# 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:** Where possible, spatial data used in our analyses and modelling outputs will be made available in ag github repository, located at <https://github.com/asarum-ecological/StewartHoodMartin_Typha_Undetected>. 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 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% or 500,000 m2 of FRE tidal marshes. Though never formally recorded in the estuary previously, *Typha × glauca* appears to be the more abundant taxon, suggesting that heterosis may be facilitating this invasion. We describe these taxa as cryptic invasive species, as their resemblance to native broad-leaved cattail (*Typha latifolia)* likely inhibited their earlier detection. In our species distribution model, we distinguish between site suitability (ability to establish and persist) and susceptibility (risk of being colonized when suitable). Our model predicts that the scale of this invasion may increase over time, as 29% and 20% of the estuary has moderate or high suitability and susceptibility probabilities, while 16% and 24% of these habitats are currently occupied. Restoration projects had proportionally more non-cattails, suitable habitat, and susceptible habitat than the overall estuary, casting doubt on their mitigation effectiveness. Estuary-wide containment and eradication is unlikely given the extent of this invasion, so management should prioritize areas of high conservation and cultural value.

# 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 established, 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. 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 nativebroad-leaved cattail (*T. latifolia*; Kuehn et al. 1999; Ball & Freeland 2013). 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).

Both *T. angustifolia* and *T*. *× glauca* areconsidered problematic wetland invasive species 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 established. There is inconclusive evidence of niche partitioning among native and non-native cattailin 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 native broad-leaved cattail (*Typha 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).

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 and fragmentation (Marijnissen & Stefan 2017), 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).

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).

Spectral 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 spectral 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 and susceptibility for species. Habitat suitability 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. Suitability 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). SDMs may also integrate propagule pressure to model the susceptibility of habitats to invasion. This is an important consideration for cattail, as they are highly effective dispersers that colonise sites via sexual and asexual reproduction. Seeds number in the tens or hundreds of thousands per infloresecense, which can then disperse > 1 km via wind, water, and wildlife (Yeo 1964; Baldwin & Cannon 2007). At one time first-generation *T. × glauca* hybrids were 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). Asexual reproduction occurs via rapid clonal expnasion (Boers & Zedler 2008; Travis et al. 2011; Larkin et al. 2012a) and through water-borne plant fragments (Bansal et al. 2019).

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 FRE 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 the isolated habitats 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 three-square bulrush(*Schoenoplectus pungens*), seacoast bulrush (*Bolboschoenus maritimus*), and salt grass (*Distichilis spicant*)dominate significant portions of the estuary leading edge. The oligohaline-associated Lyngbye’s sedge (*Carex lyngbyei*) dominates much of the remaining study area, along with other locally-abundant species such as soft-stemmed bulrush (*Schoenoplectus tabernaemontani*), common spike-rush (*Eleocharis palustris*), reed canarygrass (*Phalaris arundinacea*) and *T. latifolia.*

## Spectral Analysis

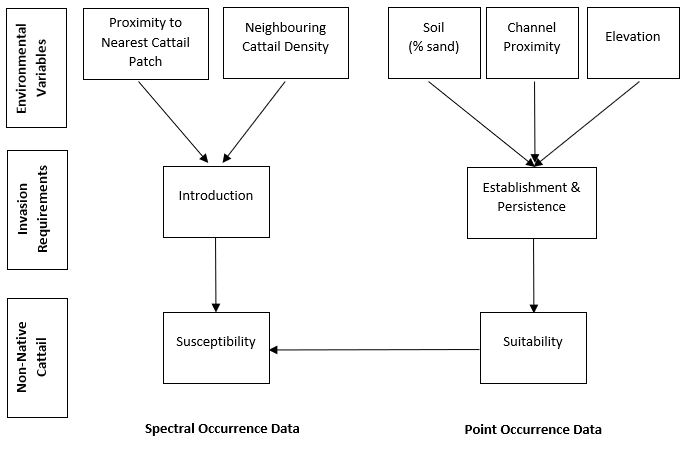
Imagery used in our spectral analysis was acquired from the Vancouver Fraser Port Authority (VFPA) and GeoBC. The datasets were identical in their respective specifications (10 cm, 8bit RGB stereo), however VFPA imagery was taken 19–24 April 2018 while GeoBC imagery was taken in June 2016**.** Both datasets 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 sweet gale (*Myrica 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 prior 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 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 cattails observed. As a hybrid, *T. × glauca* possesses intermediate traits that may confound its field identification. Certain macroscopic traits have 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 manuals (Tompkins & Taylor 1983; Smith 1986, 2000; Kuehn & White 1999; Snow et al. 2010; Kirk et al. 2011; see Supplementary Materials for key). We then evaluated the accuracy of this key by applying it to 15 plants occurring in discrete patches, 5 per presumed taxa, at 3 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 those of the molecular analysis, demonstrating the key was somewhat reliable at differentiating the three *Typh*a taxa (D. Stewart, G. Buckholtz & Q. Cronk, unpublished data). The classification 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 non-native cattail occurrence data were not available from external sources due to data deficiency, so we used our personal observations from work related to this study, and from > 5 years of previous fieldwork in FRE marshes, for example a study that involved > 50 tidal marsh creation sites and several reference marshes throughout the study area in 2015 (Lievesley et al. 2016). Given that observations were recorded throughout our study area in both remote and accessible habitats over this 5-year span, 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, so 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). Identically-sized datasets are optimal for regression and machine learning models (Barbet-Massin et al. 2012), so 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 estuarine plant 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 (v4.6.14; Liaw & Wiener 2002), dismo (v1.14; Hijmans et al. 2017), and kernlab (v0.9.29; 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 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, and (3) potential changes in *Typha* behaviour over time due to continued hybridization (e.g., demographic swamping). The probability of propagule introduction was estimated based on proximity to the nearest non-native cattail occurrence, and density of non-native cattails in nearby marsh. We based these calculations on the locations of non-native cattail identified in our spectral analysis (see 2.2). 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. 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 rate 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 cattails 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 Supplementary Materials for a patch size map)

