

# Undetected but widespread: the cryptic invasion of non-native cattail (*Typha* spp.) in a Pacific Northwest estuary

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## Research Article

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# Abstract

Early detection of invasive species is an important predictor of management success. Non-native narrow-leaved cattail (*Typha angustifolia*) has been detected in the Fraser River Estuary (FRE) in recent decades, but questions around their degree of establishment, and the potential emergence of hybrid cattail (*Typha x glauca*), remain unanswered. This study models the current and potential future distribution of non-native cattails in the FRE using a unique combination of spectral imagery analysis and species distribution modelling. Contrary to our expectation, we find that non-native cattails are already widespread, currently occupying approximately 4% of FRE tidal marshes. Though never formally recorded in the FRE, hybrid cattail is the more abundant of the two taxa, suggesting that heterosis may be facilitating this invasion. In our species distribution model, we distinguish between site suitability (ability to establish and persist) and site susceptibility (risk of being colonized when suitable). Our model predicts that 28% of the estuary has > 50% probability of suitability, and 21% has > 50% probability of susceptibility to non-native *Typha*, indicating the scale of this invasion may increase over time. Restoration projects had proportionally more cattail, susceptible habitat, and suitable habitat than the overall estuary, casting doubt on their effectiveness at mitigating wetland destruction. Due to their resemblance to native *Typha latifolia*, these cattails qualify as cryptic invaders, which explains how they were able to establish and remain undetected for decades. Regional eradication is unlikely given the extent of invasion, therefore management should prioritize areas of high conservation and cultural values.

## 1 Introduction

Invasion biology research is often reactive, occurring when a non-native species is well-established, and therefore eradication, containment, and other management efforts are limited by effort and cost, which compound temporally (Smith et al. 1999; Rejmánek & Pitcairn 2002; Simberloff et al. 2013). Proactive research, investigating the ecological threat potential of non-native species in habitats where they are not yet present or have only recently arrived, may more likely lead to successful management outcomes (Hobbs et al. 2009; Martin et al. 2015). We examine the threat of two potential invaders to tidal marsh ecosystems in the Pacific Northwest, narrow-leaved cattail (*Typha angustifolia* L.), and hybrid cattail (*Typha x glauca* Godr.), to understand their current distribution and future risk of expansion.

Narrow-leaved and hybrid cattail are considered problematic wetland invaders throughout North America. Recent assessments indicate *T. angustifolia* was likely introduced to North America from Europe (Ciotir et al. 2013; Ciotir & Freeland 2016), though it has been present on the east coast since at least the early 19th century (Shih & Finkelstein 2008). Concurrent with its establishment was the emergence of hybrid *T. x glauca*, the offspring of *T. angustifolia* and native *T. latifolia* (Kuehn et al. 1999; Ball & Freeland 2013). The F1 *T. x glauca* hybrid is often sterile (Smith 1967; Kuehn et al. 1999), but backcrosses and advanced generation hybrids have been recently detected in the Great Lakes Region (Travis et al. 2010; Snow et al. 2010; Kirk et al. 2011; Zapfe & Freeland 2015). Initially restricted to the eastern margins of the continent,

these taxa have rapidly expanded westward because of habitat alteration, habitat disturbance, and commercial sales (Shih & Finkelstein 2008; Ciotir & Freeland 2016).

Most research aimed at identifying the impacts of non-native *Typha* invasions has occurred in central and eastern North America, where they are more widely-recognized as a conservation concern. Impacts vary from the intrageneric level, where competition is occurring between *Typha* taxa, to intergeneric and multitrophic levels. At an intrageneric level there is mixed evidence of niche differentiation between native and non-native cattail in North America; some studies find no niche separation (McKenzie-Gopsill et al. 2012; Pieper et al. 2018), while others find non-native lineages to be tolerant of greater and more prolonged water depths (Weisner 1993; Chow-Fraser et al. 1998; Grace & Wetzel 1998) and higher salinity (Hotchkiss & Dozier 1949; Smith et al. 2015). Regardless of whether niche partitioning exists, hybrid *T. x glauca* is widely considered more competitive than either parent, often replacing them over time through either direct competition, gradual introgression, or a combination of both mechanisms (Travis et al. 2010; Kirk et al. 2011; Bunbury-Blanchette et al. 2015).

The multitrophic impacts of non-native cattail have been increasingly investigated in recent decades. Monodominant invasive *Typha* stands displace native marsh plant communities (Frieswyk & Zedler 2007; Wilcox et al. 2008), via high growth rates (Grace & Wetzel 1998; Zapfe & Freeland 2015), leaf litter (Larkin et al. 2012; Farrer & Goldberg 2014; Szabo et al. 2018), nutrient-induced plasticity (Woo & Zedler 2002), and allelopathy (Jarchow & Cook 2009) that inhibit and outcompete sympatric natives. These community-level changes are linked to changes at other trophic levels, such as the direct and indirect exclusion of waterfowl (Kostecke et al. 2004; Hood 2013; Lishawa et al. 2020), reduction in marsh-associated birds (Meyer et al. 2010), and reduction in macroinvertebrate and insect biomass (Kostecke et al. 2005; Lawrence et al. 2016).

At the northwest limit of this continental invasion lies the Fraser River Estuary (FRE), western Canada's largest and most productive estuary. Though non-native cattail are known to be present, occurrence data are limited. No herbarium vouchers of *T. angustifolia* exist prior to 1990, and only a handful of formal occurrence records have been found in grey literature, all after the late 1980s. Prior to our research no formal record existed of *T. x glauca* in the FRE, though specimens had been collected in recent decades from wetlands in nearby Puget Sound (CPNWH 2020). Lack of occurrence data may reflect actual limited abundance of these taxa, but may also reflect other confounding factors, such as site inaccessibility, limited survey resources, or morphological similarities to other species that may prevent detection. The true extent of non-native cattail in the FRE was therefore uncertain, as was the potential for their continued establishment, should they remain unmanaged.

Reflectance analyses and other remote sensing techniques have emerged as powerful and cost-effective tools for mapping the past and present distributions of invasive plant species (Parker Williams & Hunt 2002; Bradley 2014). They are useful in instances such as this where occurrence data are deficient, resources for field surveys are limited, and habitats are difficult to access (Hestir et al. 2008). Marshes are excellent candidates for these analyses because vegetation tends to form expansive monocultures in

these environments, and canopy-forming woody vegetation is generally absent. Several remote sensing studies have effectively mapped the distribution of marsh species, including cattail (Lishawa et al. 2017; Wilcox et al. 2018; Clifton et al. 2018).

Species distribution models (SDMs) are regularly used to predict environmental suitability for species. These models use occurrence and spatial data to compare the similarity of occurrence conditions to other sites, and then generate spatial and temporal predictions for a given species (Elith & Leathwick 2009). Such models have been used to infer the potential distribution of invasive species (e.g. Bradley et al. 2010; Martin et al. 2015; Kramer et al. 2017), but often at regional or continental scales where predictor resolution is coarse (e.g. climate, precipitation), and more available. Models that operate at the scale of a single estuary are less frequent in the literature, likely due to limitations in high-resolution predictor data, and the overall complexity of predicting within these dynamic ecosystems. To our knowledge there are no instances of an SDM being used to predict an invasive plant in an estuary, apart from modelling by Hood (2013) for predicting *T. angustifolia* distributions in small restoration sites.

Using a combination of spectral analysis and species distribution modelling, we investigate the threat of non-native cattail to the FRE. Knowing that the distribution and abundance of these taxa have significant implications on the cost, effort, and incentives behind their management (Martin et al. 2015), we ask:

1. What is the current distribution of non-native cattail in the FRE?
2. What is the projected distribution of non-native cattail, should they remain unmanaged?
3. Are certain habitat types (e.g. protected areas, non-protected areas, restoration sites) more prone to cattail invasions?

## 2 Methods

### 2.1 Study Area

Our research was located in the tidal marshes of the Fraser River Estuary, British Columbia, Canada. At over 21,000 hectares, the Fraser is one of the largest estuaries in Pacific North America, and the largest of western Canada. Widely recognized for its ecological importance, the FRE historically supported the largest annual salmon run of any river in North America, with multiple species using highly-productive estuarine tidal marshes for their juvenile life stages (Chalifour et al. 2019). Globally recognized as an Important Bird and Biodiversity Area (IBA), the FRE hosts over 300 species of birds, the highest concentration of migratory birds in Canada, including over 600,000 Western Sandpipers and 200,000 Dunlins annually, and over 100 plants and animals designated as “at risk” (Kehoe et al. 2020). The FRE has also been assigned the term “Living Working River” for its high economic and social value that predates European arrival. For millennia, First Nations have traded, resided, and been sustained by the abundant resources of the FRE, which range from fisheries to waterfowl, to extensive cultivation of marsh

plants for both food and technology. The modern economic value of the FRE is also significant. It contains the largest port by export tonnage in North America, an estimated \$50 billion CAD worth of human development, and fertile agricultural land that generates \$1.6 billion CAD annually (Richmond Chamber of Commerce 2014). In addition, it supports the most populous metropolitan area in western Canada, with over 2.5 million residents in Greater Vancouver, 300,000 of which reside on the floodplain.

As a result of urban and agricultural development, the FRE has experienced wetland losses of 70-90% since European settlement (Hoos & Packman 1974; Boyle 1997). Remnant marsh habitats, approximately 70% of which are now protected by governments and NGOs, continue to be degraded by a multitude of historical and emerging threats, including invasive plants, sea level rise (Bornhold et al. 2008; Kirwan & Murray 2008), climate change (Taylor 2004), habitat loss (Balke 2017), habitat fragmentation, and excessive waterfowl herbivory (Demarchi 2006). These threats are likely to compound, because the human population in the region is projected to increase at a 1.4% annual rate until 2041 (Ip & Lavoie 2019). Research that investigates and improves our understanding of these threats is therefore critical for conserving and restoring these important remnant habitats.

