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Invasive species and carbon flux: the case of invasive beavers (*Castor canadensis*) in riparian *Nothofagus* forests of Tierra del Fuego, Chile

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Abstract

Forests are important moderators of global atmospheric CO_2 emissions, making them a key focus of terrestrial C-cycling research. The 5th assessment report of the Intergovernmental Panel on Climate Change explicitly calls upon nations to enhance C-stock accounting and mitigate losses of global forest C sinks, which inherently will require more accurate and higher spatial resolution carbon accounting. Monitoring and predicting how disturbances, such as invasive species, influence forest C stocks and the transfer of C from live to dead pools remains a high priority both in the scientific and policy communities. We documented the effects of invasive North American beavers (*Castor canadensis*) on C-sequestration of riparian *Nothofagus* forests in Tierra del Fuego, Chile. Our paired plot sampling design quantified significant losses from beaver invasion in total aboveground, live standing, dead standing, and dead and downed C stocks ($P < 0.001$, paired t tests). We extrapolated stand-level C losses to the entire study area using a Maxent habitat suitability model and estimated that 1.177 (± 0.103) Tg C would be lost if all of the predicted 18,384 ha of invasible habitat (14% of the total forested area) were colonized by beavers. These results document the impacts of invasive mammals on large terrestrial C sinks and highlight the need for understanding the magnitude of such effects across both landscape- and regional-scales.

1 Introduction

Forests play a pivotal role in global carbon cycling (Pan et al. 2011a; Smith et al. 2014), sequestering an estimated 25% of annual global anthropogenic C-emissions (Ciais et al. 2014); yet, the mechanisms underpinning forest C sink-source transitions remain poorly understood (Pan et al. 2011b; Running 2008). Assessing the relationships between forest disturbances and terrestrial C-cycling is paramount for improved carbon accounting (Grassi et al. 2017).

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Disturbances including fires, pests, natural disasters, and pathogens can have profound effects on forest ecosystems and their long-term carbon capture and storage capacities, which often occurs through the conversion of forest carbon sinks to sources (Ellison et al. 2011; Trumbore et al. 2015; Turner 2010). Invasive species also act as major disturbance agents over large areas (Charles and Dukes 2008; Dukes and Mooney 2004) and are significant drivers of environmental change. Through the alteration of energy fluxes and biogeochemical cycles, forest-dwelling alien species pose a major threat to global forest stability (Tylianakis, 2008; Charles and Dukes 2008; Liao et al. 2008; Ehrenfeld 2010; Hicke et al. 2012).

Forests comprise a recent major focus of international climate agreements due to their capacity to moderate atmospheric CO_2 concentrations (Berndes et al. 2016; Grassi et al. 2017; Houghton et al. 2015). The 2015 Paris Agreement called for developed nations to begin making payments to developing nations as compensation for conserving forests as a part of REDD+ (Reducing Emissions from Deforestation, forest Degradation and other forest activities) and to report Nationally Determined Contributions (NDC) on a country-by-country basis (Grassi et al. 2017; IPCC 2008; UNFCCC 2017) that outline national mitigation objectives with forests as the basis for a quarter of emissions reductions through 2030. The effective implementation of REDD+ and NDCs hinges on more accurate and transparent measurement, reporting, and verification (MRV) of greenhouse gas inventories and C-flux from forests at the national level (Trumbore et al. 2015). Understanding the mechanisms responsible for forest C-flux provides the basis for predicting future atmospheric CO_2 levels, bolstering forest C sinks, and mitigating the effects of forest loss on C budgets (Trumbore et al. 2015; Pan et al. 2011a, b).

Invasive species can influence global biogeochemical cycling and can thereby represent a major global carbon emissions factor (Hicke et al. 2012). Nonnative forest pests such as the emerald ash borer, gypsy moth, mountain pine beetle, and hemlock wooly adelgid are causing massive C stock losses, as are invasive pathogens such as chestnut blight (Anagnostakis 1987), beech bark disease (Xu et al. 2016), and Dutch elm disease (Hicke et al. 2012; Loo 2009). While there is a growing body of literature on the effects of invasive insects and pathogens on forest C-sequestration, nonnative mammal impacts on forest C-cycling are largely lacking (but see Wardle et al. 2001, 2007). This signals the need for studies investigating such relationships, especially since the effects of invasive species are often unpredictable in their magnitude, direction, and duration. Reducing uncertainty about how nonnative biotic disturbance agents influence global forest C-cycling is a key step towards developing international agreements for monitoring forest C stocks and flux.

In this study, we sought to develop an easily replicable protocol that could be used to rapidly estimate (at regional- and national-scales) the effects of an invasive mammal on aboveground forest C storage. We quantified the effects of the invasive North American beaver, *Castor canadensis*, on aboveground C stocks and changes to this C pool in response to land cover conversion from forest to wetland in riparian *Nothofagus* forests of Tierra del Fuego, South America. We also modeled the regional potential distribution of aboveground C pool transitions due to potential future beaver invasion. The study, from a remote and heavily forested region of the globe, adds to the growing body of literature on invasive species' effects on forest C-cycling.

