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

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**keywords**: cryptic invasion, estuary, cattail, pacific northwest, suitability modelling, wetland

# Declarations

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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/asarum-ecological/StewartHoodMartin_Typha_Undetected>. 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 above github repository, located at <https://github.com/asarum-ecological/StewartHoodMartin_Typha_Undetected>.

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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 × 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.

# 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 hindered by effort and cost, which compound temporally (Smith et al. 1999; Rejmánek & Pitcairn 2002; Simberloff et al. 2013; Ahmed et al. 2022). 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). 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 × glauca* Godr.), to understand their current distribution and future risk of expansion.

Both *T. angustifolia* and *T*. *× glauca* areconsidered problematic wetland invaders in North America, and most research related to their impacts has occurred in the central and eastern parts of the continent where they are more widely recognized as a conservation issue. At an intrageneric level there is inconclusive evidence of niche partitioning among *Typha* in modern freshwater studies (Travis et al. 2010; McKenzie-Gopsill et al. 2012; Bunbury-Blanchette et al. 2015; Zapfe & Freeland 2015; Pieper et al. 2018); however, niche partitioning may be more pronounced in coastal marshes, as *T. angustifolia* is considered more salt-tolerant than *T. latifolia* (McMillan 1959; Hutchinson 1988; Galatowitsch et al. 1999). Where they co-occur, hybrid *T. × glauca* is widely considered more competitive than either parent, often replacing them over time through direct competition or introgression (Bunbury-Blanchette et al. 2015; Geddes et al. 2021). Non-native cattails are known to displace native marsh plant communities (Frieswyk & Zedler 2007; Wilcox et al. 2008) via high growth rates (Grace & Wetzel 1998; Zapfe & Freeland 2015), shading by leaf litter (Larkin et al. 2012a; Farrer & Goldberg 2014; Szabo et al. 2018), phenotypic plasticity (Waters & Shay 1990; Woo & Zedler 2002), and allelopathic compounds (Jarchow & Cook 2009; Szabo et al. 2018). These community-level impacts are linked to changes at other trophic levels, such as the exclusion of waterfowl (Kostecke et al. 2004; Hood 2013; Lishawa et al. 2020), reduction of marsh-associated birds (Meyer et al. 2010), and reduction in macroinvertebrate and insect biomass (Kostecke et al. 2005; Lawrence et al. 2016a; Lee 2021).

Recent assessments suggest *T. angustifolia* was likely introduced to North America from Europe (Ciotir et al. 2013; Ciotir & Freeland 2016), though it has been present on the Atlantic Coast since at least the early 19th century (Shih & Finkelstein 2008). Concurrent with its continental establishment was the emergence of hybrid *T. × glauca*, the offspring of *T. angustifolia* and native *T. latifolia* (Kuehn et al. 1999; Ball & Freeland 2013). First-generation hybrids were once considered sterile (Smith 1967), but backcrosses and advanced generation hybrids have been recently detected in the Great Lakes and Maritime Regions (Travis et al. 2010; Snow et al. 2010; Kirk et al. 2011; Zapfe & Freeland 2015; Pieper et al. 2017), and genetic evidence suggests asexual and sexual reproduction is similar among taxa (Pieper et al. 2020). Initially restricted to the eastern margins of the continent, these taxa have rapidly expanded westward over the last century due to habitat alteration, disturbance, and commercial sales (Shih & Finkelstein 2008; Ciotir & Freeland 2016).

At the northwest limit of this continental invasion lies the Fraser River Estuary (FRE), western Canada’s largest and most productive estuary, and home to Canada’s third largest metropolitan area, Greater Vancouver. Widely recognized for its ecological importance, the FRE historically supported the largest annual salmon run of any river in North America (Chalifour et al. 2019), is globally recognized as an Important Bird and Biodiversity Area (IBA), and supports over 100 plants and animals designated as “at risk” (Kehoe et al. 2020). 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; Dorcey 2004). Remaining habitats, approximately 70% of which are now protected by governments and non-government organizations (NGOs), continue to be degraded by a multitude of historical and emerging threats (Kehoe et al. 2020), including invasive plants (Stewart et al. 2022), sea level rise (Kirwan & Murray 2008), climate change (Taylor 2004), habitat loss (Marijnissen & Stefan 2017), habitat fragmentation, and excessive waterfowl herbivory (Demarchi 2006). These threats are likely to compound, as the human population in Greater Vancouver 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.