## 2.2 Spectral Analysis

Imagery for our analysis was provided by the Vancouver Fraser Port Authority (VFPA) and GeoBC. The datasets were identical in their spatial (10 cm) and spectral (8bit RGB stereo) resolutions, however VFPA imagery was taken 19-24 April 2018 while GeoBC imagery was taken in summer of 2016. Both imagery datasets were acquired at low tide using manned aerial vehicles. Before analyzing the imagery, we catalogued the dominant land cover types of the estuary, which varied from monoculture-forming herbaceous species (e.g. *Phalaris arundinacea*, *Carex lyngbyei*) and shrubs (e.g. *Myrica gale*) to exposed substrates and log debris accumulations. Training polygons of each land cover type were manually drawn in ArcMap (Esri Inc. 2020) using 2019 field data and notes from our previous work throughout the study area. These ground-verified data were used as training sites to calculate the unique spectral signature of each land cover class. Training data varied from 55 - 1,925 pixels per class ( $\bar{x}$  = 663.6). Low training sizes were infrequent, occurring only in instances where verified training sites were lacking, but deemed important to include. High training sizes reflect instances where larger samples were necessary for effectively distinguishing similar classes. Separate classes and training polygons were created for each imagery dataset due to temporal, technological, and spatial differences, with 21 classes in the GeoBC dataset, and 31 in the VFPA respectively.

To enhance processing performance, we removed all non-suitable habitat from the analysis prior to classification. Non-suitable habitat was defined as (1) terrestrial habitats above the high-tide mark, (2) open water, including significant tidal channels (3) tidal mudflats, (4) areas shaded/covered by nearby woody plants, and (5) anthropogenic structures (e.g. riprap, docks, pavement). Remaining imagery was classified in ArcMap using a supervised Bayes Maximum Likelihood Classification, a probabilistic approach that characterizes each land cover class by their mean vector and covariance matrix, and then

assigns each cell to the class to which it has the greatest likelihood of being a member (Richards 2013). Classified rasters were aggregated from 0.1 to 1.0 m pixel size using median class values, as the high spatial resolution of the imagery, combined with the effects of varying stem densities, substrates and shadows, produced an undesirable amount of noise in our outputs.

The GeoBC dataset was more effective at classifying vegetation in much of the study area, likely because it was taken later in the growing season when aboveground biomass was fully developed. We therefore used it wherever possible, and used the VFPA imagery in the outer estuary where GeoBC imagery was not available. Non-native *T. angustifolia* and *T. x glauca* often had overlapping spectral signatures in our exploratory analyses, perhaps due to similarities in their respective stem densities and flower abundances. To avoid confusion, the two taxa were combined as “non-native cattail” for the final classification. Native *T. latifolia* was rarely confused with non-native *Typha*, likely due to factors such as leaf colour, fewer flowering plants (Grace & Wetzel 1982), and physical differences, as *T. latifolia* rarely achieves densities that are comparable to its exotic congeners in the FRE.

Classification accuracy was determined through post-analysis field verification conducted between 14 November 2019 and 3 January 2020. We divided the study area into 500 m x 500 m grid cells, equalling a total of 486 cells, and randomly selected 30 for field verification, with 8 occurring in the lower estuary classified dataset and 22 in the upper estuary. The disparity of grid cells between datasets reflected the marsh being less abundant in the upper estuary (some grid cells contained no marsh), so more grid cells had to be sampled to verify a comparable amount of habitat between datasets. Field verification included visiting all 30 grid cells, and mapping all non-native cattail. As a hybrid, *T. x glauca* possesses many intermediate traits that confound its field identification, particularly with *T. angustifolia*. Molecular analyses and microscopic traits, such as stigma width (Kuehn & White 1999) and pollen shape (Finkelstein 2003) have been used to definitively identify the hybrid, but a combination of macroscopic traits can also be accurate (Smith 1967; Tompkins & Taylor 1983; Grace & Harrison 1986; Kuehn & White 1999). To assist in our cattail identification, we created a multi-access key of macroscopic traits, based on available literature (see Supplementary Material). We then evaluated the accuracy of this key by testing it on several plants of each presumed taxa in July 2019. These identifications were then compared to pollen collected from the same plants, and the key was accurate in all instances.

The accuracy assessment focused on two simplified classes: (1) non-native cattail and (2) other. A total of 200 random-stratified assessment points were generated within the grid cells of each dataset (100 per class), and at each point the classified value (i.e. non-native cattail, Y/N), was compared to field-verified data using a confusion matrix (Congalton 1991). Confusion matrix outputs included the overall accuracy (*fraction of correct values assigned to a class*), commission errors (*fraction of incorrect values assigned to a class*), omission errors (*fraction of values that were incorrectly assigned to a different class*) and Kappa Coefficient, a statistic used in classifications to compare observed accuracy with expected accuracy, thereby accounting for random chance (Cohen 1960).

## 2.3 Species Distribution Model

To investigate the potential distribution of non-native cattail in the FRE we constructed an SDM that predicts habitat suitability (i.e. probability of establishment and persistence given environmental conditions) and habitat susceptibility (i.e. probability of colonization given propagule pressure and habitat suitability; Martin et al. 2015). This model accounted for introduction, establishment and persistence requirements using a combination of distance-based probabilities and environmental data (Fig. 1).

Predictions were restricted to tidal marsh habitats from the Port Mann Bridge west to the estuary mouth. Marsh habitats were delineated using the BC Land Use spatial layer provided by GeoBC for high water boundaries. Low water boundaries were based on 0.2 m ASL elevation using a Digital Elevation Model (DEM) data (see 2.3.1 for specifications), an elevation determined in our baseline surveys as generally demarking the lower limits of marsh vegetation. Though included in our spectral analysis, a portion of Roberts Bank Wildlife Management Area, located in the southwest corner of the estuary, was excluded from predictions due to missing elevation data. Given that estuarine marshes are highly heterogenous with environmental changes occurring along minute spatial scales, we ran our predictive models at 1.0 m<sup>2</sup> resolution, the highest resolution available based on the specifications of our predictor data. The result was a modeled marsh area of 12.3 km<sup>2</sup>, which at a resolution of 1.0 m<sup>2</sup> represented >12 million data points.

### 2.3.1 Habitat Suitability

Habitat suitability models are dependent on presence or abundance data that can be related to various environmental predictors; accurate presence data are critical. Thus, we refrained from using the outputs of our spectral analysis (see 2.2) as a proxy for presence data, as it would introduce error into our suitability predictions. Verified occurrence data for non-native cattail were not available for our study area from any external source, so we used our personal observations from >5 years of field experience in the FRE. Given that many remote areas of the estuary were visited over this period, and many marsh habitats were surveyed systematically for this and other studies (Lievesley et al. 2016), we concluded that any effects of spatial bias were marginal. The high resolution of our model resulted in 344,846 presence data points produced from our 239 verified polygons. To improve processing performance we selected a randomized subsample of 100,000 data points for use in the model, after comparing the processing time and model performances of models that included 1,000, 10,000, 100,000 and all data points.

Though presence data were ascertained from our personal field records, accurate and spatially-unbiased absence points were unavailable without additional surveys. As an alternative, we created and utilized background data, which characterizes the environmental conditions of the modeled area, regardless of whether cattail is present or not (Phillips et al. 2009). Because identically-sized datasets are optimal for

regression and machine learning models (Barbet-Massin et al. 2012), we randomly selected 100,000 data points within our study area to match our presence data sub-sample.

The distribution and abundance of estuarine plants are driven by many interdependent factors including elevation, proximity to channel margins salinity, available nutrients, soil sulfide concentration, sediment grain size, organic content, competition, facilitation, grazing, disturbance, tides, climate, and atmospheric CO<sub>2</sub> concentrations (Adams 1963; Hutchinson 1982; Snow & Vince 1984; Vince & Snow 1984; Bertness & Leonard 1997; Zedler et al. 1999; Sanderson et al. 2000; Crain et al. 2004; Sullivan et al. 2010; Hood 2013). For this study we were limited to datasets that were deemed relevant to *Typha* distributions and freely available, so our predictors were elevation, proximity to nearest channel, and percent sand.

Elevation is considered a powerful predictor of estuarine marsh plant distributions, including *T. angustifolia* (Hood 2013), likely due to correlations with a host of factors including inundation duration and frequency, and edaphic properties such as soil salinity. Elevation data were comprised of a 1 m gridded bare earth Digital Elevation Model (DEM) provided by GeoBC from their National Disaster Mitigation Program dataset, generated from Lidar Data acquired during low tides between June - September 2016 (12 points/m<sup>2</sup>, vertical accuracy +/- 15 cm RMS).

Tidal channels also have a significant influence on marsh vegetation due to edaphic correlations (Zedler et al. 1999; Sanderson et al. 2000), and likely other mechanisms such as disturbance and seed dispersal. No channel dataset was accessible at the time of this study, so we used our DEM to designate all pixels with elevations below 0.2 m ASL as channels, an elevation deemed to be the lower limit of emergent marsh vegetation based on our preliminary surveys. Proximity to nearest channel was then calculated in ArcMap using the Euclidean Distance Tool, resulting in a Euclidean distance raster where each 1 m<sup>2</sup> pixel was assigned a distance value to the nearest channel.

Percent sand data were acquired through National Resources Canada, and were based on data collation and interpretation by Barrie & Currie (2000) for the Geological Survey of Canada. At 50 m<sup>2</sup> resolution, their interpretations were based on textural analyses of over 1500 surficial grab samples collected from throughout the river and delta front, as well as geophysical and core data provided by Hart & Barrie (1995) and Hart et al. (1998).