2 Background

North American beavers are ecosystem engineers that dramatically modify their habitat by clearing, damming, and flooding forested areas (Allen 1983). Within their native range, they comprise a major riparian disturbance agent. As both an ecosystem engineer and herbivore, *C. canadensis* has the ability to affect both ecosystem function and species diversity (Nummi and Kuuluvainen 2013). Their impacts influence nearly all levels of the carbon and methane cycles within their native range, including streams, wetlands, and floodplains (Naiman et al. 1988; Roulet et al. 1997; Whitfield et al. 2015; Wohl et al. 2012).

Dramatic land cover alteration by beavers also triggers major ecosystem-level changes in this species' invaded range in South America (Allen 1983; Anderson et al. 2009). The invasion of *C. canadensis* in South America has been recognized as the largest disturbance agent to the forests of Tierra Del Fuego (TDF) since the last ice age (Anderson et al. 2009). TDF is home to the southernmost forest on the planet, and it was recently named one of the most pristine wilderness areas in the world because of its extensive size, remoteness, and lack of human disturbance (Mittermeier et al. 2002).

Beavers were introduced to Isla Grande, TDF in 1946 by the Argentinian government for the fur trade industry (Anderson et al. 2009). They have since expanded to most of the islands in the archipelago and, more recently, to mainland South America (Pietrek et al. 2017; Westbrook et al. 2017). Their population has expanded exponentially in the absence of predators and with abundant available habitat (Lizarralde 1993; Westbrook et al. 2017). Current *C. canadensis* population densities in TDF range from 0.2 to 5.8 colonies km^{-2} compared to a range of 0.08 to 1.4 colonies km^{-2} within their native range (Anderson et al. 2006; Gurnell 1998; Lizarralde 1993; Westbrook et al. 2017). While their dam building can have myriad negative impacts on Tierra del Fuego riparian ecosystem function, including shifts in understory succession (Pastur et al. 2006), pond formation resulting in methane emissions (Whitfield et al. 2015), and changes in inorganic and organic soil nitrogen concentrations (Lizarralde et al. 1996), neither the local- or regional-scale effects of beaver invasion on forest carbon sequestration have been estimated in South America.

3 Methods

3.1 Study area description

The study was conducted in Karukinka Park (53° 42′ 0″ S, 69° 19′ 0″ W), which is owned and managed by the Wildlife Conservation Society. Karukinka is located on the Chilean side of Tierra Del Fuego's main island, Isla Grande, and is approximately 300,000 ha in size (Tapia 2010) (Fig. 1). The study area consists mainly of sphagnum bogs and beech forests, both of which play an important role in carbon capture and storage (Saavedra et al. 2011). The forests of Karukinka are dominated by two deciduous tree species, *Nothofagus pumilio and N. antarctica*, and one evergreen species, *N. betuloides* which dominates the coastline (Barrera et al. 2000; Pisano 1977; Saavedra et al. 2011`). Mean annual temperatures range from 2.6 to 6.6 °C, with mean monthly temperatures of 9.5 °C in January and 0 °C in July (Hobbs et al. 1998; Tuhkanen 1992). The average annual precipitation ranges from 408 to 620 mm (Pisano 1977).

3.2 Species biology

The native range of *C. canadensis* includes all of North America, except for the arctic tundra and Florida (Jenkins and Busher 1979). Beavers are generalized herbivores, but they show

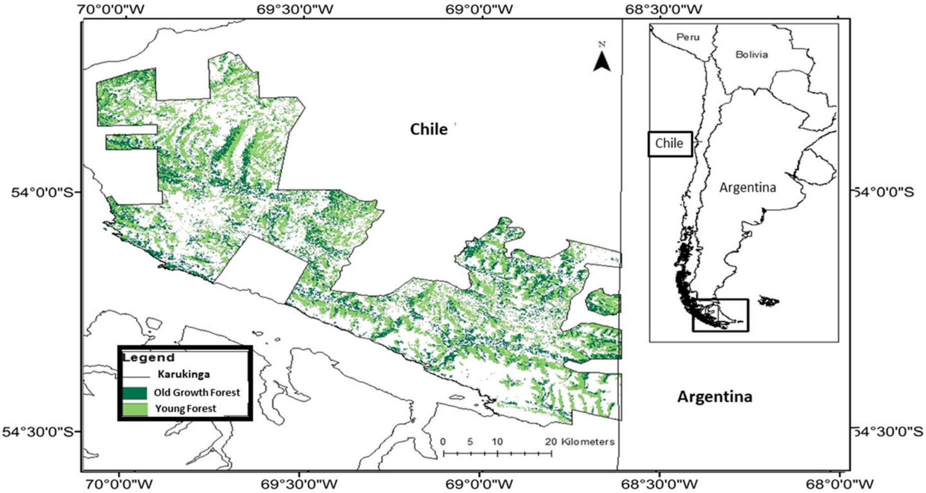

Fig. 1 Map of the study area and forest cover (Tapia 2010) within Karukinka Park, WCS, Tierra del Fuego, Chile

preference for particular tree species in both their native range in North America and their invaded range in South America. In Tierra del Fuego, they have a preference for *N. pumilio* and avoid *Drimys winteri* and *Maytenus magellanica* (Wallem et al. 2007). Bank slope, stream gradient, hardwood canopy cover, and stream width and depth are important factors influencing beaver dam construction and subsequent colony formation for *C. canadensis* in their native range (Howard and Larson 1985; McComb et al. 1990; Slough and Sadleir 1977). However, the extent to which these factors influence beaver dam construction and colonization within this species' invaded range is not well documented.

