

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

Daniel Stewart^{1*}, W. Gregory Hood², Tara G. Martin³

*Corresponding Author: daniel.stewart@asarum.org, +1 778 873-0867

¹Asarum Ecological Consulting, Burnaby, BC, Canada.

²Skagit River System Cooperative, PO Box 368, LaConner, WA 98257, USA.

³University of British Columbia, Department of Forest and Conservation Sciences, 2424 Main

13 Mall, Vancouver, BC V6T 1Z4, Canada.

ORCID id:

Daniel Stewart (0000-0003-4258-6110)

W. Gregory Hood (0000-0001-6286-7935)

Tara G. Martin (0000-0001-7165-9812)

Submitted on 14 December 2022

Acknowledgements

The authors would like to acknowledge the financial support of our funders, including the National Sciences and Engineering Research Council of Canada Graduate Scholarship program, Ducks Unlimited Canada, and Mitacs Accelerate for DS, and Liber Ero Conservation Chair and NSERC DG 2019-04535 for TGM. We wish to thank Amy Angert, Professor in the UBC Department of Botany for her guidance throughout this research, and the reviewers who dedicated their time to improving this manuscript. Finally, we thank the BC Ministry of Environment, Natural Resources Canada, and Vancouver Fraser Port Authority for contributing their spatial datasets, which proved invaluable for this research.

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 cattail in the FRE using a combination of spectral imagery analysis and species distribution modelling. Contrary to our expectation, we find that non-native cattail are widespread, currently occupying approximately 4% or 50 ha of FRE tidal marshes. Though never formally recorded in the estuary previously, *T.* × *glauca* appears to be the more abundant taxon, suggesting heterosis may be facilitating this invasion. We describe these taxa as cryptic invasive species, as their resemblance to native cattail (*Typha latifolia*) likely inhibited their detection. In our species distribution model, we distinguish between site suitability (ability to establish and persist) and susceptibility (risk of colonization when suitable). Our model predicts the scale of this invasion may increase over time, as 29% and 20% of the estuary has moderate or high suitability and susceptibility probabilities, respectively, while 16% and 24% of these habitats are currently occupied. Estuary-wide containment and eradication is unlikely given the extent of this invasion. Consequently, we recommend management prioritize monitoring and early eradication in areas of high conservation and cultural value. This study highlights the vulnerability of estuaries to cryptic invasions, and the invasibility of Pacific Northwest estuaries by non-native cattail.

keywords: cryptic invasion, estuary, cattail, suitability modelling, invasive species

1 Introduction

Invasion biology research is often reactive, occurring when a non-native species is well-established, and therefore eradication, containment, and other management efforts are hindered by effort and cost, which compound temporally (Smith et al. 1999; Rejmánek and 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). In river deltas throughout the world, increasing population density and subsequent land use intensity and nutrient pollution is facilitating non-native plant invasions and altering ecological communities. Novel species and genotypes are arriving through human introduction, and via range shifts resulting from landscape alteration and climate change (Levine et al. 1998; Galatowitsch et al. 1999; Parmesan and Yohe 2003; Chen et al. 2011; Lu et al. 2019). These anthropogenic stresses are likely to increasingly impact and restructure ecological communities in tidal marshes, with difficult to forecast consequences on valuable fish and wildlife resources (Bertness et al. 2002; Bertness et al. 2004; Gedan et al. 2009; Hobbs et al. 2009).

We examine the threat of two potential non-native invaders to tidal marsh ecosystems in the Pacific Northwest (PNW), 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 possibly introduced to North America from Europe (Ciotir et al. 2013; Ciotir and Freeland 2016), though it has been present on the East Coast since at least the early 19th century (Shih and Finkelstein 2008). Concurrent with its continental establishment was the emergence of hybrid *T.* × *glauca*, the offspring of *T. angustifolia* and native broad-leaved cattail (*Typha latifolia*). Initially restricted to the eastern margins of the continent, these non-native taxa have rapidly expanded westward over the last century due to habitat disturbance, and commercial sales (Shih and Finkelstein 2008; Ciotir and Freeland 2016).

Both *T. angustifolia* and *T.* × *glauca* are considered problematic wetland invasive species in North America. 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 cattail in freshwater studies (Travis et al. 2010; McKenzie-Gopsill et al. 2012; Bunbury-Blanchette et al. 2015; Zapfe and 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 *T. latifolia* (McMillan 1959, Hutchinson 1988;

Galatowitsch et al. 1999). Where they co-occur, hybrid *T. × glauca* is widely considered more competitive than either parent, often replacing them over time through direct competition or introgression (Bunbury-Blanchette et al. 2015; Geddes et al. 2021). Non-native cattail are known to displace native marsh plant communities through a suite of mechanisms, including high growth rates and size (Bunbury-Blanchette et al. 2015; Zapfe and Freeland 2015), nutrient appropriation (Larkin et al. 2012), leaf litter accumulation (Farrer and Goldberg 2009; Larkin et al. 2011; Mitchell et al. 2011; Farrer and Goldberg 2014; Szabo et al. 2018), phenotypic plasticity (Waters and Shay 1990; Woo and Zedler 2002), and allelopathic compounds (Jarchow and Cook 2009; Szabo et al. 2018). These community-level impacts are linked to changes at other trophic levels, such as the degradation of waterfowl habitats (Kantrud 1986; Kostecke et al. 2004; Hood 2013; Lishawa et al. 2020) and reduction of macroinvertebrate and insect biomass (Kostecke et al. 2005; Lawrence, Bourke, et al. 2016; 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 one of the largest annual salmon runs among North American rivers (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. 2021). As a result of urban and agricultural development, the FRE has experienced wetland losses of 70 – 90% since European settlement (Boyle 1997; Dorsey 2004; Finn et al. 2021). Remaining habitats, approximately 70% of which are now protected by governments and non-government organizations (NGOs), continue to be degraded by multiple threats (Kehoe et al. 2021), including invasive plants (Stewart et al. 2022), sea level rise (Kirwan and Murray 2008), climate change impacts to river flow (Taylor 2004), habitat loss and fragmentation (Marijnissen and Stefan 2017), and excessive waterfowl herbivory (Demarchi 2006; Lievesley et al. 2016; Stewart et al. 2022; Fig. S1). 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 and Lavoie 2019).

Though non-native cattail are present in the FRE, occurrence data are limited. No herbarium vouchers of *T. angustifolia* exist prior to 1990, and few records have been found in grey literature, all after the mid 1980s (Brayshaw 1985; Williams 1998; Adams and 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 and Pocock 2015; Morais and 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 (Williams and 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 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; Clifton et al. 2018; Wilcox 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 and 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 common, likely due to limited availability of high-resolution predictor data.

