# Title Page

**Passive recovery risks invasion of non-native graminoids following intensive herbivory by Canada geese in two Salish Sea estuaries.**

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## Abstract

Tidal marsh plant communities in the Pacific Northwest are characterized by graminoids (grasses, rushes, and sedges), which provide forage for herbivores such as Canada geese. Excessive grazing by Canada geese leads to loss of marsh habitat, and removal of grazing pressure is required for the vegetation to recover. Grazing exclosures (fences) are used to allow time and space for vegetation to recover following intensive herbivory; however, whether the technique is effective for native plant communities to recover has not been tested. We used generalized linear models to compare graminoid species identity and abundance of above-ground vegetation and surface seed banks in 1-year old and 10-year old exclosures to areas of the marsh that had no known history of grazing (undisturbed) and areas still actively grazed.

We found surface seed banks lacked seed of native graminoids in actively grazed and 1-year old exclosures, while 10-year old enclosures and undisturbed areas of the marsh had equal or greater abundance of non-native graminoid seed compared to native graminoid seeds. Further, we found 10-year old exclosures had significantly greater non-native graminoid cover in the above-ground vegetation, indicating vegetation may not recover towards comparable historic conditions through grazing exclusion alone. These results indicate active restoration techniques may be required following intensive grazing, especially in estuaries where the vegetation community and surface seed bank has a high abundance of non-native, invasive species.

## Keywords

Active restoration; conservation land management; invasive species; alternative stable states;

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# Introduction

Estuaries around the world are subject to disturbance and cumulative effects of stressors from a variety of natural and anthropogenic disturbances (Lotze, 2010; Zedler, 2017). Sources of disturbance or stressors may occur on a variety of spatial and temporal scales, from extensive conversion of estuarine floodplain for municipal and industrial use (Finn et al., 2021), to local disturbances such as intensive storms or tidal surges (Pasternack, 2009). These cumulative impacts can have negative consequences on plant communities comprising estuarine habitat, such as native species biodiversity loss or species homogenization, leading to altered community structure and functional processes (Price et al., 2020; Simberloff et al., 2013). Not only does this directly impact the biodiversity and function of an estuary, but it can erode resistance to subsequent disturbance as historically abundant species become locally extirpated (Diefenderfer et al., 2021; Johnstone et al., 2016; Schaefer, 2011).

Following disturbance, life history strategies of colonizing species may drive alternative successional trajectories, leading to alternative species composition and abundance in the recovering habitat (Connell & Slatyer, 1977; Ricklefs, 1987). If life history traits are sufficiently competitive, early colonizers may inhibit recruitment of species diversity present in the pre-disturbance community, thus shifting it to an alternative stable state (Connell & Slatyer, 1977; Scheffer & Carpenter, 2003). How successional trajectories proceed in estuarine plant communities depends on abiotic conditions (e.g., elevation, salinity), as well as availability of viable plant propagules. Propagules may be present in the form of seeds deposited into the sediment surface (hereafter, surface seed bank), or vegetative clonal growth at the site. Local propagule inputs may be derived from seed rain from parent plants or extension of clonal stems within the site, and dependent on species-specific growth strategies such as seed limitation in favor of clonal growth (Morzaria-Luna & Zedler, 2007). However, dispersal of propagules from distant sites is possible through water, with seed or clonal fragments of some species able to float on tidal currents for weeks to months to reach new colonization sites (Koutstaal et al., 1987). Novel species (e.g., non-native or invasive species) locally encroaching from terrestrial habitat or dispersed through water into an estuary may shift propagule loads, and thus shift potential recovery trajectories of a site via priority effects (Connell & Slatyer, 1977) before a disturbance event occurs. Following disturbance, propagule pressure may overshadow recruitment advantages of historically dominant species (Lavorel & Lebreton, 1992).

Post-disturbance propagule recruitment and establishment, especially in tidal marshes, depends on abiotic conditions including disturbance-free temporal niches, termed windows of opportunity (Balke et al., 2014), where germinating seeds must anchor and elongate their roots before they are subject to dislodging during subsequent tidal inundation. Because seedlings are susceptible to dislodging or drowning during tidal inundation, successful establishment favors clonal fragments over seed-based establishment at tidal elevations with greater erosion and inundation stress (Silinski et al., 2016). However, increases in the frequency or duration of local disturbances can impact the recruitment window of opportunity for historically successful propagules (Hu et al., 2015). For example, stronger storms or tidal currents due to changing climate, or increased human disturbances such as boat waves can become a compounding feedback loop between altered propagule availability and altered windows of opportunity for successful species to establish, resulting in an environmental filter influencing which species may successfully establish within the new windows of opportunity.