3.3 Beaver presence data

Beaver dam presence data were generated using Google Earth Pro satellite imagery ($n = 2068$ dams) for Karukinka Park. Google Earth Pro imagery was used exclusively to identify points where beavers were present for subsequent maximum entropy (MaxEnt) (Phillips et al. 2006) species distribution modeling and to identify dams to be located for field data collection. Dams were easily identified in the imagery by the characteristic triangular shape of water behind each dam which was surrounded by an irregular perimeter of standing dead trees that had died from intermittent dam flooding events during the period of beaver dam occupation. The match between beaver presence in the field and the aerial triangular shape of the dam was also validated via field visits and drone flights by Karukinka Park manager, Daniel Terán, in 2015 prior to satellite imagery interpretation (Fig. 2). Dams were defined as single barriers to water flow created by *C. canadensis.* Each individual dam was marked at its centroid in the imagery. We used cloud-free satellite imagery for the study area from Google Earth Pro for 2004, 2014, and 2015. Stands of dead riparian trees resulting from other causes were also evident in the imagery. However, such sites lacked the characteristic triangular beaver dam shape and were thereby excluded in the generation of the beaver dam presence dataset.

3.4 Raster environmental data

A suite of raster environmental data layers was derived from 30-m-resolution ASTER GDEM V2 (USGS NASA Earth Explorer) digital elevation data for the spatial extent of Karukinka Park.

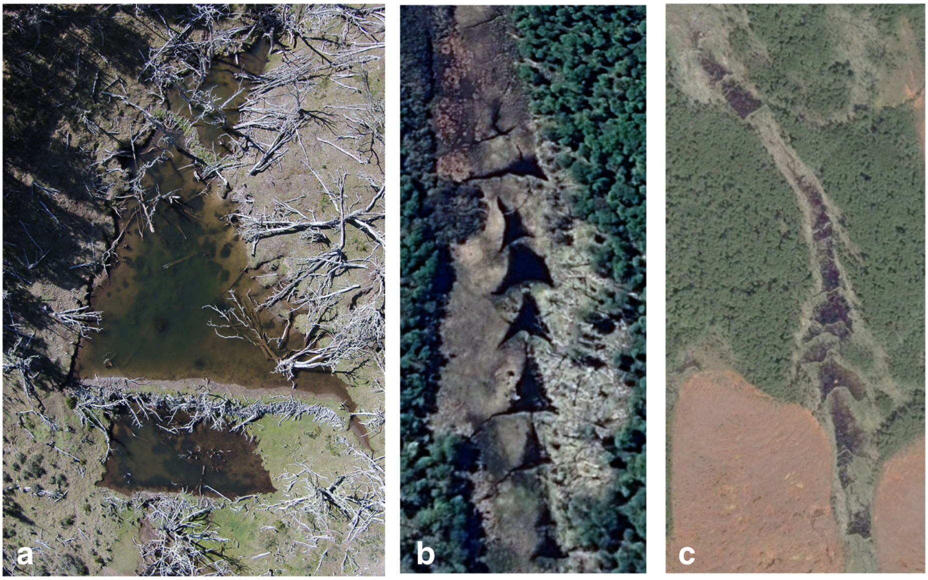

Fig. 2 Aerial imagery of dams created by *C. canadensis* in Tierra del Fuego, Chile depicted in **a** aerial image of beaver dam taken by a drone (Daniel Terán, unpublished data), **b** the same beaver dam in Google Earth Pro imagery, and **c** other beaver dams identified in Google Earth imagery (Google Earth Pro, Digital Globe 2017) for the beaver dam presence points in the MaxEnt modeling procedure. Standing dead trees surrounding the beaver dams themselves occurred in response to intermittent flooding events during the period of beaver dam occupation and were therefore attributable to beaver activity

Elevation, upstream flow, downstream flow, distance to stream, and slope were all produced in ArcMap 10.4.1 (ESRI 2017) and were projected to WGS 1984 UTM 19S (Table 1). The raster data layers included in the modeling procedure were chosen based upon their relevance to riparian habitats and upon the previously mentioned factors that influence beaver distributions within their native range (Howard and Larson 1985; McComb et al. 1990; Slough and Sadleir 1977). A Landsat 8, 30-m-resolution vegetation map by Tapia (2010) was also used as an environmental predictor variable with six vegetation cover-types: bog, closed forest, open forest, meadow and pasture, rocky outcrop, and bodies of water. We were conservative in the environmental predictors we used in our model; we included only biologically meaningful variables and that would be indicative of *C. canadensis* activity in the model construction.

