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Why Do Beavers Leave Home? Lodge Abandonment in an Invasive Population in Patagonia

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Abstract: *Research Highlights:* Lodge abandonment by beavers is apparently a common phenomenon in Patagonia, but it is still poorly understood and we ignore what drives it. In relatively slow growth *Nothofagus* forests, resource depletion can impact abandonment while water availability may be a major driver in the semiarid steppe. *Background and Objectives:* North American beaver (*Castor canadensis*) was introduced in 1946 on the island of Tierra del Fuego (TDF) in southern Argentina. Since then, beavers have become a major disturbance affecting not only forest but also treeless steppe landscapes. Our goal was to determine the factors affecting lodge abandonment by beavers in two habitats of TDF: forest and steppe. *Materials and Methods:* A total of 47 lodges were surveyed between February and March from 2012 to 2014 in both habitat types, 22 in the forest and 25 in the steppe. To explain factors involved in lodge abandonment by beavers, we measured the following variables: water level variation, stream gradient, vegetation cover adjacent to shore and forest structure. *Results:* We recorded 24 abandonments events, with a similar proportion of lodges abandoned in both habitats. Our results revealed that lodge abandonment was mostly linked to water level fluctuations irrespective of habitat type. The water level at the entrances of the lodge generally decreased in abandoned lodges. Variables that characterize understory cover had some influence on lodge abandonment in the forest, and no effect in the steppe. *Conclusions:* Water level variation was associated with lodge abandonment in both habitats, and we found some evidence of resource depletion in the forest. However, we caution that changes in water level may be not only due to extrinsic factors but rather to beaver's own activities or to a decay in pond maintenance following abandonment.

Keywords: Argentina; biological invasions; ecosystem engineer; lodge occupancy; *Nothofagus*

1. Introduction

Abiotic agents of natural disturbance such as wind and fire influence ecosystem functioning and biodiversity [1–3], but biotic agents, most notably ecosystem engineers such as North American beavers, can have a comparable impact on ecosystems [4–6]. Although positive effects of ecosystem engineers on diversity and habitat heterogeneity have been widely documented in their native range, the opposite has been shown to be true for many alien ecosystem engineers [7–9]. This is particularly worrying as alien ecosystem engineers, by impacting on the environment and its biota, can have a much larger impact than other invasive species. For instance, North American beaver in Patagonia, as an invasive ecosystem engineer, by modifying the environment, may spread faster on suboptimal habitats than species that do not [10]. This highlights the need to control them to prevent widespread impacts on biodiversity.

The North American beaver (*Castor canadensis*) is an ecosystem engineer initially introduced in 1946 on the island of Tierra del Fuego (TDF) in southern Argentina. Since the release of twenty individuals from Manitoba, Canada [11], the population in the archipelago has increased to more than a hundred thousand individuals [12]. The lack of predators and natural competitors, and the abundant food resources facilitated the spread of beavers on the island. Originally, beavers established in the forests of TDF, but in the last 20 years they have spread rapidly over the adjacent steppe [13–15]. Economic losses associated with the beaver invasion of Argentina and Chile were estimated at approximately USD 4 million/year, due to flooding and damage to civil infrastructures [16]. More importantly, beavers have impacted dramatically the riparian Southern beech forest and its associated biodiversity [17].

By transforming narrow lotic environments to a mix of lotic and lentic habitats through the construction of dams [18–20], beavers increase habitat heterogeneity, plant and amphibian diversity and generate new habitat for birds in their native range [21–23]. However in TDF, where beavers affect on average 30% of watershed surfaces, they reduce the diversity of aquatic macroinvertebrates [7], provide greater food subsidies for non-native trout [24], and affect the nutrient cycle by increasing sediment and organic matter retention [25]. Beavers particularly alter the structure and tree species composition of riparian southern beech (*Nothofagus* spp.) forests used for food and dam construction, and favour the invasion of other exotic herbaceous species [17,26]. A long-standing question is how the loss of these riparian forests feeds back on beaver colonies, particularly given these forests likely recover slower than forests in North America [27]. Near-shore vegetation has been cited repeatedly as a driver of pond occupancy and colony size [21,28,29] and beavers rarely travel farther than 100 m on land from their pond to feed to minimize predation risk [30]. Over longer time scales, population growth rates of beavers may decline in *Nothofagus* depleted areas (or in densely populated areas where territoriality may hinder juvenile settlement), but in the short-term beavers may move and select areas where resources are more abundant.

The causes behind lodge abandonment go beyond resource depletion and remain understudied despite its ubiquity. Juveniles leave the parental colony after 2 years usually, either to form a new colony or join one already established [31,32]. However, often an entire colony can abandon a lodge and move to a new settlement site (translocation) [33]. Studies have also linked lodge abandonment with adult mortality [34] and pond desiccation, which exposes the entrances to the lodge [35]. Water is a key resource and slight water level fluctuations can have substantial effects on the colony [36–38]. Beavers can adjust to changes in water level through excavation of entrances or by adding material to the lodge (branches or mud) [39]. In cold climates, beavers need a minimum water depth to dive under frozen ponds and feed on their food cache [40].

Another related physical feature that may affect habitat selection by beavers is the stream gradient [41,42]. The stream gradient indicates the degree to which beavers might handle the maintenance of beaver constructions after snow melting in spring [38]. Often, beavers prefer low-gradient streams [42], and do not tend to colonize river courses that drain hillside fronts or slopes that are greater than 40° [43]. Lodges in high slope areas are susceptible to removal by large thaws [37,44], while those in low slope areas allow beavers to increase their safe foraging area by

building dams, making them more stable over time. Nevertheless, none of these studies discussed stream gradient in relation to lodge abandonment.

Our main goal is to understand the causes that determine the abandonment of beaver lodges in the two major habitats types in Patagonia: forest and steppe. Lodge occupancy has been only partially studied in North America [35,45], but no studies have addressed this within their invaded range in Patagonia. The long history of beaver occupation, in conjunction with the slow regeneration of *Nothofagus* stands, may favor the movement to new areas with greater availability of resources. Furthermore, in these southern habitats closer to the Andes and with higher water flows, the stream gradient may have a larger effect on abandonment compared to the steppe habitats, located in relatively flat environments. Therefore, we hypothesize that in the semiarid steppe, water is the limiting factor and changes in the water table will lead to lodge abandonment. On the contrary, we predict that in the forest, abandonment of lodges is related to depletion of southern beech and topography.