## Species Distribution Model

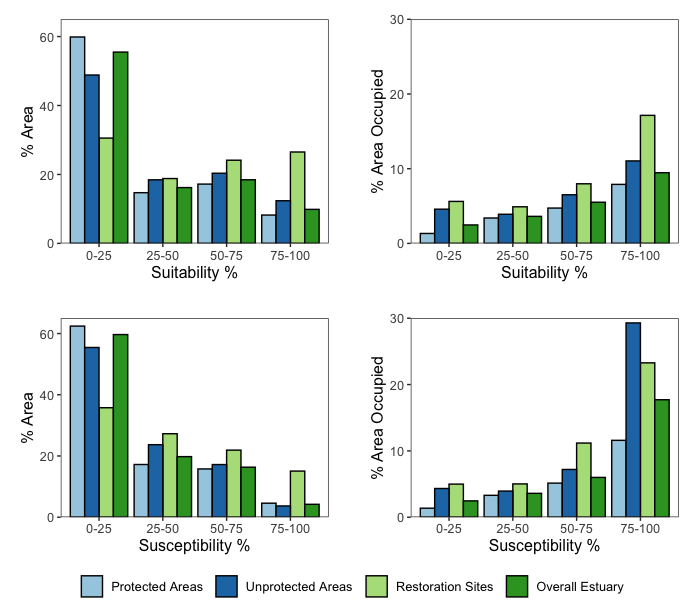
**Fig. 2** Heat map of classified non-native cattail pixels in the Fraser River Estuary, British Columbia. Lower and upper estuary imagery datasets are delineated by the dotted line

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 cattails (Fig. 4). Based on our spectral analysis, cattail currently occupies 10%, 6%, 4% and 2% of these areas respectively. The majority of protected (75%) and unprotected (67%) are comprised of very low and low suitability habitats. 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.



**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.

Currently 4% of the modelled estuary has high, 16% has moderate, 20% has low, and 60% has very low susceptibility probabilities for non-native cattails. 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.

# Discussion

## Cryptic Cattail Invasions in the Pacific Northwest

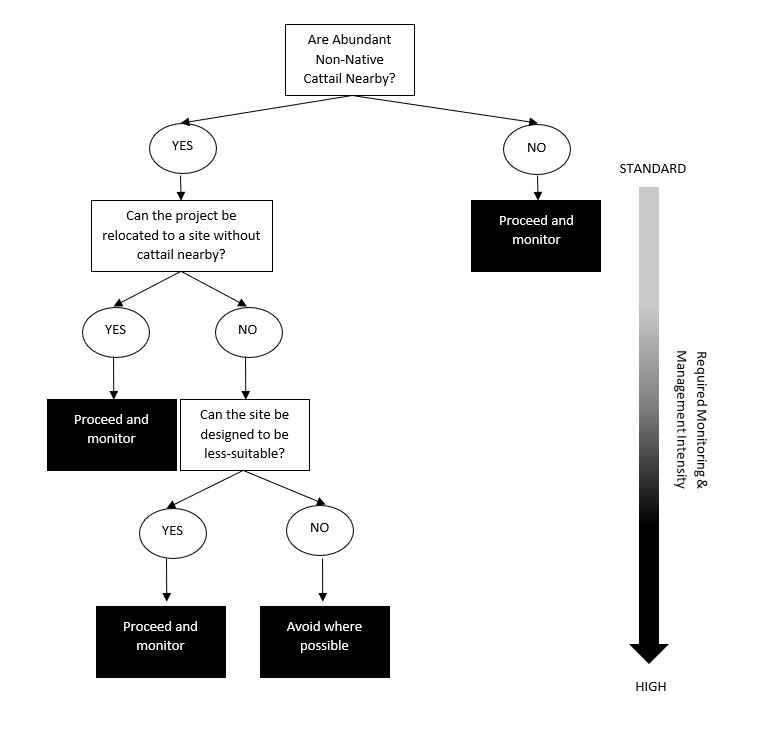
This study offers new information on the distribution, abundance, and behaviour of non-native cattails in Western Canada. Prior to this research *T. angustifolia* was sporadically known in the FRE, but there was no understanding of how established it was, nor whether hybridization with *T. latifolia* was occurring. Our research addresses these knowledge gaps, demonstrating that non-native cattails are 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. Human access to these tidal marsh habitats may have also been 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. 2012a; 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 cattails in protected areas, which contain 57.0% of non-native *Typha* 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 several factors, including high propagule pressure, which can overwhelm ecological resistance of a system to invasion (Holle & Simberloff 2005). Available nutrients, which are elevated in urban estuaries due to inputs from both marine and terrestrial environments, may also promote *Typha* dominance, as cattails are known to use excess nitrogen and phosphorous more efficiently than sympatric native species (Lorenzen et al. 2001; Woo & Zedler 2002; Larkin et al. 2012b). Finally, recurring disturbance processes that are inherent to estuaries, such as erosion, intense waterfowl grazing, debris deposition, and accretion, may promote cattail colonization due to the ongoing creation of bare spaces (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 priority effect advantages due to the high dispersal ability and rapid growth of cattail (Dickson et al. 2012), and lack of consideration for cattails 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 cattails should be considered in the design of new restoration projects, which we have framed through a decision tree (Fig. 6). 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 cattails 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. Several removal methods have been recently 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 cattails, and the first verified occurrence of hybrid *T. × glauca* in British Columbia, 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. This invasion is likely continue should 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 cattails than the overall estuary and contained more suitable and susceptible habitat, casting doubt on past approaches to mitigating habitat losses. Containment and estuary-wide eradiction of non-native cattails is no longer feasible, and we propose that future management should prioritise monitoring and eradication efforts in areas of high cultural and ecological value.

