# 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 ecological 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). 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), shading by leaf litter (Larkin et al. 2012; Farrer & Goldberg 2014; Szabo et al. 2018), phenotypic plasticity (Waters & Shay 1990; Woo & Zedler 2002a), and allelopathic compounds (Jarchow & Cook 2009; Szabo et al. 2018). These community-level changes are linked to changes at other trophic levels, such as the exclusion of waterfowl (Kostecke et al. 2004; Hood 2013a; 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; 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 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 (tidal) 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 cattail 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 a digital elevation model (DEM) data (see 2.3.1 for specifications), an elevation determined in our 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 estuary mouth, particularly in marshes isolated from direct 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 areas mentioned above, while surface water salinity can reach 4.0 ppt approximately 10 km upstream in the South Arm during the 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

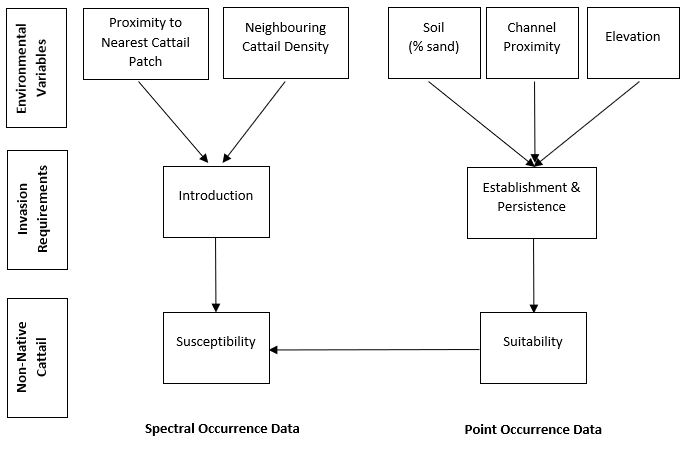
Spectral analysis imagery was acquired from the Vancouver Fraser Port Authority (VFPA) and GeoBC. The datasets were identical in their respective specifications (10 cm, 8bit RGB stereo), however VFPA imagery was taken 19–24 April 2018 while GeoBC imagery was taken in June 2016**.** Both datasets were 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 areas. 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 it was taken later in the growing season when aboveground biomass was fully 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 of habitat 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 five 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 cattail (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 2002a) 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

The outputs of our confusion matrix indicate 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%), while unprotected marshes were 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 (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

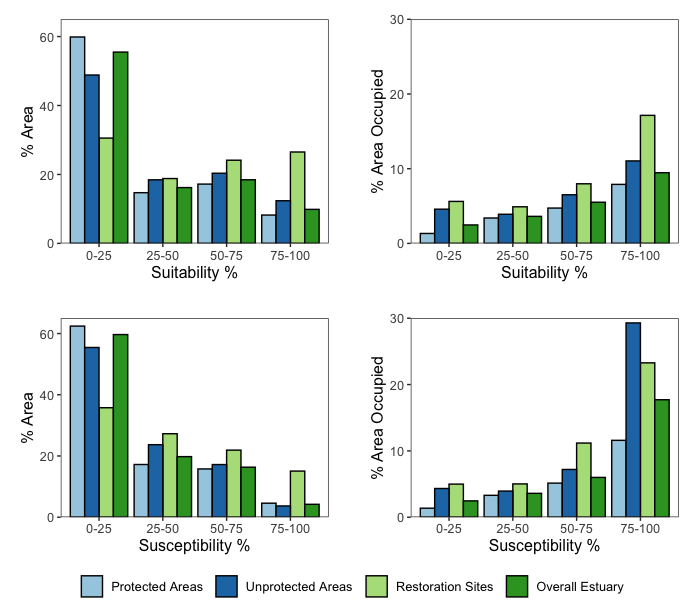
**Fig. 2** Heat map of classified non-native cattail pixels in the Fraser River Estuary, British Columbia. Lower and upper estuary imagery datasets are delineated by the dotted line

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

## Non-Native Cattail as a Cryptic Invasive Species

We found that *T. angustifolia* and *T. × glauca* qualify as cryptic invaders in the FRE, as evidence suggests they have been present and establishing for decades with minimal documentation. Evidence of their long duration in the estuary includes their coverage (~500,000 m2), widespread distribution over the 40 km of riverine habitat in our study area, and an evaluation of herbarium specimens, where we found collections that appear to be misidentified hybrids dating to the late 1970s from the FRE (D. Stewart, unpublished data). This raises the question of how these non-native taxa could be widespread for so long without detection, despite the vegetation of the FRE being well-documented historically. Potential reasons include the morphological similarity between native and non-native taxa, which are often sympatric in the FRE, 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*, 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. × glauca* with its intermediate and at times confounding traits, were misidentified as a native forma. 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. Whatever the cause behind this decades-long oversight, our findings underline the importance of preventative efforts that can assist in “decrypting” cryptic invasions, particularly on the fringes of an invasion where (1) regional awareness around a species 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 wetlands in many parts of North America, little data exists on the behaviour and impact of these taxa in the ecological context of Pacific Northwest estuaries. Alleging economic, social, and/or ecological losses is therefore speculative, though local evidence suggests these species qualify as “invasive” to this region. Non-native cattail has been acknowledged as problematic invader in the nearby Skagit River Delta of Puget Sound, where cattail is estimated to cover approximately 226 ha or 12.5% of tidal habitats, and may represent the largest concentration in Washington State (Heimer & Parsons 2013). Here, non-native cattail have been mechanically cut to increase native vegetation and habitat use by waterfowl (Hood 2013b). Recent work in the FRE indicates monodominant non-native *Typha* stands possess lowerplant community diversity (Stewart 2021), and proportionally less salmon-associated invertebrate species than native marshes (Lee 2021). It is therefore reasonable to assume that 500,000 m2 of native marsh replacement by non-native *Typha* has implications for regional biodiversity. Studies that further clarify the regional impacts of non-native *Typha* on marsh habitat function, and on certain priority species such as Pacific Salmon, should be prioritised to inform their future management.

## 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).

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 2013a), 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 CO2 (Sullivan et al. 2010), sea level rise (Hood 2013a), and eutrophication (Woo & Zedler 2002b), 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. × 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).

## 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 × more abundant in these sites than the overall estuary and 4 × 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 m2 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 2013a), 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 shouldshould not proceed unless monitoring and management efforts, which increase with each step down the decision tree, can counteract the invasion risk.

## Management Response

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

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.* × *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. × 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).

# Conclusion

Contrary to our expectations, non-native *T. angustifolia* and *T. × 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 propabilities of > 50% respectively. Marsh restoration sites contained 3 × 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 eradiction 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 safegaurd areas of high conservation and cultural value from exotic cattail invasion in the Fraser River estuary is a priority.

EXTRA TEXT

*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.* 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 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.

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.

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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