2. Material and Methods

2.1. Study Area

Our research was conducted in the island of Tierra del Fuego (TDF)—Southern Argentina. The study area extended from 52° and 55° latitude south to 65° and 69° longitude west (Figure 1). The climate is temperate cold. Annual mean temperature is 5.9 °C and annual mean precipitation ranges from 300 mm at our sites in the steppe to 600 mm in the forest [46,47]. Soils are relatively deep with a humid moisture regime [48]. The main economic activities in TDF are oil and gas extraction, timber harvesting, tourism, livestock grazing and sheep farming [49,50]. Beavers primarily affect forestry. Due to the fact that only 30% of the total forest area is considered productive, timber harvesting is concentrated in the most accessible areas and on the highest quality forests [51].
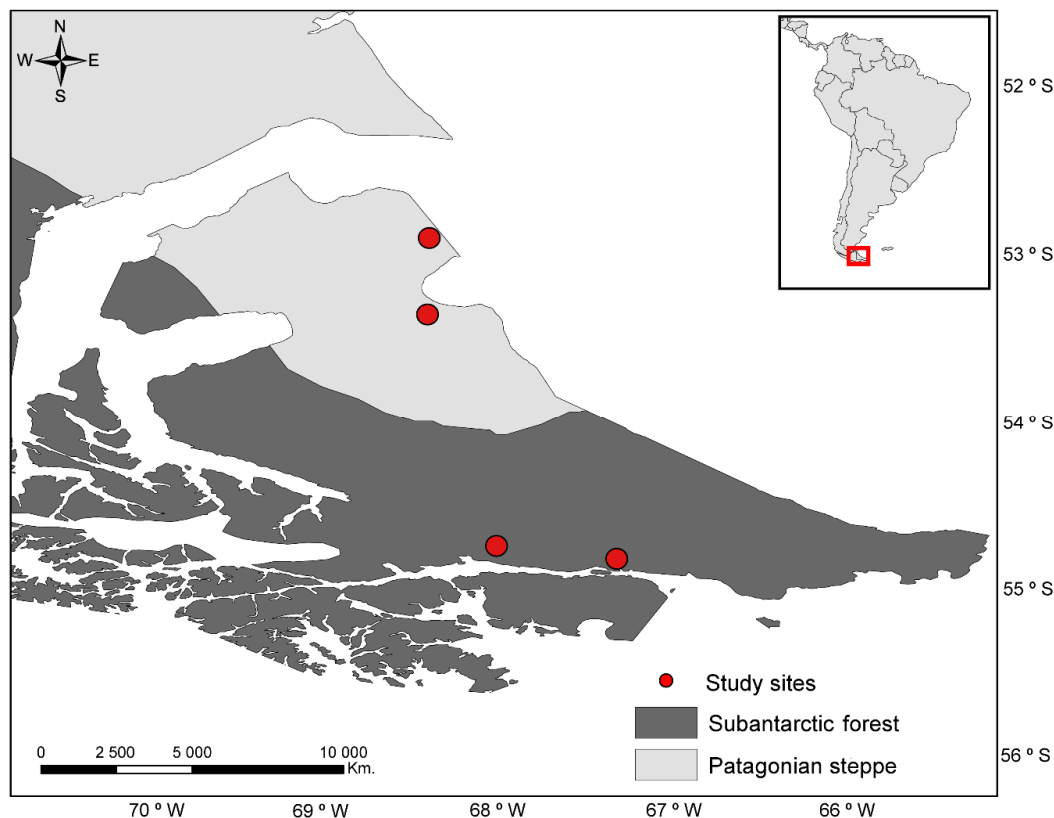

Figure 1. Location of study areas in Tierra del Fuego Island. Red circles indicate study sites.

The study area is composed by two major habitat types: forest and steppe. The forest ecoregion in TDF is part of the Magellan Sub-Antarctic biome and covers 35% of the surface of the Argentinean side [52,53]. Snowfall precipitation (mean annual of 160 mm) covers the study area from May to September, and the soil is frozen during this period from 10 cm to 1 m deep [26]. Since North American beavers were initially introduced in 1946 at less than 40 km from our study sites, these areas have a long-term history of occupation [14]. The study sites in the forest include the valley of the Submarine River (54°43'40" S 68°4'25" W) and Estancia Harberton (54°52'18" S 67°25'15" W). The dominant tree species is the Lenga beech (*Nothofagus pumilio* (Poepp. & Endl.) Krasser). Other less important species are the Magellan's beech or Guindo (*Nothofagus betuloides* (Mirb.) Oerst.) and the Antarctic Beech (*Nothofagus Antarctica* (G. Forst) Oerst.) [26,51].

The Patagonian steppe is a mixed steppe with mesic and xeric grasslands and variable shrub cover of *mata negra* (*Chilliotrichum diffusum* (G. Fort.) Kuntze) and Magellan barberry (*Berberis microphylla* G. Forst.) both used by beavers as food and for dam construction [54]. The first beaver records in the steppe date from the early 1990s [11], therefore, this habitat represents an intermediate stage of colonization within the beaver invasion history in TDF. Beaver activity such as flooding, which destroys bridges and roads and reduces the quality of livestock pastures, together with cattle are the main disturbance agent in the steppe [50]. The selected sites in the steppe were *Estancia Sara* (53°20'54" S 68°31'35" W) and *Estancia Cullen* (52°53'36" S 68°27'8" W) in the northern portion of the TDF.

2.2. Experimental Design and Site Selection

We surveyed a total of 47 lodges between February and March from 2012 to 2014 in both habitat types, 22 and 25 lodges in the forest and the steppe, respectively. The first year of monitoring (2012), we took measurements in lodges occupied by beavers, while the following years (2013 and 2014) we took measurements in the same lodges and then assessed its occupation status (occupied or abandoned). Lodges abandoned during the first period (2012–2013) were not included in the dataset during the following period (2013–2014).