Though non-native cattails are present in the FRE, occurrence data are limited. No herbarium vouchers of *T. angustifolia* exist prior to 1990, and only a small number of records have been found in grey literature, all after the mid 1980s (Brayshaw 1985; Williams 1998; Adams & Williams 2004; Lievesley et al. 2016). Prior to this research no formal record existed of *T.* × *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 the actual limited abundance of these taxa, but may also reflect observer biases related to site inaccessibility, limited survey resources, or morphological similarities to other species (Isaac & Pocock 2015; Morais & Reichard 2018).

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 where occurrence data are deficient, resources for field surveys are limited, and habitats are difficult to access (Hestir et al. 2008). Tidal marshes are excellent candidates for reflectance analyses because they tend to be dominated by a small number of monodominant species, 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 habitat 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 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, a necessity for estuarine plants given the small environmental scales in which they occur, and the overall complexity of predicting within these dynamic ecosystems. Several environmental factors are known to influence species distributions in coastal marshes, including salinity, submergence stress, proximity to channel margins, available nutrients, numerous edaphic properties, disturbance, and climate (Adams 1963; Hutchinson 1982; Ewing 1983; Snow & Vince 1984; Zedler et al. 1999; Sanderson et al. 2000; Cronk & Fennessy 2001; Crain et al. 2004; Sullivan et al. 2010).

Using a combination of spectral analysis and species distribution modelling, we investigate the threat of non-native cattails to the FRE. Knowing that the distribution and abundance of these taxa have significant implications on the cost, effort, and incentives behind their future management, 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 more prone to cattail invasions than others?

# Methods

## Study Area

This study occurred in the tidal marshes of the Fraser River Estuary, British Columbia, Canada (10 U 501906 5446049). At over 21,000 hectares, the Fraser is one of the largest estuaries in Pacific North America, and the largest of western Canada. For the purposes of this study, we included all habitats downstream of the Port Mann Bridge, located approximately 35 km upstream from the river mouth via channel distance (10 U 513641 5451852). 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 data extracted from a digital elevation model (DEM; see 2.3.1 for specifications), an elevation determined in exploratory surveys as generally demarking the lower limits of marsh vegetation.

These marsh habitats possess a mixed diurnal and semi-diurnal tidal regime, where the timing and amplitude of tides are influenced by seasonal river discharge and distance upriver (Ages & Woollard 1976; Wu et al. 2022). The effects of salinity are greatest at the estuary mouth, particularly in marshes isolated from river flows by jetties, where soil pore water ranges from approximately 3.5–15.5 ppt during high river flows (Hutchinson 1982). Saltwater intrusion diminishes with distance upriver, influenced primarily by tides and river discharge. During high river flows (mid-May to mid-August) surface waters are fresh in most of the study area, apart from isolated areas mentioned above. Surface water salinity can reach 4.0 ppt approximately 10 km upstream during low-flow winter months (Ages & Woollard 1994; Adams & Williams 2004). The composition of dominant vegetation in the estuary reflects these environmental differences. Species with high relative salt tolerance such as *Schoenoplectus pungens* (three-square bulrush), *Bolboschoenus maritimus* (seacoast bulrush), and *Distichilis spicant* (saltgrass) dominate significant portions of the estuary leading edge, while the oligohaline-associated *Carex lyngbyei* (Lyngbye’s sedge) dominates much of the remaining study area, along with other locally-abundant species such as *Schoenoplectus tabernaemontani* (soft-stemmed bulrush), *Eleocharis palustris* (common spike-rush), *T. latifolia,* and reed *Phalaris arundinacea* (reed canarygrass)*.*

