.

Twenty North American beavers were introduced to the island of Tierra del Fuego in 1946 (Pietrek and Fasola 2014), and studies suggest that at least 100,000 beavers currently populate the Fuegian archipelago and cause significant economic damage (Choi 2008; Soto Simeone and Soza-Amigo 2014). In Tierra del Fuego beavers are responsible for the most drastic landscape alteration in the Holocene, impacting between 20 and 40% of the total stream length (Anderson et al. 2014). Beavers cause changes in the structure and composition of *Nothofagus* forests (Martínez Pastur et al. 2006), impact fish and aquatic macroinvertebrate assemblages populations (Anderson and Rosemond 2007; Moorman et al. 2009) and alter stream food webs (Anderson and Rosemond 2010). Perhaps more importantly, beavers create entirely new habitats (beaver meadows) that allow establishment of many invasive plant species and require active restoration to return to their original state (Anderson et al. 2006; Henn et al. 2014).

Beavers were reported in mainland Chile in the early 1990s, but recent dendrochronological studies suggest beavers may have arrived on the continent between the late 1960s and early 1970s (Graells et al. 2015). In 2013 a beaver was detected close to the city of Puerto Natales (Sanguinetti et al. 2014) (Fig. 1). This relatively rapid northward

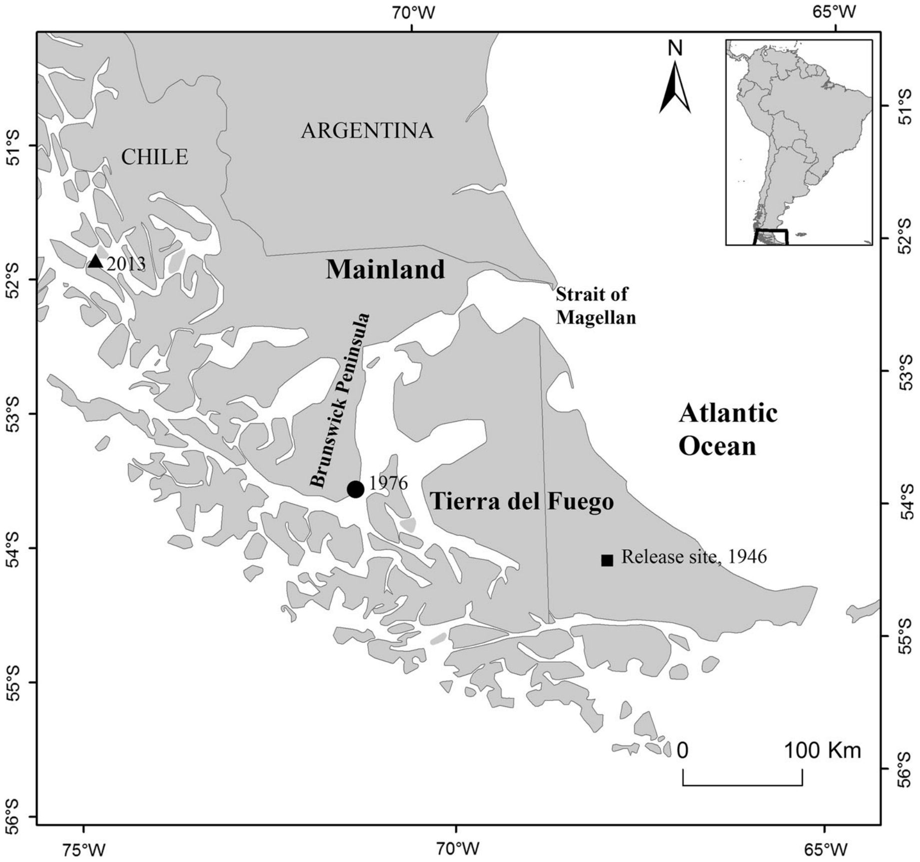

Fig. 1 Spread of introduced beavers in the Patagonia region of South America. The *square* indicates the site were the first 20 beavers were released. The *circle* represent the site in the continent where beavers arrived in 1976 according to the dendrochronological record. The *triangle* represents the northernmost point where a beaver has been captured (near the town of Puerto Natales in 2013)

expansion has highlighted the urgent need to control further northward spread of beavers and has prompted the governments of Argentina and Chile to design a binational strategy to eradicate the invader. For beavers, a buffer zone strategy could be an alternative to eradication in Patagonia. A buffer zone would be a strip of land running perpendicular to the direction of spread within which a fraction of beavers are culled (i.e., removed by trapping or shooting). To allocate resources most efficiently, we would like to know if control can be achieved in this way and if so, what are the narrowest width of the buffer zone and the lowest culling rate within the buffer zone that are compatible with achieving control of the invasion. Realistic simulation models can provide a cost-effective means to evaluate this proposed strategy before embarking on costly measures that may be doomed to fail.

An increase in computational power has led to an increase in the use of individual-based models (IBMs), also called agent-based models (Grimm and Railsback 2013; Grimm et al. 2005). IBMs simulate the behavior of individuals in space and time and allow for interactions with other agents and with their environment. Population-level patterns arise as an emergent property of the behavior of individuals as they interact with each other and their local environment. The appeal of individual based models is that they can easily incorporate a wide range of behaviors and traits that analytical models cannot. Further, the parallel development of geographic information systems (GIS) has led to an explosion of spatially explicit individual-based models (SEIBMs) that can realistically represent the interaction of individuals across heterogeneous landscapes (Adams et al. 2015; Travis et al. 2011).