Some natural disturbance events, like grazing by ungulates or waterfowl, may occur as either discrete, short-term events, or as long-term disturbance agents in an ecosystem. Historically, grazing would have occurred as species like waterfowl moved through on migration routes, and forage preference would be related to seasonal plant phenology (Buchsbaum & Valiela, 1987). Under these grazing regimes, plant communities were able to passively recover through natural recruitment and succession (Meli et al., 2017). However, intensive or persistent grazing in conservation areas such as estuaries is becoming more common with the introduction of novel grazers within a region, compounded by the loss of conservation habitat due to anthropogenic landscape changes (Clausen & Percival, 1998; Prowse et al., 2019). These new grazing pressures can effectively reset successional processes through total removal of mature vegetation by opening space with reduced or absent competition, and thus potentially set the plant community on a recovery trajectory towards an alternative stable state via seed bank recruitment (Abernethy & Willby, 1999; Srivastava & Jefferies, 1996). Through alternative competitive strategies, these novel species can shift recovery trajectories to a new compositional palette.

Estuaries around the Salish Sea in the Pacific Northwest of North America are dominated by swards of graminoids (sedges, rushes, grasses) whose competitive strategies include clonal vegetative reproduction and tall (> 1 m) canopy cover, interspersed with a diversity of broadleaf, flowering species (“forbs”) (Borde et al., 2020). Many estuaries in this region are overgrazed by non-native, hyperabundant Canada geese (*Branta canadensis* ssp. *Fulva*) (Dawe et al., 2011; Dawe & Stewart, 2010). In addition to removing leafy above-ground vegetation, Canada geese will rip out or “grub” starchy rhizomes capable of clonal reproduction, which in turn increases erosion of marsh sediments and their seed banks. Estuary plant communities impacted by intensive goose herbivory and associated sediment disturbances can recover either by clonal expansion from adjacent remnant patches, or through seed recruitment from seed dispersed and retained on the eroded site. For graminoids that are seed-limited, such as *Carex* sp. (Kettenring & Galatowitsch, 2011; Schütz, 2000), recovery of these species to pre-disturbance abundance may be more dependent on the presence of intact, clonally dominated communities adjacent to the grazed areas.

Our main objective of this study was to understand propagule composition and availability within surface seed banks, and above-ground vegetation compositional changes at discrete stages since removal of grazing by Canada geese in two Salish Sea estuaries. Traditional succession models relate the most competitive species will increasingly dominate the plant community as time since disturbance increases (Tilman, 1990). This would particularly be the case in a community dominated by clonal species, where recovery is driven by species spreading clonally from adjacent undisturbed patches, in addition to potential recruitment from the seed bank. If succession is happening the way inhibition models explain, then:

1. Composition and abundance of dominant tall, perennial graminoids in above ground vegetation at older disturbance sites will have greater similarity to undisturbed (reference) vegetation than recently disturbed sites. Alternatively, the grazing disturbance to remove vegetation and altered propagule availability can lead to alternative succession pathways, where new species can achieve competitive dominance through seed or clonal recruitment, derailing the slow clonal encroachment of historically dominant species from neighboring sites. If this is the case, we expect compositional abundance of competitively dominant species in the older disturbance sites will be significantly different from that of undisturbed sites.
2. Because a longer post-grazing recovery period should allow for recruitment of more species diversity into the above-ground vegetation and surface seed bank, we expect composition and abundance of surface seed banks should closely resemble that of above-ground vegetation in recently disturbed sites (e.g., via direct seed rain) and become more species-rich and dissimilar from above-ground vegetation (i.e., via dispersal) with time since disturbance.

# Methods

## Study area & site history

The Little Qualicum River Estuary (LQRE) and Nanaimo River Estuary (NRE) are situated on the east coast of Vancouver Island along the Strait of Georgia, British Columbia, Canada (Fig. 1), and are on the ancestral, unceded territories of Coast Salish Peoples, including the K’ómoks, Snuneymuxw, Qualicum Band, and Nanoose Nations. Prior to European colonial settlement, traditional practices by Indigenous Peoples around the Salish Sea would have included managing estuaries as root gardens to promote the abundance of broadleaf flowering species with starchy roots, rather than the perennial graminoids that competitively dominate the estuaries today (Turner et al., 2013). Colonial settlement of the LQRE began in 1887, with cattle grazing, log booming, and sawmill operations being the chief uses of the estuary until 1974 when 29 ha of the estuary were donated to the Canadian Wildlife Service for conservation purposes, and subsequently designated as a provincially protected Wildlife Management Area (WMA) in 1993 (Clermont, 2010). The NRE was similarly settled through the late 19th and early 20th centuries, and heavily augmented through construction of a ferry terminal, logging operations, and coal mining. While the NRE is part of the UNESCO-designated Mount Arrowsmith Biosphere Region and portions fall under conservation management, it is not provincially protected through designation as a WMA.