## Spectral Analysis

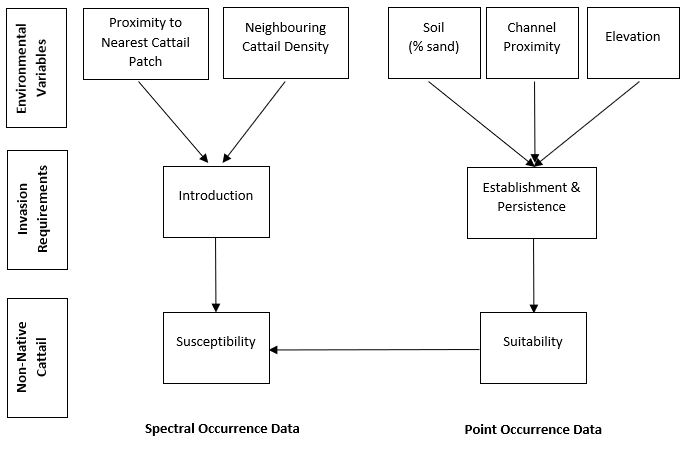
Imagery used in our spectral was acquired from the Vancouver Fraser Port Authority (VFPA) and GeoBC. The datasets were identical in their respective specifications (10 cm, 8bit RGB stereo), however VFPA imagery was taken 19–24 April 2018 while GeoBC imagery was taken in June 2016**.** Both datasets were acquired at low tide using manned aerial vehicles. Prior to analyzing the imagery we catalogued the dominant land cover types of the estuary, which varied from monodominant herbaceous species such as *P. arundinacea* and *C. lyngbyei*, to shrubs such as *Myrica gale* (sweet gale), to bare mud and log debris. Training polygons of each land cover type were manually drawn in ArcMap (v10.6.1; Esri Inc. 2020) using 2019 field data and notes from previous work in 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 (x̃ = 663.6). Low training sizes were infrequent, occurring only 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, with 21 and 31 classes in the GeoBC and VFPA datasets 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 probabilistic supervised Bayes Maximum Likelihood Classification, a probabilistic approach that characterizes each land cover class by its mean vector and covariance matrix, and then assigns each cell to the class in which it has the greatest likelihood of being a member (Richards 2013).

Based on preliminary outputs, certain adjustments were made to improve classification accuracy. 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. We also noted the outputs of the GeoBC dataset were superior to the VFPA dataset, likely because the imagery was taken later in the growing season when aboveground biomass was more developed. We therefore used it wherever possible and only used the VFPA imagery in the outer estuary, where GeoBC imagery was not available. Though classified separately, non-native *T. angustifolia* and *T. × glauca* often had overlapping spectral signatures in our exploratory analyses, perhaps due to similarities in their respective ramet densities and flower abundances. To avoid confusion, the two taxa were combined as “non-native cattail” for the final classification.

Classification accuracy was determined through field verification conducted between 14 November 2019 and 3 January 2020. We divided the study area into 500 m × 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 reflects marsh habitat being less abundant in the upper estuary, so more grid cells had to be sampled to verify a comparable amount between datasets. Field verification included visiting all 30 grid cells, and mapping all non-native cattail observed. As a hybrid, *T. × glauca* possesses intermediate traits that may confound its field identification. Certain macroscopic traits have also been used by past investigators (Tompkins & Taylor 1983; Smith 1986; Kirk et al. 2011), however the usefulness of this approach has been questioned, particularly where advanced generation hybrids are abundant (Geddes et al. 2021). Acknowledging these challenges, we created a multi-access key of six macroscopic traits, based on previous morphological studies and field manuals (see Supplementary Material). We then evaluated the accuracy of this key by applying it to 15 plants, 5 per presumed taxa, at 3 discrete locations in the estuary. Leaf tissue was collected from the same plants for later molecular analysis. We found the results of our field identifications were identical to our molecular analysis, demonstrating the key was reliable at differentiating the three *Typh*a taxa (D. Stewart, G. Buckholtz & Q. Cronk, unpublished data). The accuracy assessment included two simplified classes: (1) non-native cattail and (2) other. For each imagery dataset, 200 random-stratified assessment points were generated, comprised of 100 non-native cattail points and 100 other points. At each point the classified value was compared to field-verified data using a confusion matrix (Congalton 1991). Confusion matrix outputs included the overall accuracy, commission errors, omission errors, and Kappa Coefficient, a statistic used in classifications to compare observed accuracy with expected accuracy, thereby accounting for random chance (Cohen 1960).