SDMs can include environmental factors 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 and Vince 1984; Zedler et al. 1999; Sanderson et al. 2000; Cronk and Fennessy 2001; Crain et al. 2004; Sullivan et al. 2010). These models may also integrate propagule pressure to model the susceptibility of habitats to invasion. This is an important consideration for cattail, because they are highly effective dispersers that colonize sites via sexual and asexual reproduction. Seeds number in the tens or hundreds of thousands per inflorescence, which can then disperse > 1 km via wind, water, and wildlife (Yeo 1964; Voss 1972; Baldwin and Cannon 2007). First-generation *T. × glauca* hybrids were previously considered sterile (Smith 1967), but backcrosses and advanced generation hybrids have been recently detected in the Great Lakes and Canadian Maritimes (Snow et al. 2010; Travis et al. 2010; Kirk et al. 2011; Zapfe and Freeland

2015; Pieper et al. 2017), and genetic evidence suggests asexual and sexual reproduction is similar among *T. latifolia*, *T. angustifolia*, and *T. × glauca* (Pieper et al. 2020). Asexual reproduction occurs via rapid clonal expansion (Boers and Zedler 2008; Larkin et al. 2011; Travis et al. 2011) 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 cattail to the FRE, with potential implications for other PNW estuaries. Knowing that the distribution and abundance of these taxa have significant influence 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?

2 Methods

2.1 Study Area

This study occurred in the tidal marshes of the Fraser River Estuary, British Columbia, Canada (10 U 501906 5446049; Fig. 1). At over 21,000 hectares, the FRE is one of the largest estuaries in Pacific North America, and the largest of Western Canada. This study included all habitats downstream of the Port Mann Bridge, located 35 river-km (rkm) upstream from the river mouth (10 U 513641 5451852). Marsh habitats were delineated using the BC Land Use spatial layer provided by GeoBC for high water boundaries. Using data extracted from a digital elevation model (DEM; see 2.3.1 for specifications), low water boundaries were delimited by the 0.2 m ASL elevation, which was determined in exploratory field surveys to generally mark the lower limits of marsh vegetation.

The marshes have 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 and 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. Surface water salinity can reach 4.0 ppt at rkm 10 during low-flow winter months (Ages and Woollard 1994; Adams and 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 (*Distichlis spicata*) dominate significant portions of the estuary leading edge. Lyngbye's sedge (*Carex lyngbyei*) dominates much of the remaining oligohaline 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*.

2.2 Spectral Analysis

Imagery in our spectral analysis was acquired from the Vancouver Fraser Port Authority (VFPA) and GeoBC. The datasets had identical specifications (10 cm, 8bit RGB stereo), except 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. Before 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 ($\bar{x} = 663.6$). Classes with low training sizes were only included if deemed important (i.e., their respective class was likely to have high coverage). High training sizes reflected 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. 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, 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 – 3 January 2020. We divided the study area into 500 m × 500 m grid cells, equalling a total of 486 cells, and randomly selected 30 for field verification, with 8 occurring in the lower estuary classified dataset and 22 in the upper estuary. The disparity of grid cells between datasets reflects marsh habitat being less abundant in the upper estuary, so more grid cells had to be sampled to verify a comparable amount between datasets. Field verification included visiting all 30 grid cells, and mapping all non-native cattail observed.

As a hybrid, *T. × glauca* possesses intermediate traits that may confound its field identification. Certain macroscopic traits have been used by past investigators (Tompkins and 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 developed an identification key of six macroscopic traits based on previous morphological studies and manuals (Tompkins and Taylor 1983; Smith 1986; Kuehn and White 1999; Smith 2000; Snow et al. 2010; Kirk et al. 2011). 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 ($n = 45$). 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 reliable at differentiating the three *Typha* taxa (Stewart, Buckholtz, et al. 2022). 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).

2.3 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. 2). We defined habitat suitability as the probability of new plants establishing (recruiting) and persisting (reaching maturity) based on environmental conditions. Susceptibility was defined as the probability of colonization by non-native cattail, which accounted for both the probability of propagule introduction, 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 environmental 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.

2.3.1 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, including 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 characterized the environmental conditions of the modeled area, regardless of whether cattail were 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 to 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”, which included both riverine and marine waters. The 0.2 m ASL threshold was deemed to be the approximate 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 and Bell 1997), which partitioned the presence and background data into five sets, one of which was used for training while the remainder were combined to test 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 were averaged across the five runs to produce a mean AUC value with variance. AUC values are frequently used to evaluate SDMs, and measure 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 and 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.

2.3.2 Habitat Susceptibility

Habitat susceptibility was calculated by multiplying the estimated probability of propagule introduction in 25 years with the probability values of our habitat suitability model (Fig. 2). 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 regional *Typha* behaviour over time due to ongoing 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 cattail 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 heterogeneous landscape. To account for spatial differences in propagule and seed dispersal effectiveness, we generated a cost raster based on land cover types, assigning cost values ranging from 1 (no cost) for marshes to 5 ($5 \times$ cost) for developed terrestrial areas (Table 1). These cost values accounted for both water and air-dispersed seeds and 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).

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 and Zedler 2002) and vary in the literature from 0.76 m/year (Bansal et al. 2019) to patch diameter increases of 3.9 and 2.5 m/year with *T. × glauca* and *T. angustifolia* respectively (Boers and 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. Only patches with a

minimum of 10 years of interpretable imagery were selected, all between 2004 – 2019. 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 2). 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.

3 Results

3.1 Spectral Analysis

The spectral analysis estimated the distribution of non-native cattail in the FRE with a high level of accuracy, indicated by the results of our confusion matrix. Both imagery datasets were similar in classification performance, with an overall accuracy of 85.5% in the lower and 86.0% in the upper estuary (Table 3). 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 and Koch 1977).

In total, 494,759 or 4.0% of the 12,264,353 pixels were classified as non-native cattail, representing nearly 50 ha of occupied marsh habitat in the estuary (Table 4). Though not differentiated in our spectral analysis, the non-native cattail observed during field verification was more often identified in the field as *T. \times glauca*. Non-native cattail was observed in 18 of the 30 field-verified grid cells, with ten containing only *T. \times 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%; Fig. S1).

Occurrences were distributed across the entire study area, with higher densities occurring in the lower estuary dataset (5.3% of cells) than the upper (2.8%; Fig. 1). The majority of sampled habitat was low in detection density, while dense hotspots, which we define as pixels that were surrounded by > 20 m² of non-native cattail within the surrounding 100 m² circular area, were primarily concentrated near the estuary mouth. The majority of detected non-native cattail patches were small, as 55% were ≤ 3 m², 77% were ≤ 10 m², and < 1% exceeded 1000 m². Similar to density hotspots, large patches were confined to the outer limits of the estuary, including a single patch in southwest Vancouver measuring > 10 ha in size, over three times the size of the next largest patch (see patch size map Fig. S2).