# Reference List

Adams DA. 1963. Factors Influencing Vascular Plant Zonation in North Carolina Salt Marshes. Ecology **44**:445–456. Ecological Society of America.

Adams MA, Williams GL. 2004. Tidal marshes of the Fraser River estuary: composition, structure, and a history of marsh creation efforts to 1997. Pages 147–172 in Groulx DC, Luternauer JL, Bilderback DE, editors. Fraser River Delta, British Columbia: Issues of an Urban Estuary.

Ages A, Woollard A. 1976. The tides in the Fraser Estuary. Page 113. Pacific Marine Science Report 76–5. Institute of Ocean Sciences, Patricia Bay, Victoria, B.C.

Ages AB, Woollard AL. 1994. The salinity intrusion in the Fraser River: observations of salinities, temperatures and currents by profiles and bottom time series 1988, 1989. Page 239. 133, Canadian Data Report of Hydrography and Ocean Sciences.

Ahmed DA et al. 2022. Managing biological invasions: the cost of inaction. Biological InvasionsDOI: 10.1007/s10530-022-02755-0. Available from https://link.springer.com/10.1007/s10530-022-02755-0 (accessed March 23, 2022).

Baldwin B, Cannon A. 2007. *Typha review*. Available from http:// files.cfc.umt.edu/cesu/NPS/USU/2006/06Baldwin\_GRKO\_ Typha%20review\_frpt.pdf (accessed April 1, 2022).

Ball D, Freeland JR. 2013. Synchronous flowering times and asymmetrical hybridization in Typha latifolia and T. angustifolia in northeastern North America. Aquatic Botany **104**:224–227.

Bansal S et al. 2019. Typha (Cattail) Invasion in North American Wetlands: Biology, Regional Problems, Impacts, Ecosystem Services, and Management. Wetlands **39**:645–684.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many?: How to use pseudo-absences in niche modelling? Methods in Ecology and Evolution **3**:327–338.

Barrie JV, Currie RG. 2000. Human Impact on the Sedimentary Regime of the Fraser River Delta, Canada. Journal of Coastal Research **16**:747–755. Coastal Education & Research Foundation, Inc.

Bearup D, Blasius B. 2017. Ecotone formation induced by the effects of tidal flooding: A conceptual model of the mud flat-coastal wetland ecosystem. Ecological Complexity **32**:217–227.

Boers AM, Veltman RLD, Zedler JB. 2007. Typha×glauca dominance and extended hydroperiod constrain restoration of wetland diversity. Ecological Engineering **29**:232–244.

Boers AM, Zedler JB. 2008. Stabilized water levels and Typha invasiveness. Wetlands **28**:676–685.

Boyle CA. 1997. Changes in land cover and subsequent effects on Lower Fraser Basin ecosystems from 1827 to 1990. Environmental Management **21**:185–196.

Bradfield GE, Porter GL. 1982. Vegetation structure and diversity components of a Fraser estuary tidal marsh. Canadian Journal of Botany **60**:440–451.

Bradley BA. 2014. Remote detection of invasive plants: a review of spectral, textural and phenological approaches. Biological Invasions **16**:1411–1425.

Bradley BA, Wilcove DS, Oppenheimer M. 2010. Climate change increases risk of plant invasion in the Eastern United States. Biological Invasions **12**:1855–1872.

Brayshaw TC. 1985. Pondweeds and Bur-reeds, and Their Relatives, of British Columbia. British Columbia Museum.

Buckley YM, Bolker BM, Rees M. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecology Letters **10**:809–817.