Lodges were classified as "occupied" (regardless if this was a first occupation or a re-occupation) when they presented evidences of recent foraging along shore, dam or lodge construction, as well as different signs of maintenance such as fresh mud, freshly gnawed trees, scent mounds, footprints or an associated winter food cache adjacent to a lodge [33,55]. On the contrary, abandoned lodges, were confirmed if none of those evidences of occupation were found. We used additional data from Pietrek et al. [56] to determine the presence of beavers at all focal lodges. These measurements included 2–3 repeated observations per beaver pond between 2012 and 2014 from January to April. During each observation, trained observers recorded the total number and composition of the beaver colony using binoculars. Observations were performed when beavers are active i.e., 2 h before dusk, usually on non-rainy days.

2.3. Data Compilation and Measurements

To assess the causes of abandonment, we measured ecological variables involved in the lodge occupation based in habitat indicators previously reported for beavers [15,42]. Habitat variables included the variation in water level, the stream gradient, the vegetation cover adjacent to shore and the forest structure (only for the forest) (Table 1).

Table 1. Description of the variables used in the models to predict the probability of abandonment.

Habitat Variables	Description	Type of Variable and Units
HAB	Habitat where the lodge was identified	Categorical
WLV	Difference of the water level of the lodge entrance between the year of first recording and the following abandonment year	Continuous (cm)
GRA	Slope of the watercourse 50 m from the lodge downstream	Continuous (°)
COV	Proportion of the total length of the transect covered by shrub cover in the steppe and understory cover in the forest.	Continuous (%)
FSTR	Median diameter of standing trees registered up to 50 m from the edge of the pond	Continuous (cm)

### 2.3.1. Water Level Variation

To quantify the water level, we measured the height of the water at the entrance of the lodge and at the front of the dam using a folding wooden rule [35] between February and March of each year. For lodges without dams, only the height of the water at the lodge entrance was measured. For lodges with multiple entrances, we considered for the analysis the one that had the greatest variation between years.

2.3.2. Stream Gradient

We quantified stream gradient by sighting a clinometer over the distance of 50 m downstream from the dam [44].

2.3.3. Shrub Cover in the Steppe and Understory Cover in the Forest

We determined the abundance of food and woody building resources by quantifying the percent of woody vegetation around each focal pond. We placed transects of 20 m perpendicular to the pond shoreline of each focal colony (Figure 2). We set the length of the transects according to various studies that describe the average foraging distance between 10 and 30 m from the edge [17,36,57]. Along each transect, we recorded the species of woody shrub, the length of the transect intercepted by vegetation and its height. We used four transects for ponds smaller than 1 ha, and six transects for ponds larger than 1 ha, equally spaced.
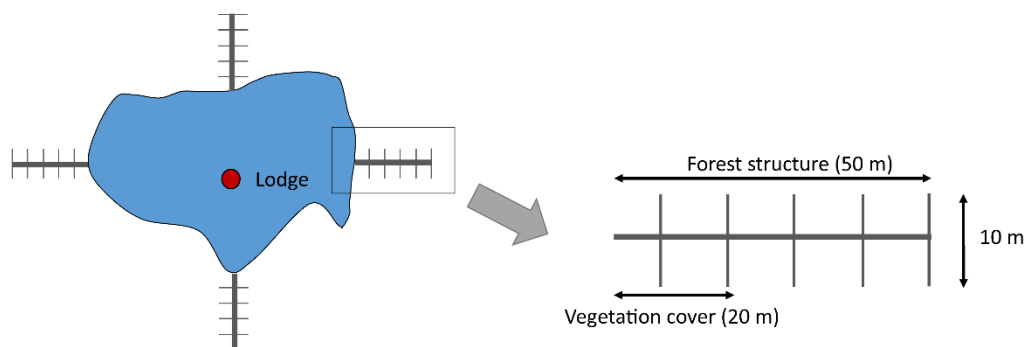
Figure 2. Schematic diagram of transect placement around beaver pond samples.

2.3.4. Forest Structure

To measure the structure of the deciduous vegetation in the forest, an additional transect was established. We took a 50 m transect in the same transect line used for the vegetation cover to

characterize the forest structure. In each transect, we settled blocks of 5 × 10 m wide (perpendicular to the transect line) separated by 5 m. The blocks were centered on 7.5, 17.5, 27.5, 37.5 and 47.5 m along the 50 m transect line (Figure 2). At each block, we recorded the number of standing trees higher than 1.5 m, their diameter 20 cm above the ground, and the number and diameter of dead trees cut by beavers.

2.4. Data Analysis

We used generalized linear mixed models (GLMM) of the binomial family to determine which variables affected the probability of lodge abandonment [58]. First, we tested a between-habitats model, which included as predictor variables the habitat type (forest or steppe), the water level variation (WLV) and the stream gradient (GRA).

A second GLMM analysis was performed to look at the variables predicting lodge abandonment within the forest and steppe (within-habitat models). For these models, we included the WLV, GRA and shrub (in the steppe) or understory cover (COV) as predictor variables. In the case of the forest model, the median tree diameter of standing trees (FSTR) was also considered [56]. Based on the number of sampled lodges, combinations including more than three variables were not included among candidate models [59].

All variables were treated as fixed effects, with the exception of the lodge (occupied lodge in the initial year) that was included as a random effect in all models of both analysis. To rank and select the best models, we used the Akaike Information Criterion adjusted for small samples (AIC$_C$) [59]. Akaike Information criteria compare a set of candidate models, ranking high those minimizing the log-likelihood and penalizing additional parameters. Comparisons between the models were made with AICc deltas, which is the difference between the lowest AICc value (that is, the model best supported by the data) and the AICc of the other models. We considered a model competitive if it differed by less than 2 AICc units with the best model. In addition, we determined the relative support of each model by generating Akaike (w_i) weight ratios [59]. We also calculated the relative variable importance (RVI) for each predictor as the sum of Akaike weights of the candidate models in which the predictor appeared. This value represents the weighted evidence that the models containing each variable were in fact the best models [60]. Finally, we checked for overdispersion in both between and within habitats full models by estimating the ratio between the residual deviance and the residual degrees of freedom (c-hat). All statistical analyses, models and graphic were performed using R (v 3.5.0) and the "lmer" and "sjPlot" package [61] implemented in R studio, version 1.2.5 [62].