3.5 Habitat suitability modeling

We utilized the maximum entropy (MaxEnt) algorithm (Elith et al. 2011; Phillips et al. 2006), version 3.3.3k to produce a habitat suitability map for *C. canadensis* within the study area to assess the invasion potential of this species in Karukinka Park. MaxEnt is a well-known and high-performing niche modeling method (Elith et al. 2011; Jarnevich and Reynolds 2011; Ward 2007) that uses a simple deterministic algorithm to identify the most suitable habitat across a given area with specified environmental covariates. MaxEnt has previously performed well in modeling species distributions of aquatic invasive species, especially since it is a presence-only niche modeling algorithm (Bouska et al. 2015; Hayer et al. 2014; Leidenberger et al. 2015; Poulos et al. 2012). We acknowledge that one limitation of invasive species niche models is that species on the invasion front comprise the species' realized niche, but that the species may not yet occupy their fundamental

Table 1 Environmental predictors with their native spatial resolution and source. All predictors were included in the habitat suitability model

Layer	Type	Description	Spatial resolution (m)	Source
Elevation	Raster-continuous	Acquired from NASA USGS in Earth Explorer	30	ASTER GDEM USGS[1]
Upstream flow	Raster-continuous	Upslope distance flow path in the Flow Length toolbox in ArcGIS	30	ASTER GDEM USGS
Downstream flow	Raster-continuous	Downslope flowpath in the Flow Length toolbox in ArcGIS	30	ASTER GDEM USGS
Distance to stream	Raster-continuous	Euclidean distance to flow accumulation raster from ArcHydro extension of ArcGIS	30	ASTER DEM USGS
Vegetation	Raster-categorical	Six distinct vegetation types as derived by Tapia (2010)	30	Tapia 2010
Slope	Raster-continuous	Surface toolbox in ArcGIS	30	ASTER GDEM USGS

[1] ASTER GDEM United States Geologic Survey: ASTER GDEM is a product of METI and NASA. Accessed through: https://earthexplorer.usgs.gov

niche space within the invaded habitat (e.g., Elith and Leathwick 2009; Rödder and Lötters 2009). We accounted for this limitation in this study in our choice of a presence only algorithm and through the incorporation of a bias file into the modeling procedure, as described below. MaxEnt uses presence only data and takes random background points as pseudo-absence. The use of background points as pseudo-absence could negatively affect the model performance due to selection bias. Selection bias can happen in different ways; it can come from presence data that is biased in a study area because of ease of accessibility to certain areas (because of roads or because an area is near to shelter) or through the placement of pseudo-absence points in areas that have not yet but could be invaded by beavers. Our use of Google Earth Imagery for identifying beaver dam presence points allowed accessibility to remote areas and thus reduced biases associated with access to remote areas of the Karukinka Park. However, we also attempted to reduce biases associated with the placement of pseudo-absence points in potentially invasible areas by generating a bias file in ArcMap 10.2 (ESRI 2017) that limited the extents of pseudo-absence points to areas that were > 200 m from a beaver dam presence location, thereby making pseudo-absences a better approximation of actual absences.

Maxent evaluates model performance by calculating area under the curve (AUC) of the receiver operator characteristic plot. The AUC is a threshold-independent measure of model performance and ranges in value from 0 to 1 with 1 being the highest performance possible. Values greater than 0.9 indicate high accuracy, values within the range 0.7–0.9 indicate good accuracy, and values below 0.7 indicate low accuracy (Swets 1988).

The final model was run 25 times with random substitution and replacement of training and testing data (55% training and 45% testing subsampling). Maps of the mean performance and standard deviation from the mean over the 25 runs were produced following Jarnevich and Reynolds (2011). We applied a threshold to the final MaxEnt habitat suitability map using equal training sensitivity and specificity to create a binary presence/absence map, which is considered a robust thresholding approach (Liu et al. 2005). We used this binary map to determine the total area vulnerable to beaver invasion in hectares within the study area. We further categorized this area by vegetation type and used the total hectares of vulnerable forest to estimate potential aboveground C loss by beaver invasion.

3.6 Quantifying carbon loss

Riparian dams were first identified via Google Earth imagery. Dams for field sampling were chosen based upon accessibility and whether they were still occupied and therefore flooded. Unoccupied dams were selected for field measurements so that surface coarse woody biomass could be sampled. Dams were located in the field using a handheld GPS unit, and plot centers were chosen randomly upon arrival by picking a random azimuth from the center of the dam and walking ten paces in that direction. We employed a paired plot sampling design where plots were placed at an invaded dam site and then in adjacent, intact, and un-invaded forest stand. Adjacent, intact, forest stands were selected by walking more than 50 m into the intact forest away from the beaver dam. Edge effects of the beaver dam on forest structure were minimized by ensuring that plots were placed well within the living closed canopy forest so that no portion of the intact forest plot was influenced by the nearby beaver dam.

Circular, variable-radius plots were used to inventory all live and standing dead trees using a metric, two-basal area factor prism. The only species encountered in our study was *N. pumilio*, and thus, standing C stocks were estimated for each plot using an allometric equation for this species according to Schmidt et al. (2009). Plot radii ranged from 10 to 18 m depending on forest density so that intact forest plots contained between 40 and 50 trees each. For each tree in each plot, we recorded diameter at breast height (DBH), species identity, and condition (standing dead or living). Coarse woody debris, or surface C stocks, were estimated using point relascope sampling with a 20° angle of inclusion according to Gove et al. (1999). The diameter of each log end and its length was recorded for each tree that fell within the inclusion angle (Gove et al. 1999). Biomass was calculated following Gove et al. (1999), and surface C from coarse woody debris was estimated using the bulk density of *N. pumilio* reported in Schmidt et al. (2009). Carbon stocks were estimated for standing live trees, standing dead trees, and dead and downed trees, and total carbon was calculated in megagrams per hectare in all paired (invaded and un-invaded) plots. Differences between C stocks in invaded and un-invaded forest stands were statistically assessed via paired t tests in R (R Development Core Team 2018).