Bunbury-Blanchette AL, Freeland JR, Dorken ME. 2015. Hybrid Typha×glauca outperforms native T. latifolia under contrasting water depths in a common garden. Basic and Applied Ecology **16**:394–402.

Chalifour L, Scott D, MacDuffee M, Iacarella J, Martin T, Baum J. 2019. Habitat use by juvenile salmon, other migratory fish, and resident fish species underscores the importance of estuarine habitat mosaics. Marine Ecology Progress Series **625**:145–162.

Ciotir C, Freeland J. 2016. Cryptic intercontinental dispersal, commercial retailers, and the genetic diversity of native and non-native cattails (Typha spp.) in North America. Hydrobiologia **768**:137–150.

Ciotir C, Kirk H, Row JR, Freeland JR. 2013. Intercontinental dispersal of Typha angustifolia and T. latifolia between Europe and North America has implications for Typha invasions. Biological Invasions **15**:1377–1390.

Cohen J. 1960. A Coefficient of Agreement for Nominal Scales. Educational and Psychological Measurement **20**:37–46.

Congalton RG. 1991. A review of assessing the accuracy of classifications of remotely sensed data. Remote Sensing of Environment **37**:35–46.

Consortium of Pacific Northwest Herbaria Specimen Database (CPNWH). 2020. Available from https://www.pnwherbaria.org (accessed July 31, 2020).

Crain CM, Silliman BR, Bertness SL, Bertness MD. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology **85**:2539–2549.

Cronk JK, Fennessy MS. 2001. Wetland plants: biology and ecology. Lewis Publishers, Boca Raton, Fla.

Demarchi MW. 2006. Are Lesser Snow Geese, Chen caerulescens caerulescens, Exceeding the Carrying Capacity of the Fraser River Delta’s Brackish Marshes? The Canadian Field-Naturalist **120**:213.

Dickson TL, Hopwood JL, Wilsey BJ. 2012. Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. Biological Invasions **14**:2617–2624.

Dorcey HJ. 2004. Evolution of estuarine governance in a metropolitan region: collaborating for sustainability in the Fraser River estuary. Pages 247–262 in Groulx DC, Luternauer JL, Bilderback DE, editors. Fraser River Delta, British Columbia: Issues of an Urban Estuary.

Elgersma KJ, Martina JP, Goldberg DE, Currie WS. 2017. Effectiveness of cattail ( *Typha* spp.) management techniques depends on exogenous nitrogen inputs. Elementa: Science of the Anthropocene **5**:19.

Elith J et al. 2006. Novel methods improve prediction of species’ distributions from occurrence data. Ecography **29**:129–151.

Elith J, Leathwick JR. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics **40**:677–697. Annual Reviews.

Esri Inc. 2020. ArcGIS Pro. Esri Inc. Available from https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Ewing K. 1983. Environmental controls in Pacific Northwest intertidal marsh plant communities. Canadian Journal of Botany **61**:1105–1116.

Farrer EC, Goldberg DE. 2014. Mechanisms and reversibility of the effects of hybrid cattail on a Great Lakes marsh. Aquatic Botany **116**:35–43.

Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38–49.

Freeland J, Ciotir C, Kirk H. 2013. Regional differences in the abundance of native, introduced, and hybrid Typha spp. in northeastern North America influence wetland invasions. Biological Invasions **15**:2651–2665.

Frieswyk CB, Zedler JB. 2007. Vegetation Change in Great Lakes Coastal Wetlands: Deviation from the Historical Cycle. Journal of Great Lakes Research **33**:366–380.

Galatowitsch SM, Anderson NO, Ascher PD. 1999. Invasiveness in wetland plants in temperate North America. Wetlands **19**:733–755.

Geddes P, Murphy L, Astudillo-Scalia Y, Blasini D, Nugent S, Ríos MJ, Schirmer AE, Olfelt JP. 2021. Microsatellite Markers Reveal Unprecedented High Frequencies of Hybridization among Typha Species in the Midwestern US. Wetlands **41**:24.

Grace JB, Wetzel RG. 1998. Long-term dynamics of Typha populations. Aquatic Botany **61**:137–146.

Hanley JA, McNeil BJ. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology **143**:29–36.

Hart BS, Hamilton TS, Barrie JV. 1998. Sedimentation on the Fraser Delta slope and prodelta, Canada, based on high resolution seismic stratigraphy, lithofacies and 137Cs fallout stratigraphy. Journal of Sedimentary Research **68**:556–568.

Hart HS, Barrie JV. 1995. Environmental geology of the Fraser Delta, Vancouver **22**:172–183.

Heimer D, Parsons J. 2013. A Request to List All non-Native Typhas (Typha angustifolia L, Typha x glauca, Typha domingensis Pers. and related hybrids) as B-Class Noxious Weeds for 2014.

Hestir EL, Khanna S, Andrew ME, Santos MJ, Viers JH, Greenberg JA, Rajapakse SS, Ustin SL. 2008. Identification of invasive vegetation using hyperspectral remote sensing in the California Delta ecosystem. Remote Sensing of Environment **112**:4034–4047.

Hijmans RJ, Leathwick J, Elith J. 2017. dismo: Species Distribution Modeling. Available from https://CRAN.R-project.org/package=dismo.