3. Results

3.1. General Abandonment Pattern

The general abandonment pattern was similar between years. Out of all lodges occupied during 2012 (*n* = 35), 37% were abandoned the following year, and these were not considered for the measurements for the period 2013/14. Of the lodges occupied in 2013 (*n* = 32), 34% were abandoned in the following season (Table 2). Thus, we accounted for a total of 24 abandonment events, with a similar proportion in both habitats (46% for forest and 54% for steppe). Water level variation measurements between lodge entrances and front dam were correlated (Pearson correlation = 0.69, *n* = 47); thus, we kept the variation at the lodge entrances as a covariate.

Table 2. Summary of the number of beaver lodges occupied and abandoned in both periods. Note that from the 32 lodges sampled in 2013/2014, $N = 20$ were already sampled in 2012/2013 resulting in 47 different lodges in the total.

Habitat	State	2012/2013	2013/2014	Total
Forest	Occupied	12	9	21
	Abandoned	5	6	11
Steppe	Occupied	10	12	22
	Abandoned	8	5	13
Total		35	32	67

3.2. Between-Habitat Models

The top-ranked model revealed that the most important factor associated with abandonment was the water level variation (WLV; Table 3). However, differences in AICc values between the first model and models combining water level and gradient ($w_i = 0.25$) and water level and habitat ($w_i = 0.17$) were lower than two AICc units. Both gradient and habitat are likely uninformative parameters as the likelihoods of these models are similar to the top-ranked model and 90% confidence intervals for both variables overlapping zero [63,64].

Table 3. Model selection of seven candidate models for predicting the probability of beaver lodge abandonment in the between-habitat models. All models included a random intercept for the beaver lodge unit.

Candidate Model	K	AICc	Δ AIC$_C$	Akaike Weight (w_i)	Log-Likelihood
WLV	**3**	**78.41**	**0.00**	**0.45**	**−35.99**
WLV + GRA	4	79.55	1.14	0.25	−35.42
WLV + HAB	4	80.38	1.97	0.17	−35.83
WLV + GRA + HAB	5	81.92	3.51	0.08	−35.42

HAB: Habitat; WLV: Water level variation; GRA: Stream gradient; K: number of parameters estimated; AICc, Akaike Information Criteria adjusted for small samples; Δ AIC$_C$, difference in the value of AIC between the AIC of the model obtained and the most parsimonious model (lowest value of AIC$_C$); w_i, relative weight of the model. Log-likelihood describes the goodness of fit of a statistical model to a sample of data. Higher, i.e., less negative log-likelihood values show a better fit of models to data. Bold means the best models.

Interestingly, WLV was included in all the models that fitted best (RVI = 0.95), which indicates the dominance of this variable for lodge abandonment. Based on the best model, decrease in water levels increased chances of lodge abandonment (Figure 3). In our study, water levels dropped after a year in 42% of the abandoned lodges.

3.3. Within-Habitat Models

For the forest, the best model included the water level variation, the gradient and the understory cover as predictors (Table 4). According to this model, the probability of abandonment is linked with a drop in the water level, a decrease in the understory cover, and smaller stream gradient (Table 5). Although these results should be taken cautiously due to the low number of lodges analyzed ($N = 25$), the log-likelihood value suggests that this model fits the best compared to the three other models. In addition, the variation of water level was included in all the models that best fit our data (RVI = 0.84), which indicates, again, the importance of this variable in the probability of abandonment of lodges in the subantarctic forest. Both the first and third models included the understory cover. Models including forest structure (FSTR) ranked poorly with weights lower than 0.06 (Table 4).
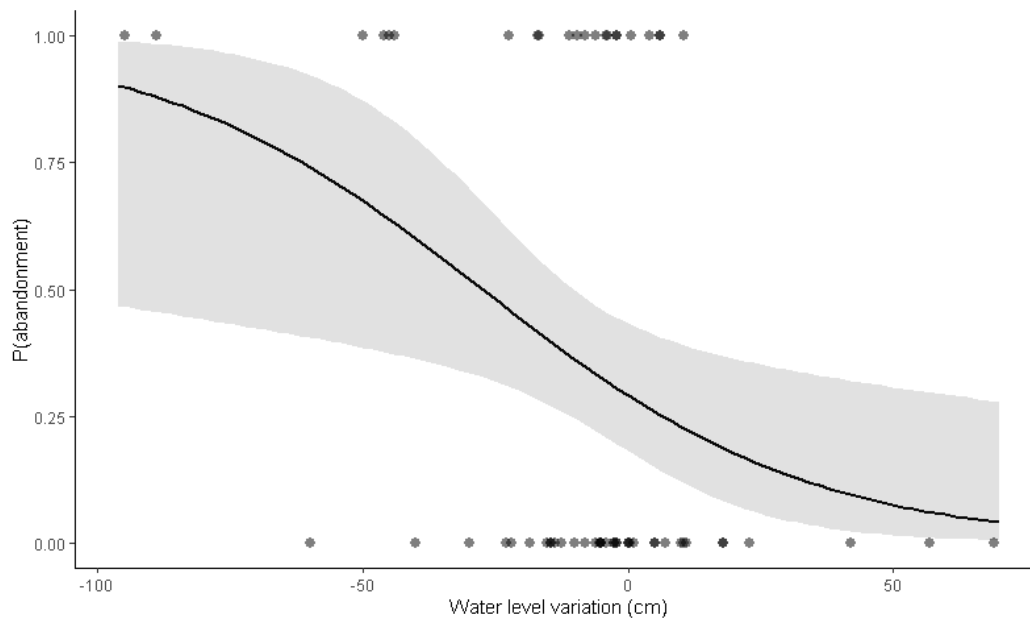
Figure 3. Probability of lodge abandonment and water level variation. Water level variation represents the increase or decrease in water level compared to the previous year's level. Gray area denotes 95% confidence intervals. Points represent sampled lodges.

Table 4. Ranking of candidate models to determine the probability of abandonment in within-habitat models.