While a disadvantage of SEIBMs is that they can require a large amount of data to parameterize, they are especially appropriate to model the spread of beavers in Patagonia for at least three reasons. First, beavers move mainly through watercourses, and dispersing juveniles will select only certain sites to settle based on geomorphology, vegetation cover and vicinity to other beavers (Muller-Schwarze 2011). Second, IBMs can incorporate stochasticity relatively more easily than can analytical invasion models. For instance, population growth near the front, where density is low, can be affected by demographic stochasticity. Also, the few established beaver families at the invasion front may or may not increase the speed of the invasion in a given year, as by chance juveniles may disperse behind the invasion front. Third, beavers are highly territorial animals that actively seek mates during dispersal, and we can expect dispersal behavior to respond in complex ways to density. Beavers may move longer distances to search for mates in low-density areas near the front, or to find new territories and avoid intraspecific competition at high densities behind the front. Conversely, beavers may move shorter distances if a mate is available at a site nearby. All these features can be easily incorporated into an SEIBM but cannot easily be captured with a diffusion or integro-difference equation model.

In summary, we constructed a realistic SEIBM for the spread of beavers in South America, parameterized the model with vital rate data collected in Tierra del Fuego, incorporated density-dependent dispersal, and used the model to estimate the dispersal parameters that matched observed rates of spread of beavers in Patagonia. Subsequently, we used the fully parameterized model to assess whether a buffer zone could prevent further spread of the invasion under two different widths and two levels of detection (and therefore, culling rates) within the buffer zone.

Materials and methods

We built the SEIBM in Netlogo 5.3 (Wilensky 1999). The model describes the position of each beaver each year on a two-dimensional landscape. Because watercourses define potential breeding sites for beavers, we constructed detailed hydrological maps (90 m cell size) using a Digital elevation model (DEM) of our study area that included only streams below the tree line (600 m) located on slopes of <20°, where beavers are more likely to settle (Allen et al. 1983; Coronato et al. 2003).

We refer to a beaver family that shares a common territory as a colony. Colony composition varies from a single pair of adults to a family composed of the adult pair, the kits born that year and one or more offspring born in previous years. We defined four beaver age classes in our simulation, assuming we census the population just after the birth season in the austral spring: kits, yearlings, and juveniles (born zero, one, and two birth seasons before the current census, respectively), and adults (three or more years old). Juveniles generally leave the natal colony when they are 2 years old, and while some can remain longer, we assume all juveniles dispersed in our model. Colonies are founded when either a male and a female juvenile settle at the same site and mate the following year or when a juvenile arrives at a site already occupied by an unmated adult of the opposite sex. Once dispersing juveniles choose a site, we assume that they never disperse again .

At each one-year time step in the model, beavers age or die, potentially reproduce, and potentially move, in that order. Using age-specific vital rates the model determines the fate of each beaver (survive and move to the next age class or die) stochastically using a Bernoulli distribution, then updates the number of colonies present. For each colony the model first determines stochastically whether the breeding pair would produce kits and if so, draws the number of kits, n, from a zero-truncated Poisson distribution. All demographic parameters were based on empirical estimates obtained for beavers in Tierra del Fuego for two habitats: forest and steppe (Pietrek et al. 2016) (see Table 1 for model parameters). All our simulated landscapes encompass areas covered primarily by forest, but as population growth at low, rather than high, density determines the speed of an invasion (Kot et al. 1996), the mean number of kits produced per colony in our simulations was the value obtained in the steppe, where colonization was more recent and populations were thus less likely to be affected by negative density dependence [all other vital rates were found to be habitat-independent; Pietrek et al. (2016)].

After survival and reproduction (which occurs in spring), juvenile beavers disperse to seek mates. Juvenile beavers cannot disperse to sites already occupied by a colony. However, they can disperse to a site occupied by a lone juvenile or adult of the opposite sex. Beavers use chemical communication through scent mounds (piles of mud and debris

Table 1 Parameters used in the SEIBM first to fit the observed rates of spread of invasive beavers, then to test buffer zone effectiveness

Parameter	Value	Distribution	Description
Beaver propagule size	20	–	Numbers of beavers released (Pietrek and Fasola 2014)
Initial location of beavers	0–10 km	Uniform	Randomly placed in a 10 km radius of known traslocation site
Probability of producing kits	0.72	Bernoulli	Mean proportion of Tierra del Fuego colonies with kits (Pietrek et al. 2016)
Number of kits per colony	2.75	Poisson	Mean number of kits produced per colony (Pietrek et al. 2016)
Annual survival of kits	0.66	Bernoulli	Mean survival of kits produced per colony (Pietrek et al. 2016)
Annual survival of yearlings	0.97	Bernoulli	Mean survival of yearlings (Pietrek et al. 2016)
Annual survival of juveniles	0.97	Bernoulli	Mean survival of juveniles (Pietrek et al. 2016)
Annual survival of adults	0.97	Bernoulli	Mean survival of adults (Pietrek et al. 2016)
Minimum dispersal distance	0.72 km		Based on inter-colony distances at high densities (Muller-Schwarze 2011)
Mean dispersal distance	17	Exponential	Estimated by matching observed spread rates to model output
Radius to search for mates	0–2.5 km	Uniform	Beavers mate with a random unpaired beaver within this radius

where they place territorial marks) and visual communication through cut and gnawed trees and damming to assess the presence of other beavers. In our simulation, beavers cannot establish a colony closer than 700 m from an existing colony, based on estimates of colony density reported in the literature (Muller-Schwarze 2011).