Hobbs RJ, Higgs E, Harris JA. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution **24**:599–605.

Holle BV, Simberloff D. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology **86**:3212–3218.

Hood WG. 2013. Applying and testing a predictive vegetation model to management of the invasive cattail, Typha angustifolia L., in an oligohaline tidal marsh reveals priority effects caused by non-stationarity. Wetlands Ecology and Management **21**:229–242.

Hoos LM, Packman GA. 1974. The Fraser River Estuary: status of environmental knowledge to 1974. Report of the Estuary Working Group, Department of the Environment, Regional Board Pacific Region. Environment Canada, Ottawa.

Hutchinson I. 1982. Vegetation–environment relations in a brackish marsh, Lulu Island, Richmond, B.C. Canadian Journal of Botany **60**:452–462.

Hutchinson I. 1988. Salinity tolerance of plants of estuarine wetlands and associated uplands. Page 81. Washington State Shorelands and Coasstal Zone Management Program: Wetlands Section.

Ip F, Lavoie S. 2019. PEOPLE 2019: BC Sub-Provincial Population Projections. BC STATS. Available from https://www2.gov.bc.ca/assets/gov/data/statistics/people-population-community/population/people\_2019\_population\_projections-highlights.pdf.

Isaac NJB, Pocock MJO. 2015. Bias and information in biological records: Bias and information in biological records. Biological Journal of the Linnean Society **115**:522–531.

Jarchow ME, Cook BJ. 2009. Allelopathy as a mechanism for the invasion of Typha angustifolia. Plant Ecology **204**:113–124.

Karatzoglou A, Smola A, Hornik K, Zeileis A. 2004. kernlab -- An {S4} Package for Kernel Methods in R. Journal of Statistical Software **11**:1–20.

Kehoe LJ et al. 2020. Conservation in heavily urbanized biodiverse regions requires urgent management action and attention to governance. Conservation Science and Practice.

Kirk H, Connolly C, Freeland JR. 2011. Molecular genetic data reveal hybridization between Typha angustifolia and Typha latifolia across a broad spatial scale in eastern North America. Aquatic Botany **95**:189–193.

Kirwan ML, Murray AB. 2008. Ecological and morphological response of brackish tidal marshland to the next century of sea level rise: Westham Island, British Columbia. Global and Planetary Change **60**:471–486.

Kostecke RM, Smith LM, Hands HM. 2004. Vegetation Response to Cattail Management at Cheyenne Bottoms, Kansas. J. Aquat. Plant Manage. **42**:39–45.

Kostecke RM, Smith LM, Hands HM. 2005. Macroinvertebrate response to cattail management at Cheyenne Bottoms, Kansas, USA. Wetlands **25**:758–763.

Kramer AM, Annis G, Wittmann ME, Chadderton WL, Rutherford ES, Lodge DM, Mason L, Beletsky D, Riseng C, Drake JM. 2017. Suitability of Laurentian Great Lakes for invasive species based on global species distribution models and local habitat. Ecosphere **8**:e01883.

Kuehn MM, Minor JE, White BN. 1999. An examination of hybridization between the cattail species Typha latifolia and Typha angustifolia using random amplified polymorphic DNA and chloroplast DNA markers. Molecular Ecology **8**:1981–1990.

Kuehn MM, White BN. 1999. Morphological analysis of genetically identified cattails *Typha latifolia* , *Typha angustifolia* , and *Typha ×glauca*. Canadian Journal of Botany **77**:906–912.

Landis JR, Koch GG. 1977. The Measurement of Observer Agreement for Categorical Data. Biometrics **33**:159.

Larkin DJ, Freyman MJ, Lishawa SC, Geddes P, Tuchman NC. 2012a. Mechanisms of dominance by the invasive hybrid cattail Typha × glauca. Biological Invasions **14**:65–77.

Larkin DJ, Lishawa SC, Tuchman NC. 2012b. Appropriation of nitrogen by the invasive cattail Typha×glauca. Aquatic Botany **100**:62–66.

Lawrence BA, Bourke K, Lishawa SC, Tuchman NC. 2016a. Typha invasion associated with reduced aquatic macroinvertebrate abundance in northern Lake Huron coastal wetlands. Journal of Great Lakes Research **42**:1412–1419.

Lawrence BA, Lishawa SC, Rodriguez Y, Tuchman NC. 2016b. Herbicide management of invasive cattail (Typha × glauca) increases porewater nutrient concentrations. Wetlands Ecology and Management **24**:457–467.

Lee JJ. 2021. The impacts of exotic *Typha* on benthic invertebrate communities in the South Arm of the Fraser River Estuary. Pages 1–33. Master’s Project. Simon Fraser University & British Columbia Institute of Technology, Burnaby.

Liaw A, Wiener M. 2002. Classification and Regression by randomForest. R News **2**:18–22.

Lievesley M, Stewart D, Knight R, Mason B. 2016. Assessing habitat compensation and examining limitations to native plant establishment in the lower Fraser River Estuary. Pages 1–63. Available from https://www.cmnbc.ca/wp-content/uploads/2018/11/Assessing-Habitat-Compensation\_2016Appendix-I-IV.pdf.