Before selecting our final models, we evaluated the results of several approaches including profile, regression, machine learning, presence-only, and presence-absence models in RStudio v. 4.0 (R Core Team 2020). The predictive performance of models were evaluated using a five-fold verification process (Fielding & Bell 1997), which partitioned the presence and background data into five sets, one of which was used for training while the remainder were combined for testing purposes for each model run. Each model was run five times so that each partition was used as training data once, and the Area Under the Curve (AUC) values of each model was averaged across the five runs to produce a mean AUC value with variance. Area Under the Curve is frequently used to evaluate SDMs, and measures the ability of a model to discriminate between sites where a species is present versus where it is absent on a 0 to 1 scale, with 1



being perfect and 0.5 equal to random (Hanley & McNeil 1982; Elith et al. 2006). To increase accuracy, we excluded models whose minimum mean Area Under the Curve (AUC) fell below a threshold of 0.8. The result was the inclusion of three modelling methods: Random Forest, Maxent, and Support Vector, which were run using randomForest (version 4.6.14; Liaw & Wiener 2002), dismo (version 1.14; Hijmans et al. 2017), and kernlab (version 0.9.29; Karatzoglou et al. 2004) packages. Maxent was run using default settings, while the number of trees in our Random Forest model was reduced from 500 to 200 to improve processing speeds, as out of bag error stabilized around 200 trees. A radial basis kernel (Gaussian) was selected in our Support Vector model due to its widespread use in literature, and it produced the highest mean AUC value among all kernel options. Finally, we combined the predictions of the methods with AUC values above the threshold into an ensemble model weighted by their AUC values.

### 2.3.2 Habitat Susceptibility

We defined susceptibility as the risk of marsh habitat being colonized by non-native cattail within 25 years, accounting for both propagule pressure and habitat suitability. The duration of 25 years was selected because greater durations were likely to diminish prediction effectiveness, due to the highly-fecund nature of cattail (i.e. seeds would likely reach most habitats given enough time) and due to the unpredictable environmental changes expected to occur this century, such as sea level rise (Bornhold et al. 2008; Kirwan & Murray 2008), altered river flows due to climate change (Taylor 2004), and chronic herbivory by overabundant waterfowl (Demarchi 2006). Susceptibility was calculated by multiplying the estimated probability of propagule introduction in 25 years with the probability outputs of our habitat suitability model (Fig. 1; see 2.3.1).

The probability of propagule introduction was estimated based on proximity to nearest non-native cattail occurrence, and non-native cattail density in nearby marsh. Proximity was calculated using a cost distance analysis in ArcMap, a variation of Euclidean distance that calculates the least-costly path between a pixel and an object (i.e.,... known cattail occurrences), accounting for both the actual distance and any associated costs of travelling through a heterogenous landscape. We based our distance calculations on the locations of non-native cattail determined in our spectral analysis (see 2.2). To account for spatial differences in seed dispersal effectiveness, we generated a cost raster based on land cover types, assigning cost values ranging from 1 for marsh (no added cost) to 5 for developed terrestrial areas (5 x cost; Table 1). These cost values accounted for both water and air-dispersed propagules and factors that inhibit their dispersal in each land cover type. Distances were then calculated for each pixel of our study area, ranging from 0 – 3114 least cost meters (i.e. cost-adjusted euclidean distance to nearest cattail).

**Table 1** Land cover types and their associated distance costs used for estimating non-native cattail propagule dispersal probabilities. A cost value of 1 is equal to the actual (Euclidean) distance.

Land Cover Type	Cost	Cost Value Rationale
Marsh	1	Seeds and plant fragments freely move via wind and water. Sheltered from excessive wind and river flows.
Open Water	3	Seeds and plant fragments freely move via wind and water, but are subjected to deleterious effects of river flows.
Agriculture Fields	4	Waterborne plant fragments and seeds excluded. Airborne seeds freely move, with no tall structures or forests present. Agricultural ditches may transport seeds to suitable habitats.
Developed Areas	5	Waterborne plant fragments and seeds excluded. Airborne seeds potentially inhibited by developed landscape including tall buildings and tall vegetation.

To translate cost distances to probabilities we considered two potential pathways of expansion: clonal growth of existing patches, and dispersal through seeds and plant fragments. Clonal growth rates vary in the literature from 0.76 m/year (Bansal et al. 2019) to patch diameter increases of 4 m/year (Boers & Zedler 2008), and are likely driven by environmental variables such as inundation, and available nutrients (Woo & Zedler 2002). To obtain an annual clonal growth rate specific to conditions in the FRE we compared the size of eleven verified patches over time using historical imagery. Lateral growth rates varied from 0.53 – 1.52 m/year and averaged 1 m/year ( $\bar{x}$  = 1.05, SD = 0.36).

Seed recruitment is not considered the primary means of reproduction by *T. x glauca* during early site colonization (Travis et al. 2010, 2011), and it is often considered a partially sterile hybrid (Smith 1967; Kuehn et al. 1999). This may be the case in the FRE, as pistillate flowers have been observed to contain very few or no seeds, and advanced hybrid generations are yet to be molecularly confirmed. However, in their study of cattail clones, Travis et al. (2011) observed that *T. x glauca* stands grew more genetically diverse over time, suggesting seedling recruitment of backcrossed and advanced-generation hybrids could supersede vegetative recruitment over time. Though the reproductive status of *T. x glauca* remains uncertain, the presence of *T. angustifolia* facilitates dispersal of both viable *T. angustifolia* seed and where *T. latifolia* is sympatric, viable F1 hybrids seeds, as evidenced by the abundance of these taxa in spatially-isolated habitats in and near the FRE. For these reasons, we still considered seed dispersal to be an important consideration for susceptibility.

Based on the above considerations, we assigned the maximum probability value to any pixel that was  $\leq 250$  least cost meters to non-native cattail (Table 2). The minimum probability value (0.4) was assigned to pixels > 2000 least cost meters, the value of which we justify by (1) the 25-year duration of our predictions, which increase the probability of dispersal to these isolated locations, (2) the possibility of cattail occurring in neighbouring inland habitats (e.g. ditches, ponds), and (3) the proven fecundity and dispersal ability of cattail in literature and in our personal observations.

**Table 2** Least cost distance classes and associated probabilities used for estimating the probability of propagule arrival.

Least Cost Meters to Nearest Non-Native Cattail	Probability of Propagule Arrival in 25 years
0 – 250	1.0
>250 – 1000	0.8
>1000 – 2000	0.6
>2000 – 3000	0.4

In addition to cost distance, we calculated cattail density within a 1000 m circular neighbourhood of each raster cell using the Point Density Tool in ArcMap. Neighbourhood density values varied from 0 – 1.61% and were classified using a geometric scale into four probability categories (Table 3). With the same rationale as our distance probabilities, we elected to set the minimum probability value to 0.4.

**Table 3** Density classes and associated probabilities used for estimating the probability of propagule arrival.

% Area Occupied by Non-Native Cattail in Surrounding 1000 m Radius	Probability of Propagule Arrival in 25 years
>0.500 – 2.000%	1.0
>0.200 – 0.500%	0.8
>0.005 – 0.200%	0.6
0.000 – 0.005%	0.4

Proximity and density-based probability values were then averaged to generate an overall propagule introduction probability. This value was then multiplied with our habitat suitability values to generate susceptibility probabilities for each raster cell in our modelled area:

## 3 Results

### 3.1 Spectral Analysis

Our spectral analysis identified non-native cattail with a high level of accuracy throughout the FRE. Confusion matrix results indicate both classified datasets were similar in accuracy, with an overall accuracy of 85.5% in the lower and 86.0% in the upper estuary (Table 4). Commission (overestimate) error was higher in the upper estuary (21.0%) than the lower estuary (11.0%), while omission (underestimate) error was higher in the lower estuary (16.8%) than upper (8.1%). Kappa Coefficients ( $k$ ) were near-identical between datasets, with values indicating strong similarity between classified data and ground-verified data when accounting for expected accuracy (Landis & Koch 1977).

Table 4  
Confusion matrix for lower and upper estuary image classifications.

Ground-Verified Data					
		Non-native Cattail	Other Species	Commission Error	Kappa Coefficient
Classified Data	Non-native Cattail	89	11	11.0%	–
	Other Species	18	82	18.0%	–
	Omission Error	16.8%	11.8%		71%
	Non-native Cattail	79	21	21.0%	–
	Other Species	7	93	7.0%	–
	Omission Error	8.1%	18.4%		72%

Non-native cattail are well-established in the FRE, with 494,759 out of the 12,264,353 cells (4.0%) classified as non-native cattail, representing nearly 500,000 m<sup>2</sup> of occupied marsh habitat (Table 5). Though only representing about 2.3% of overall marsh habitat, restoration sites, consisting of habitat compensation, enhancement, restoration and banking projects created within the last 30 years, have the highest proportion of cattail (14.9%), with over 3 x greater proportions than the overall estuary. Conversely, protected area marshes, defined as marshes legally protected by government agencies and NGOs (e.g. Wildlife Management Areas, Conservancy Lands), have the lowest proportion (3.4%), while unprotected marshes were only slightly higher (5.5%).

Table 5  
Percent area and abundance of non-native cattail-classified pixels in restoration sites, protected areas, and unprotected areas in the Fraser River Estuary.