We simulated dispersal as follows (Fig. 2). Before dispersing, beavers usually venture on short sallies to prospect the area surrounding the natal colony; thus, to simulate exploratory behavior, we set a fixed radius of 2.5 km to search for nearby mates (Muller-Schwarze 2011). In our model, juveniles will first attempt to move to sites within this radius that are occupied by juveniles or adults of the opposite sex and that do not have a mate (this can include sites that previously contained a colony, but where one of the members of the breeding pair died), choosing from among all such sites at random. However, if no mates are available within the search radius, beavers move a distance randomly draw from an exponential distribution. If a beaver does not find a suitable site at the randomly chosen distance (±1 km), it dies. This was intended to simulate negative density dependent survival, as may occur when highly territorial animals such as beavers disperse at high density and die as a result of territorial fights. If a beaver does find a site at the randomly drawn distance, it searches for a mate within a 2.5 km radius of the destination site as described above. If no potential mate is found in the search radius the beaver settles by itself in its destination site.

Estimating dispersal parameters and fitting observed rates of spread

While survival and reproduction rates were estimated from field data, we lacked information on individual dispersal. Thus, we estimated the mean dispersal distance of the

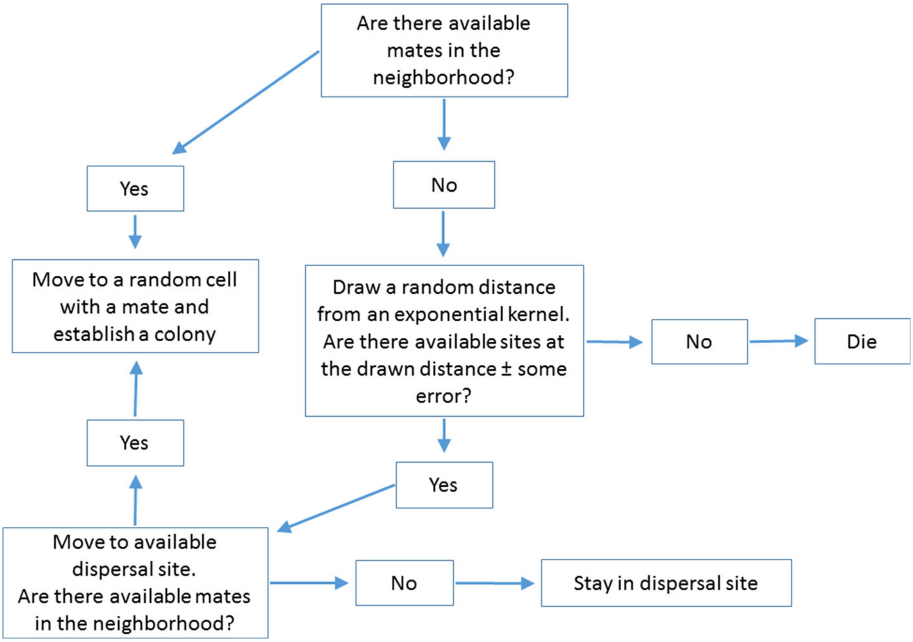

Fig. 2 Flow diagram describing dispersal of juvenile beavers in the model

exponential kernel by varying it in the model until the model predicted the observed rate of spread of the invasion.

There are no published estimates of how quickly beavers colonized Patagonia, so to estimate the rate of spread, we measured the time it took for beaver populations to expand from their original introduction site at Cami Lake on the island of Tierra del Fuego in 1946, to mainland Chile. The most reliable estimates of beavers' first arrival on the mainland come from dendrochronological data (Graells et al. 2015). Of the three sites on mainland Chile with the earliest evidence of beaver presence, one was estimated to have been colonized in 1968 and two in 1976 (Fig. 1). To estimate the observed rate of spread, we chose the site (Rio Yumbel, colonized in 1976) deemed the most precise estimate of beaver arrival time on the continent. The precision of the estimate was determined by the correlation ($r = 0.78$) between the estimated age of beaver cut trees and ages of a sample of live trees in the same site. The mean observed rate of spread was 7.66 km/year [=distance from Lake Cami to Rio Yumbel/(1976−1946)].

To simulate the spread of beavers and fit the exponential dispersal kernel we used a rectangular strip of our landscape running southeast to northwest 250 km long by 50 km wide that included the release point, Cami Lake, in southeastern Tierra del Fuego at the southeastern edge of the rectangle and the sites first invaded on the continent at the northwestern edge of the rectangle. At time 0 we placed twenty beavers (the original propagule size) at the release point in Cami Lake and we assumed beavers paired up in ten colonies within a 10 km radius of the release point. To make the simulation feasible with our available computing power and allow beavers to move freely, we allowed beavers to leave the right edge of the rectangle and reemerge on the left edge and vice versa (i.e., our simulated landscape represented a cylinder). We let our simulations run from $t = 0$ to a maximum of $t = 20$, when the invasion was approaching asymptotic rates of spread. We calculated the speed of the simulated invasion as the distance from the release point to the beaver farthest from that point, divided by the number of years since simulation began. To determine the dispersal distance that best matched the observed speed of the invasion we varied the mean dispersal distance of the exponential kernel (for beavers who do not find mates within the 2.5 km radius). We ran 200 simulations for each mean dispersal distance value and averaged the invasion speed over all simulations. After exploring a range of dispersal distances, we chose the estimate that best matched the observed rate of spread.