Aboveground C-storage change due to *C. canadensis* invasion was estimated by first calculating the mean difference in C stocks between the paired ($n = 34$ pairs) un-invaded and invaded stands. We estimated C loss for the entire study area by multiplying the total vulnerable forested area (from the Maxent model in hectares) by the difference in C stocks (Mg ha^{-1}) as an estimate of C losses if the entire potential habitat was invaded by beavers. As a more conservative estimate of loses, we also estimated C loss if beavers were to invade just half of the potential invasible habitat.

4 Results and discussion

4.1 Beaver habitat suitability modeling

The MaxEnt model performance revealed a mean AUC (area under the curve of the receiver characteristic plot) value across all runs was 0.846 (SD = 0.004), indicating good overall model performance predictors including distance to a stream, vegetation cover, and slope as the most important predictors of *C. canadensis* habitat, consistent with its known habitat requirements. Other minor contributors to the model (> 10%) included upstream flow, elevation, and downstream flow (Fig. 3; Table 3). The Maxent environmental response curves also identified sites in Karukinka Park that were suitable for beaver dam establishment (Figs. 4 and 5). These characteristics were consistent with known habitat selection preferences in the native and invaded range (Anderson et al. 2009; Howard and Larson 1985; Lizarralde 2004; McComb et al. 1990; Slough and Sadleir 1977) suggesting that flat, lowland habitats near streams are a primary forest conservation and beaver eradication target. In addition to providing an estimate of the total invasible area, the habitat suitability model for Karukinka can also be used as a decision support

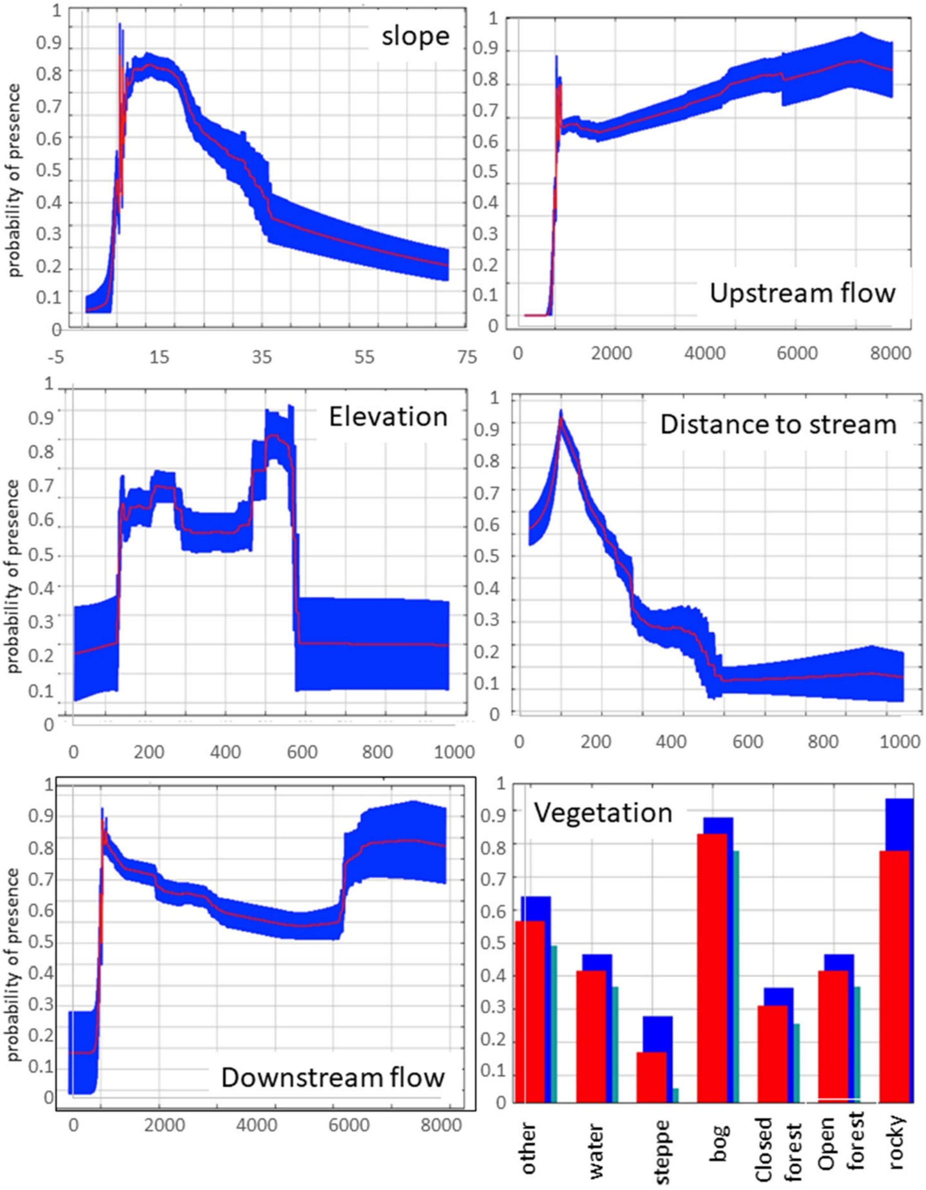

Fig. 3 Environmental response curves for all environmental predictor variables included in the final Maxent potential *C. canadensis* distribution model for Karukinka Park, Chile. Red lines indicate mean values for the 25 iterations of the model. Blue shading indicates ± SD. Probability by vegetation type is shown in the bottom left panel in red + one (dark blue) – one (light blue) SD