Habitat Type	% of Estuary	Non-Native Cattail Pixels	Total Pixels	Non-Native Cattail (%)
Restoration Sites	2.3	41656	278825	14.9
Protected Areas	68.5	281836	8404145	3.4
Unprotected Areas	31.5	212923	3860208	5.5
Total Estuary	100	494759	12264353	4.0

Occurrences are distributed across the entire study area (Figs. 2 & 3), with higher densities occurring in the lower estuary dataset (5.3% of cells) than the upper (2.8%). Density data were right-skewed in their distribution, as the majority of sampled habitat was relatively low in detection density ( $0.5 \text{ m}^2/100 \text{ m}^2$  radius), while dense hotspots ( $> 20.0 \text{ m}^2/100 \text{ m}^2$  radius) were primarily restricted to a small number of locations near the estuary mouth.

The spatial distribution of large patches appears to correspond with areas of greatest density (Fig. 2), with the majority of large patches occurring in the outer limits of the estuary and a small number of sites up river (Fig. 3). Patch sizes were also right-skewed in their distribution, as 55% of patches were  $\leq 3 \text{ m}^2$ , 77% were  $\leq 10 \text{ m}^2$ , and  $< 1\%$  exceeded  $1000 \text{ m}^2$ . The largest patch occurs in southwest Vancouver, exceeding 10 hectares in size, over three times the size of the next largest patch.

Though not distinguished in our spectral analysis, in nearly all instances the non-native cattail observed during field verification was *T. x glauca*, which is surprising considering there were no formal records of this taxa in British Columbia prior to our study. Non-native cattail was observed in 18 of the 30 field-verified grid cells, with ten containing *T. x glauca*, two containing *T. angustifolia*, and six containing both taxa. In instances where multiple *Typha* taxa were present (including *T. latifolia*), *Typha x glauca* was consistently the most abundant, often representing an estimated  $> 90\%$  of cattail present.

## 3.2 Species Distribution Model

### 3.2.1 Suitability to Further Invasion

The results of our cross validation indicates our Maxent, Random Forest, and Support Vector models are effectively predicting cattail habitat suitability, with mean AUC values ranging from a minimum of 0.842 (Maxent) to a maximum of 0.871 (Random Forest; Table 6). Areas with high suitability probabilities reflect where non-native cattail are confirmed, and low probabilities reflect where cattail is not known to be present. Variance and standard deviation values were  $< 0.4$  for all models, indicating the models were effectively applying their predictions to both training and non-training datasets.

Table 6  
Area Under the Curve (AUC) values of the three models  
included in the ensemble habitat suitability model.

AUC VALUES			
Partition #	Maxent	Random Forest	Support Vector
1	0.846	.867	.846
2	0.848	.871	.848
3	0.846	.871	.848
4	0.842	.866	.839
5	0.847	.871	.843
Mean AUC	0.846	.869	.844
Mean $\sigma$	0.002	0.002	.004
Mean $\sigma^2$	0.001	0.001	.001

Substantial unoccupied portions of the FRE are suitable for the establishment and persistence of non-native cattail, as 10% of the estuary has suitability probabilities of > 75%, and 19% has values 50–75%, while currently only 10% and 6% of these habitats, respectively, are occupied based on our spectral analysis (Figs. 4 and 5). Our spectral analysis, which assessed a larger area than the SDM, indicated 4.0% of the estuary is currently occupied, so these findings suggest the invasion threat posed by non-native cattail is ongoing, as many highly-suitable areas remain unoccupied.

All habitat types are similar in having proportionally more low-suitability (< 25%) habitats than high (> 75%), and higher proportions of non-native cattail in high-suitability habitats based on our spectral analysis results (Fig. 5). Restoration sites are the greatest outlier, as 26.5% of their habitats have suitability values > 75%, representing over double the proportions of unprotected areas, and triple that of protected areas. In addition, suitable habitats in restoration sites appear more likely to be invaded, with 17.1% occupancy in habitats > 75%, while equally-suitable habitats in protected and unprotected areas are 7.9% and 11.0% occupied respectively. Although protected areas possess the highest proportion of low-suitable habitat, the least amount of high-suitable habitat, and the lowest area occupied area across all classes, there is still significant risk of invasion, as 25.4% of their area has suitability values > 50%, and currently only 12.8% of these habitats are currently occupied.

### 3.2.2 Susceptibility

As with suitable habitats, we found that unoccupied susceptible habitats are also abundant in the FRE (Fig. 6). Currently 4% of the modelled estuary has a susceptibility probability of > 75% or more, 16% has values of 50–75%, while currently only 18% and 6%, respectively of these habitats are occupied. The most susceptible areas in the estuary resemble the current distribution of cattail (Figs. 2 and 3), which is

likely a by-product of (1) high cattail density and thus high propagule pressure in these areas, and (2) the high suitability of these sites. Our findings suggest the most susceptible areas to invasion are those immediately adjacent to existing patches. Invasion could occur clonally in contiguous habitats, or via seed or vegetative dispersal across greater distances or in fragmented habitats.

Though susceptibility probabilities follow similar trends across all habitat types, habitat restoration sites are noticeably more susceptible to cattail invasion, as evidenced by the presence of proportionally less low-susceptible (0–25%), and significantly more high-susceptible (> 75%) habitat than other habitat types (Fig. 7). When overlaid with the presence data acquired from our spectral analysis, this is further confirmed by the comparatively high percent area occupied by cattail across all susceptibility classes in restoration sites vs. other sites. The lone exception are high-susceptible habitats in unprotected areas, which have the highest cattail occupancy of any habitat type. This anomaly can likely be explained by the largest cattail patch in the estuary, which occurs in a large, contiguous, unprotected marsh (see 3.1). Restoration sites therefore appear to not only be more suitable environmentally (as indicated in our suitability mode), but in most instances also more susceptible, suggesting that practitioners are creating these sites in areas of high propagule pressure.

Protected and unprotected areas differ very little in most classes, apart from the 75–100% class, where 29.3% of unprotected areas are occupied (the highest of any habitat type), versus 11.6% of protected areas. This difference can likely be attributed to the largest non-native cattail patch in the estuary, which occurs in unprotected marshes of southwest Vancouver (see 3.1). Protected areas appear to show some degree of invasion resilience in possessing the highest proportion of low-susceptibility habitat, the least amount of high-susceptibility habitat, and the lowest area occupied across all classes. However, there is still risk of expansion in these areas, as 25.4% of their habitats have probabilities of > 50%, and a mere 16.7% of these habitats are currently occupied.

## 4 Discussion

### 4.1 Non-native Cattail as a Cryptic Invasive Species

Awareness and concern around cryptic invasive species, i.e., non-native species that are either not recognized as alien or not distinguished from known species in a region (Novak 2011), has increased in recent decades. Though studies that quantify their impacts are infrequent, Morais & Reichard (2018) identified three overarching threats presented by cryptic invaders: (1) hybridization-induced losses in genetic diversity, (2) replacement of native species and lineages, and (3) cascading ecosystem impacts due to compositional changes. Despite these threats, cryptic invasions are often not recognized until long-after they occur, and proactive strategies are subsequently rare or poorly defined.

We found that non-native cattail, (in particular *T. x glauca*) qualify as cryptic invaders in the FRE, as they are well-established and have likely been present for several decades without detection. Evidence of their long duration in the estuary includes their large extent (~ 500,000 m<sup>2</sup>) and widespread distribution,

particularly in habitats deemed to be highly-suitable in our models. This suggests enough time has passed to allow propagules to disperse over great distances between highly-fragmented habitats, and successfully establish in most large, optimal sites. Also, although *T. angustifolia* has been commercially-available in the region till recently (Ciotir & Freeland 2016), there is no evidence of the commercial sale of *T. x glauca*. This suggests its presence in the estuary is likely the product of natural hybridization, which presumably occurred after the establishment of its non-native parent, *T. angustifolia*.

This raises the question of how these non-native taxa could be widespread for so long without detection. One explanation is the morphological similarity between native and non-native cattails (Kuehn & White 1999), which are often sympatric in the FRE. Without prior knowledge of non-native *Typha*, any cattail observed in the FRE would be assumed to be native *T. latifolia*. Another reason for this oversight may have been the taxonomic uncertainty of *Typha* in the region. Historical herbarium specimens and technical guides in British Columbia refer to *T. latifolia* forma *ambigua*, described as “[often resembling] *T. angustifolia* in gross appearance, and may be mistaken for this species being identifiable correctly and unquestionably only with the aid of a microscope” (Brayshaw 1985). This taxon was never formally recognized, and due to this misnomer, it is possible that non-native cattail, particularly *T. x glauca* with its intermediate and at times confounding traits, were misidentified as a native forma. This could explain how *T. x glauca* remained overlooked for so long, despite the vegetation of the FRE being well-documented historically (e.g. McLaren 1972; Yamanaka 1975; Bradfield & Porter 1982). A final explanation may be that human access to these habitats is severely limited by hazardous topography, tidal cycles, and often geographical isolation. Thus, many of the worst invaded areas, which presumably underwent compositional change within decades, were not under regular observation.

The cryptic resemblance of these non-native cattail to *T. latifolia* may also reduce the likelihood that decision makers will perceive them to be an ecological hazard requiring management. Already, one of the emerging counterarguments to these *Typha* being labelled “invasive species” (i.e. species that threaten economic, social, and environmental values), has been the assumption that they share identical functional traits to *T. latifolia*, so their impacts would largely be intrageneric. This assumption is supported by research where no niche differentiation between *Typha* species has been observed (e.g. McKenzie-Gopsill et al. 2012; Pieper et al. 2018). However, all of these studies were situated in freshwater environments, where several known limiting environmental factors (e.g. salinity and tidal fluctuations) were absent. Contrary to this assumption, our findings suggest that niche partitioning is occurring in the FRE, as (1) current invaded areas were not *T. latifolia* monocultures historically, and (2) many uninvaded habitats with the highest suitability probabilities are currently occupied by other native species, such as *C. lyngbyei*. Functional differences have been well-described between *Typha* species in the literature. Native *T. latifolia* is known to have shorter and wider leaves, higher leaf surface area, greater allocation to leaves and vegetative reproduction, later emergence, more and smaller rhizomes, lower stem density, and expend less allocation to sexual reproduction than *T. angustifolia* (Grace & Wetzel 1982; Weisner 1993; Kuehn & White 1999). When placed in an estuarine environment where species niches occur along minute environmental gradients, these functional differences, however small, likely translate to niche partitioning. Such inferences have been made by Grace & Wetzel (1982), who theorized that the narrow leaves and



large rhizomes of *T. angustifolia* explain its competitive dominance over *T. latifolia* in lower, wetter marsh elevations.