Simulating management scenarios

Using the fitted mean dispersal distance that reproduced the speed of the invasion, we simulated four management scenarios, representing all combinations of two buffer zone widths (50 and 100 km) and two realistic detection probabilities within the buffer zone (0.6 and 0.9) (Schiavini et al. 2016). Detection probability was defined as the likelihood that a site occupied by one or more beavers is found by managers during culling efforts in a given year. As even lone beavers can build dams, alter the surrounding habitat, and build a visible winter food cache, we assumed that the probability of detecting an invaded site was the same regardless of the number of beavers at the site. To simulate culling, once an occupied site was detected, all the individuals were removed. In addition to these four scenarios, we ran two control scenarios (one for each width) with the same parametrization in which no culling was performed within the buffer zone.

We ran our model on a rectangular strip of mainland Patagonia, northwest from Brunswick Peninsula, 300 km long by 50 km wide that included the northernmost point where a lone beaver was recorded in 2013. Since juveniles that will advance the invasion front disperse from colonies, and we were interested in testing how effective the buffer zone would be, we placed the start of the buffer zone 10 km north of the southern edge of our landscape and filled suitable sites south of the buffer zone with beaver colonies. The colony composition of the invaded area below the buffer was simulated using density and colony composition from our previous dispersal kernel simulations. We ran 200 simulations (each 10 years long) for each management and control scenario, and we recorded the time of first arrival to the other side of the buffer zone, the number of beavers that crossed the buffer zone in 10 years, the final number of colonies within the buffer zone, the number of beavers removed within the buffer zone, and the distance and type of dispersal of each individual beaver in the entire landscape. Specifically, we considered three types of dispersal: short-distance (2.5 km) mate finding (M); long-distance dispersal followed by successful mating (DM), in which beavers dispersed a distance drawn from the dispersal kernel and then found a mate within a 2.5 km radius of their dispersal site; and long-distance dispersal without mating (D), in which beavers dispersed a distance drawn from the dispersal kernel, found a suitable site, but failed to find a mate, and thus remained by themselves in that time step at the destination site.

Results

The mean dispersal distance that best matched the observed rate of spread was 17 km, on the higher side of mean dispersal distances of beavers given literature estimates (3.5–17.1 km, Muller-Schwarze 2011). An SEIBM that incorporated this mean dispersal distance produced a mean invasion speed 8.1 km/year, close to the observed speed of 7.66 km/year.

In the management scenario simulations, at both levels of detection and removal, the mean number of colonies within the buffer zone at the end of the 10-year simulation was drastically reduced relative to the control simulations (Fig. 3). The mean number of colonies with 90% removal was close to seven, while an average of 49 colonies remained after 10 years when 60% of the colonies were culled, compared to close to 1000 in the control. Both buffer zone widths reduced to half the number of individuals that crossed the

Fig. 3 Number of colonies within the buffer zone after 10 years under the different management scenarios. Error bars indicate standard deviation among simulations

buffer zone compared to a strip of comparable width where no beavers were removed (the controls, Fig. 4a). Not surprisingly, wider buffer zones resulted in fewer individuals crossing the buffer zone. Somewhat counterintuitively, removing 60% of the colonies resulted in a larger total number of beavers culled over ten years (Fig. 4b). In the 100 km buffer zone scenario, culling 60% of the colonies lead to an additional 19 beavers removed on average every year, compared to the 90% colony removal scenario.

The number of beavers that crossed the 100 km buffer zone did not differ under the two culling rates (mean, SD; 60%: 4.15, 2.15; 90%: 3.79, 2.1), even though more colonies were left within the buffer zone with 60% removal. This unanticipated outcome means that most beavers that crossed the buffer zone originated from the colonies located south of the southern edge of the buffer zone, rather than representing dispersing juveniles that were born within the buffer zone. For instance, with both 60 and 90% removal, almost all beavers crossing the buffer zone dispersed 100 km or more in a single move (Fig. 6 in Appendix).

The median time it took the first beaver to cross the buffer zone varied with buffer zone width but not with the fraction of beaver colonies removed (including no culling). Regardless of culling levels, the median time for the first beaver to arrive to the other side of the buffer zone was one year when the buffer zone was 50 km wide and, for a 100 km buffer zone, averaged 4 years (mean, median, SD; no removal: 4.1, 4, 2.5; 60%: 4.1, 4, 2.4; 90%: 3.7, 3, 2.4). Beavers crossed the buffer zone in all simulations under the control scenario, but in 5–10% of our removal simulations beavers did not make it to the other side of the buffer zone within 10 years. Comparing the distributions (rather than just the means) of crossing times for the control versus the two removal scenarios, the distributions are significantly different (χ^2 test, $\chi^2 = 36.46$, df = 18, p = 0.006) (Fig. 7 in Appendix) but the distributions did not differ between the two culling scenarios (χ^2 test, $\chi^2 = 8.612$, df = 9, p = 0.47). Thus, culling in general, may slightly slow crossing, but the difference between moderate and high culling is negligible.