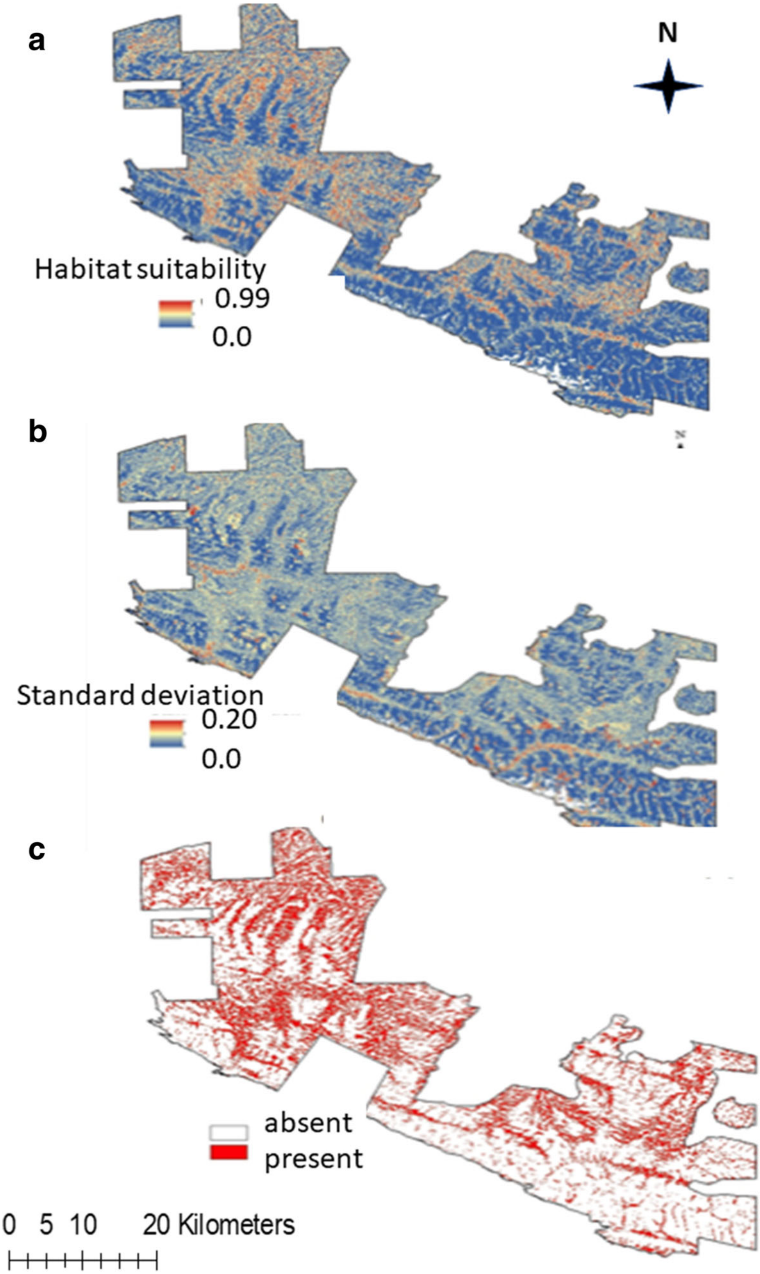

Fig. 4 Maxent potential distribution maps for *C. canadensis* in Karukinka Park, Chile. **a** The habitat prediction map derived from the mean of the 25 iterations. **b** The standard deviation among the 25 iterations using different subsets of the presence points for training (55%) and testing (45%). **c** The presence–absence map after thresholding. Maximum sensitivity plus specificity was used as the threshold to derive the binary prediction map product

tool for informing efforts focused on limiting the spread of beavers and for guiding eradication efforts at the invasion front (Elith et al. 2011).