***Fig. 1*** *The extent of watershed catchments flowing into the Salish Sea (A, outlined in green) spans the US-Canadian border on the Pacific Coast of North America (A, inset). Sampling took place within the polygons outlined in gold dash at the Little Qualicum River Estuary (B) and Nanaimo River Estuary (C) along the southeast coast of Vancouver Island, near the towns of Qualicum Beach and Nanaimo, respectively.*

## Goose introduction & grazing exclusion

Canada geese (*Branta canadensis* spp. *fulva*) were historically a migratory species to Vancouver Island (Dawe & Stewart, 2010), however in the late 20th century populations from eastern North America were introduced to the island to promote hunting tourism. These populations lost their migratory behavior and have since established resident populations. In the absence of sufficient hunting pressure, these resident populations have grown hyperabundant (Dawe & Stewart, 2010). These hyperabundant populations place heavy pressure on estuaries through sustained herbivory and grubbing (the digging and uprooting of plant roots and rhizomes, Fig. 2C), leading to complete loss of above- and below-ground plant structures, denuded marsh platforms, and subsequent sediment and seed bank loss through erosion.

Fences or “exclosures” are commonly used to exclude herbivores, including Canada geese, from continued grazing. A history of exclosure construction since 2010 in the LQRE, and recent history of exclosure construction in NRE since 2020 afford the opportunity to develop a coarse chronosequence of recovery at discrete time periods since grazing disturbance, including Grubbed (denuded mudflat), 1-year old exclosures, 10-year old exclosures, and areas that have no known history of grazing by Canada geese (Undisturbed or “reference”) (Table 3). Exclosures are constructed along the edges of vegetation impacted by grazing activity (Fig. 2D, E, F), with the rationale that remnant vegetation should recover towards a desired Undisturbed or “reference” condition (Fig. 2A, B) once grazing pressure is relieved.

**Fig. 2** *Reference vegetation for this study was defined as areas with no known grazing disturbance and dominated by native species, including Carex lyngbyei in the Little Qualicum River Estuary (A), and Juncus balticus or Deschampsia caespitosa in the Nanaimo River Estuary (B). Intensive grubbing (C) by Canada geese (Branta canadensis) removes rhizomes and contributes to sediment loss, resulting in large areas of bare or “denuded” mudflat (D). Exclosures were constructed around the edges of these grubbed/grazed areas to promote vegetation recovery in 2010 in the Little Qualicum River Estuary (E) and Nanaimo River Estuary in 2020 (F). Photo credits (A) D. Clermont, 2021, (B) S. Lane, 2021, (C) G. Fairbrother, date unknown, (D) G. Ashley, 2021, (E) N. Dawe, 2011, (F) T. Clermont, 2020*

**Table 3** *Grazing disturbance conditions in the Little Qualicum River and Nanaimo Estuaries resulted in conversion of vegetated marsh to partially or fully grubbed mudflats; exclosures were installed to prevent further degradation into the marsh platform. We sampled n = 4 sites in each estuary, with two 1 m2 vegetation plots per site, and two surface seed bank samples per plot.*

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Estuary** | **Time Since Disturbance** | **Disturbance condition** | **Protected by exclosure?** | **Total vegetation plots** | **Total surface seed bank samples** |
| Little Qualicum, Nanaimo | 0 years | Actively grazed and grubbed | No | 16 | 32 |
| Nanaimo | 1-year post-grazing/grubbing disturbance | Recovering | Yes | 8 | 16 |
| Little Qualicum | 10 years post-grazing/grubbing disturbance | Recovering | Yes | 8 | 16 |
| Little Qualicum, Nanaimo | No known grazing/grubbing disturbance | Undisturbed | No | 16 | 32 |
| Total |  |  |  | 48 | 96 |

## Vegetation sampling

Above-ground vegetation were surveyed across all vegetation plots (Table 3) once in mid-July, 2021. Two 1 m2 vegetation plots were placed within the exclosures (“sites,” n = 4 per disturbance condition in each estuary, Table 3), at least 1 m from the bank edge and any exclosure boundary, and at least 3 m apart within the exclosure. Quadrats were placed so that the plot edge nearest creek was parallel to the bank.