## Species Distribution Model

We constructed a SDM based on environmental data and distance-based probabilities that predicts the suitability and susceptibility of habitats to non-native cattails (Fig. 1). We defined suitability as the probability of non-native cattail establishment and persistence based on environmental conditions, and susceptibility as the probability of non-native cattail colonization, accounting for both propagule pressure and habitat suitability (Smith et al. 2012; Martin et al. 2015). Predictive models were run at 1.0 m2 resolution, the highest resolution available based on the specifications of our predictor data, to account for habitat heterogeneity and the sensitivity of estuarine plants to small enviornmental changes. The result was a modeled marsh area of 12.3 km2, which at a resolution of 1.0 m2 represented > 12 million data points.

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

### Habitat Suitability

Verified occurrence data for non-native cattail were not available from any external source, so we used our personal observations from > 5 years of field activites in FRE marshes. 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, 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. Accurate and spatially-unbiased absence points were unavailable without additional surveys. As an alternative, we used 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.

Environmental variables were limited to datasets that were both relevant to *Typha* distributions and available, which included elevation, proximity to nearest channel, and percent sand. Elevation data were comprised of a 1 m gridded bare earth DEM provided by GeoBC, generated from lidar Data acquired during low tides in June 2016 (12 points/m2, vertical accuracy +/- 15 cm RMS). 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 m2 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 m2 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).

We evaluated the results of several modeling approaches including profile, regression, machine learning, presence-only, and presence-absence models in R (v4.0; R Core Team 2021). 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. AUC values are 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 AUC fell below a threshold of 0.8. The result was the inclusion of three models: 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 respectively. 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. Finally, we combined the predictions of the three remaining models into a single AUC-weighted ensemble model.

### Habitat Susceptibility

Habitat svalues The duration of 25 years was selected because longer time frames were likely to diminish the effectiveness of predictions, due to (1) the highly-fecund nature of cattail, whereby propagules would likely reach most habitats given enough time, and (2) uncertainty around future environmental conditions in the estuary, due to factors such as relative sea level rise and climate change. The probability of propagule introduction was estimated based on proximity to nearest non-native cattail occurrence, and density of non-native cattail 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, in this case 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 propagule dispersal effectiveness, we generated a cost raster based on land cover types, assigning cost values ranging from 1 (no cost) for marshes to 5 (5 × cost) for developed terrestrial areas (Table 1). These cost values accounted for both water and air-dispersed propagules, and factors that facilitate or 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 (LCM).

**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 river flows that may transport seeds downriver. |
| Agricultural Fields | 4 | Impassible to waterborne plant fragments and seeds, though agricultural ditches may serve as transport corridors. Airborne seeds freely move, as few tall structures or forests are present. |
| Developed Areas | 5 | Impassible to waterborne plant fragments and seeds. Airborne seeds potentially inhibited by developed landscape, tall buildings, and urban vegetation. |

To translate cost distances to introduction probabilities we considered two potential pathways of expansion: vegetative growth of existing patches, and dispersal through seeds and plant fragments. Vegetative growth rates are likely driven by environmental factors such as inundation and available nutrients (Woo & Zedler 2002) and vary in the literature from 0.76 m/year (Bansal et al. 2019) to patch diameter increases of 3.9 m and 2.5 m/year with *T. × glauca* and *T. angustifolia* respectively (Boers & Zedler 2008). To obtain an estimate of annual vegetative growth rate specific to conditions in the FRE, we compared the size of eleven verified patches over time using historical imagery. Only patches with a minimum of 10 years of interpretable imagery were selected. Lateral growth rates varied from 0.53 – 1.52 m/year and averaged 1.05 m/year (SD = 0.36).