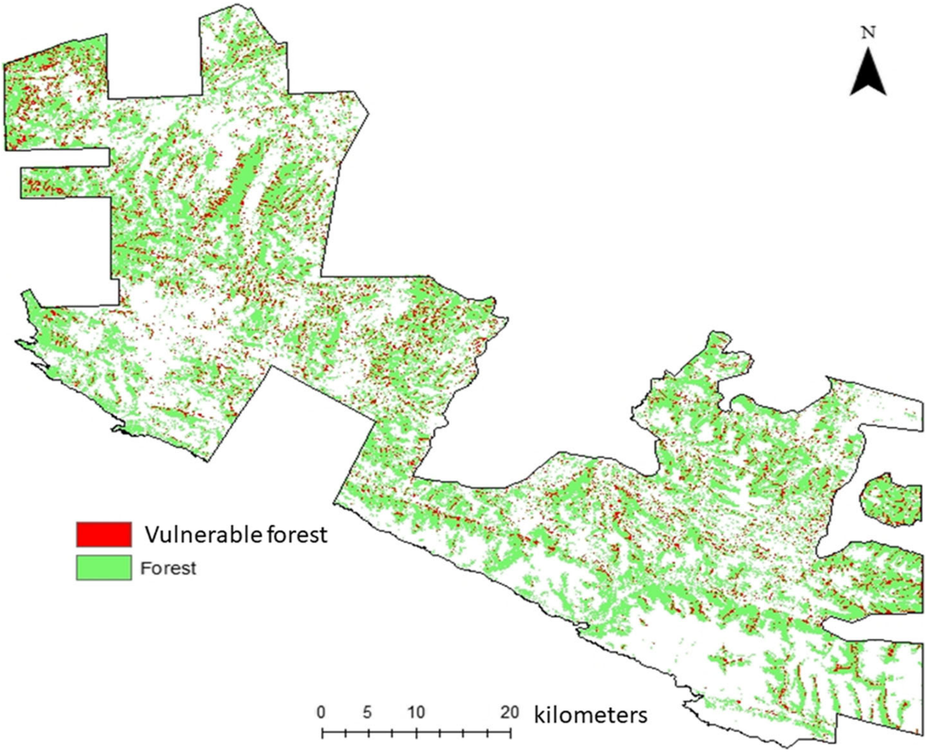

Fig. 5 Forests (Tapia 2010) that are vulnerable (18,384.48 ha) to invasion by *C. canadensis* in Karukinka Park, Chile as predicted by Maxent

4.2 Effects of beaver activity on aboveground C stocks

North American beaver activity in Tierra del Fuego has triggered significant losses of *Nothofagus* aboveground C stocks via land cover conversion from forest to wetland. The aboveground field carbon inventories revealed that beaver-invaded areas experienced significantly lower total aboveground C stocks relative to adjacent intact forests (paired *t* test, df = 33; *f* value = 208.8; *p* value < 0.0001). Standing dead (df = 33; *f* value = 11.65; *p* value = 0.0017), dead and downed (df = 33; *f* value = 34.43; *p* value < 0.0001), and total carbon (df = 33; *f* value = 137.97; *p* value < 0.0001) stocks also differed significantly between invaded and uninvaded areas (Table 2). Mean C conversion from live to dead pools due to *C. canadensis* invasion was 64 ± 5.6 Mg ha^{-1}, which we estimated by taking the difference in C stocks between the paired invaded and uninvaded forest stands.

Table 2 Effect on aboveground carbon from invasion of *C. canadensis* in riparian forests. Mean (± SE) aboveground carbon storage in both invaded and un-invaded riparian forests were estimated in un-invaded (*n* = 34) and invaded (*n* = 34) plots in Karukinka Park, Tierra del Fuego, Chile

	Un-invaded (Mg ha^{-1})	Invaded (Mg ha^{-1})
Living aboveground	80.7 (± 5.43)	2.01 (± 1.45)
Standing dead	9.65 (± 1.99)	20.96 (± 2.68)
Coarse woody debris	2.68 (± 0.31)	5.83 (± 0.48)
Total carbon	93.05 (± 5.69)	28.81 (± 2.82)

Our results suggest that beaver invasion can result in major differences between aboveground C stocks in invaded versus un-invaded forest stands. However, they also highlight differences in the compartmentalization of the aboveground C stock. In un-invaded stands, most of the C was stored in live standing trees, while in beaver-invaded and recently abandoned beaver colonies, the majority of the C stock was stored in standing dead and dead and downed trees. Other authors have observed that post-abandonment beaver ponds do not revert back to *Nothofagus* forest stands over the long-term, but rather convert to sedge- and grass-dominated meadows that persist indefinitely (Anderson et al. 2009; Pastur et al. 2006). While the soils of the plant communities that form after dam abandonment and pond drainage are C-rich following the incorporation of coarse and fine organic matter from the forest die-off event, they also comprise significant carbon dioxide and methane greenhouse gas emissions “hot spots” (Scanlon and Moore 2000; Updegraff et al. 1995; Vecherskiy et al. 2011), or emissions factors.

The prolonged inundation of forest stands from beaver damming and subsequent sedimentation and nutrient deposition amplifies these effects and prevents tree regeneration from the seed bank following beaver colonization (Anderson et al. 2009; Pastur et al. 2006). Although other major forest die-off events release carbon slowly from dead trees, (Moore et al. 2013), the rapid conversion of *Nothofagus* forests in TDF from intact forest to flooded beaver dam precludes rapid forest recolonization and recovery at these sites, at least over the short-term. Our field data and observations indicate that tree recruitment has yet to occur at older, abandoned dam sites, even 10 years after beaver dam abandonment. This suggests that beaver invasion stimulates a persistent loss of riparian forests and that future invasion of beavers will likely have major consequences for forest C sequestration across the region.