Differences in density driven by culling affected the frequency of dispersal types. At high density within the buffer zone (control) a higher proportion of potentially dispersing beavers died because they failed to find either mates or suitable sites (Fig. 5). Thus,

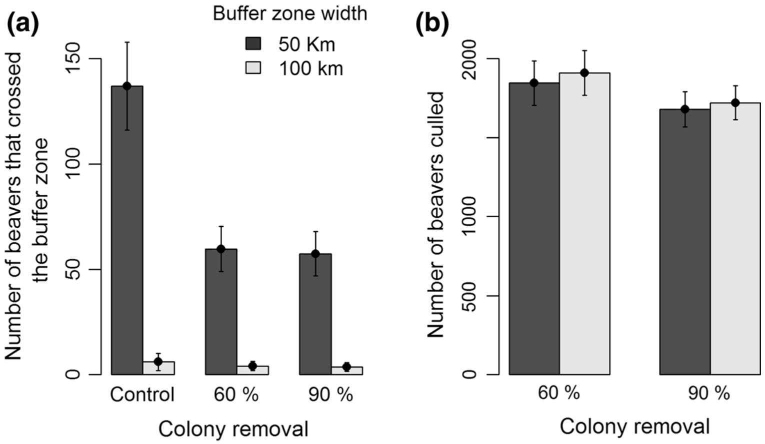

Fig. 4 **a** Mean number of beavers that crossed the buffer zone in ten years for three different removal scenarios and two buffer zone widths. **b** Mean number of beavers culled in the two removal scenarios. Error bars indicate standard deviation. Each scenario was run 200 times

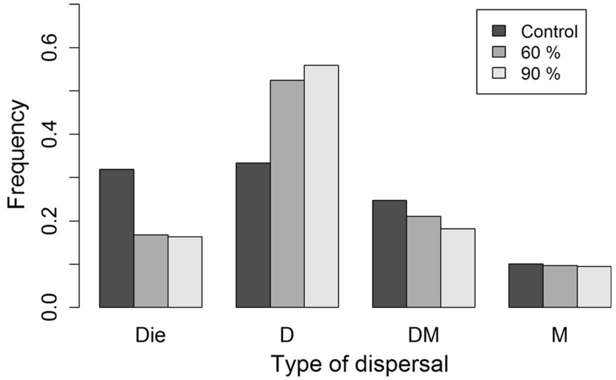

Fig. 5 Frequency of dispersal types among treatments. Each scenario was simulated 200 times. *Die* unsuccessful dispersal and death, *D* long-distance dispersal to a suitable site, but without finding a mate, *DM* long-distance dispersal in which a mate was found, and *M* short-distance mate finding

beavers needed to move longer distances to successfully disperse as density built up behind the invasion front. For instance, mean dispersal distance was close to 15 km at the beginning of our control simulations, but near 24 km after 10 years. At low density (as occurs when the culling rate is high), beavers also tended to move long distances (D and DM dispersal types), because they were less likely to find mates in their neighborhood. Lower culling resulted in a higher proportion of individuals that found a mate after dispersal (60% culling: 21% of 85,503 dispersal events; 90% culling: 18% of 101,232 dispersal events, test of equal proportions, $\chi^2 = 216$, df = 1, p = 0.00) which may favor the spread of beavers in the 60% culling scenarios at longer simulation times due to higher reproduction rates.

Discussion

Our study shows that only a 100 km buffer zone will work as a management strategy. Interestingly, we found that a higher fraction of beavers culled did not decrease the mean number of individuals crossing the buffer zone within the timeframe of our simulation, but given higher rates of density-driven mate finding dispersal (DM type dispersals) under the lower culling rate, higher culling could result in a slower invasion over longer time frames. Although a few colonies persisted within the buffer zone in the culling scenarios, most beavers that crossed the buffer zone dispersed from colonies outside the buffer zone, not within it. Below, we discuss these results and try to provide some insights on the spread of beavers in Patagonia and the broader issue of slowing or stopping invasions using a buffer zone strategy.

The mean number of beavers that crossed the buffer zone decreased as the width of the buffer zone increased. As expected, a 50 km wide buffer zone reduced the density of beavers at the invasion front but was insufficient to altogether halt further spread. Beavers can travel long distances. Saveljev et al. (2002) reported a beaver that migrated more than 500 km in Russia. Beer (1955) found a mean dispersal distance of 17 km in Minnesota, which agrees with the estimates of dispersal derived from our model. Under our model, as many as 3 out of 1000 dispersal events can surpass 100 km if mates are not found close by. In a previous study we conducted in Tierra del Fuego (Pietrek 2015), one of ten dispersing beavers tracked by radio telemetry moved 19 km, and we believe our ability to relocate other tagged beavers was constrained by the long distances they move. Long-distance dispersal events have been one of the main factors driving the spread of rabies in raccoons (*Procyon lotor*) in Ohio, where a buffer zone strategy was unsuccessful in preventing spread of the disease (Russell et al. 2005). Similarly, rare long dispersal in badgers has been linked to failure of buffer zone strategies to stop the spread of bovine TB (Byrne et al. 2014).

For beavers, movement along drainage basins is probably more frequent than movement between basins. However, in areas with relatively high drainage density (such as the one we studied), beavers can easily move between basins. In Tierra del Fuego, three out of the ten dispersal events we tracked by radio telemetry involved inter-basin movement (Pietrek 2015). Beavers in Wisconsin moved as far as 11 km from the nearest body of water, suggesting they can travel long distances over land (Muller-Schwarze 2011). This ability could have facilitated dispersal in Tierra del Fuego, where juvenile beavers do not have any predators, by allowing them to disperse longer distances and by increasing their chances of successful establishment. Beavers have also colonized mainland Chile and several of the islands in the archipelago of Tierra del Fuego by swimming across bodies of salt water such as the Strait of Magellan, demonstrating their extraordinary dispersal capabilities.