All vascular species were identified according Hitchcock and Cronquist (2018). Species were considered in the plot if at least half of their basal stem(s) were inside the quadrat boundary; overhanging vegetation originating from basal stems outside the plot was not considered. Aerial vegetated cover was estimated to the nearest 3 % (1/32 m2). For any species present with less than 3 % cover, species were assigned 2 % cover if > 20 individuals were present, 1 % cover if 2-20 individuals were present, and 0.1% cover for single individuals. Bare ground was estimated as the remainder of the plot area not covered by above-ground vegetation. Any plots with > 100 % cover were standardized relative to 100 % to allow for comparison across plots and to constrain values to fit statistical distributions. To characterize plant structure, all species were assigned to a height category tall (> 1 m), medium (50-100 cm), or short (< 50 cm) based on their maximum reported height in the Illustrated Flora of British Columbia (Douglas et al., 1998). Our key species of interest, tall perennial graminoids (TPGs), were defined as any grass (Poaceae), sedge (Cyperaceae), or rush (Juncaceae) with a biennial or perennial life history and mature height of at least 1 m.

## Surface seed bank sampling & germination

Two surface seed bank samples were taken from each plot (n = 16 per disturbance condition in each estuary, Table 3) in summer (July 2020), fall (October 2020), and spring (March 2021). A 10 cm diameter handheld bulb planter (e.g., Husky 9 in. stainless Steel Bulb Planter, Home Depot, USA) was used to excise sediment 1 cm deep to capture the most recent seeds deposited into the marsh sediment, which we call the “surface seed bank.” Vegetative roots, rhizomes, or other viable rooted material were removed before placing sample in a plastic zipper bag. All surface seed bank samples from the same estuary and disturbance condition were then homogenized in a clean bucket with 100 mL dechlorinated water. Samples were hand-sifted for any remaining root, rhizome, or vegetative material, then the homogenized sample was transferred to a clean plastic zipper bag. Summer and fall 2020 samples were stored at 4o C for approx. 12 weeks to simulate overwinter cold stratification to release seed dormancy (Rosbakh et al., 2019); samples collected in the spring of 2021 underwent natural winter conditions within the estuaries and were not subjected to cold stratification.

Germination trials were conducted under greenhouse conditions with 15 hr. daylength at ~ 20o C. Seedling pots (9 cm x 13 cm x 5.7 cm (depth)) were filled with moist, sterile potting media (Sunshine Mix No. 4, Sun Gro Horticulture, Agawam, MA, United States). Pots were placed in solid cache trays and constantly bottom-watered with municipal tap water. Seeds were sown by adding 75 mL of sampled sediments to the top of each seedling pot (n = 8 per estuary and disturbance condition) while constantly agitating the homogenized seed bank sample to prevent seeds from settling to the bottom of the sediment mixture. Seeds were allowed to germinate for 5 weeks, at which time all individuals were identified, counted and removed. The seedling trays were observed for any further germination for another 7-10 days, at which time the samples were discarded. Any species that could not be identified to species at germination were labelled and transplanted into 38 P plug trays with the same growing media and growing conditions until a positive identification could be made.

## Statistical analyses

All analyses were performed in R Studio (v. 4.2.2). Because tall, perennial graminoids (TPGs) are the dominant species group in intact tidal marsh plant communities, we focused most of our analyses on this taxonomic group, however we summarized compositional characteristics for all species. Mean species richness was calculated for all species in the above-ground vegetation and surface seed banks for each disturbance category. For all species, we defined dominance within the above-ground vegetation plots or surface seed bank samples as species having > 25% mean relative abundance. Although a species may be dominant within the vegetation at a site, dominance may not indicate specificity or fidelity to a specific disturbance category. To understand which species could be used to significantly characterize each grazing disturbance condition in the above-ground vegetation and surface seed, we used indicator species analysis (“indicspecies,” R package De Caceres & Jansen, 2016). Species significantly driving compositional abundance in each disturbance category were defined by a biserial correlation coefficient (multipatt func = “r.g.”) and permutational analysis (Dufrene & Legendre, 1997).

Relative abundance in the above ground vegetation was calculated as the proportion of one species relative to the total plot cover, defined as the sum of all vegetation cover and bare ground. Relative abundance in the seed bank sample was calculated as the proportion of one species represented in the total germinants to fit a binomial distribution. To test whether species relative abundance differed among disturbance recovery categories we used separate generalized linear models for the above-ground vegetation and surface seed bank, each with a binomial distribution and logit link function from the R *stats* package (R Core Team, 2022). Our response variable, the proportion of graminoid abundance in each sample of above-ground vegetation or the surface seed banks, was fit against each disturbance category as the primary predictor, with estuary location as an additional fixed effect to test for geographic differences., and model residuals were visually inspected for normality (Fig. S1). For each model we used the predict() function with type = “response” (*stats*, R Core Team 2022) to calculate the probability of finding TPG relative abundance proportional to Undisturbed above-ground vegetation or surface seed banks.