Habitat	Candidate Model	K	AICc	Δ AIC$_C$	wi	Log-Likelihood
Forest	**WLV + GRA + COV**	**5**	**29.21**	**0.00**	**0.40**	**−8.02**
	WLV + GRA	4	30.19	0.99	0.24	−10.10
	WLV + COV	4	31.37	2.16	0.14	−10.68
	WLV + GRA + FSTR	5	33.09	3.88	0.06	−9.96
Steppe	**WLV**	**3**	**49.04**	**0.00**	**0.35**	**−21.13**
	NULL	2	50.48	1.44	0.17	−23.05
	WLV + GRA	4	50.72	1.68	0.15	−20.69
	WLV + COV	4	51.39	2.35	0.11	−21.03
	WLV + GRA	4	51.78	2.74	0.09	−22.50
	COV	3	52.72	3.68	0.06	−22.97

HAB, Habitat; WLV: Water level variation; GRA: Stream gradient; COV: shrub cover in the steppe and understory cover in the forest; FSTR: forest structure; k: number of parameters estimated; AICc, Akaike Information Criteria adjusted for small samples; ΔAIC, difference in the value of AIC between the AIC of the model obtained and the most parsimonious model (lowest value of AIC$_C$); w$_i$, relative weight of the model. Log-likelihood describes the goodness of fit of a statistical model to a sample of data. Higher, i.e., less negative log-likelihood values show a better fit of models to data. Bold means the best models.

Table 5. Parameters and relative variable importance (RVI) of the best models selected for forest and steppe habitats to estimate the probability of lodge abandonment.

Habitat	Coefficients	Slope	95% CI	*p* Value	RVI
Forest	Water level variation (WLV)	−0.13	−0.3; −0.04	0.08	0.84
	Stream gradient (GRA)	−0.55	−1.46; −0.11	0.13	0.70
	Understory cover (COV)	−0.15	−0.49; −0.02	0.23	0.54
Steppe	Water level variation (WLV)	−0.04	−0.09; −0.007	0.07	0.70

In the case of steppe habitats, of all the possible models (*n* = 8), only those with a ΔAIC$_C$ less than four are presented (Table 4). The most parsimonious model explaining the probability of lodge

abandonment included only the variation of water level as a predictor, followed by a null model that only includes lodge as a random effect. A third model was ranked competitive (WLV + GRA), but gradient was an uninformative parameter for the same reasons mentioned before. More complex models with three predictors, all of them including WLV, ranked more than three units below the best model. Two models weighted similarly (w_i = 0.06). Models combining three variables can be dismissed since AICc deltas are close to or above 4, and AICc weights are near or below 0.06 [64].

4. Discussion

Despite the fact that lodge abandonment by beavers is ubiquitous both in their native range and in Patagonia, few studies have looked at the variables behind it. Our observations suggest that abandonment is common at short temporal scales, occur with similar frequency in two contrasting habitats and that changes in water level are the most common feature of abandoned lodges in Tierra del Fuego. Furthermore, our results indicate that understory cover and the stream gradient may also affect the probability of lodge abandonment in the forest. In the next paragraphs, we will discuss in detail potential mechanisms associated with lodge abandonment by beavers in Tierra del Fuego.

We showed here that water level variation was associated with abandonment both in the forest and the steppe. The methods we use in this paper do not allow us to discriminate whether the drop in water causes abandonment, is a consequence of it, or if initial decreases in water level may lead to abandonment and may be accentuated later. Our visual surveys of lodges continued until May when beaver build their food caches and mobility is reduced, but in theory abandonment could have happened anywhere between September and December in the austral spring. Water level fluctuations are known to trigger beavers to move and relocate in the northern hemisphere [65,66]. Smith and Peterson [35] observed that when the water level dropped at the entrance of the lodge, beavers left the focal pond. We can think of at least three reasons driving this behavior. First, a submerged lodge entrance reduces the risk of predation by terrestrial predators. As predators of beavers are mostly absent in TDF with the exception of culpeo foxes in the forest or feral dogs, this behavior may be an evolutionary relic. Second, moving on land is likely more energetically demanding for beavers. While beavers need to operate both under water and on land, they are much better swimmers than walkers and spend less energy when moving under water than on land [67]. Last, in cold environments when water bodies can freeze, beavers need to dive under the ice and feed from the food cache without having to leave the proximity of the lodge in winter [39]. Hence, a minimum water level ensures a quick and safe access to the lodge under ice.

Can water level decrease only as a result of lodge abandonment? Decay of the pond and sediment deposition may occur, particularly at log time-scales, but as quintessential engineers, beavers can dramatically modify their habitat [68]. For instance, beavers' colonies upstream can limit water flow downstream pushing colonies to search for alternative water sources. The expansion of the pond to reach new saplings may cause changes in the water table. Snow melting in spring may increase transient water flows that can be temporally exploited by beavers. All these factors may ultimately impact lodge occupancy. Along these lines, we found that in the most water-limited habitats (steppe) lodge abandonment was higher (44 vs. 29%) in the rainiest year, which happened to be among the wettest years in the decade. This unexpected result indicates wet periods may favor use of previously unsuitable areas ultimately increasing abandonment. What seems clear given the high frequency of abandoned lodges, is that costs of a abandoning a lodge are relatively low or are easily offset by other potential benefits. As indicated by Müller-Schwarze and Sun [33], beavers can build a lodge in only two nights. Higher time resolution of lodge occupancy surveys or real time tracking of beavers may help elucidate if decreases in the water table lead to lodge abandonment, follow abandonment or both.

Contrary to our expectations, vegetation variables had a minor influence on patterns of lodge abandonment. Forest structural variables, such as the median diameter of living trees, which were intended to index the food supply, did not affect the probability of lodge abandonment. However, the best supported model in the forest included understory cover, suggesting fewer *Nothofagus* saplings

may lead to lodge abandonment. Beavers prefer to feed on understory vegetation rather than large trees, which are generally selected as building materials [36,37,69]. The slow regeneration and depletion of *Nothofagus* saplings may push beavers to move to new areas with greater availability of resources. Future studies should aim to increase sample sizes to confirm this trend particularly given beaver colonies seem to be regulated by density dependent phenomena such as resource availability [56,70].