3.2 Species Distribution Model

Cross validation indicates our Maxent, Random Forest, and Support Vector models are effectively predicting non-native cattail habitat suitability, with mean AUC values ranging from a minimum of 0.842 (Maxent) to a maximum of 0.871 (Random Forest; Table S3). 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. 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 (Figs. 3, S4). 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%) areas 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. 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 (Figs. 3, S5). Restoration sites are also more proportionally invaded in all susceptibility classes, apart from high-susceptible habitats, where unprotected areas have the highest cattail occupancy.

4 Discussion

4.1 Cryptic Cattail Invasions in the Pacific Northwest

Plant species invasions are a threat to estuaries globally, and are facilitated by human activity and global change. Climate change, landscape modification, and the transport of propagules by humans can lead to range shifts and the dispersal of species over great distances (Galatowitsch et al. 1999; Parmesan and Yohe 2003; Chen et al. 2011). Particularly in urban estuaries, population growth and land use changes have elevated disturbance and available nutrients, promoting the establishment and dominance of invasive species (Levine et al. 1998; Zedler and Kercher 2004; Lu et al. 2019). As the demands on finite resources increase for mitigating these threats, so too does the need for proactive research that can evaluate the current and potential threat of invasive species.

This study offers new information on the distribution, abundance, and behaviour of non-native cattail in the PNW. Prior to this research *T. angustifolia* was sporadically known in the FRE, but there was no understanding of how established it was, nor whether hybridization with *T. latifolia* was occurring. Our research addresses these knowledge gaps, demonstrating that non-native cattail are well-adapted to reproduce, establish, and persist in tidal marshes in the region, as evidenced by the 50 ha of occupied habitat in the FRE. 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, or in the case of *T. × glauca*, no 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 is presumably under regular observation. One explanation may be 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, even by students and trained professionals regularly working in the estuary. These students and professionals, many of whom were not plant specialists, were likely the only eyes on many FRE marshes, as public access is frequently limited by hazardous topography, tidal cycles, and geographical isolation, despite being in a major metropolitan area. Poor detection may also reflect a deficiency in long-term vegetation monitoring programs in the FRE, which to our knowledge has been limited to a small number of infrequent, coarse scale, and non-standardized studies that were unlikely to detect an emerging cryptic invader. 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; Fisher et al. 2022).

Though considered invasive in many parts of North America, few studies have documented the impacts of non-native cattail in PNW estuaries. Non-native cattail have been recognised and actively managed as invasive species for decades in the Skagit River Delta, located 100 km south of the FRE 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 and Parsons 2013). Our observations suggest a substantial portion of cattail in the FRE estuary is *T. × glauca*, echoing the findings of studies conducted in the Prairie Pothole, Great Lakes, 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 and Freeland 2015), nutrient appropriation and use (Woo and Zedler 2002; Larkin et al. 2012), and excessive leaf litter (Vaccaro et al. 2009; Larkin et al. 2011; Mitchell et al. 2011; Farrer and Goldberg 2014; Stewart 2021), which suppresses competition by inhibiting germination (Vaccaro et al. 2009; Szabo et al. 2018) and adversely altering the growth environment for sympatric native species (Farrer and Goldberg 2009; Larkin et al. 2011), may be effective in the environmental context of the PNW.

Though more investigation is required, the biotic impacts of cattail invasions in the FRE appear to mirror other regions of North America, suggesting the displacement of 50 ha of marsh is not without ecological consequence. Our observations indicate that cattail monocultures in the FRE primarily occur in areas previously dominated by native *C. lyngbyei*, a species strongly associated with juvenile salmonid habitat. Cattail monocultures possess lower native plant diversity and richness than nearby reference 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 and Goldberg 2014). Macroinvertebrate abundance was found to be lower in cattail-invaded sites than native marshes (Lee 2021), which is consistent with studies in Kansas (Kostecke et al. 2005) and the Great Lakes (Lawrence, Bourke, et al. 2016). We suspect other impacts are likely occurring without detection in the FRE, for example the reduction of important forage species for birds (Kantrud 1986; Hood 2013; Lishawa et al. 2020), and degradation of fish and wildlife habitats through sedimentation and structural homogenization. Given the importance of these ecosystems to numerous fish and wildlife species (Chalifour et al. 2019; Kehoe et al. 2021), it is paramount that future studies investigate these impacts further.

4.2 Management Implications

Our results suggest non-native 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 respective habitats are currently occupied. 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, but the widespread establishment of non-native cattail in *protected areas* (Fig. S1), 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 seed or propagule pressure, which can overwhelm ecological resistance of a system to invasion (Werner and Zedler 2002; Holle and Simberloff 2005; Lawrence, Bourke, et al. 2016). Available nutrients, which are elevated in urban estuaries due to inputs from both marine and terrestrial environments, may also promote *Typha* dominance, as cattail are known to appropriate and use excess nitrogen and phosphorous more efficiently than sympatric native species (Lorenzen et al. 2001; Woo and Zedler 2002; Larkin et al. 2012). 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 and Kercher 2004; Bearup and Blasius 2017).

Though protected areas possess the majority of non-native cattail in the FRE, habitat restoration sites contain proportionally $3 \times$ more cattail than the overall estuary, and higher proportions of suitable and susceptible habitat. As a result many restoration sites are no longer meeting their intended objectives (Lievesley et al. 2016; Stewart et al. 2022). This issue likely extends to other invasive species, and to restoration sites in other PNW estuaries. For example, *P. arundinacea* presents challenges for freshwater wetland restoration in the Columbia River Estuary, which has led to the development of several management strategies, including pre- and post- restoration control efforts, topographic modification, strategic seeding, limiting nutrient availability (Diefenderfer et al. 2018; Sinks et al. 2021). The initial disturbance associated with restoration projects may increase their invasibility, offering a window of opportunity for problematic species to colonise before native competitors can establish (Hobbs and Huenneke 1992). This may be further pronounced by priority effects, which favours the establishment and later dominance of species such as *Typha* spp. due to their high fecundity, dispersal ability, and rapid growth (Dickson et al. 2012). The higher invasibility of restoration sites may also reflect a lack of consideration for invasive species, particularly cryptic ones, in their respective designs, locations, and monitoring strategies.