The virtual absence of differences in the mean number of beavers that crossed the buffer zone as a function of culling can be ascribed to the fact that very few crossing events originate within the buffer zone. Most of the beavers crossing the buffer zone originated outside it, probably because the number of colonies within the buffer zone remained low. This interesting result suggest that even moderate rates of culling may suffice to control the spread of beavers if wide buffer zones are used. Although lower rates of culling resulted in more beavers culled due to population build-up within the buffer zone, the associated cost of culling more beavers under 60% detection rate will probably be offset by the much higher costs necessary to detect a larger proportion of colonies (at the 90% detection rate).

The increase in the mean dispersal distances both at high density behind the invasion front and at low density near the front may shed light on the mechanisms of beaver spread in Tierra del Fuego. At high densities, survival of dispersers decreases because they are unable to find suitable sites and they may face an increase in conspecific attacks. Thus, beavers are forced to move longer distances when they are born far behind the invasion front, where density is high. When the numbers of suitable sites and available mates are relatively high, as they were in the forest habitats of Tierra del Fuego as populations were increasing, beavers do not need to travel long distances. But when suitable sites decrease as a result of overcrowding or simply because there are no unpaired mates nearby (negative density dependence) or fewer high quality sites (steppe, Pietrek and González-Roglich 2015) they may disperse farther (Altwegg et al. 2013), which is consistent with a more rapid spread of beavers in the steppe habitat of Tierra del Fuego (Skewes et al. 2006). In our model, we have included high dispersal at both low and high densities, which we think best describes beaver behavior, but previous studies on effects of density on dispersal have usually assumed more linear responses to density (Altwegg et al. 2013; Travis et al. 1999).

Even if the long-term strategy to control the invader is eradication and subsequent restoration of the affected ecosystems (Henn et al. 2014; Malmierca et al. 2011;

Menvielle et al. 2010), our results suggest buffer zones may provide good short-term solutions. First, buffer zones will slow further spread of beavers in the continent by decreasing the number of dispersers behind the front. Second, buffer zones will reduce the ecological and economic impact of beavers on the ecosystem by reducing their population numbers. Third, buffer zones may act as population sinks by making available previously occupied territories. Last, they may pave the road for long-term eradication. For instance, use of sequential buffer zones starting at the invasion front may slow the spread of the invasion at the first buffer by increasing the distance to the source of propagules in the short-run, and facilitate eradication in the long-run by lowering densities within subsequent buffer zones.

In conclusion, our results suggest that a 100 km buffer zone is likely to contain the beaver spread in Patagonia. However, these results should be taken with caution. Seven North American beavers were the founders of the entire invasive beaver population in Finland and only ten pairs initiated Tierra del Fuego population (Parker et al. 2012; Pietrek and Fasola 2014). Our simulations with high culling have shown as much as ten beavers can cross the 100 km buffer zone in ten years, but is true this was over a 10 years period. Even wider buffer zones (or multiple sequential zones) may be more effective at containing the spread of beavers, but the cost of actively surveilling and culling in one or more buffer zones that are, for example, 200 km wide may be economically unfeasible or unsustainable over time. We do not have detailed estimates for how much eradication would cost or how much it would cost to implement the most effective buffer zones, but knowing the level of effectiveness of butter zones will allow managers to better weigh the costs and benefits of the various management options (including eradication). More generally, our study shows buffer zones may be a good management strategy on their own, or as part of a multi-pronged approach to contain invasions although we caution relatively good data on dispersal is needed, particularly for highly vagile species.

Our work shows that realistic SEIBMs can be an inexpensive way to assess different management scenarios, and are particularly cost effective if these strategies are doomed to fail. Further, our work highlights the importance of incorporating into invasion models both real landscapes and density dependent dispersal responses. This is particularly true for species that actively select sites and search for mates, features common to many animal invaders. In the future, we expect these models, with the incorporation of finer scale data on beaver habitat availability, will guide the efforts to eradicate invasive beavers of Patagonia.

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Appendix

See Figs. 6 and 7.

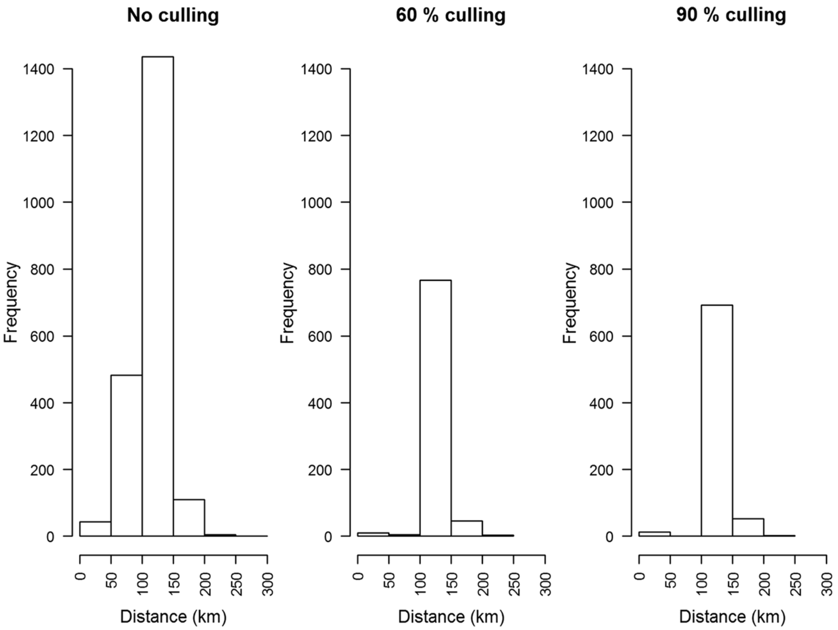

Fig. 6 Distribution of dispersal distances of successful crossings with a 100 km width buffer zone under different culling scenarios