In our study, the lack of effect of the shrub cover and the persistence of colonies in the steppe where woody resources are limited, also indicates that other types of vegetation may be important for beavers. Previous studies found seasonal changes on the beaver diet, with beavers relying more on wood sources during winter, and herbaceous and aquatic vegetation during summer [42,71]. Moreover, beavers in sub-arctic regions have shown a diet dominated by aquatic vegetation where this is abundant [28,72]. We have recorded rhizomes, aquatic vegetation, roots and perennial creeping shrubs such as *Empetrum rubrum* Vahl ex Willd. on food caches in the steppe. It is also likely that beavers may still graze in the steppe in winter-time. Despite the low temperatures, the steppe may remain free of snow for part of the winter, particularly compared to the forest. As other biological invasions, the plasticity in the diet of the species could have been key for the spread of beavers in Fuegian lands [73–75].

Surprisingly, we found a tendency towards lower chances of abandonment with higher stream gradients in the forest. We believe this result may be due to the fact that most surveyed colonies in high-gradient areas are located on minor watercourses, lateral to the course of higher order rivers towards those that drain. This implies that the variations in the flow at the time of snow melting may have less impact on these lodges compared to lodges located on high order water courses. A better model for abandonment could incorporate an interaction between the order of the watercourse and the stream gradient, which was already found to be important [42,76]. The addition of a larger number of colonies in watercourses of different orders and gradients could help to better understand the real importance of this variable in the forest.

5. Conclusions

To our knowledge, this study is the first attempt to elucidate the factors affecting lodge occupancy in two contrasting habitats. Our study shows that beaver abandonment in forest and steppe habitats is related to water level fluctuations which can be a by-product of beaver activities. Unexpectedly, the proportion of lodges abandoned was similar between habitats, despite the fact that the steppe is comparatively a water limited environment. We found an interaction between habitat type and vegetation cover, such that areas with low understory cover in the forest are more prone to be abandoned, while shrub cover had no influence in the probability of lodge abandonment in the steppe. This suggest movement on beaver colonies may be driven by density dependent processes in the forest, where *Nothofagus* saplings can be depleted or may take years to recover, and highlights the need for conducting active eradication in the riparian forests of Tierra del Fuego, arguably the most impacted ecosystem in all Patagonia. This new contribution improves our understanding of the factors affecting habitat occupancy of an invasive ecosystem engineer that can be integrated into management strategies for the restoration of the unique and vulnerable ecosystems of Tierra del Fuego.

Conflicts of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

1. Bergeron, Y.; Gauthier, S.; Kafka, V.; Lefort, P.; Lesieur, D. Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry. *Can. J. For. Res.* **2001**, *31*, 384–391. [CrossRef]

2. Pickett, S.T.; White, P.S. *The Ecology of Natural Disturbance and Patch Dynamics*; Academic Press: Cambridge, MA, USA, 1985.

3. Mitchell, S.J. Wind as a natural disturbance agent in forests: A synthesis. *Forestry* **2013**, *86*, 147–157. [CrossRef]

4. Wright, J.P.; Jones, C.G.; Flecker, A.S. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **2002**, *132*, 96–101. [CrossRef] [PubMed]

5. Badano, E.I.; Marquet, P.A. Ecosystem engineering affects ecosystem functioning in high-Andean landscapes. *Oecologia* **2008**, *155*, 821–829. [CrossRef] [PubMed]

6. Fox-Dobbs, K.; Doak, D.F.; Brody, A.K.; Palmer, T.M. Termites create spatial structure and govern ecosystem function by affecting N_2 fixation in an East African savanna. *Ecology* **2010**, *91*, 1296–1307. [CrossRef] [PubMed]

7. Anderson, C.B.; Rosemond, A.D. Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia* **2007**, *154*, 141–153. [CrossRef] [PubMed]

8. Tait, L.W.; Lohrer, A.M.; Townsend, M.; Atalah, J.; Floerl, O.; Inglis, G.J. Invasive ecosystem engineers threaten benthic nitrogen cycling by altering native infaunal and biofouling communities. *Sci. Rep.* **2020**, *10*, 1581. [CrossRef] [PubMed]

9. Barrios-Garcia, M.N.; Ballari, S.A. Impact of wild boar (*Sus scrofa*) in its introduced and native range: A review. *Biol. Invasions* **2012**, *14*, 2283–2300. [CrossRef]

10. Cuddington, K.; Hastings, A. Invasive engineers. *Ecol. Model.* **2004**, *178*, 335–347. [CrossRef]

11. Pietrek, A.G.; Fasola, L. Origin and history of the beaver introduction in South America. *Mastozool. Neotrop.* **2014**, *21*, 355–359.

12. Choi, C. Tierra del Fuego: The beavers must die. *Nature* **2008**, *453*, 968. [CrossRef]

13. Pietrek, A.G.; González-Roglich, M. Post-establishment changes in habitat selection by an invasive species: Beavers in the Patagonian steppe. *Biol. Invasions* **2015**, *17*, 3225–3235. [CrossRef]

14. Skewes, O.; Gonzalez, F.; Olave, R.; Avila, A.; Vargas, V.; Paulsen, P.; Konig, H.E. Abundance and distribution of American beaver, *Castor canadensis* (Kuhl 1820), in Tierra del Fuego and Navarino islands, Chile. *Eur. J. Wildl. Res.* **2006**, *52*, 292–296. [CrossRef]

15. Wallem, P.K.; Jones, C.G.; Marquet, P.A.; Jaksic, F.M. Identifying the mechanisms underlying the invasion of *Castor canadensis* (Rodentia) into Tierra del Fuego archipelago, Chile. *Rev. Chil. Hist. Nat.* **2007**, *80*, 309–325. [CrossRef]

16. Parkes, J.; Paulson, J.; Donlan, C.; Campbell, K. *Control of North American Beavers in Tierra del Fuego: Feasibility of Eradication and Alternative Management Options*; Landcare Research Contract Report LC0708/084; Landcare Research New Zealand Ltd.: Lincoln, New Zealand, 2008.