We propose that non-native cattail should be considered in the design of future restoration projects in the FRE and in similar PNW systems, which we have framed through a decision tree (Fig. 4). At the project outset, practitioners should first ask whether non-native cattail is present and/or abundant in the vicinity. We prioritised cattail abundance over environmental suitability with the rationale that regardless of suitability a site can only be invaded if propagules enter it, and because non-native cattail appear to occupy a wide niche in the FRE, as indicated by our occupancy analysis (Fig. 3). If non-native cattail is abundant nearby, relocation of the project should be considered, if feasible. If not, practitioners should aim to make their site less suitable to non-native cattail. Manipulating a site to be less suitable for cattail is challenging, considering their environmental limits are poorly understood in PNW estuaries, and these systems possess many interacting abiotic factors (e.g., salinity, tidal inundation, nutrient pollution) and biotic factors (e.g., competitive interactions) that are both difficult to manipulate and vary geographically. Possible manipulation approaches may include improving site drainage (Stewart et al. 2022), and lowering site elevations (Hood 2013) to promote the dominance of native species. Predictive vegetation

models (PVMs) may also be used to predict and compare the outcomes of various restoration designs before they are implemented (Hood 2013). In addition to environmental manipulation, rapid and dense plantings may be used to mitigate invasion by reducing colonizable empty spaces and giving native species a “head start”, thus reducing priority effects. 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.

Despite the proactive intent of this investigation, we found that non-native cattail have established to the point where containment and estuary-wide eradication is no longer feasible. We therefore recommend management efforts in the FRE shift towards asset-based management. Such actions include monitoring and immediate removal of newly established patches in areas of high cultural and conservation value, and strategic removal and restoration of established invasion sites, if appropriate. Though we used morphological characters as a reliable identifier of *Typha* taxa in this study, we recommend that genetic verification be central to future monitoring efforts. Genetic verification would assist in reliably tracking the expansion of these taxa, avoiding non-target damage to native *T. latifolia*, and also clarifying the state of local *Typha* genetics, as factors such as hybridization and introgression may have implications for future cattail behavior and management in the estuary (Zapfe and Freeland 2015; Bhargav et al. 2022).

Future eradication and restoration 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 tenure. Several cattail management methods have been applied in North America, including grazing, repeated cutting/disking, flooding, mowing, burning, biomass removal, and herbicides (Kostecke et al. 2005; Hood 2013; Lawrence, Lishawa, et al. 2016; Elgersma et al. 2017; Lishawa et al. 2017; Wilcox et al. 2018). Applying many of these methods is not possible in the FRE, due to factors ranging from site inaccessibility to air quality regulations, to strict Canadian herbicide legislation for aquatic ecosystems. Mechanical cutting is the most feasible method at this time and has been experimentally applied in the FRE since 2019. Thus far experiments have demonstrated limited success, even after annual or biannual cuts over four growing seasons (D. Stewart, unpublished data). Site-level treatments are therefore unlikely to be cost-effective, requiring repeated cuts over multiple years, while small-scale prevention and containment measures should be emphasized. Even where eradication is successful, 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 proposed for restoration sites (Fig. 4).

5 Conclusion

Invasive species represent a major threat to global estuaries. This study documents the undetected establishment of non-native cattail in the FRE, and thus demonstrates the vulnerability of estuaries to cryptic invasions, even those located within a major metropolitan area. We attribute the absence of occurrence data for these taxa to a lack of local awareness, morphological similarity to native *T. latifolia*, and inaccessibility of habitats. Cryptic invasions are common and will only be overcome by ‘decrypting’ these species through research (e.g., genetic studies), monitoring, public outreach and responding to these potential invasions in a timely way. With containment and estuary-wide eradication of non-native cattail no longer feasible, we propose that future management prioritise monitoring and eradication efforts in areas of high cultural and ecological value.

Reference List

- Adams, D. A. 1963. Factors Influencing Vascular Plant Zonation in North Carolina Salt Marshes. *Ecology* 44. Ecological Society of America: 445–456. JSTOR. <https://doi.org/10.2307/1932523>.
- Adams, M. A., and G. L. Williams. 2004. Tidal marshes of the Fraser River estuary: composition, structure, and a history of marsh creation efforts to 1997. In *Fraser River Delta, British Columbia: Issues of an Urban Estuary*, ed. D. C. Groulx, J. L. Luterbauer, and D. E. Bilderback, 567:147–172. Geological Survey of Canada, Bulletin. <https://doi.org/10.4095/215772>.
- Ages, A. B., and A. L. Woollard. 1994. *The salinity intrusion in the Fraser River: observations of salinities, temperatures and currents by profiles and bottom time series 1988, 1989*. 133. Canadian Data Report of Hydrography and Ocean Sciences.
- Ages, A., and A. Woollard. 1976. *The tides in the Fraser Estuary*. Pacific Marine Science Report 76–5. Victoria, B.C.: Institute of Ocean Sciences, Patricia Bay.
- Ahmed, D. A., E. J. Hudgins, R. N. Cuthbert, M. Kourantidou, C. Diagne, P. J. Haubrock, B. Leung, et al. 2022. Managing biological invasions: the cost of inaction. *Biological Invasions*. <https://doi.org/10.1007/s10530-022-02755-0>.
- Baldwin, B., and A. Cannon. 2007. *Typha* review. Utah State University.
- Bansal, S., S. C. Lishawa, S. Newman, B. A. Tangen, D. Wilcox, D. Albert, M. J. Anteau, et al. 2019. *Typha* (Cattail) Invasion in North American Wetlands: Biology, Regional Problems, Impacts, Ecosystem Services, and Management. *Wetlands* 39: 645–684. <https://doi.org/10.1007/s13157-019-01174-7>.
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 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. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>.
- Barrie, J. V., and R. G. Currie. 2000. Human Impact on the Sedimentary Regime of the Fraser River Delta, Canada. *Journal of Coastal Research* 16. Coastal Education & Research Foundation, Inc.: 747–755. JSTOR.
- Bearup, D., and B. Blasius. 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. <https://doi.org/10.1016/j.ecocom.2016.11.005>.
- Bertness, M. D., P. J. Ewanchuk, and B. R. Silliman. 2002. Anthropogenic modification of New England salt marsh landscapes. *Proceedings of the National Academy of Sciences* 99: 1395–1398. <https://doi.org/10.1073/pnas.022447299>.
- Bertness, M., B. Silliman, and R. Jeffries. 2004. Salt Marshes Under Siege. *American Scientist* 92: 54. <https://doi.org/10.1511/2004.1.54>.
- Bhargav, V. V., J. R. Freeland, and M. E. Dorken. 2022. Evidence of hybrid breakdown among invasive hybrid cattails (*Typha* × *glauca*). *Heredity* 129: 195–201. <https://doi.org/10.1038/s41437-022-00557-7>.
- Boers, A. M., R. L. D. Veltman, and J. B. Zedler. 2007. *Typha* × *glauca* dominance and extended hydroperiod constrain restoration of wetland diversity. *Ecological Engineering* 29: 232–244. <https://doi.org/10.1016/j.ecoleng.2006.04.011>.
- Boers, A. M., and J. B. Zedler. 2008. Stabilized water levels and *Typha* invasiveness. *Wetlands* 28: 676–685. <https://doi.org/10.1672/07-223.1>.
- Boyle, C. A. 1997. Changes in land cover and subsequent effects on Lower Fraser Basin ecosystems from 1827 to 1990. *Environmental Management* 21: 185–196. <https://doi.org/10.1007/s002679900017>.
- Bradley, B. A. 2014. Remote detection of invasive plants: a review of spectral, textural and phenological approaches. *Biological Invasions* 16: 1411–1425. <https://doi.org/10.1007/s10530-013-0578-9>.
- Bradley, B. A., D. S. Wilcove, and M. Oppenheimer. 2010. Climate change increases risk of plant invasion in the Eastern United States. *Biological Invasions* 12: 1855–1872. <https://doi.org/10.1007/s10530-009-9597-y>.
- Brayshaw, T. C. 1985. *Pondweeds and Bur-reeds, and Their Relatives, of British Columbia*. Occasional Papers of the British Columbia Museum 26. Victoria, B.C.: British Columbia Museum.
- Buckley, Y. M., B. M. Bolker, and M. Rees. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters* 10: 809–817. <https://doi.org/10.1111/j.1461-0248.2007.01067.x>.
- Bunbury-Blanchette, A. L., J. R. Freeland, and M. E. Dorken. 2015. Hybrid *Typha* × *glauca* outperforms native *T. latifolia* under contrasting water depths in a common garden. *Basic and Applied Ecology* 16: 394–402. <https://doi.org/10.1016/j.baae.2015.04.006>.