Based on these growth estimates and seed dispersal, we assigned the maximum introduction probability value (1.0) to any pixel that was ≤ 250 LCM to non-native cattail (Table 2). The minimum probability value (0.4) was assigned to pixels > 2000 LCM, 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 such as ponds and ditches that were outside of our spectral analysis, and (3) the proven fecundity and dispersal ability of cattail in literature and in our personal observations. In addition to LCM, 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. Probabilities based on LCM and density 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.

**Table 2** Least cost distance classes, density 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 |
| **% area occupied by non-native cattail within 1000 m radius** |  |
| > 0.500 – 2.000% | 1.0 |
| > 0.200 – 0.500% | 0.8 |
| > 0.005 - 0.200% | 0.6 |
| 0.000 – 0.005% | 0.4 |



# Results

## Spectral Analysis

Our confusion matrix indicates the spectral analysis identified non-native cattail with a high level of accuracy throughout the FRE. Both classified datasets were similar in performance, 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 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** | **Commission Error** | **Kappa**  **Coefficient** |  |
| **Classified Data** | **Non-native Cattail** | 89 | 11 | 11.0% | -- | **Lower Estuary** |
| **Other** | 18 | 82 | 18.0% | -- |
| **Omission Error** | 16.8% | 11.8% |  | 71% |
| **Non-native Cattail** | 79 | 21 | 21.0% | -- | **Upper Estuary** |
| **Other** | 7 | 93 | 7.0% | -- |
| **Omission Error** | 8.1% | 18.4% |  | 72% |

In total, 494,759 or 4.0% of the 12,264,353 cells were classified as non-native cattail, representing nearly 500,000 m2 of occupied marsh habitat in the estuary (Table 5). Though not differentiated in our spectral analysis, the non-native cattail observed during field verification was more often identified in the field as *T. × glauca*. Non-native cattail was observed in 18 of the 30 field-verified grid cells, with ten containing only *T. × glauca,* two containing only *T. angustifolia*, and six containing both taxa*.* Restoration sites, comprised of > 100 habitat compensation, offset, and banking projects created within the last 40 years, have the highest proportion of cattail occupancy (14.9%), with over 3 × greater proportions than the overall estuary. Protected area marshes, defined as marshes legally protected by government agencies and NGOs, have the lowest proportional occupancy (3.4%), but since they comprise 68.5% of the estuary, still contain the majority of cattail (57.0%).

**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 (Fig. 2), with higher densities occurring in the lower estuary dataset (5.3% of cells) than the upper (2.8%). The majority of sampled habitat was low in detection density, while dense hotspots (> 20.0 m2/100 m2 radius) were primarily restricted to a small number of locations near the estuary mouth. Among patches, ≤ ≤ Similar to density hotspots, large are confined to the, including a singlepatch measuring > a (see patch size map in supplementary materials)

## Species Distribution Model

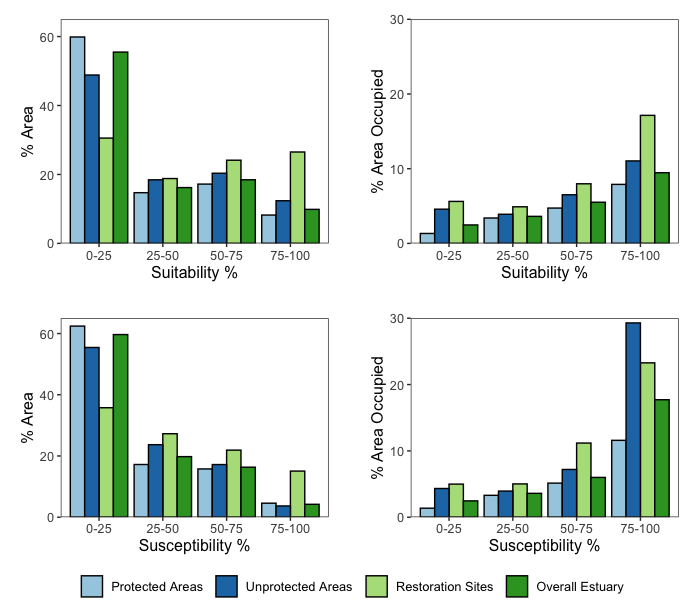
**Fig. 2** Heat map of classified non-native cattail pixels in the Fraser River Estuary, British Columbia. Lower and upper estuary imagery datasets are delineated by the dotted line