While this study documents the conversion of an aboveground C from a sink to a source, we also recognize that this process likely occurs over time-scales spanning from months to decades. Flooding caused by dam creation kills trees over short time-scales (i.e., months), but the loss of carbon and CO_2 emissions to the atmosphere can occur over longer time-scales, depending on the permanency of the dam (Johnston 2014, 2017). Standing dead snags can persist for years after tree death, and the pool created by the beaver dam subsequently traps and submerges woody debris and sediments in an anoxic environment that can store organic C for years to decades post-dam abandonment (Johnston 2014; Naiman et al. 1988, 1994). The process by which stored C-stocks in standing live trees are either released into the atmosphere as CO_2 after tree death or remain trapped in underwater organic sediments is complex. Our knowledge of how and when such changes occur is largely restricted to northern latitudes within the native range of the species. Such processes warrant further study within this species’ invaded range as a means of elucidating the long-term consequences beaver invasion on C-cycling. Longitudinal studies that examine how long beaver dam sites remain ponds that can trap organic sediments after abandonment could facilitate our understanding of the rate of C sink-source transitions, as could research that evaluates pond–meadow–pond transitions in response to the recolonization of former dam sites by beavers.

4.3 Landscape-scale aboveground C losses

Our Maxent habitat suitability model predicted that 18,384 ha (14% of the total forested area) of forested land is vulnerable to invasion by *C. canadensis* (Fig. 4; Table 3). If the entire potential invasible forested area (18,384 ha) of Karukinka was invaded by beavers, 1.177 (± 0.103) Tg C, or 10% of the total carbon stored in the forests of the park, would be lost based on the potential invasible area and our field-based estimates of C storage). A more modest calculation of 0.588 (+ 0.051) Tg C would be lost if only half of the potential invasible area were colonized by

Table 3 Relative contribution of the environmental covariates to the Maxent model. Percent contribution reports the gain by including that specific variable at each step of the Maxent algorithm. The permutation importance reports the percent contribution of each environmental covariate

Environmental predictor	% Contribution	Permutation importance
Distance to stream	42.1	35
Vegetation	24	20.1
Slope	13.9	19.1
Upstream flow	9.4	12
Elevation	5.4	6.9
Downstream flow	5.3	6.9

C. canadensis. We acknowledge that it is unlikely that beavers would invade all of the predicted suitable habitat, but the invasion of even half of the potential habitat would result in significant forest conversion and aboveground C stock losses. To put these losses into context, between 2006 and 2010, C loss due to deforestation for the entire conterminous United States (which contains approximately 1800 times the forested area as is within Park Karukinka) was 6 ± 1 Tg C year^{-1} (Harris et al. 2016), highlighting the magnitude of this potential disturbance on global C-sequestration due to beaver activity.

5 Conclusion

Our study presents a novel method for quantifying the effects of invasive species on terrestrial C-cycling by combining a habitat suitability model with field-based C stock data—an approach that could be easily applied elsewhere to quantifying the effects of other invasive species on aboveground C budgets. Modeling the species' range provided a means for estimating the potential large-scale effects of beaver invasion on forest carbon sequestration and allowed us to extrapolate field C-inventory data across a wide geographical area. Such an approach provides a mechanism for generating landscape- and regional-scale estimates of the conversion of C from live to dead pools in response to mammal invasion, which is useful for newly-mandated national carbon-accounting in this region and elsewhere.

The study also highlights the magnitude of change that an invasive mammal can have on forest C-cycling and storage. The estimated loss of above-ground forest C caused by beaver invasion, combined with poor post-invasion forest regeneration potential (Pastur et al. 2006), suggests that active restoration of previously invaded areas will be necessary for mitigating the effects of beaver invasion on South American C-storage. While this study estimates aboveground C loss, further research could contribute to a greater understanding the effects of beavers, as well as other invasive mammals on aboveground C-storage and biogeochemical cycling within the ecosystem, including in-stream effects and effects on the archipelagos peat bogs that result from forest conversion by beavers. Globally, including South America, *C. canadensis* has already been recognized as a significant source of methane emissions via pond formation (Whitfield et al. 2015), although data are lacking from within this species' invaded range. Thus, a combined mitigation approach that focuses on beaver spread prevention, population reduction through beaver eradication efforts, and forest restoration will be necessary for ameliorating the negative effects of invasive beaver activities on C budgets (Anderson et al. 2009; Pastur et al. 2006).

Preventing and reducing deforestation has been specifically identified by the IPCC as one of the largest and most immediate ways to decrease global CO_2 emissions in the short term (IPCC 2008;

Smith et al. 2014). The signing of the Paris Agreement has placed increased international attention on the importance of forests in reducing atmospheric CO_2. The successful implementation of REDD+ and reduction of emissions by a quarter through 2030 depends on more accurate and transparent C-monitoring, reporting, and verification. More detailed and process-based studies of the mechanisms responsible for alterations to the C cycle within forests are needed for generating accurate forest C stocks and emissions factors. Not only does *C. canadensis* pose a serious threat to the forests of TDF but they also threaten mainland South American forests, and the effects of the widespread invasion of this invasive mammal could have effects on C-cycling that spread well beyond the study area. Thus, incorporating invasive species as a C emissions factor in land use/land cover change carbon accounting represents an important step in achieving more accurate IPCC Tier II and Tier III C-accounting standards.

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Author contribution Chloe Papier designed the study, did all of the field work and analysis, and wrote the paper. Helen Poulos designed the study, assisted with analyses, and helped write the paper. Alejandro Kusch assisted with the study design and the field component of the study.

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