- Chalifour, L., D. Scott, M. MacDuffee, J. Iacarella, T. Martin, and J. Baum. 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. <https://doi.org/10.3354/meps13064>.
- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* 333: 1024–1026. <https://doi.org/10.1126/science.1206432>.
- Ciotir, C., and J. Freeland. 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. <https://doi.org/10.1007/s10750-015-2538-0>.
- Ciotir, C., H. Kirk, J. R. Row, and J. R. Freeland. 2013. Intercontinental dispersal of *Typha angustifolia* and *T. latifolia* between Europe and North America has implications for *Typha* invasions. *Biological Invasions* 15: 1377–1390. <https://doi.org/10.1007/s10530-012-0377-8>.
- Clifton, B. C., W. G. Hood, and S. R. Hinton. 2018. Floristic Development in Three Oligohaline Tidal Wetlands after Dike Removal. *Ecological Restoration* 36: 238–251. <https://doi.org/10.3368/er.36.3.238>.
- Cohen, J. 1960. A Coefficient of Agreement for Nominal Scales. *Educational and Psychological Measurement* 20: 37–46. <https://doi.org/10.1177/001316446002000104>.
- Congalton, R. G. 1991. A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing of Environment* 37: 35–46. [https://doi.org/10.1016/0034-4257\(91\)90048-B](https://doi.org/10.1016/0034-4257(91)90048-B).
- Consortium of Pacific Northwest Herbaria Specimen Database (CPNWH). 2020. *Consortium of Pacific Northwest Herbaria*.
- Crain, C. M., B. R. Silliman, S. L. Bertness, and M. D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85: 2539–2549. <https://doi.org/10.1890/03-0745>.
- Cronk, J. K., and M. S. Fennessy. 2001. *Wetland plants: biology and ecology*. Boca Raton, Fla: Lewis Publishers.
- Demarchi, M. W. 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. <https://doi.org/10.22621/cfn.v120i2.290>.
- Dickson, T. L., J. L. Hopwood, and B. J. Wilsey. 2012. Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. *Biological Invasions* 14: 2617–2624. <https://doi.org/10.1007/s10530-012-0257-2>.
- Diefenderfer, H. L., I. A. Sinks, S. A. Zimmerman, V. I. Cullinan, and A. B. Borde. 2018. Designing topographic heterogeneity for tidal wetland restoration. *Ecological Engineering* 123: 212–225. <https://doi.org/10.1016/j.ecoleng.2018.07.027>.
- Dorcey, H. J. 2004. Evolution of estuarine governance in a metropolitan region: collaborating for sustainability in the Fraser River estuary. In *Fraser River Delta, British Columbia: Issues of an Urban Estuary*, ed. D. C. Groulx, J. L. Luternauer, and D. E. Bilderback, 567:247–262. Geological Survey of Canada, Bulletin. <https://doi.org/10.4095/215772>.
- Elgersma, K. J., J. P. Martina, D. E. Goldberg, and W. S. Currie. 2017. Effectiveness of cattail (*Typha* spp.) management techniques depends on exogenous nitrogen inputs. Edited by Donald R. Zak and Lauren B. Buckley. *Elementa: Science of the Anthropocene* 5: 19. <https://doi.org/10.1525/elementa.147>.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>.
- Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40. Annual Reviews: 677–697.
- Esri Inc. 2020. ArcGIS Pro (version 10.6.1.). Esri Inc.
- Ewing, K. 1983. Environmental controls in Pacific Northwest intertidal marsh plant communities. *Canadian Journal of Botany* 61: 1105–1116.
- Farrer, E. C., and D. E. Goldberg. 2009. Litter drives ecosystem and plant community changes in cattail invasion. *Ecological Applications* 19: 398–412. <https://doi.org/10.1890/08-0485.1>.
- Farrer, E. C., and D. E. Goldberg. 2014. Mechanisms and reversibility of the effects of hybrid cattail on a Great Lakes marsh. *Aquatic Botany* 116: 35–43. <https://doi.org/10.1016/j.aquabot.2014.01.002>.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49. <https://doi.org/10.1017/S0376892997000088>.