17. Anderson, C.B.; Griffith, C.R.; Rosemond, A.D.; Rozzi, R.; Dollenz, O. 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.* **2006**, *128*, 467–474. [CrossRef]

18. Naiman, R.J.; Melillo, J.M.; Hobbie, J.E. Ecosystem alteation of boreal forest streams by beaver (*Castor canadensis*). *Ecology* **1986**, *67*, 1254–1269. [CrossRef]

19. Martell, K.A.; Foote, A.L.; Cumming, S.G. Riparian disturbance due to beavers (*Castor canadensis*) in Alberta's boreal mixedwood forests: Implications for forest management. *Ecoscience* **2006**, *13*, 164–171. [CrossRef]

20. Touihri, M.; Labbé, J.; Imbeau, L.; Darveau, M. North American beaver (*Castor canadensis* Kuhl) key habitat characteristics: Review of the relative effects of geomorphology, food availability and anthropogenic infrastructure. *Ecoscience* **2018**, *25*, 9–23. [CrossRef]

21. Cunningham, J.M.; Calhoun, A.J.; Glanz, W.E. Patterns of beaver colonization and wetland change in Acadia National Park. *Northeast. Nat.* **2006**, *13*, 583–596. [CrossRef]

22. Westbrook, C.J.; Cooper, D.J.; Baker, B.W. Beaver assisted river valley formation. *River Res. Appl.* **2011**, *27*, 247–256. [CrossRef]

23. Nummi, P.; Kuuluvaine, T. Forest disturbance by an ecosystem engineer: Beaver in boreal forest landscapes. *Boreal Environ. Res.* **2013**, *18*, 13–24.

24. Arismendi, I.; Penaluna, B.E.; Jara, C.G. Introduced beaver improve growth of non-native trout in Tierra del Fuego, South America. *Ecol. Evol.* **2020**, *10*, 9454–9465. [CrossRef] [PubMed]

25. Lizarralde, M.S.; Escobar, J.M.; Deferrari, G. Invader species in Argentina: A review about the beaver (*Castor canadensis*) population situation on Tierra del Fuego ecosystem. *Interciencia* **2004**, *29*, 352–356.

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

27. Anderson, C.B.; Pastur, G.M.; Lencinas, M.V.; Wallem, P.K.; Moorman, M.C.; Rosemond, A.D. Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration. *Mammal Rev.* **2009**, *39*, 33–52. [CrossRef]

28. Fryxell, J.M. Habitat suitability and source–sink dynamics of beavers. *J. Anim. Ecol.* **2001**, *70*, 310–316.

29. Barnes, D.M.; Mallik, A.U. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. *J. Wildl. Manag.* **1997**, *61*, 1371–1377. [CrossRef]

30. Jenkins, S.H. A size-distance relation in food selection by beavers. *Ecology* **1980**, *61*, 740–746. [CrossRef]

31. Townsend, J.E. Beaver ecology in western Montana with special reference to movements. *J. Mammal.* **1953**, *34*, 459–479. [CrossRef]

32. Jenkins, S.H.; Busher, P.E. Castor canadensis. *Mamm. Species* **1979**, *120*, 1–8. [CrossRef]

33. Müller-Schwarze, D.; Sun, L. *The Beaver: Natural History of A Wetlands Engineer*; Cornell University Press: Ithaca, NY, USA, 2003.

34. Svendsen, G.E. Pair formation, duration of pair-bonds, and mate replacement in a population of beavers (*Castor canadensis*). *Can. J. Zool.* **1989**, *67*, 336–340. [CrossRef]

35. Smith, D.W.; Peterson, R.O. Behavior of beaver in lakes with varying water levels in northern Minnesota. *Environ. Manag.* **1991**, *15*, 395. [CrossRef]

36. Dieter, C.D.; McCabe, T.R. Factors influencing beaver lodge-site selection on a prairie river. *Am. Midl. Nat.* **1989**, *122*, 408–411. [CrossRef]

37. Gurnell, A.M. The hydrogeomorphological effects of beaver dam-building activity. *Prog. Phys. Geogr.* **1998**, *22*, 167–189. [CrossRef]

38. Beier, P.; Barrett, R.H. Beaver habitat use and impact in Truckee River basin, California. *J. Wildl. Manag.* **1987**, *51*, 794–799. [CrossRef]

39. Collen, P.; Gibson, R. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish–a review. *Rev. Fish Biol. Fish.* **2001**, *10*, 439–461. [CrossRef]

40. Bloomquist, C.K.; Nielsen, C.K.; Shew, J.J. Spatial organization of unexploited beavers (*Castor canadensis*) in southern Illinois. *Am. Midl. Nat.* **2012**, *167*, 188–197. [CrossRef]

41. Slough, B.G.; Sadleir, R. A land capability classification system for beaver (*Castor canadensis* Kuhl). *Can. J. Zool.* **1977**, *55*, 1324–1335. [CrossRef]

42. Howard, R.J.; Larson, J.S. A stream habitat classification system for beaver. *J. Wildl. Manag.* **1985**, *49*, 19–25. [CrossRef]

43. Coronato, A.; Escobar, J.; Mallea, C.; Roig, C.; Lizarralde, M. Características geomorfológicas de ríos de montaña colonizados por *Castor canadensis* en Tierra del Fuego, Argentina. *Ecol. Austral* **2003**, *13*, 15–26.

44. Suzuki, N.; McComb, W.C. Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon Coast Range. *Nofihwest Sci.* **1998**, *72*, 102–110.

45. Labrecque-Foy, J.P.; Morin, H.; Girona, M.M. Dynamics of Territorial Occupation by North American Beavers in Canadian Boreal Forests: A Novel Dendroecological Approach. *Forests* **2020**, *11*, 221. [CrossRef]

46. Oliveira, M.; Pérez-Alberti, A.; Crujeiras, R.M.; Rodríguez-Casal, A.; Castillo-Rodríguez, F. A new method for analysing and representing ground temperature variations in cold environments. The Fuegian Andes, Tierra del Fuego, Argentina. *Cuad. Investig. Geogr.* **2018**, *44*, 293–320. [CrossRef]

47. Oliva, G.; González, L.; Rial, P.; Livraghi, E. El ambiente en la Patagonia Austral. In *Ganadería ovina Sustentable en la Patagonia Austral. Tecnología de Manejo Extensivo*; Borelli, P., Oliva, G., Eds.; INTA: Santa Cruz, Argentina, 2001; pp. 17–80.