# Results

## Above-ground vegetation

Native species richness was consistently greater than non-native richness across all disturbance categories, although the Little Qualicum River Estuary (LQRE) had the lowest mean native species richness in the Undisturbed and 10-year old exclosures (Fig. 3). We found that cover abundance of the dominant group of tall, perennial graminoids (TPGs) was similar to Undisturbed sites after grazing exclusion, however compositional abundance became dominated by non-native, invasive species in the 10-year old exclosure sites (Fig. 4). Dominant species were often the same as those identified by indicator species analysis (Table 3) in each disturbance category, although indicator species were not always dominant (Fig. 5).

**Fig. 3** *Species richness of native vs. non-native plants among disturbance categories in both Nanaimo and Little Qualicum River Estuaries for both above-ground vegetation and surface seed banks*

**Fig. 4** *Above-ground cover abundance of key functional group ‘tall, perennial graminoids’ is not significantly different from undisturbed (reference) sites after 10 years. However, indicator species analysis reveals this above-ground cover is dominated by non-native graminoid species Agrostis stolonifera. Moreover, seed bank abundance of tall, perennial graminoids is significantly higher in 10-year old exclosures compared to other disturbance conditions, including undisturbed (reference) sites. Notably, there is a nearly equal abundance of non-native and native graminoid seed in 10-year old exclosures, and significantly greater representation of non-native than native graminoid seed in Undisturbed sites in Little Qualicum Estuary*

Above-ground vegetation in undisturbed sites in both estuaries (n = 8) was dominated by several TPGs (non-native *Agrostis stolonifera*, and native species *Carex lyngbyei* and *Juncus balticus*), in addition to native broadleaf flowering species *Potentilla pacifica* in LQRE, and *Symphyotrichum subspicatum* in both estuaries (Fig. 5). The 10-year old exclosures in LQRE (n = 4) shared similar dominant species, however non-native *A. stolonifera* had greater abundance than native *C. lyngbyei*; native TPG *J. balticus* was not dominant, and *S. subspicatum* was not present. Indicator species analysis identified non-native graminoid *A. stolonifera* and native forb *P. pacifica* as significantly characterizing the 10-year old exclosures, while Undisturbed sites included two native graminoids and one forb (*J. balticus*, *C. lyngbyei*, *Triglochin maritima*) (Table 4).

**Table 4** Indicator species analysis identified which species significantly characterize the above-ground vegetation (left panel) and surface seed bank (right panel) for each disturbance condition of “recently disturbed” (1-year old exclosures and Grubbed sites) and “recovered” (10-year old exclosures), and Undisturbed sites. No species significantly indicated surface seed banks in 1-year old exclosures. Non-native species are indicated by asterisk (\*); tall perennial graminoids indicated by plus sign (+).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Above Ground Vegetation | | |  | Below Ground Seed Bank | | |
| **Disturbance** | **Species** | **p-value** |  | **Disturbance** | **Species** | **p-value** |
| Undisturbed | *Juncus balticus+* | 0.03 |  | Undisturbed | *Carex lyngbyei+* | 0.01 |
| *Carex lyngbyei+* | 0.02 |  | *Cotula coronopifolia\** | 0.03 |
| *Triglochin maritima* | 0.04 |  | *Juncus articulatus+* | 0.05 |
| 10-year old exclosures | *Agrostis stolonifera\*+* | < 0.01 |  | 10-year old exclosures | *Juncus balticus+* | < 0.01 |
| *Potentilla pacifica* | 0.04 |  | *Agrostis stolonifera\*+* | < 0.01 |
|  |  |  | *Triglochin maritima* | 0.04 |
| 1-year old exclosures | *Spergularia canadensis* | 0.03 |  | 1-year old exclosures | None |  |
| *Glaux maritima* | 0.04 |  |  |  |
| Grubbed | *Eleocharis parvula* | < 0.01 |  | Grubbed | *Salicornia depressa* | < 0.01 |
| *Cotula coronopifolia\** | 0.04 |  |  |  |

**Fig. 5** *Mean relative abundance of species identified in indicator species analysis in above-ground vegetation and surface seed bank at each estuary sampled. Non-native species indicated with (\*). Notably, abundance of key native TPGs such as Carex lyngbyei are absent from the seed bank, while others such as Juncus balticus are dominant (> 25% relative abundance) in the seed bank but not dominant in above-ground vegetation, such as observed in 10-year old exclosures at Little Qualicum Estuary*