Lishawa SC, Carson BD, Brandt JS, Tallant JM, Reo NJ, Albert DA, Monks AM, Lautenbach JM, Clark E. 2017. Mechanical Harvesting Effectively Controls Young Typha spp. Invasion and Unmanned Aerial Vehicle Data Enhances Post-treatment Monitoring. Frontiers in Plant Science **8**:619.

Lishawa SC, Dunton EM, Pearsall DR, Monks AM, Himmler KB, Carson BD, Loges B, Albert DA. 2020. Wetland Waterbird Food Resources Increased by Harvesting Invasive Cattails. The Journal of Wildlife Management **84**:1326–1337.

Lorenzen B, Brix H, Mendelssohn IA, McKee KL, Miao SL. 2001. Growth, biomass allocation and nutrient use efficiency in Cladium jamaicense and Typha domingensis as affected by phosphorus and oxygen availability. Aquatic Botany **70**:117–133.

Marijnissen R, Stefan A. 2017. Marsh recession and erosion study of the Fraser Delta, B.C., Canada from historic satellite imagery. Communications on Hydraulic and Geotechnical Engineering **2017–1**:59.

Martin TG, Murphy H, Liedloff A, Thomas C, Chadès I, Cook G, Fensham R, McIvor J, van Klinken RD. 2015. Buffel grass and climate change: a framework for projecting invasive species distributions when data are scarce. Biological Invasions **17**:3197–3210.

McKenzie-Gopsill A, Kirk H, Drunen WV, Freeland JR, Dorken ME. 2012. No evidence for niche segregation in a North American Cattail ( *Typha* ) species complex: Niche Segregation in Cattails. Ecology and Evolution **2**:952–961.

McLaren KA. 1972. A Vegetation Study of the Islands and Associated Marshes in the South Arm of the Fraser River, B.C., From the Deas Island Tunnel to Westham Island Foreshore. Fish & Wildlife Branch, B.C. Department of Recreation & Conservation.

McMillan C. 1959. Salt Tolerance Within a Typha Population. American Journal of Botany **46**:521–526.

Meyer SW, Badzinski SS, Petrie SA, Ankney CD. 2010. Seasonal Abundance and Species Richness of Birds in Common Reed Habitats in Lake Erie. Journal of Wildlife Management **74**:1559–1567.

Morais P, Reichard M. 2018. Cryptic invasions: A review. Science of The Total Environment **613–614**:1438–1448.

Parker Williams A, Hunt ER. 2002. Estimation of leafy spurge cover from hyperspectral imagery using mixture tuned matched filtering. Remote Sensing of Environment **82**:446–456.

Phillips SJ, Dudik M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S. 2009. Sample Selection Bias and Presence-Only Distribution Models: Implications for Background and Pseudo-Absence Data. Ecological Applications **19**:181–197. [Wiley, Ecological Society of America].

Pieper S, Dorken M, Freeland J. 2020. Genetic structure in hybrids and progenitors provides insight into processes underlying an invasive cattail (Typha × glauca) hybrid zone. Heredity **124**:714–725.

Pieper SJ, Freeland JR, Dorken ME. 2018. Coexistence of Typha latifolia, T. angustifolia (Typhaceae) and their invasive hybrid is not explained by niche partitioning across water depths. Aquatic Botany **144**:46–53.

Pieper SJ, Nicholls AA, Freeland JR, Dorken ME. 2017. Asymmetric Hybridization in Cattails (Typha spp.) and Its Implications for the Evolutionary Maintenance of Native Typha latifolia. Journal of Heredity **108**:479–487.

Rejmánek M, Pitcairn MJ. 2002. When is eradication of exotic pest plants a realistic goal? Pages 249–252 in Veitch CR, Clout MN, editors. Turning the tide: the eradication of invasive species.

Sanderson EW, Ustin SL, Foin TC. 2000. The Influence of Tidal Channels on the Distribution of Salt Marsh Plant Species in Petaluma Marsh, CA, USA. Plant Ecology **146**:29–41. Springer.

Shih JG, Finkelstein SA. 2008. Range dynamics and invasive tendencies in Typha latifolia and Typha angustifolia in eastern North America derived from herbarium and pollen records. Wetlands **28**:1–16.

Simberloff D et al. 2013. Impacts of biological invasions: what’s what and the way forward. Trends in Ecology & Evolution **28**:58–66.

Smith C, van Klinken RD, Seabrook L, McAlpine C. 2012. Estimating the influence of land management change on weed invasion potential using expert knowledge: Estimating weed invasion potential using experts. Diversity and Distributions **18**:818–831.

Smith HA, Johnson WS, Shonkwiler JS, Swanson SR. 1999. The implications of variable or constant expansion rates in invasive weed infestations. Weed Science **47**:62–66.

Smith SG. 1967. Experimental and Natural Hybrids in North American Typha (Typhaceae). American Midland Naturalist **78**:257.

Smith SG. 1986. The cattails ( *Typha*  ): Interspecific Ecological Differences and Problems of Identification. Lake and Reservoir Management **2**:357–362.