It is challenging to infer what changes have occurred in the displacement of approximately 500,000 m<sup>2</sup> of native plant communities, and what future changes will occur should these taxa remain unmanaged. Alleging economic, social, and environmental losses is speculative, but likely given the scale of invasion. Researchers have investigated the impacts of *Typha* invasions in eastern North America (e.g. Travis et al. 2010; Snow et al. 2010; Kirk et al. 2011), but little data exists on impacts to the unique flora and fauna of Pacific Northwest estuaries, including juvenile salmonids whose reliance on marsh habitat for rearing in the FRE has recently been highlighted (Chalifour et al. 2019). Studies that investigate the regional impacts of *Typha* invasions on plant species composition and marsh habitat function should be a management priority, as this will significantly influence management responses to this invasion.

## 4.2 Limitations of Estuarine Habitat Protection

Prior to this study, a large portion of non-native cattail detections in the FRE occurred in recently disturbed habitats such as habitat restoration sites (Lievesley et al. 2016) and roadside ditches. Based on these initial observations, one could infer that disturbance is a major vector for cattail invasion (cf., Bansal et al. 2019). If non-native cattails adhere to competition-colonisation tradeoff theory (Tilman 1994), one could predict that they allocate energy towards reproduction, and therefore (1) invaded areas such as mature restoration sites would see reduced cattail abundance over time as more competitive species establish, and (2) protected areas should be more resilient to invasion due to the lack of large-scale disturbances, and higher degree of competition by established plant communities.

Contrary to these predictions, we found colonization-competition trade-offs appear to be negligible for these taxa in the FRE; they appear capable of both successfully colonizing and persisting. Their colonization ability in the FRE is demonstrated by the high proportion of cattail in recently-created restoration sites, by their widespread distribution across the estuary over a short period of time, and by their high occupancy in suitability and susceptibility hotspots. Strong competitiveness is evident in the ability of these cattail to successfully establish in protected and remote habitats, many of which have been buffered from direct human disturbance for decades and presumably possess more intact, resilient plant communities. It is also demonstrated in the multi-decade persistence of cattail in invaded sites, as evidenced by herbarium vouchers dating to the early 1990s and historical imagery. This resilience could be explained by various theories in invasion science, including ecological release (Kohn 1978), Novel Weapons Hypothesis (Callaway & Ridenour 2004), priority effects (Dickson et al. 2012; Hood 2013), and mechanisms such as allelopathy (Jarchow & Cook 2009) and overabundant leaf litter (Larkin et al. 2012; Farrer & Goldberg 2014; Szabo et al. 2018).

Spectral analysis indicated non-native cattail are well-established in protected areas, occupying 3.4% of protected vegetated tidal marshes. Though this average is slightly below that of the overall estuary (4.0%) and of unprotected areas (5.5%), protected areas comprise about 70% of existing FRE tidal marshes in our study area, and therefore contain 57.0% of all non-native cattail in the estuary. That invasive cattail

were capable of establishing so successfully in the protected areas of the FRE is of concern, but consistent with protected areas being subject to ongoing degradation (Sinclair et al. 1995) and estuaries being inherently dynamic, with recurring disturbance processes such as erosion, log deposition, and accretion that may facilitate colonization (Bearup & Blasius 2017). Other impacts such as climate change, rising atmospheric CO<sup>2</sup> (Sullivan et al. 2010), sea level rise (Hood 2013), and eutrophication (Woo & Zedler 2002), may also promote the dominance of non-native “passenger” species that are better-adapted to novel conditions than natives, resulting in gradual shifts in species composition (MacDougall & Turkington 2005). These environmental processes, in combination with the elevated propagule pressure of non-native species in an urban estuary, pose a constant invasion threat to the FRE, regardless of protection status.

Addressing this issue in the FRE is complex, as ownership and governance over these tidal environments is shared across multiple government agencies, First Nations, private landholders, and industry. In some instances, ownership is unknown. As a result, these habitats are an often overlooked “space between” jurisdictions where non-native species and other ecological threats are able to incubate with little notice or management intervention. Though jurisdictional issues are not likely to be resolved in the immediate future, the cryptic invasion outlined in this paper demonstrates the need for changes in how these protected areas are managed and maintained. First, habitat protection alone is not sufficient to maintain ecological integrity. Diligent monitoring, and where necessary, strategic renewal activities (e.g. habitat restoration, although see below for important caveats) should be promoted (Sinclair et al. 1995). Second, coordination between governments and FRE stakeholders must improve, involving the open sharing of data, collaborative research, and expending collective resources to identify potential or emerging threats while they can still be addressed. Few FRE stakeholders have been willing to fund floristic surveys in recent decades, so the identification of novel species has been largely dependent on in-kind labour and incidental observations. The presence of novel species, including *T. x glauca*, was known in the region for decades among a select few naturalists, but these findings were not communicated to decision-makers. Coordination of governments and stakeholders has been attempted in the past. For example, the Fraser River Estuary Management Program (FREMP) aimed to bridge ecological and economic values in the estuary. However, it had several shortcomings, e.g., exclusion of First Nations, and was abruptly disbanded by the Federal government in 2011. No entity has replaced FREMP, so the estuary remains highly vulnerable to the lack of coordinated environmental governance (Kehoe et al. 2020).

## 4.3 Invasibility of Habitat Restoration Sites

Our findings demonstrate the need for change in how habitat restoration projects, which in the FRE primarily consist of banking and compensation sites, are designed and managed. Spectral analysis showed that cattail was proportionally 3 x more abundant in these sites than the overall estuary and 4 x more abundant than in protected areas. Similarly, our models predicted that restoration sites are more suitable and susceptible to cattail invasion than marsh habitats elsewhere. This suggests the threats posed by non-native cattail were not considered in the design, location, and monitoring of these sites. Many are now invaded and no longer meeting their intended objectives (Lievesley et al. 2016). These

findings have significant conservation implications, as these invaded habitats were built in most instances to offset, and therefore enable the destruction of marsh habitats elsewhere. The high proportion of cattail in restoration sites versus the whole estuary indicates that in some instances, restoration sites may adversely serve as major propagule sources to surrounding marshes.

Managers and practitioners should plan for non-native cattail in the design of new restoration projects, which we have framed through a decision tree (Fig. 8). At the project outset, practitioners must understand the landscape context of their restoration project, and determine whether non-native cattail is present and/or abundant in the vicinity (i.e. 1000 m<sup>2</sup> radius). The cryptic nature of these taxa has prevented this step to date. Large-scale habitat banking projects continue to be planned in susceptible regions, including a proposed 41.1 ha project next to the largest patch of cattail in the estuary. If a proposed restoration site is located in a cattail-abundant region, relocation should be considered, if feasible. If not, restoration practitioners should aim to make their site less suitable to cattail. This could be achieved through [1] dense plantings of native species, to reduce the amount of available habitat and increase the resiliency of the site to invasion, [2] monitoring and early eradication of invasive individuals, [3] and by using predictive vegetation models (Hood 2013), available literature, and other sources to design sites that are less environmentally optimal for cattail. Where none of these preventative measures can be employed, projects should not proceed unless monitoring and management efforts, which increase with each step down the decision tree, can counteract the invasion risk.

## 4.4 Management Response

Our findings indicate non-native cattail are both widespread and abundant, to the point where comprehensive prevention and eradication actions are likely infeasible. This raises two questions: (1) What can managers learn from this invasion to prevent similar narratives from occurring? (2) What management responses are now appropriate, acknowledging the unlikelihood of regional eradication, but also the social, economic, and ecological importance of these threatened marsh ecosystems?

The BC provincial government Invasive Plant Program has evaluated the threat potential of almost 300 terrestrial and aquatic plants, including *T. angustifolia* in 2011. Of those assessments, 48 species have been identified as candidates for management through the provincial Invasive Species Early Detection Rapid Response (EDRR) Program, none of which are cattails. The inability of this system to identify non-native *Typha* as a priority for management, even long after their establishment, suggests gaps may exist in current defences, offering an opportunity for constructive change. One potential gap is the apparent sensitivity of these assessments to available occurrence data, as no *T. x glauca* and fewer than ten *T. angustifolia* herbarium records existed in the FRE at the time of the 2011 evaluation. Data deficiency led decision makers to believe these cattails were not present (i.e. *T. x glauca*) or sporadic (i.e. *T. angustifolia*), despite both taxa being present and abundant for decades according to historical imagery. Minimal occurrence data were therefore not an indicator of low abundance, but likely of the inaccessibility of these habitats, lack of communication between applied researchers and managers (see 4.2), and their cryptic nature. To prevent similar cryptic invasions, future assessments should account for

probability of detection during the risk assessment process. A second explanation is the frequency at which species are re-evaluated in BC. After its evaluation in 2011, *T. angustifolia* was scheduled to be reassessed in 2016, but this has not occurred to date. Around 2016 non-native cattail began to garner local attention (e.g. Lievesley et al. 2016) so a timely re-evaluation may have facilitated an earlier management response.