- Finn, R. J. R., L. Chalifour, S. E. Gergel, S. G. Hinch, D. C. Scott, and T. G. Martin. 2021. Quantifying lost and inaccessible habitat for Pacific salmon in Canada's Lower Fraser River. *Ecosphere* 12. <https://doi.org/10.1002/ecs2.3646>.
- Fisher, S., R. N. Fisher, and G. B. Pauly. 2022. Hidden in Plain Sight: Detecting Invasive Species When They Are Morphologically Similar to Native Species. *Frontiers in Conservation Science* 3: 846431. <https://doi.org/10.3389/fcsc.2022.846431>.
- Freeland, J., C. Ciotir, and H. Kirk. 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. <https://doi.org/10.1007/s10530-013-0481-4>.
- Galatowitsch, S. M., N. O. Anderson, and P. D. Ascher. 1999. Invasiveness in wetland plants in temperate North America. *Wetlands* 19: 733–755. <https://doi.org/10.1007/BF03161781>.
- Gedan, K. B., B. R. Silliman, and M. D. Bertness. 2009. Centuries of Human-Driven Change in Salt Marsh Ecosystems. *Annual Review of Marine Science* 1: 117–141. <https://doi.org/10.1146/annurev.marine.010908.163930>.
- Geddes, P., L. Murphy, Y. Astudillo-Scalia, D. Blasini, S. Nugent, M. J. Rios, A. E. Schirmer, and J. P. Olfelt. 2021. Microsatellite Markers Reveal Unprecedented High Frequencies of Hybridization among *Typha* Species in the Midwestern US. *Wetlands* 41: 24. <https://doi.org/10.1007/s13157-021-01429-2>.
- Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143: 29–36. <https://doi.org/10.1148/radiology.143.1.7063747>.
- Hart, B. S., T. S. Hamilton, and J. V. Barrie. 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, H. S., and J. V. Barrie. 1995. Environmental geology of the Fraser Delta, Vancouver 22. Geoscience Canada: 172–183.
- Heimer, D., and J. Parsons. 2013. A Request to List All Non-Native *Typhas* (*Typha angustifolia* L., *Typha* × *glauca*, *Typha domingensis* Pers. and related hybrids) as B-Class Noxious Weeds for 2014.
- Hestir, E. L., S. Khanna, M. E. Andrew, M. J. Santos, J. H. Viers, J. A. Greenberg, S. S. Rajapakse, and S. L. Ustin. 2008. Identification of invasive vegetation using hyperspectral remote sensing in the California Delta ecosystem. *Remote Sensing of Environment* 112: 4034–4047. <https://doi.org/10.1016/j.rse.2008.01.022>.
- Hijmans, R. J., J. Leathwick, and J. Elith. 2017. dismo: Species Distribution Modelling (version R package version 1.1-4).
- Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24: 599–605. <https://doi.org/10.1016/j.tree.2009.05.012>.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology* 6: 14.
- Holle, B. V., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86: 3212–3218. <https://doi.org/10.1890/05-0427>.
- Hood, W. G. 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. <https://doi.org/10.1007/s11273-013-9294-6>.
- Hutchinson, I. 1982. Vegetation–environment relations in a brackish marsh, Lulu Island, Richmond, B.C. *Canadian Journal of Botany* 60: 452–462. <https://doi.org/10.1139/b82-061>.
- Hutchinson, I. 1988. *Salinity tolerance of plants of estuarine wetlands and associated uplands*. Washington State Shorelands and Coastal Zone Management Program: Wetlands Section.
- Ip, F., and S. Lavoie. 2019. *PEOPLE 2019: BC Sub-Provincial Population Projections*. BC STATS.
- Isaac, N. J. B., and M. J. O. Pocock. 2015. Bias and information in biological records: Bias and information in biological records. *Biological Journal of the Linnean Society* 115: 522–531. <https://doi.org/10.1111/bij.12532>.
- Jarchow, M. E., and B. J. Cook. 2009. Allelopathy as a mechanism for the invasion of *Typha angustifolia*. *Plant Ecology* 204: 113–124. <https://doi.org/10.1007/s11258-009-9573-8>.
- Kantrud, H. A. 1986. *Effects of vegetation manipulation on breeding waterfowl in prairie wetlands-a literature review*.
- Karatzoglou, A., A. Smola, K. Hornik, and A. Zeileis. 2004. kernlab -- An {S4} Package for Kernel Methods in R. *Journal of Statistical Software* 11: 1–20.

- Kehoe, L. J., J. Lund, L. Chalifour, Y. Asadian, E. Balke, S. Boyd, D. Carlson, et al. 2021. Conservation in heavily urbanized biodiverse regions requires urgent management action and attention to governance. *Conservation Science and Practice* 3. <https://doi.org/10.1111/csp2.310>.
- Kirk, H., C. Connolly, and J. R. Freeland. 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. <https://doi.org/10.1016/j.aquabot.2011.05.007>.
- Kirwan, M. L., and A. B. Murray. 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. <https://doi.org/10.1016/j.gloplacha.2007.05.005>.
- Kostecke, R. M., L. M. Smith, and H. M. Hands. 2004. Vegetation Response to Cattail Management at Cheyenne Bottoms, Kansas. *J. Aquat. Plant Manage.* 42: 39–45.
- Kostecke, R. M., L. M. Smith, and H. M. Hands. 2005. Macroinvertebrate response to cattail management at Cheyenne Bottoms, Kansas, USA. *Wetlands* 25: 758–763. [https://doi.org/10.1672/0277-5212\(2005\)025\[0758:MRTCMA\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2005)025[0758:MRTCMA]2.0.CO;2).
- Kramer, A. M., G. Annis, M. E. Wittmann, W. L. Chadderton, E. S. Rutherford, D. M. Lodge, L. Mason, D. Beletsky, C. Riseng, and J. M. Drake. 2017. Suitability of Laurentian Great Lakes for invasive species based on global species distribution models and local habitat. *Ecosphere* 8: e01883. <https://doi.org/10.1002/ecs2.1883>.
- Kuehn, M. M., and B. N. White. 1999. Morphological analysis of genetically identified cattails *Typha latifolia*, *Typha angustifolia*, and *Typha* \times *glaucia*. *Canadian Journal of Botany* 77: 906–912. <https://doi.org/10.1139/b99-037>.
- Landis, J. R., and G. G. Koch. 1977. The Measurement of Observer Agreement for Categorical Data. *Biometrics* 33: 159. <https://doi.org/10.2307/2529310>.
- Larkin, D. J., M. J. Freyman, S. C. Lishawa, P. Geddes, and N. C. Tuchman. 2011. Mechanisms of dominance by the invasive hybrid cattail *Typha* \times *glaucia*. *Biological Invasions* 14: 65–77. <https://doi.org/10.1007/s10530-011-0059-y>.
- Larkin, D. J., S. C. Lishawa, and N. C. Tuchman. 2012. Appropriation of nitrogen by the invasive cattail *Typha* \times *glaucia*. *Aquatic Botany* 100: 62–66. <https://doi.org/10.1016/j.aquabot.2012.03.001>.
- Lawrence, B. A., K. Bourke, S. C. Lishawa, and N. C. Tuchman. 2016. *Typha* invasion associated with reduced aquatic macroinvertebrate abundance in northern Lake Huron coastal wetlands. *Journal of Great Lakes Research* 42: 1412–1419. <https://doi.org/10.1016/j.jglr.2016.08.009>.
- Lawrence, B. A., S. C. Lishawa, Y. Rodriguez, and N. C. Tuchman. 2016. Herbicide management of invasive cattail (*Typha* \times *glaucia*) increases porewater nutrient concentrations. *Wetlands Ecology and Management* 24: 457–467. <https://doi.org/10.1007/s11273-015-9471-x>.
- Lee, J. J. 2021. *The impacts of exotic Typha on benthic invertebrate communities in the South Arm of the Fraser River Estuary*. Applied Research Project. Burnaby: Simon Fraser University & British Columbia Institute of Technology.
- Levine, J. M., S. D. Hacker, C. D. G. Harley, and M. D. Bertness. 1998. Nitrogen effects on an interaction chain in a salt marsh community. *Oecologia* 117: 266–272. <https://doi.org/10.1007/s004420050657>.
- Liaw, A., and M. Wiener. 2002. Classification and Regression by randomForest. *R News* 2: 18–22.
- Lievesley, M., D. Stewart, R. Knight, and B. Mason. 2016. *Assessing habitat compensation and examining limitations to native plant establishment in the lower Fraser River Estuary*. Technical Report.
- Lishawa, S. C., B. D. Carson, J. S. Brandt, J. M. Tallant, N. J. Reo, D. A. Albert, A. M. Monks, J. M. Lautenbach, and E. Clark. 2017. Mechanical Harvesting Effectively Controls Young *Typha* spp. Invasion and Unmanned Aerial Vehicle Data Enhances Post-treatment Monitoring. *Frontiers in Plant Science* 8: 619. <https://doi.org/10.3389/fpls.2017.00619>.
- Lishawa, S. C., E. M. Dunton, D. R. Pearsall, A. M. Monks, K. B. Himmler, B. D. Carson, B. Loges, and D. A. Albert. 2020. Wetland Waterbird Food Resources Increased by Harvesting Invasive Cattails. *The Journal of Wildlife Management* 84: 1326–1337. <https://doi.org/10.1002/jwmg.21912>.
- Lorenzen, B., H. Brix, I. A. Mendelssohn, K. L. McKee, and S. L. Miao. 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. [https://doi.org/10.1016/S0304-3770\(01\)00155-3](https://doi.org/10.1016/S0304-3770(01)00155-3).
- Lu, M., E. R. Herbert, J. A. Langley, M. L. Kirwan, and J. P. Megonigal. 2019. Nitrogen status regulates morphological adaptation of marsh plants to elevated CO₂. *Nature Climate Change* 9: 764–768. <https://doi.org/10.1038/s41558-019-0582-x>.