Grubbed sites in both estuaries (n = 8) and 1-year old exclosures in the Nanaimo River Estuary (NRE, n = 4) shared common dominant species, however only the 1-year old exclosures were dominated by a single TPG (*C. lyngbyei*). In Grubbed sites, dominant species in both estuaries included native species *Eleocharis parvula* (very short perennial graminoid, < 10 cm tall) and *Glaux maritima* (short perennial forb, < 30 cm tall), with the additional dominant native species *Spergularia canadensis* (short annual forb, < 30 cm tall) in LQRE (Fig. 5). In NRE, 1-year old exclosures were dominated by the same species as in all Grubbed sites (*E. parvula, G. maritima, S. canadensis*), but remnant TPG species *C. lyngbyei* also maintained cover dominance in above-ground vegetation (Fig. 5).

Indicator species analysis identified *S. canadensis* and *G. maritima* as species significantly characterizing 1-year old exclosures, while native, short graminoid *E. parvula* and non-native forb *Cotula coronopifolia* (short (< 30 cm) perennial forb) significantly characterized just the Grubbed sites (Table 4). Generalized linear models showed Grubbed sites had significantly lower TPG above-ground cover as compared to Undisturbed sites (p = 0.02), however 1-year old exclosures in NRE did not have significantly lower TPG cover than Undisturbed sites (p = 0.09) (Fig. 6).

## Surface seed banks and comparison to above-ground vegetation

As with above-ground vegetation, native species richness was greater than non-native richness, and mean species richness was comparable between all disturbance categories (Fig. 3). Relative abundance of TPG seeds was greater in the 10-year old exclosures at LQRE than in Undisturbed sites at both estuaries, however seed of any TPG species was nearly absent from Grubbed sites in both estuaries, and 1-year old exclosures at NRE (Fig. 4). Additionally, we found surface seed banks had fewer dominant species in each of the disturbance categories than above-ground vegetation (Fig. 5). Relative abundance of all species found in the above-ground vegetation and surface seed banks are found in Table S1.

Dominant surface seed bank species in Undisturbed sites varied by estuary, with no TPG species dominating in NRE (Table 4). In LQRE, both the Undisturbed and 10-year old exclosures were dominated by the same two species (non-native *A. stolonifera* and native *J. balticus*) (Fig. 5). Indicator species for the surface seed bank in 10-year old exclosures in LQRE included non-native *A. stolonifera*, native *J. balticus*, and native *T. maritima.* Indicators of Undisturbed surface seed banks in both estuaries included native TPGs *C. lyngbyei* and *Juncus articulatus*, as well as non-native forb *C. coronopifolia* (Table 4). This was contrasted by no dominant or indicator species in the surface seed banks of 1-year old exclosures, and the only indicator of Grubbed sites was native forb *Salicornia depressa*. Grubbed sites in both estuaries were dominated by native, short graminoid *E. parvula*, while native forb *S. canadensis* was dominant only in seed bank samples from Grubbed sites at LQRE. No species were seed-dominant in 1-year old exclosures in NRE. Our generalized linear models showed Nanaimo River Estuary had significantly lower TPG seed abundance overall (p = 0.02), and Grubbed sites had significantly lower TPG seed abundance, regardless of estuary (p = 0.05) (Fig. 6).

We found surface seed bank compositional abundance differed from vegetation at Grubbed sites, as many of the species found in the above-ground vegetation were not present in the surface seed bank (Fig. 5). In 10-year old exclosures, native *C. lyngbyei* recovered as dominant vegetation, but abundance of its seed in the surface seed bank was much lower than that in Undisturbed sites. This was contrasted by non-native invasive *A. stolonifera*, whose seed dominated surface seed banks in 10-year old exclosures and Undisturbed sites, and its dominance in above-ground vegetation was greater at 10-year old sites than in Undisturbed sites. Though the native forb *Symphyotrichum subspicatum* was dominant in vegetation at Undisturbed sites, it was absent from the vegetation and surface seed bank in 10-year old exclosures.

***Fig. 6*** *Actual vs. predicted values for proportion of tall, perennial graminoid in above-ground vegetation cover (top panel) and surface seed bank samples (bottom panel) based on disturbance condition. Actual values plotted as colored points (blue) for Little Qualicum River Estuary and Nanaimo River Estuary; estimated mean values shown in black as means (points) with standard error*

# Discussion

We wanted to understand whether the competitively dominant tall, perennial graminoids (TPGs) recovered following grazing disturbance, and whether recovery of surface seed banks resembled above-ground vegetation composition. We found that after 10 years of grazing exclusion, the dominant plant group of tall, perennial graminoids (TPGs) recovered in the above-ground vegetation according to our expectations, however non-native species *Agrostis stolonifera* had become the dominant species in both the vegetation and surface seed banks. Additionally, we found significantly lower relative abundance of TPGs in the above-ground vegetation and surface seed bank in the Grubbed sites at both estuaries, and significantly lower relative abundance of TPG species in the surface seed banks at 1-year old exclosures at Nanaimo River Estuary (NRE) (Fig. 6). Given that non-native species dominate the recovered vegetation and surface seed banks after 10 years of grazing exclusion at Little Qualicum River Estuary (LQRE), we suggest that these disturbed habitats are recovering towards an alternative compositional state, reflecting the prevalence of non-native grasses throughout the region.