Estuary-wide eradication is no longer possible without considerable cost and effort, so we recommend efforts in the FRE shift towards asset-based management. Such actions include (1) monitoring and immediate removal of newly established patches in areas of high cultural and conservation value, and (2) strategic removal and restoration of established invasion sites, where appropriate. These efforts should be prioritized based on factors such as cost and feasibility, propagule pressure from nearby infestations, cultural values, presence of at-risk species, and land ownership. Recently several removal methods have been investigated in North America, with some success (e.g. Kostecke et al. 2005; Hood 2013; Lawrence et al. 2016; Lishawa et al. 2017; Elgersma et al. 2017; Wilcox et al. 2018). However, applying these methods in the FRE may prove challenging due to factors such as site inaccessibility and strict herbicide legislation for aquatic ecosystems. Also, the wide-scale distribution and abundance of cattail in the FRE indicates that propagule pressure is likely high in many areas. Additionally, conditions are likely to remain suitable for non-native cattail post-removal, so successful removal efforts risk generating highly-susceptible “weed-shaped holes” (Buckley et al. 2007) that are re-invaded post-restoration. We advise caution before pursuing eradication activities, following a similar decision framework to that propose for restoration sites (Fig. 8).

## 5 Conclusion

Contrary to our expectations, non-native *T. angustifolia* and *T. x glauca* are well-established in the FRE, occupying nearly 4% of the tidal marsh habitats. Expansion is likely should these cattail remain unmanaged, with 28% and 21% of the estuary having suitability and susceptibility probabilities of > 50% respectively. Marsh restoration sites contained 3 x more non-native cattail than the overall estuary proportionally, and contained more suitable and susceptible habitat, casting doubt on the advisability of habitat banking used to mitigate wetland destruction. Regional eradication is no longer an option for these species, and localized management will be necessary to avoid further expansion. We attribute the lack of data for these taxa to their cryptic nature, specifically their resemblance to native *T. latifolia*, which impaired their detection. Going forward, the development of management and restoration strategies to safeguard areas of high conservation and cultural value from exotic cattail invasion in the Fraser River estuary is a priority.

## Declarations

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## Declarations

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### **Conflicts of Interest/Competing Interests:**

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**Ethics approval:** The authors have no ethics approvals to declare that are relevant to the content of this article.

**Consent to participate:** The authors have no consent to participate declarations that are relevant to the content of this article.

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**Data Availability:** A portion of the datasets analyzed during the study and all of the generated results will be available in the StewartHoodMartin2020 repository, located at <https://github.com/dstewart86/StewartHoodMartin2020>. The imagery datasets and most of the model predictors belong to partner agencies, and are not publicly available.

**Code Availability:** The code used during the current study will be available in the StewartHoodMartin2020 repository, located at <https://github.com/dstewart86/StewartHoodMartin2020>.

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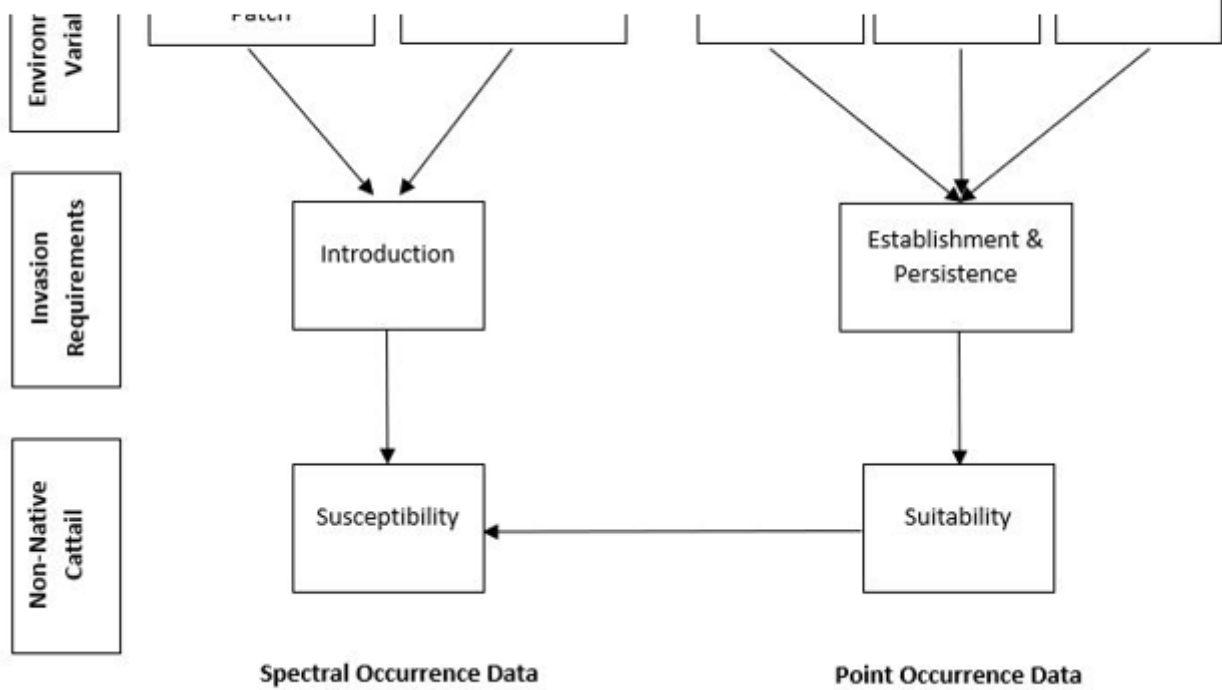
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## Figures

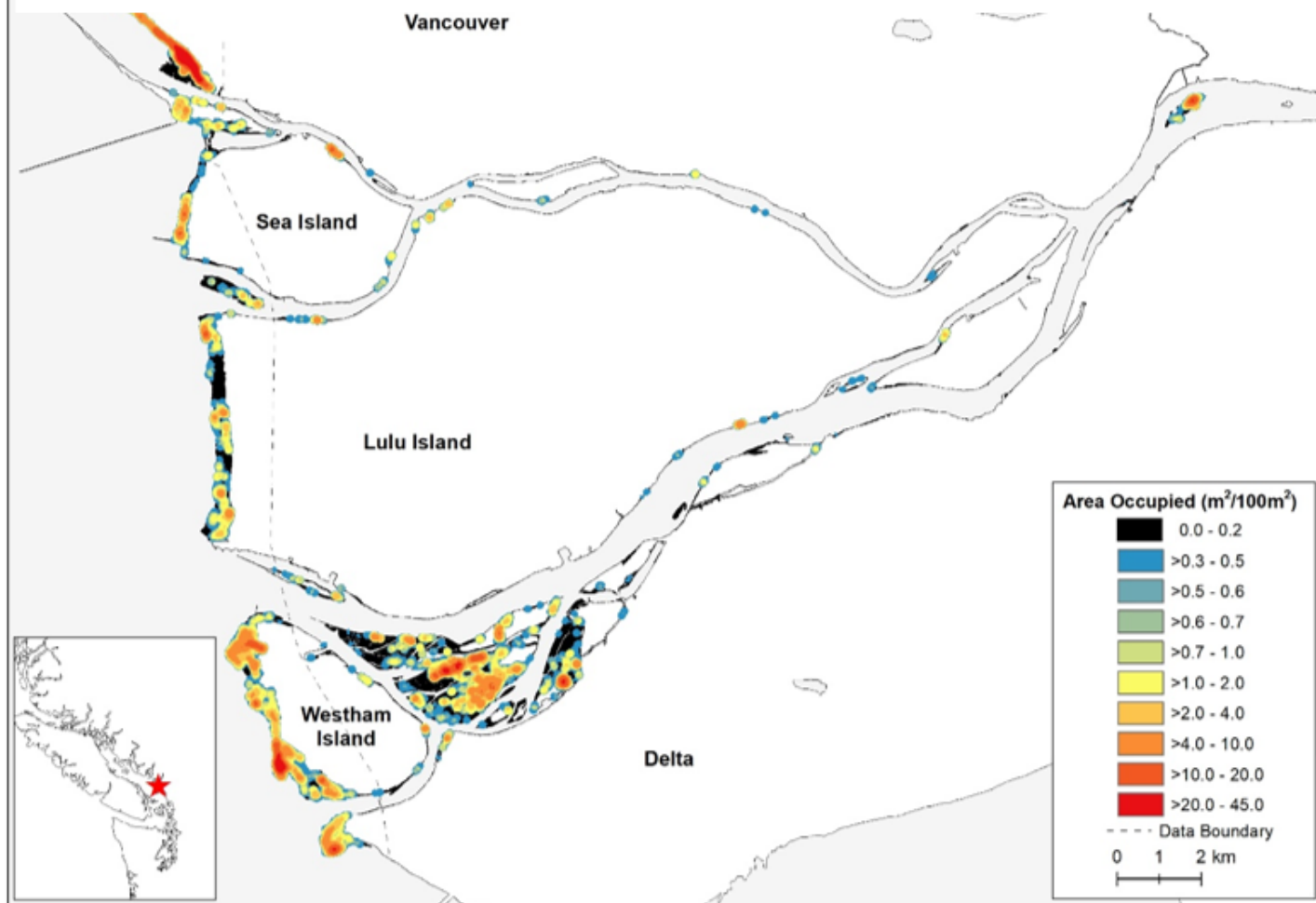
Fig. 1 Conceptual model of environmental variables and invasion requirements used to model the suitability and susceptibility of the FRE to non-native cattail invasion



**Figure 1**

Conceptual model of environmental variables and invasion requirements used to model the suitability and susceptibility of the FRE to non-native cattail invasion

**Fig. 2** Heat map of classified non-native cattail pixels in the Fraser River Estuary, British Columbia. Lower and upper estuary imagery datasets are delineated by the dotted line