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). Variance and standard deviation values were < 0.004 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 σ | 0.002 | 0.002 | .004 |
| Mean σ² | 0.001 | 0.001 | .001 |
|  |  |  |  |

Our model predicts that 10% of the estuary has high (> 75%), 19% has moderate (50 – 75%), 16% has low (25 – 50%), and 55% has very low (< 25%) habitat suitability probabilities for non-native cattail (Fig. 4). Based on our spectral analysis, cattail currently occupies 10%, 6%, 4% and 2% of these areas respectively. The majority of protected and unprotected areas are comprised of very low and low suitability habitats, totaling 75% and 67% respectively. Restoration sites differ, as 24% of their habitats had moderate and 27% had high suitability values, the latter representing over double the proportions of unprotected areas, and triple that of protected areas (Fig. 5). High suitability habitats in restoration sites are also more proportionally invaded, with 17% occupancy, while comparable habitats in protected and unprotected areas are 8% and 11% occupied respectively.

Currently 4% of the modelled estuary has high, 16% has moderate, 20% has low, and 60% has very low susceptibility probabilities for non-native cattail. Occupancy, determined by our spectral analysis, is currently 18%, 6%, 4% and 2% in these habitats respectively. Susceptibility probabilities follow similar trends across all habitat types; however, restoration sites contain significantly less low-susceptibility, and more high-susceptibility habitat than other habitat types (Fig. 4). Restoration sites are also more proportionally invaded in all susceptibility classes, apart from high-susceptible habitats, where unprotected areas have the highest cattail occupancy. This anomaly may be attributed to the largest non-native cattail patch in the estuary, which occurs in unprotected marshes of southwest Vancouver (see 3.1).

**Fig 4** Percent area (left) and percent area occupied by non-native cattail (right)l based on suitability and susceptibility class for protected areas, unprotected areas, restoration sites, and the overall estuary.

# Discussion

## Cryptic Cattail Invasions in the Pacific Northwest

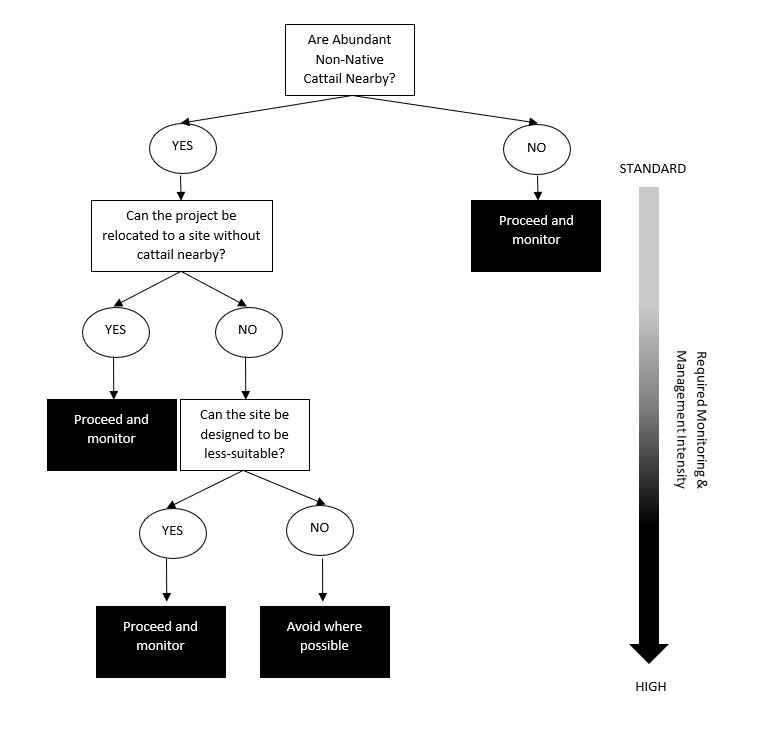
This study offers new information on the distribution, abundance, and behaviour of non-native cattail in western Canada. Prior to this research *T. angustifolia* was sporadically known in the FRE, but there was no understanding of how established it was, nor whether hybridization with *T. latifolia* was occurring. Our research addresses these knowledge gaps, demonstrating that non-native cattail is well-adapted to reproduce, establish, and persist in tidal marshes in the region, as evidenced by the 500,000 m2 of occupied habitat in the FRE. We also confirm for the first time that *T. × glauca* is present in the estuary, which is significant considering the FRE occurs outside of the known continental distribution of this taxon, and it had not been formally documented in British Columbia prior.