Non-native TPGs may have a greater competitive recruitment advantage, contributing to this alternative recovery trajectory following disturbance by grubbing. This may be driven at least in part by high seed production, resulting in a “weighted lottery” (Lavorel & Lebreton, 1992) of seed propagules from which the plant community can recover. In addition, it is likely that these species are also characterized by more competitive recruitment strategies than native TPGs. For example, the two TPG species with greatest representation in surface seed banks in Undisturbed sites at both estuaries and 10-year old exclosures in LQRE were native *J. balticus* and non-native, invasive *A. stolonifera* (Fig. 5). Despite these two species having similar seed propagule loads, native *J. balticus* is not dominant in the above-ground vegetation, suggesting that its seed and clonal recruitment strategies were not sufficient to out-compete those of *A. stolonifera*. If these two species had comparable competitive recruitment traits, we might expect a similar proportion of cover abundance in the above ground vegetation in 10-year old exclosures (Aicher et al., 2011). Additionally, seed limitation of some species like *Carex lyngbyei* result in reliance on recovery from clonal reproduction which may be insufficient to out-compete non-native, invasive species like *A. stolonifera* (Kettenring & Galatowitsch, 2011).

These results could imply that even when ecological memory remains through clonal fragments, it may be overwhelmed by the novel propagule pressures from the surrounding landscape. This post-disturbance recovery dominated by novel species may also exacerbate disturbance-driven losses of ecological memory, and hinder efforts to passively restore native composition (Johnstone et al., 2016). However, such intensely altered propagule loads were site-specific. We note that the sites sampled at Little Qualicum River Estuary appear to have a greater threat of non-native invasive species encroachment than sites sampled at Nanaimo River Estuary (Fig. 5), despite its status as a protected Wildlife Management Area since 1993. Non-native species *A. stolonifera* was not dominant in the surface seed banks in Undisturbed sites in NRE, nor did it appear in the surface seed banks of 1-year old exclosures in this estuary. It is notable that indicator species analysis did not identify any species as significantly characterizing 1-year old exclosures at NRE (Table 3). This suggests that overgrazing and grubbing removes not only vegetative growth but contributes to the loss of propagules in the surface seed bank via erosion when vegetation is stripped away. Additionally, some native, clonally reproductive species did not appear to recover following disturbance. For example, *S. subspicatum* was dominant in the above-ground vegetation and present in surface seed banks at Undisturbed sites in both estuaries, but neither plants nor seed were found in any other disturbance categories, including the 10-year old exclosures at LQRE (Fig. 5). This may indicate that there are critical windows of opportunity in which native species propagule loads must recover (Fivash et al., 2021). If they are unlikely to disperse from the surrounding landscape, land managers may need to actively intervene through seed and plant addition to preserve their presence in the landscape. As with many restoration projects in degraded lands, this will likely need to be coupled with suppression of competitive non-native species invasion to offset the disproportionate representation of those species in the arriving propagule pool.

Successful passive restoration methods are dependent on the extent and duration of the disturbance (Meli et al., 2017), and may be inappropriate in ecosystems with a history of invasive species (Shackelford et al., 2019). If propagules of non-native, invasive species are competitively successful within the available windows of opportunity to the point of excluding native species richness and abundance, then passive restoration methods such as grazing exclosures are insufficient to restore habitat conditions comparable to the pre-disturbance state. We suggest that in these estuaries, passive recovery creates a temporal window of opportunity in which non-native invasive species like *A. stolonifera* can gain dominance, and therefore active restoration is required for native communities to recover. Because the cumulative impacts of overgrazing and high propagule loads of non-native species may reset the recovery trajectory with unknown consequences for ecosystem function (Mack et al., 2000), we recommend actively restoring a diversity of native species as soon as possible following removal of grazing disturbance to expedite habitat recovery. Sites with a known abundance of non-native, invasive species may benefit from transplanting rooted plants (rather than seed), especially in areas of low to moderate salinity to increase recovery through clonal vegetative expansion (Crain et al., 2008). Seed additions may offer a cost-effective way to increase species diversity recruited to the restoration site, however reliance on seed alone to restore a disturbed area may not be successful due to uncertain germination and seedling survival rates. While a species may grow robustly across a given salinity and/or elevation gradient, the species’ germination and establishment success is highly restricted by microsite variation in salinity and elevation (Janousek & Folger, 2013; Lane, 2022).