**Figure 2**

Heat map of classified non-native cattail pixels in the Fraser River Estuary, British Columbia. Lower and upper estuary imagery datasets are delineated by the dotted line

Fig. 3 Proportional map of non-native cattail patch sizes in the Fraser River Estuary, British Columbia. Lower and upper estuary imagery datasets are delineated with a dotted line

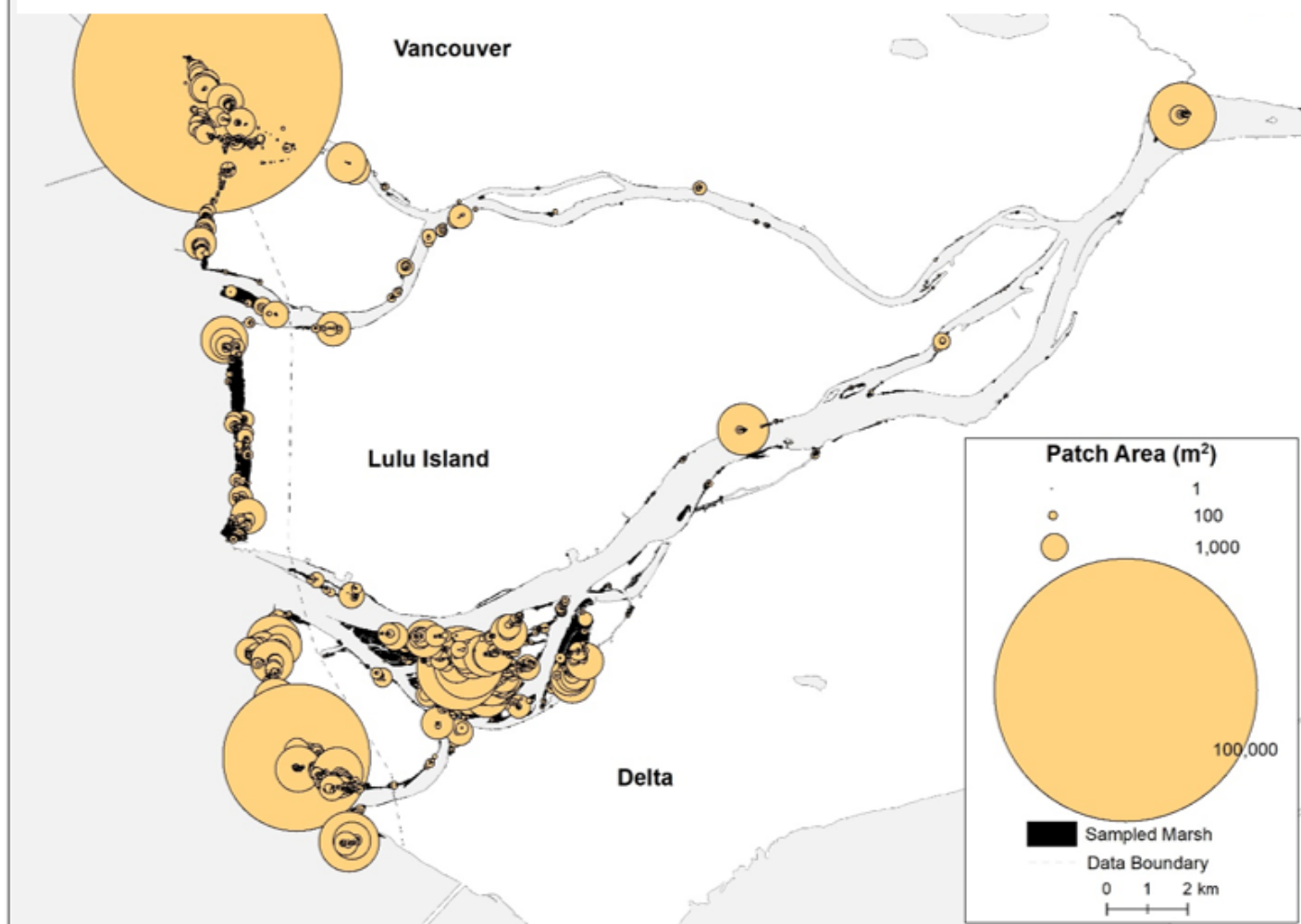
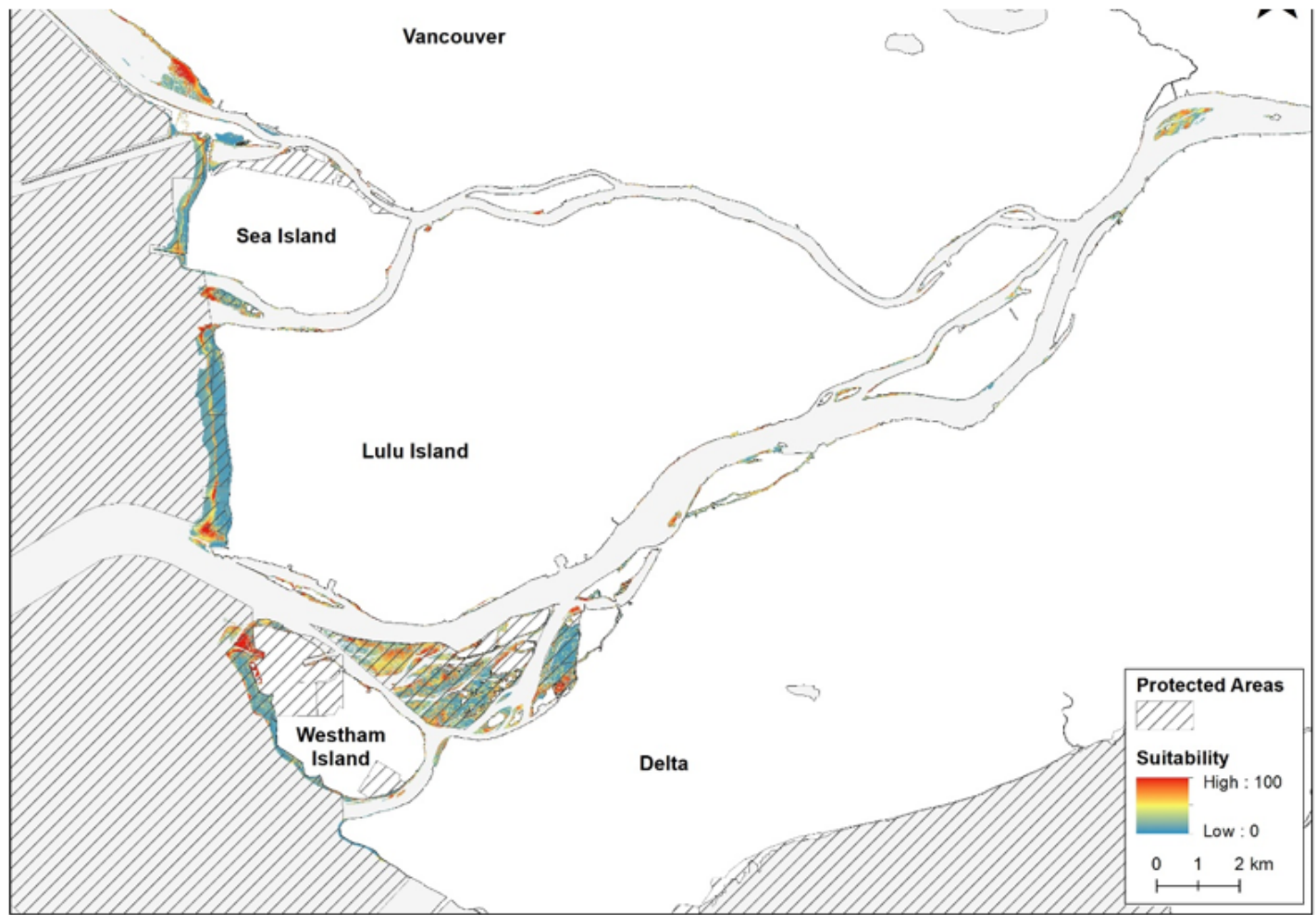


Figure 3

Proportional map of non-native cattail patch sizes in the Fraser River Estuary, British Columbia. Lower and upper estuary imagery datasets are delineated with a dotted line

**Fig. 4** Probability of high suitability for non-native cattail in the Fraser River Estuary. Protected area boundaries are shown in lined polygons

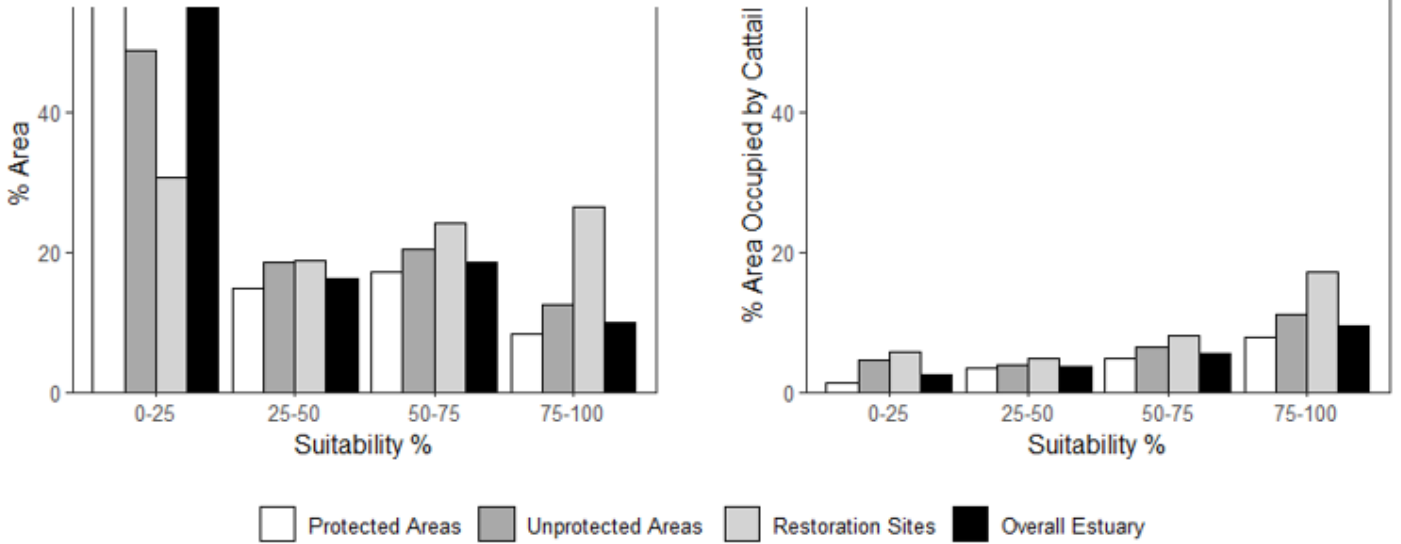


**Figure 4**

Probability of high suitability for non-native cattail in the Fraser River Estuary. Protected area boundaries are shown in lined polygons