We propose that *T. angustifolia* and *T. × glauca* qualify as cryptic invasive species to the FRE, as evidence suggests they have been present and establishing for decades with minimal detection. Evidence of their long duration in the estuary includes their extensive coverage, widespread distribution over our study area, and herbarium records, where we found collections that appear to be misidentified *T. × glauca* dating to the late 1970s (D. Stewart, unpublished data). This raises the question of how these non-native taxa could be present for so long without detection, particularly in an urban estuary that has undergone significant study (e.g., McLaren 1972; Bradfield & Porter 1982; Hutchinson 1982). Potential reasons include the morphological similarity between native and non-native taxa, and the overall taxonomic uncertainty of *Typha* in the region. Historical herbarium specimens and technical guides in British Columbia refer to *T. latifolia* forma *ambigua* (Sonder), described as “[having] narrower than average leaves and relatively slender spikes…[often resembling] *T. angustifolia* in gross appearance, and may be reported as that species” (Brayshaw 1985). Due to this misnomer, it is possible that *T. × glauca* was misidentified for decades as a native forma. A final explanation may be that human access to these tidal marsh habitats is limited by hazardous topography, tidal cycles, and geographical isolation, despite being in a major metropolitan area. Thus, many of the worst invaded areas, which presumably underwent compositional change within decades, were not under regular observation. Whatever the cause, our findings underline the importance of preventative measures that can assist in “decrypting” invasive species, particularly on the margins of a continental invasion where (1) regional awareness may be lacking, and (2) the importance of early detection and rapid response measures are most pronounced (Ahmed et al. 2022).

Though considered invasive in many parts of North America, few studies have documented the impacts of these taxa in Pacific Northwest estuaries. Alleging non-native cattails qualify as invasive species in this region, and are thus linked to economic, social, or ecological losses, is therefore speculative, though supported by current evidence. First, non-native cattails have been recognised and actively managed as invasive species for decades in the Skagit River Delta, located 100 km south in Washington State (Hood 2013). Here they have also established successfully, and now comprise an estimated 226 ha or 12.5% of tidal habitat, possibly representing the largest infestation in the State (Heimer & Parsons 2013). Second, our observations suggest that a substantial portion of cattail in the estuary is *T. × glauca*, echoing the findings of studies conducted in Prairie Pothole, Great Lake, and Laurentian regions of North America (Travis et al. 2010; Kirk et al. 2011; Freeland et al. 2013; Tangen et al. 2022). This suggests that known mechanisms of dominance by *T. × glauca*, such as hybrid vigour (Bunbury-Blanchette et al. 2015; Zapfe & Freeland 2015), and excessive leaf litter, which suppresses competition (Larkin et al. 2012b; Stewart 2021) and exudes leachates that inhibit the germination of parental species (Szabo et al. 2018), may be effective in this environment. Third, new research suggests the biotic impacts of cattail in the FRE are consistent with other regions of North America. Cattail monocultures in the FRE possess lowernative plant diversity than nearby native marshes (Stewart 2021), which was also observed in urban wetlands in Illinois (Boers et al. 2007) and lacustrine marshes in the Great Lakes (Tuchman et al. 2009; Farrer & Goldberg 2014). Macroinvertebrate abundance was found to be lower in cattail-invaded sites than native marshes (Lee 2021), which is consistent to studies in Kansas (Kostecke et al. 2005) and the Great Lakes (Lawrence et al. 2016a). It is therefore reasonable to infer that the conversion of 500,000 m2 of native marsh to non-native *c*attailhas ecological implications, and future studies should investigate these biotic and abiotic impacts further.