Our findings suggest there is a window of opportunity to influence the recovery pathway of estuaries following geese removal. The blank slate produced by intensive geese grubbing and grazing creates a weed-shaped hole (Buckley et al., 2007) unless management intervenes. High levels of non-native species invasion have been found in other protected Pacific Northwest estuaries, and our findings reiterate the need for regular monitoring and active management of estuarine systems (see also Stewart et al., 2023, Lane et al., in review). Moreover, estuaries throughout the Pacific Northwest comprise complex Indigenous food systems supporting many culturally important plant species often referred to as root gardens (Deur et al., 2013; Turner et al., 2013). Restoration following Canada geese removal creates an opportunity for the re-instatement of Indigenous stewardship practices to revive these ancient food systems and broader land management practices. This will entail partnerships and support of local Indigenous communities as they work to reinstate their cultural practices and achieve food sovereignty.

# Supplemental

Table S1. Relative abundance of each species found in mature vegetation and surface seed banks, averaged across all disturbance types within each estuary.

|  |  |  |  |
| --- | --- | --- | --- |
| **Estuary** | **Species Latin Name** | **Surface Seed Bank** | **Above-ground Vegetation** |
| Nanaimo | *Agrostis stolonifera* | 5.5 | 12.6 |
| *Carex lyngbyei* | 0.3 | 26.4 |
| *Cotula coronopifolia* | 0.6 | 0.3 |
| *Deschampsia caespitosa* | 0.2 | 5.5 |
| *Distichlis spicata* | 0.0 | 4.1 |
| *Eleocharis parvula* | 84.6 | 17.8 |
| *Epilobium ciliatum* | 0.9 | 0.0 |
| *Epilobium glaberrimum* | 1.0 | 0.0 |
| *Glaux maritima* | 0.8 | 13.6 |
| *Grindelia integrifolia* | 1.0 | 0.0 |
| *Isolepis cernua* | 1.1 | 0.0 |
| *Juncus articulatus* | 1.1 | 0.0 |
| *Juncus balticus* | 3.2 | 29.3 |
| *Juncus ensifolius* | 1.8 | 0.0 |
| *Juncus tenuis* | 1.0 | 0.0 |
| *Potentilla anserina pacifica* | 1.1 | 8.9 |
| *Salicornia depressa* | 0.2 | 0.8 |
| *Spergularia canadensis* | 9.1 | 7.1 |
| *Symphyotrichum subspicatum* | 2.3 | 35.8 |
| *Trifolium wormskioldii* | 0.0 | 1.0 |
| *Triglochin maritima* | 0.0 | 4.6 |
|  |  |  |  |
| Little Qualicum | *Achillea millefolium* | 2.7 | 0.0 |
| *Agropyron repens* | 0.0 | 0.9 |
| *Agrostis stolonifera* | 34.6 | 36.4 |
| *Atriplex patula* | 0.0 | 1.0 |
| *Carex lyngbyei* | 5.6 | 28.8 |
| *Cotula coronopifolia* | 3.7 | 4.1 |
| *Eleocharis parvula* | 48.5 | 43.5 |
| *Glaux maritima* | 1.9 | 4.8 |
| *Isolepis cernua* | 0.3 | 0.0 |
| *Juncus balticus* | 20.6 | 11.3 |
| *Poa palustris* | 0.2 | 0.0 |
| *Potentilla anserina pacifica* | 2.6 | 12.2 |
| *Salicornia depressa* | 1.2 | 1.7 |
| *Spergularia canadensis* | 16.0 | 15.2 |
| *Symphyotrichum subspicatum* | 3.7 | 75.1 |
| *Triglochin maritima* | 2.0 | 2.9 |

**Fig. S1** Quantile-quantile plot residuals for above-ground vegetation and surface seed bank generalized linear models.

# Statements & Declarations

## Competing interests

The authors have no relevant financial or non-financial interests to disclose.

## Author contributions

Study conception, 2021 data collection, analysis, and interpretation were undertaken by Stefanie L. Lane. Nancy Shackelford assisted with theoretical framework and manuscript revision. Manuscript was drafted by Stefanie L. Lane; Nancy Shackelford, and Tara G. Martin participated in draft revisions on previous versions of this manuscript. All authors read and approved the final manuscript.

## Data availability

Data and code for all years of observation are available on GitHub (LINK) or via Dryad (LINK)