Smith SG. 2000. Typhaceae. In: Flora of North America Editorial Committee (eds.). Pages 278–285 Flora of North America North of Mexico. Oxford University Press, New York.

Snow AA, Travis SE, Wildová R, Fér T, Sweeney PM, Marburger JE, Windels S, Kubátová B, Goldberg DE, Mutegi E. 2010. Species-specific SSR alleles for studies of hybrid cattails ( *Typha latifolia* × *T. angustifolia* ; Typhaceae) in North America. American Journal of Botany **97**:2061–2067.

Snow AA, Vince SW. 1984. Plant Zonation in an Alaskan Salt Marsh: II. An Experimental Study of the Role of Edaphic Conditions. Journal of Ecology **72**:669–684. [Wiley, British Ecological Society].

Stewart D. 2021. Undetected but widespread: the cryptic invasion of non-native cattail (*Typha*) in the Fraser River Estuary. Master’s Thesis. University of British Columbia, Vancouver. Available from https://open.library.ubc.ca/soa/cIRcle/collections/ubctheses/24/items/1.0397016.

Stewart D, Hennigar D, Ingham R, Balke E. 2022. Factors influencing the persistence of created tidal marshes in the Fraser River Estuary. Page 63. Ducks Unlimited Canada, Surrey.

Sullivan L, Wildova R, Goldberg D, Vogel C. 2010. Growth of three cattail (Typha) taxa in response to elevated CO2. Plant Ecology **207**:121–129.

Szabo J, Freeland JR, Dorken ME. 2018. The effects of leaf litter and competition from hybrid cattails ( Typha × glauca ) on the seed germination and seedling performance of its parental species. Aquatic Botany **145**:29–36.

Tangen BA, Bansal S, Freeland JR, Travis SE, Wasko JD, McGonigle TP, Goldsborough LG, Gow K, Marburger JE, Meier JA. 2022. Distributions of native and invasive Typha (cattail) throughout the Prairie Pothole Region of North America. Wetlands Ecology and Management **30**:1–17.

Taylor E. 2004. Impacts of future climate change on the Fraser River delta and its urban estuary. Pages 99–110 in Groulx BJ, Mosher DC, Luternauer JL, Bilderback, DE, editors. Fraser River Delta, British Columbia: Issues of an Urban Estuary. Geological Survey of Canada. Available from https://geoscan.nrcan.gc.ca/starweb/geoscan/servlet.starweb?path=geoscan/fulle.web&search1=R=215772.

Tompkins TM, Taylor J. 1983. Hybridization in Typha in Genessee County, Michigan **22**:5.

Travis SE, Marburger JE, Windels S, Kubátová B. 2010. Hybridization dynamics of invasive cattail (Typhaceae) stands in the Western Great Lakes Region of North America: a molecular analysis. Journal of Ecology **98**:7–16.

Travis SE, Marburger JE, Windels SK, Kubátová B. 2011. Clonal Structure of Invasive Cattail (Typhaceae) Stands in the Upper Midwest Region of the US. Wetlands **31**:221–228.

Tuchman NC, Larkin DJ, Geddes P, Wildova R, Jankowski K, Goldberg DE. 2009. Patterns of environmental change associated withTypha xglauca invasion in a Great Lakes coastal wetland. Wetlands **29**:964–975.

Waters I, Shay JM. 1990. A field study of the morphometric response of *Typha glauca* shoots to a water depth gradient. Canadian Journal of Botany **68**:2339–2343.

Wilcox DA, Buckler K, Czayka A. 2018. Controlling Cattail Invasion in Sedge / Grass Meadows. Wetlands **38**:337–347.

Wilcox DA, Kowalski KP, Hoare HL, Carlson ML, Morgan HN. 2008. Cattail Invasion of Sedge/Grass Meadows in Lake Ontario: Photointerpretation Analysis of Sixteen Wetlands over Five Decades. Journal of Great Lakes Research **34**:301–323.

Williams GL. 1998. Ecology of bulrush and cattail - literature review for wetland design and management. Page 15. Client Report for the Greater Vancouver Regional District Parks Department. G.L. Williams & Associates Ltd., Burnaby.

Woo I, Zedler JB. 2002. Can nutrients alone shift a sedge meadow towards dominance by the invasive Typha × glauca. Wetlands **22**:509–521.

Wu Y, Hannah C, Matte P, O’Flaherty-Sproul M, Mo R, Wang X, MacAulay P. 2022. Tidal propagation in the Lower Fraser River, British Columbia, Canada. Estuarine, Coastal and Shelf Science **264**:107695.

Yeo RR. 1964. Life History of Common Cattail. Weeds **12**:284–288.

Zapfe L, Freeland JR. 2015. Heterosis in invasive F1 cattail hybrids (Typha × glauca). Aquatic Botany **125**:44–47.

Zedler JB, Callaway JC, Desmond JS, Vivian-Smith G, Williams GD, Sullivan G, Brewster AE, Bradshaw BK. 1999. Californian Salt-Marsh Vegetation: An Improved Model of Spatial Pattern. Ecosystems **2**:19–35. Springer.