- Marijnissen, R., and A. Stefan. 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, T. G., H. Murphy, A. Liedloff, C. Thomas, I. Chadès, G. Cook, R. Fensham, J. McIvor, and R. D. van Klinken. 2015. Buffel grass and climate change: a framework for projecting invasive species distributions when data are scarce. *Biological Invasions* 17: 3197–3210. <https://doi.org/10.1007/s10530-015-0945-9>.
- McKenzie-Gopsill, A., H. Kirk, W. V. Drunen, J. R. Freeland, and M. E. Dorken. 2012. No evidence for niche segregation in a North American Cattail (*Typha*) species complex: Niche Segregation in Cattails. *Ecology and Evolution* 2: 952–961. <https://doi.org/10.1002/ece3.225>.
- McMillan, C. 1959. Salt Tolerance Within a *Typha* Population. *American Journal of Botany* 46: 521–526. <https://doi.org/10.1002/j.1537-2197.1959.tb07044.x>.
- Mitchell, M. E., S. C. Lishawa, P. Geddes, D. J. Larkin, D. Treering, and N. C. Tuchman. 2011. Time-Dependent Impacts of Cattail Invasion in a Great Lakes Coastal Wetland Complex. *Wetlands* 31: 1143–1149. <https://doi.org/10.1007/s13157-011-0225-0>.
- Morais, P., and M. Reichard. 2018. Cryptic invasions: A review. *Science of The Total Environment* 613–614: 1438–1448. <https://doi.org/10.1016/j.scitotenv.2017.06.133>.
- Parnesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42. <https://doi.org/10.1038/nature01286>.
- Phillips, S. J., M. Dudik, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample Selection Bias and Presence-Only Distribution Models: Implications for Background and Pseudo-Absence Data. *Ecological Applications* 19. [Wiley, Ecological Society of America]: 181–197. JSTOR.
- Pieper, S., M. Dorken, and J. Freeland. 2020. Genetic structure in hybrids and progenitors provides insight into processes underlying an invasive cattail (*Typha* × *glauca*) hybrid zone. *Heredity* 124: 714–725. <https://doi.org/10.1038/s41437-020-0307-y>.
- Pieper, S. J., J. R. Freeland, and M. E. Dorken. 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. <https://doi.org/10.1016/j.aquabot.2017.11.001>.
- Pieper, S. J., A. A. Nicholls, J. R. Freeland, and M. E. Dorken. 2017. Asymmetric Hybridization in Cattails (*Typha* spp.) and Its Implications for the Evolutionary Maintenance of Native *Typha latifolia*. *Journal of Heredity* 108: 479–487. <https://doi.org/10.1093/jhered/esx036>.
- R Core Team. 2021. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Rejmánek, M., and M. J. Pitcairn. 2002. When is eradication of exotic pest plants a realistic goal? In *Turning the tide: the eradication of invasive species*, ed. C. R. Veitch and M. N. Clout, 249–252.
- Richards, J. A. 2013. *Remote Sensing Digital Image Analysis*. Berlin, Heidelberg: Springer Berlin Heidelberg. <https://doi.org/10.1007/978-3-642-30062-2>.
- Sanderson, E. W., S. L. Ustin, and T. C. Foin. 2000. The Influence of Tidal Channels on the Distribution of Salt Marsh Plant Species in Petaluma Marsh, CA, USA. *Plant Ecology* 146. Springer: 29–41. JSTOR.
- Shih, J. G., and S. A. Finkelstein. 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. <https://doi.org/10.1672/07-40.1>.
- Simberloff, D., J.-L. Martin, P. Genovesi, V. Maris, D. A. Wardle, J. Aronson, F. Courchamp, et al. 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 28: 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>.
- Sinks, I. A., A. B. Borde, H. L. Diefenderfer, and J. P. Karnezis. 2021. Assessment of Methods to Control Invasive Reed Canarygrass (*Phalaris arundinacea*) in Tidal Freshwater Wetlands. *Natural Areas Journal* 41. <https://doi.org/10.3375/043.041.0303>.
- Smith, C., R. D. van Klinken, L. Seabrook, and C. McAlpine. 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. <https://doi.org/10.1111/j.1472-4642.2011.00871.x>.
- Smith, H. A., W. S. Johnson, J. S. Shonkwiler, and S. R. Swanson. 1999. The implications of variable or constant expansion rates in invasive weed infestations. *Weed Science* 47: 62–66. <https://doi.org/10.1017/S0043174500090664>.
- Smith, S. Galen. 1967. Experimental and Natural Hybrids in North American *Typha* (Typhaceae). *American Midland Naturalist* 78: 257. <https://doi.org/10.2307/2485231>.
- Smith, S. Galen. 1986. The cattails (*Typha*): Interspecific Ecological Differences and Problems of Identification. *Lake and Reservoir Management* 2: 357–362. <https://doi.org/10.1080/07438148609354657>.