## Management Implications

Our results suggest that cattail are not only well-established, but are likely to continue their expansion in the FRE should they remain unmanaged. Currently 29% and 20% of the estuary has moderate or high suitability and susceptibility probabilities, yet only 16% and 24% of these habitats are currently occupied respectively. Non-native cattail are also present in low and very low suitability and susceptibility classes in smaller amounts, suggesting that less optimal areas are not immune to invasion. Species interactions were not directly accounted for in our SDM, however the widespread establishment of non-native cattail in protected areas, which contain 57.0% of non-native cattail in the estuary, indicates that even large, intact plant communities that are relatively isolated from direct human disturbances are vulnerable. This vulnerability may be linked to high propagule pressure EXPAND. Typha has also been associated with high P, which is generally not limiting in estuaries and may thus facilitate their advantage. Finally estuaries being inherently dynamic, with recurring disturbance processes such as erosion, intense waterfowl grazing, debris deposition, and accretion. The result is the ongoing creation of bare spaces in the estuary that are prone to colonization by opportunistic invasive species (Zedler & Kercher 2004; Bearup & Blasius 2017).

Though protected areas possess the majority of non-native cattail in the FRE, habitat restoration sites contain proportionally 3 × more cattail than the overall estuary and higher proportions of suitable and susceptible habitat. This can likely be attributed to two factors: priority effect advantages in newly-created habitats (Dickson et al. 2012) due to the high dispersal ability and rapid growth of cattail, and lack of consideration for cattail in the design, location, and monitoring of these sites. As a result many restoration sites are no longer meeting their intended objectives (Lievesley et al. 2016; Stewart et al. 2022), and some may represent “hot spots” in areas where cattail is not abundant in adjacent natural marshes, thus serving as propagule sources. We propose that non-native cattail should be considered in the design of new restoration projects in the FRE, which we have framed through a decision tree (Fig. 8). At the project outset, practitioners must consider whether non-native cattail is present and/or abundant in the vicinity. If cattail is abundant nearby, 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 measures such as dense plantings to reduce colonizable empty spaces, 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.

**Fig. 6** Decision tree for habitat restoration practitioners in the FRE planning for the threat of non-native cattail invasions

Despite the proactive intent of this investigation, we found that non-native cattail have established to the point where containment and estuary-wide eradication is no longer feasible. We therefore recommend management 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. 2016b; Elgersma et al. 2017; Lishawa et al. 2017; Wilcox et al. 2018). However, applying these methods in the FRE may prove challenging due to site inaccessibility, and strict herbicide legislation for aquatic ecosystems. 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. 6).

# Conclusion

Contrary to our expectations, non-native *T. angustifolia* and *T. × glauca* are well-established in the FRE, occupying nearly 4% or 500,000 m2 of tidal marsh habitats. This represents the first documented invasion of non-native cattail in British Columbia, and the first verified occurrence of hybrid *T. × glauca.* We attribute the lack of occurrence data for these taxa to a lack of local awareness, morphological similarity to native *T. latifolia,* and inaccessibiliy of habitats. Expansion is likely should these cattail remain unmanaged, as our SDM predicts that 29% and 20% of the estuary has moderate or high suitability and susceptibility propabilities, while 16% and 24% of these habitats are currently occupied. Marsh restoration sites contained proportionally 3 × more non-native cattail than the overall estuary and contained more suitable and susceptible habitat, casting doubt on past approaches to mitigating habitat losses. Given their abundance, containment and estuary-wide eradiction of non-native cattail is no longer feasible, and we propose that future management should prioritise monitoring and eradication efforts in areas of high cultural and ecological value.

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# Supplemental Materials (to be discussed)

Map

Description automatically generatedPatch density map:

**Fig. 7** 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

Diagram, map

Description automatically generated

**Fig. 8** Probability of high suitability for non-native cattail in the Fraser River Estuary. Protected area boundaries are shown in lined polygons

Diagram, map

Description automatically generated

**Fig. 9** Probability of high susceptibility for non-native cattail in the Fraser River Estuary. Protected area boundaries are shown in lined polygons