**Fig. 5** Percent area and percent area occupied by cattail based on suitability class for restoration sites, protected areas, unprotected areas, and the overall estuary



**Figure 5**

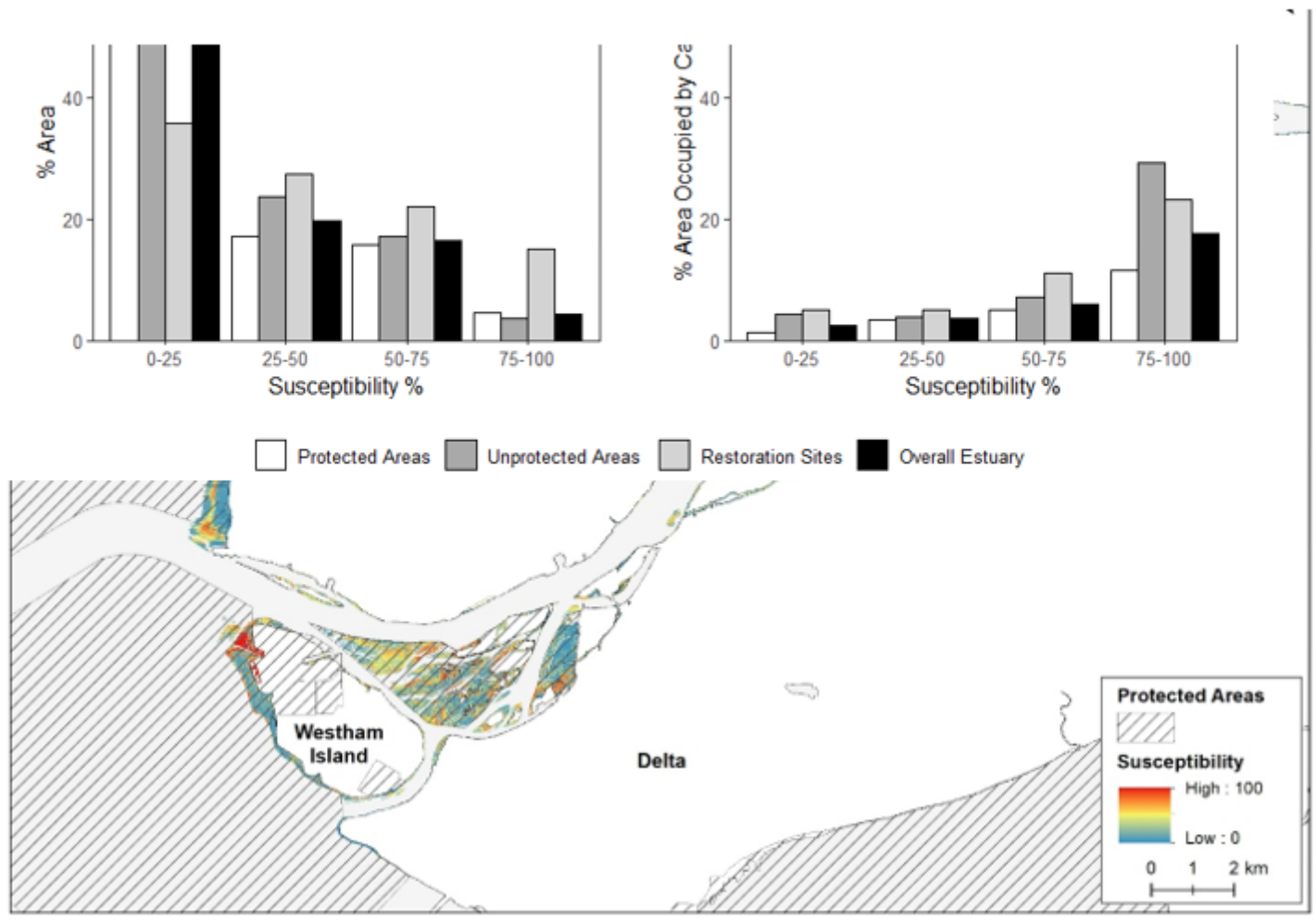
Percent area and percent area occupied by cattail based on suitability class for restoration sites, protected areas, unprotected areas, and the overall estuary

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**Figure 6**

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Fig. 7 Percent area and percent area occupied by cattail based on susceptibility class for restoration sites, protected areas, unprotected areas, and the overall estuary n in



**Figure 7**

Percent area and percent area occupied by cattail based on susceptibility class for restoration sites, protected areas, unprotected areas, and the overall estuary

Fig. 8 Decision tree for habitat restoration practitioners in the FRE planning for the threat of non-native cattail invasions

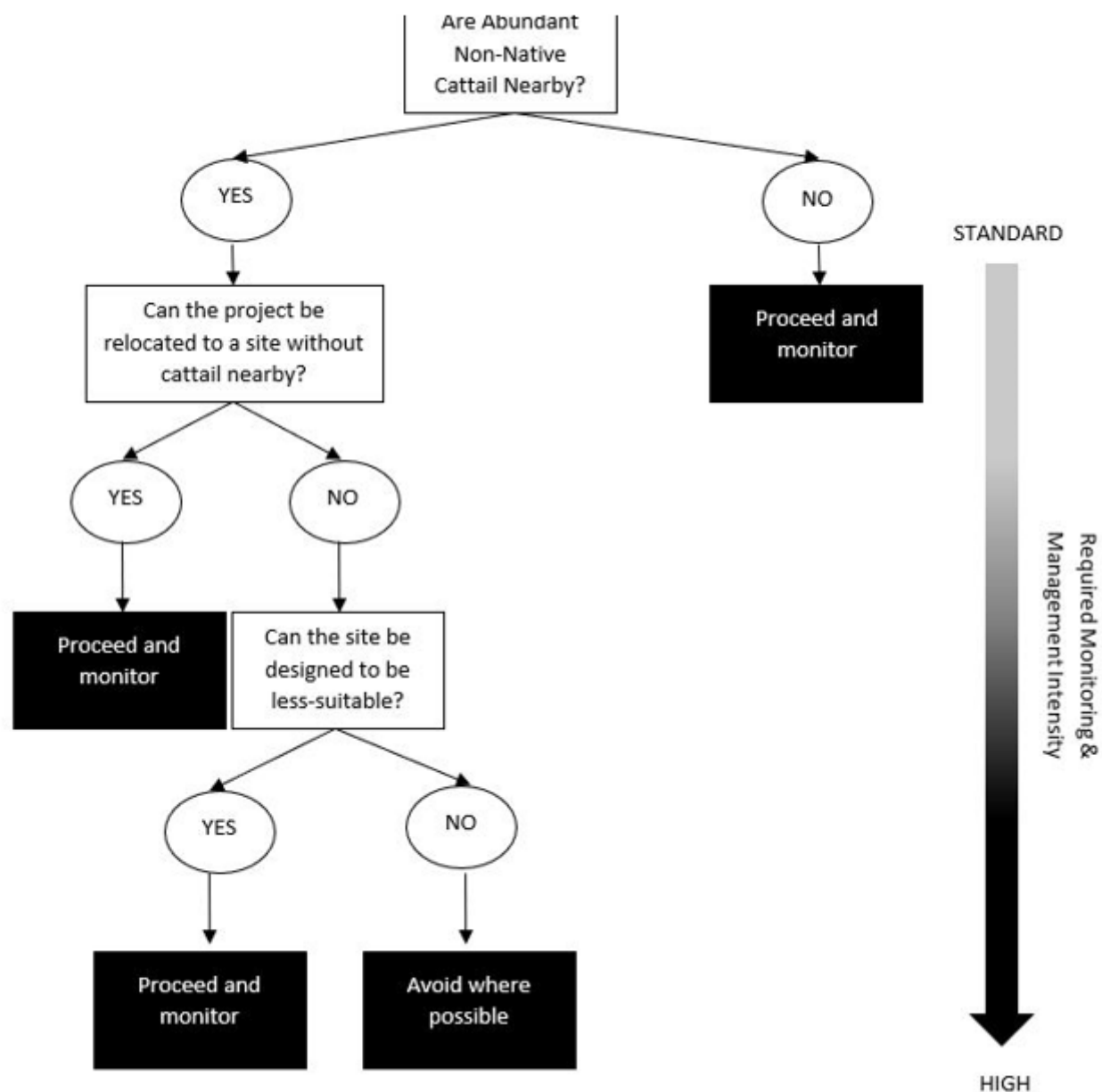


Figure 8

Decision tree for habitat restoration practitioners in the FRE planning for the threat of non-native cattail invasions

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