Zedler JB, Kercher S. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences **23**:431–452.

# Supplemental Materials (Proposed)

Morphological Key to Typha in the FRE (adapted from D. Stewart, G. Buckholtz & Q. Cronk, unpublished data).

|  |  |  |  |
| --- | --- | --- | --- |
| **Morphological Trait** | **Key Code** | **Character State (cm)** | **Taxa** |
| 1. Wet leaf width (cm) | A  B  C | <0.9  0.9 – 1.8  >1.8 | ANG  GLA/LAT  LAT |
| 2. Spike interval (cm) | A  B  C | <0.5  0.5 – 4.8  >4.8 | GLA/LAT  ANG/GLA  ANG |
| 3. Pistillate spike length (cm) | A  B  C | <10.0  10.0 – 23.0  >23.0 | ANG/LAT  ANG/GLA/LAT  ANG/GLA |
| 4. Pistillate spike width (cm) | A  B  C | <0.8  0.8 – 2.5  >2.5 | ANG  ANG/GLA/LAT  LAT |
| 5. Staminate length (cm) | A  B  C | >17.0  17.0 – 23.0  >23.0 | ANG/LAT  ANG/GLA/LAT  GLA |
| 6. Ramet height (cm) | A  B  C | <180  180 – 250  >250 | ANG/LAT  ANG/GLA/LAT  GLA |

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **CODES** | **SPECIES** |  | **CODES** | **SPECIES** | **CODES** | **SPECIES** |
| ABAAAA | TYPHANG |  | BABABB | TYPHGLA | BAABAA | TYPHLAT |
| ABAAAB | TYPHANG |  | BABABC | TYPHGLA | BAABAB | TYPHLAT |
| ABAABA | TYPHANG |  | BABACB | TYPHGLA | BAABBA | TYPHLAT |
| ABAABB | TYPHANG |  | BABACC | TYPHGLA | BAABBB | TYPHLAT |
| ABABAA | TYPHANG |  | BABBBB | TYPHGLA | BAACAA | TYPHLAT |
| ABABAB | TYPHANG |  | BABBBC | TYPHGLA | BAACAB | TYPHLAT |
| ABABBA | TYPHANG |  | BABBCB | TYPHGLA | BAACBA | TYPHLAT |
| ABABBB | TYPHANG |  | BABBCC | TYPHGLA | BAACBB | TYPHLAT |
| ABBAAA | TYPHANG |  | BACABB | TYPHGLA | BABBAA | TYPHLAT |
| ABBAAB | TYPHANG |  | BACABC | TYPHGLA | BABBAB | TYPHLAT |
| ABBABA | TYPHANG |  | BACACB | TYPHGLA | BABBBA | TYPHLAT |
| ABBABB | TYPHANG |  | BACACC | TYPHGLA | BABBBB | TYPHLAT |
| ABBBAA | TYPHANG |  | BACBBB | TYPHGLA | BABCAA | TYPHLAT |
| ABBBAB | TYPHANG |  | BACBBC | TYPHGLA | BABCAB | TYPHLAT |
| ABBBBA | TYPHANG |  | BACBCB | TYPHGLA | BABCBA | TYPHLAT |
| ABBBBB | TYPHANG |  | BACBCC | TYPHGLA | BABCBB | TYPHLAT |
| ACAAAA | TYPHANG |  | BBBABB | TYPHGLA | CAABAA | TYPHLAT |
| ACAAAB | TYPHANG |  | BBBABC | TYPHGLA | CAABAB | TYPHLAT |
| ACAABA | TYPHANG |  | BBBACB | TYPHGLA | CAABBA | TYPHLAT |
| ACAABB | TYPHANG |  | BBBACC | TYPHGLA | CAABBB | TYPHLAT |
| ACABAA | TYPHANG |  | BBBBBB | TYPHGLA | CAACAA | TYPHLAT |
| ACABAB | TYPHANG |  | BBBBBC | TYPHGLA | CAACAB | TYPHLAT |
| ACABBA | TYPHANG |  | BBBBCB | TYPHGLA | CAACBA | TYPHLAT |
| ACABBB | TYPHANG |  | BBBBCC | TYPHGLA | CAACBB | TYPHLAT |
| ACBAAA | TYPHANG |  | BBCABB | TYPHGLA | CABBAA | TYPHLAT |
| ACBAAB | TYPHANG |  | BBCABC | TYPHGLA | CABBAB | TYPHLAT |
| ACBABA | TYPHANG |  | BBCACB | TYPHGLA | CABBBA | TYPHLAT |
| ACBABB | TYPHANG |  | BBCACC | TYPHGLA | CABBBB | TYPHLAT |
| ACBBAA | TYPHANG |  | BBCBBB | TYPHGLA | CABCAA | TYPHLAT |
| ACBBAB | TYPHANG |  | BBCBBC | TYPHGLA | CABCAB | TYPHLAT |
| ACBBBA | TYPHANG |  | BBCBCB | TYPHGLA | CABCBA | TYPHLAT |
| ACBBBB | TYPHANG |  | BBCBCC | TYPHGLA | CABCBB | TYPHLAT |
|  |  |  |  |  |  |  |

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