- Smith, S.G. 2000. Typhaceae. In: Flora of North America Editorial Committee (eds.). In *Flora of North America North of Mexico*, 22:278–285. New York: Oxford University Press.
- Snow, A. A., S. E. Travis, R. Wildová, T. Fér, P. M. Sweeney, J. E. Marburger, S. Windels, B. Kubátová, D. E. Goldberg, and E. Mutege. 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. <https://doi.org/10.3732/ajb.1000187>.
- Snow, A. A., and S. W. Vince. 1984. Plant Zonation in an Alaskan Salt Marsh: II. An Experimental Study of the Role of Edaphic Conditions. *Journal of Ecology* 72. [Wiley, British Ecological Society]: 669–684. JSTOR. <https://doi.org/10.2307/2260075>.
- Stewart, D. 2021. Undetected but widespread: the cryptic invasion of non-native cattail (*Typha*) in the Fraser River Estuary. Master's Thesis, Vancouver, B.C.: University of British Columbia.
- Stewart, D., G. Buckholtz, D. Percy, and Q. Cronk. 2022. Macroscopic traits effectively identify hybrid cattail (*T. × glauca*) in the Fraser River Estuary, British Columbia. *Manuscript in preparation*.
- Stewart, D., D. Hennigar, R. Ingham, and E. Balke. 2022. *Factors influencing the persistence of created tidal marshes in the Fraser River Estuary*. Technical Report. Surrey, B.C.: Ducks Unlimited Canada.
- Sullivan, L., R. Wildova, D. Goldberg, and C. Vogel. 2010. Growth of three cattail (*Typha*) taxa in response to elevated CO₂. *Plant Ecology* 207: 121–129. <https://doi.org/10.1007/s11258-009-9658-4>.
- Szabo, J., J. R. Freeland, and M. E. Dorken. 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. <https://doi.org/10.1016/j.aquabot.2017.11.009>.
- Tangen, B. A., S. Bansal, J. R. Freeland, S. E. Travis, J. D. Wasko, T. P. McGonigle, L. G. Goldsborough, K. Gow, J. E. Marburger, and J. A. Meier. 2022. Distributions of native and invasive *Typha* (cattail) throughout the Prairie Pothole Region of North America. *Wetlands Ecology and Management* 30: 1–17. <https://doi.org/10.1007/s11273-021-09823-7>.
- Taylor, E. 2004. Impacts of future climate change on the Fraser River delta and its urban estuary. In *Fraser River Delta, British Columbia: Issues of an Urban Estuary*, ed. B. J. Groulx, D. C. Mosher, J. L. Luternauer, and Bilderback, DE, 99–110. Geological Survey of Canada.
- Tompkins, T. M., and J. Taylor. 1983. Hybridization in *Typha* in Genesee County, Michigan. *The Michigan Botanist*: 127–131.
- Travis, S. E., J. E. Marburger, S. K. Windels, and B. Kubátová. 2011. Clonal Structure of Invasive Cattail (Typhaceae) Stands in the Upper Midwest Region of the US. *Wetlands* 31: 221–228. <https://doi.org/10.1007/s13157-010-0142-7>.
- Travis, S. E., J. E. Marburger, S. Windels, and B. Kubátová. 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. <https://doi.org/10.1111/j.1365-2745.2009.01596.x>.
- Tuchman, N. C., D. J. Larkin, P. Geddes, R. Wildova, K. Jankowski, and D. E. Goldberg. 2009. Patterns of environmental change associated with *Typha × glauca* invasion in a Great Lakes coastal wetland. *Wetlands* 29: 964–975. <https://doi.org/10.1672/08-71.1>.
- Vaccaro, L. E., B. L. Bedford, and C. A. Johnston. 2009. Litter accumulation promotes dominance of invasive species of cattails (*Typha* spp.) in Lake Ontario wetlands. *Wetlands* 29: 1036–1048. <https://doi.org/10.1672/08-28.1>.
- Voss, E. 1972. *Michigan Flora, Part I: Gymnosperms and Monocots*. Bloomfield Hills, MI: Cranbrook Institute of Science.
- Waters, I., and J. M. Shay. 1990. A field study of the morphometric response of *Typha × glauca* shoots to a water depth gradient. *Canadian Journal of Botany* 68: 2339–2343. <https://doi.org/10.1139/b90-298>.
- Werner, K. J., and J. B. Zedler. 2002. How sedge meadow soils, microtopography, and vegetation respond to Sedimentation. *Wetlands* 22: 451–466. [https://doi.org/10.1672/0277-5212\(2002\)022\[0451:HSMSMA\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2002)022[0451:HSMSMA]2.0.CO;2).
- Wilcox, D. A., K. Buckler, and A. Czayka. 2018. Controlling Cattail Invasion in Sedge / Grass Meadows. *Wetlands* 38: 337–347. <https://doi.org/10.1007/s13157-017-0971-8>.
- Williams, A. P., and E. R. Hunt. 2002. Estimation of leafy spurge cover from hyperspectral imagery using mixture tuned matched filtering. *Remote Sensing of Environment* 82: 446–456. [https://doi.org/10.1016/S0034-4257\(02\)00061-5](https://doi.org/10.1016/S0034-4257(02)00061-5).
- Williams, G. L. 1998. *Ecology of bulrush and cattail - literature review for wetland design and management*. Client Report for the Greater Vancouver Regional District Parks Department. Burnaby: G.L. Williams & Associates Ltd.

- Woo, I., and J. B. Zedler. 2002. Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha* × *glauca*. *Wetlands* 22: 509–521. [https://doi.org/10.1672/0277-5212\(2002\)022\[0509:CNASAS\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2002)022[0509:CNASAS]2.0.CO;2).
- Wu, Y., C. Hannah, P. Matte, M. O’Flaherty-Sproul, R. Mo, X. Wang, and P. MacAulay. 2022. Tidal propagation in the Lower Fraser River, British Columbia, Canada. *Estuarine, Coastal and Shelf Science* 264: 107695. <https://doi.org/10.1016/j.ecss.2021.107695>.
- Yeo, R. R. 1964. Life History of Common Cattail. *Weeds* 12: 284–288.
- Zapfe, L., and J. R. Freeland. 2015. Heterosis in invasive F1 cattail hybrids (*Typha* × *glauca*). *Aquatic Botany* 125: 44–47. <https://doi.org/10.1016/j.aquabot.2015.05.004>.
- Zedler, J. B., J. C. Callaway, J. S. Desmond, G. Vivian-Smith, G. D. Williams, G. Sullivan, A. E. Brewster, and B. K. Bradshaw. 1999. Californian Salt-Marsh Vegetation: An Improved Model of Spatial Pattern. *Ecosystems* 2. Springer: 19–35. JSTOR.
- Zedler, J. B., and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences* 23: 431–452. <https://doi.org/10.1080/07352680490514673>.