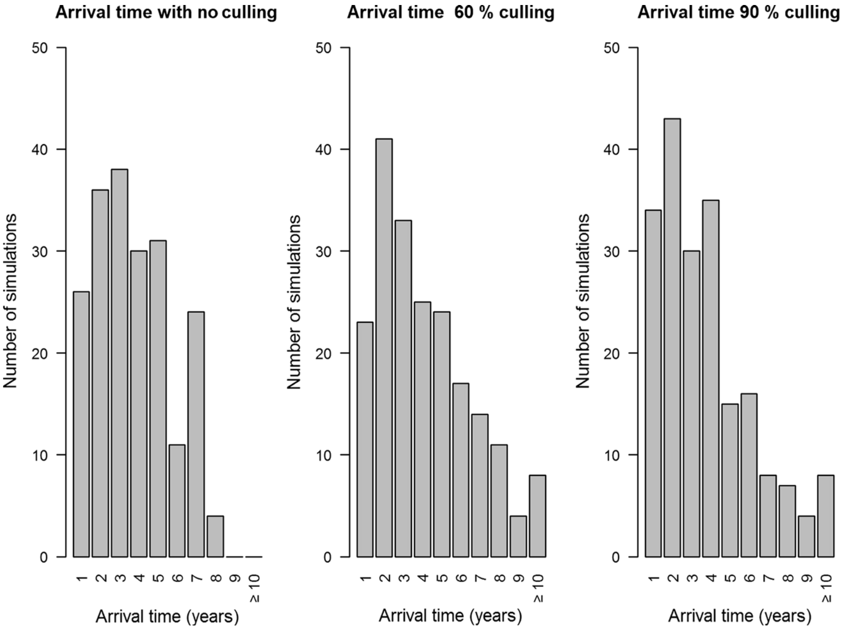

Fig. 7 Distribution of time of first arrival to the other side of the 100 km buffer zone under different culling scenarios

References

Adams VM et al (2015) Distribution, demography and dispersal model of spatial spread of invasive plant populations with limited data. Methods Ecol Evol 6:782–794. doi:10.1111/2041-210X.12392

Allen AW, Energy W, Team LU (1983) Habitat suitability index models: beaver. Western Energy and Land Use Team, Division of Biological Service, Research and Development, Fish and Wildlife Service, US Department of the Interior

Altwegg R, Collingham YC, Erni B, Huntley B (2013) Density-dependent dispersal and the speed of range expansions. Divers Distrib 19:60–68. doi:10.1111/j.1472-4642.2012.00943.x

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. doi:10.1007/s00442-007-0757-4

Anderson CB, Rosemond AD (2010) Beaver invasion alters terrestrial subsidies to subantarctic stream food webs. Hydrobiologia 652:349–361. doi:10.1007/s10750-010-0367-8

Anderson C, Griffith C, Rosemond A, Rozzi R, Dollenz O (2006) 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, Vanessa Lencinas M, Wallem PK, Valenzuela AEJ, Simanonok MP, Martínez Pastur G (2014) Engineering by an invasive species alters landscape-level ecosystem function, but does not affect biodiversity in freshwater systems. Divers Distrib 20:214–222. doi:10.1111/ddi.12147

Beer JR (1955) Movements of tagged beaver. J Wildl Manage 19:492–493

Byrne AW, Quinn JL, O'Keeffe JJ, Green S, Paddy Sleeman D, Wayne Martin S, Davenport J (2014) Large-scale movements in European badgers: has the tail of the movement kernel been underestimated? J Anim Ecol 83:991–1001. doi:10.1111/1365-2656.12197

Choi C (2008) Tierra del Fuego: the beavers must die. Nat News 453:968

Coronato A, Escobar J, Mallea C, Roig C, Lizarralde M (2003) Caracteristicas geomorfologicas de rios de montaña colonizados por *Castor canadensis* en Tierra del Fuego. Argentina Ecol Austral 13:15–26

Freuling CM, Hampson K, Selhorst T, Schröder R, Meslin FX, Mettenleiter TC, Müller T (2013) The elimination of fox rabies from Europe: determinants of success and lessons for the future. Philos Trans R Soc B. doi:10.1098/rstb.2012.0142

Graells G, Corcoran D, Aravena J (2015) Invasion of North American beaver (Castor canadensis) in the province of Magallanes, Southern Chile: comparison between dating sites through interviews with the local community and dendrochronology. Rev Chil Hist Nat 88:3

Grimm V, Railsback SF (2013) Individual-based modeling and ecology. Princeton University Press, Princeton

Grimm V et al (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987–991. doi:10.1126/science.1116681