48. Frederiksen, P. Soils of Tierra del Fuego: A satellite-based land survey approach. *Folia Geogr. Danica* **1988**, *18*, 159.

49. Pastur, G.M.; Peri, P.L.; Fernández, M.C.; Staffieri, G.; Lencinas, M.V. Changes in understory species diversity during the *Nothofagus pumilio* forest management cycle. *J. For. Res.* **2002**, *7*, 165–174. [CrossRef]

50. Peri, P.L.; Lencinas, M.V.; Martínez Pastur, G.; Wardell-Johnson, G.W.; Lasagno, R. Diversity patterns in the steppe of Argentinean southern Patagonia: Environmental drivers and impact of grazing. In *Steppe Ecosystems: Biological Diversity, Management and Restoration*; NOVA Science Publishers Inc.: New York, NY, USA, 2013; p. 346.

51. Collado, L. Los bosques de Tierra del Fuego. Análisis de su estratificación mediante imágenes satelitales para el inventario forestal de la provincia. *Multequina* **2001**, *10*, 1–15.

52. Allué, C.; Arranz, J.A.; Bava, J.O.; Beneitez, J.M.; Collado, L.; López, J.G. Caracterización y cartografía fitoclimáticas del bosque nativo subantártico en la Isla Grande de Tierra del Fuego (Patagonia, Argentina). *For. Syst.* **2010**, *19*, 189–207.

53. Barrera, M.D.; Frangi, J.L.; Richter, L.L.; Perdomo, M.H.; Pinedo, L.B. Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. *J. Veg. Sci.* **2000**, *11*, 179–188. [CrossRef]

54. Moore, D.M. Flora of Tierra del Fuego. In *Missouri Botanical Garden*; Anthony Nelson: Oswestry, UK, 1983.

55. Slough, B.G. Beaver food cache structure and utilization. *J. Wildl. Manag.* **1978**, *42*, 644–646. [CrossRef]

56. Pietrek, A.G.; Escobar, J.M.; Fasola, L.; Roesler, I.; Schiavini, A. Why invasive Patagonian beavers thrive in unlikely habitats: A demographic perspective. *J. Mammal.* **2017**, *98*, 283–292. [CrossRef]

57. Fryxell, J.; Doucet, C. Diet choice and the funcional response of beavers. *Ecology* **1993**, *74*, 1297–1306. [CrossRef]

58. Pinheiro, J.C.; Bates, D.M. *Mixed-Effects Models in S and S-PLUS*; Springer Science & Business Media: Berlin/Heidelberg, Germany, 2006.

59. Bumham, K.P.; Anderson, D.R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*; Springer: New York, NY, USA, 2002.

60. Anderson, D.R.; Burnham, K.P. Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manag.* **2002**, *66*, 912–918. [CrossRef]

61. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. *J. Stat. Softw.* **2014**, *67*, 1–48. [CrossRef]

62. R Core Team. *R: A Language and Environment for Statistical Computing [Computer Software]*; R foundation for Statistical Computing: Vienna, Austria, 2013.

63. Arnold, T.W. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *J. Wildl. Manag.* **2010**, *74*, 1175–1178. [CrossRef]

64. Leroux, S.J. On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. *PLoS ONE* **2019**, *14*, e0206711. [CrossRef] [PubMed]

65. Nixon, C.M.; Ely, J. Foods eaten by a beaver colony in southeast Ohio. *Ohio J. Sci.* **1969**, *69*, 313–319.

66. Henry, D.B.; Bookhout, T.A. Utilization of woody plants by beavers in northeastern Ohio. *Ohio J. Sci.* **1970**, *70*, 123–127.

67. Allers, D.; Culik, B.M. Energy requirements of beavers (*Castor canadensis*) swimming underwater. *Physiol. Zool.* **1997**, *70*, 456–463. [CrossRef]

68. Hood, G.A. Not all ponds are created equal: Long-term beaver (*Castor canadensis*) lodge occupancy in a heterogeneous landscape. *Can. J. Zool.* **2020**, *98*, 210–218. [CrossRef]

69. Basey, J.M.; Jenkins, S.H. Influences off predation risk and energy maximization on food selection by beavers (*Castor canadensis*). *Can. J. Zool.* **1995**, *73*, 2197–2208. [CrossRef]

70. Johnson-Bice, S.M.; Ferguson, J.M.; Erb, J.D.; Gable, T.D.; Windels, S.K. Ecological forecasts reveal limitations of common model selection methods: Predicting changes in beaver colony densities. *Ecol. Appl.* **2020**. [CrossRef] [PubMed]

71. Wang, G.; McClintic, L.F.; Taylor, J.D. Habitat selection by American beaver at multiple spatial scales. *Anim. Biotelem.* **2019**, *7*, 10. [CrossRef]

72. Milligan, H.E.; Humphries, M.M. The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic-terrestrial ecosystem linkages in a subarctic environment. *Oikos* **2010**, *119*, 1877–1886. [CrossRef]

73. González-Suárez, M.; Bacher, S.; Jeschke, J.M. Intraspecific Trait Variation Is Correlated with Establishment Success of Alien Mammals. *Am. Nat.* **2015**, *185*, 737–746. [CrossRef]

74. Sakai, A.K.; Allendorf, F.W.; Holt, J.S.; Lodge, D.M.; Molofsky, J.; With, K.A.; Baughman, S.; Cabin, R.J.; Cohen, J.E.; Ellstrand, N.C. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **2001**, *32*, 305–332. [CrossRef]

75. Piscart, C.; Rousel, J.M.; Dick, J.T.; Grosbois, G.; Marmonier, P. Effects of coexistence on habitat use and trophic ecology of interacting native and invasive amphipods. *Freshw. Biol.* **2011**, *56*, 325–334. [CrossRef]

76. Curtis, P.D.; Jensen, P.G. Habitat features affecting beaver occupancy along rfoadsides in New York state. *J. Wildl. Manag.* **2004**, *68*, 278–287. [CrossRef]