Harrington LA, Hughes J, Macdonald DW (2008) Management of American mink in the northern highlands: a proposed cordon sanitaire approach. Wildlife Conservation Research Unit, University of Oxford

Haydon D et al (2006) Low-coverage vaccination strategies for the conservation of endangered species. Nature 443:692–695

Henn JJ, Anderson CB, Kreps G, Lencinas MV, Soler R, Pastur GM (2014) Determining abiotic and biotic factors that limit transplanted *Nothofagus pumilio* Seedling success in abandoned beaver meadows in Tierra del Fuego. Ecol Restor 32:369–378. doi:10.3368/er.32.4.369

Kot M, Lewis MA, van den Driessche P (1996) Dispersal data and the spread of invading organisms. Ecology 77:2027–2042

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Malmierca L, Menvielle M, Ramadori D, Saavedra B, Saunders A, Soto N, Schiavini A (2011) Eradication of beaver (Castor canadensis), an ecosystem engineer and threat to southern Patagonia. In: Island invasives: eradication and management, International Conference on Island Invasives, 2011. pp 87-90

Manchester SJ, Bullock JM (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. J Appl Ecol 37:845–864. doi:10.1046/j.1365-2664.2000.00538.x

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

Menvielle M, Funes M, Malmierca L, Ramadori D, Saavedra B, Schiavini A, Soto Volkart N (2010) American beaver eradication in the southern tip of South America: main challenges of an ambitious project. Aliens Invasive Species Bull 29:9–16

Moorman MC, Eggleston DB, 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. doi:10.1577/t08-081.1

Muller-Schwarze D (2011) The beaver: its life and impact. Cornell University Press, Ithaca

Murray J, Stanley E, Brown D (1986) On the spatial spread of rabies among foxes. Proc R Soc London B 229:111–150

Parker H, Nummi P, Hartman G, Rosell F (2012) Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and a strategy for eradication. Wildl Biol 18:354–365

Pech R, Byrom A, Anderson D, Thomson C, Coleman M (2010) The effect of poisoned and notional vaccinated buffers on possum (*Trichosurus vulpecula*) movements: minimising the risk of bovine tuberculosis spread from forest to farmland. Wildl Res 37:283–292

Pietrek AG (2015) Demography and spread of invasive beavers in the heterogeneous landscapes of Patagonia. Dissertation, Duke University

Pietrek AG, Fasola L (2014) Origin and history of the beaver introduction in South America. Mastozoología Neotropical 21:355–359

Pietrek AG, González-Roglich M (2015) Post-establishment changes in habitat selection by an invasive species: beavers in the Patagonian steppe. Biol Invasions 17:3225–3235

Pietrek AG, Escobar JM, Fasola L, Roesler I, Schiavini A (2016) Why invasive Patagonian beavers thrive in unlikely habitats: a demographic perspective. J Mammal. doi:10.1093/jmammal/gyw169

Russell CA, Smith DL, Childs JE, Real LA (2005) Predictive spatial dynamics and strategic planning for raccoon rabies emergence in Ohio. PLoS Biol 3:382–388. doi:10.1371/journal.pbio.0030088

Sanguinetti J et al (2014) Manejo de especies exóticas invasoras en Patagonia, Argentina: Priorización, logros y desafíos de integración entre ciencia y gestión identificados desde la Administración de Parques Nacionales. Ecología austral 24:183–192

Saveljev A, Stubbe M, Stubbe A, Unzhakov V, Kononov S (2002) Natural movements of tagged beavers in Tyva. Russ J Ecol 33:434–439

Schiavini A, Carranza ML, Deferrari G, Escobar J, Malmierca L, Pietrek AG (2016) Erradicación de especies invasoras: Ciencia, actitud y entendimiento. El castor en Tierra del Fuego Mastozoología Neotropical 23:279–288

Simberloff D (2009) We can eliminate invasions or live with them. Successful management projects. Biol Invasions 11:149–157. doi:10.1007/s10530-008-9317-z

Skewes O, Gonzalez F, Olave R, Avila A, Vargas V, Paulsen P, Konig HE (2006) Abundance and distribution of American beaver, *Castor canadensis* (Kuhl 1820), in Tierra del Fuego and Navarino islands, Chile. Eur J Wildl Res 52:292–296. doi:10.1007/s10344-006-0038-2

Sleeman DP, Davenport J, More SJ, Clegg TA, Griffin JM, O'Boyle I (2008) The effectiveness of barriers to badger Meles meles immigration in the Irish Four Area project. Eur J Wildl Res 55:267–278. doi:10.1007/s10344-008-0241-4

Soto Simeone A, Soza-Amigo S (2014) Economic valuation of native forest affected by the North American beaver (*Castor canadensis*) in Tierra del Fuego. BOSQUE 35:229–234

Travis JMJ, Murrell DJ, Dytham C (1999) The evolution of density–dependent dispersal. Proc R Soc London B 266:1837–1842. doi:10.1098/rspb.1999.0854

Travis JMJ, Harris CM, Park KJ, Bullock JM (2011) Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Methods Ecol Evol 2:477–488. doi:10.1111/j.2041-210X.2011.00104.x

White A, Bell SS, Lurz PW, Boots M (2014) Conservation management within strongholds in the face of disease-mediated invasions: red and grey squirrels as a case study. J Appl Ecol 51:1631–1642

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615

Wilensky U (1999) NetLogo. Center for connected learning and computer-based modeling, Northwestern University, Evanston, IL. http://ccl.northwestern.edu/netlogo/