# Discussion

We find there have been substantive changes in species composition over time, indicating that despite conservation status and broad resilience of our ecosystem, regional pressures are influencing considerable shifts in the species composition within this habitat. We also found the three main plant assemblages, Sedge, Fescue and Bogbean, have consistently been defined by the same most dominant species over the past 40 years, supporting our expectation that these characteristic species should not change in the absence of significant environmental disturbance. Overall, we observed a decline of native species richness, an increased richness and abundance of exotic species, leading to homogenization of cover abundance within assemblages, and greater dissimilarity between assemblages. These shifts in compositional trends are also reflected in the overall loss of secondary indicator species for the Sedge and Fescue assemblages. Our results present another compelling case example of broader global trends of species homogenization, and are of critical concern to local conservation objectives in the Fraser River Estuary for salmon, water birds, and shoreline stability.

## Predominant themes

1. Loss of native species richness, and increased richness/abundance of exotic species.

Overall, native species contributing to floristic diversity have been lost, both in terms of richness and cover abundance. The trend of losing native species richness contributes to biodiversity loss, and potential loss of functional redundancy (and thus resilience) within the assemblage, and the marsh community as a whole. This trend was observed as decreasing alpha diversity and increasing beta diversity, which indicated increasing rarity of secondary species within each assemblage.

The greatest loss of native species richness occurred in the Fescue assemblage, while nominal gains in exotic richness were found in all assemblages (Fig. S5). The Fescue assemblage had an overall net loss of 18 native species between 1979 and 2019 (Table S7). Among the species lost from the assemblage, X are not found in any other assemblage. There was a net zero gain of exotics, however exotic RCG accounts for the greatest 2019 mean cover in the entire assemblage (25-50% cover). In the Bogbean assemblage, there was a net gain of 1 native species and 3 exotic species. The new native species gained included woody *Salix* sp., and cattail (*Typha latifolia*), which are different from species lost [which/how]. The new exotic species include *Phalaris arundinaceae* (reed canary grass, RCG) and *Iris pseudacorus* (yellow flag iris). Although they are presently < 25% mean 2019 cover, these species are notorious for quickly spreading to the point of near-exclusion of other species (especially natives). Within the Sedge assemblage, there was a net loss of 3 native species, and net gain of 3 exotic species, including yellow flag and RCG. As of 2019, these species accounted for < 25% mean cover, but are of significant management concern due to their potential for excluding native species to the point of exotic monocultures (cite).

These results reflect broader global trends of biodiversity loss paired with exotic invasion. The unknown consequences of this invasion and native species loss may be creating broader instability within the Fraser River Estuary ecosystem through fragmented or lost propagule dispersal networks, and altered trophic cascades such as pollinator networks or primary production.

1. Homogenization of compositional cover abundance ***within*** assemblages, but greater compositional cover dissimilarity ***between*** assemblages is related to increasing cover of exotic species

We found that species cover has become more homogenized within assemblages, but more distinct between assemblages. That is, plots were more similar in the species composition and cover abundance within an assemblage, but increasingly dissimilar between assemblages. This was shown as increasing dissimilarity distance between assemblages, but reduced dissimilarity distance between plots within an assemblage (cluster Fig.), indicating sharper contrasts in species compositional abundance between assemblages. The key driver of this trend was greater dominance in cover abundance by fewer species (FIG?), while presence and cover abundance of ‘rare’ species became rarer.

It is worth noting changes in cover abundance for SARA blue-listed species *Sidalcea hendersonii*, which may inform conservation best practices. Cover abundance of the species was greatest in the Fescue assemblage in 1979, butdecreased by 46% in 2019. However, it increased ~140% in the Sedge assemblage (< 25% cover in 2019). It is difficult to say whether shifting abiotic conditions or encroaching exotic species such as RCG (~1430% increase to 25-50% plot cover in 2019) were responsible for the decline in *S. hendersonii* abundance in the Fescue assemblage. However, these trends may represent an opportunity for new research to inform better conservation strategies.

Surprisingly, cover abundance of many the assemblage-dominant species have decreased over time. For example, in the Sedge assemblage both native keystone species *Carex lyngbyei* and exotic grass *Agrostis stolonifera* have decreased cover abundance from 1979-2019 (Fig. 3), with each species losing ~25-35% cover abundance between 1979-2019. Meanwhile, exotic species *Lythrum salicaria* and *Festuca arundinaceae* increased ~50% and 100%, respectively, in abundance (< 25% cover) by 2019 (Supp.). Similarly, in the Bogbean assemblage, cover abundance of native keystone species *Menyanthes trifoliata* had declined ~21% (50-75% cover) by 2019, while cover of exotic *Mentha aquatica* had increased ~385% (~25-50%). Overall, the ratio of native to exotic cover within assemblages is decreasing, resulting in greater proportional cover abundance of exotic species (Fig. S5b). **This indicates certain exotic species are becoming more abundant within assemblages, however few species (native or exotic) represent the majority of cover within the assemblage.**

1. Shifts in secondary indicator species

The species indicator analysis of clustered assemblages showed that assemblage-defining species (Bogbean, Fescue, Sedge) remained consistent, however there were overall losses in indicator species, and few of those indicator species were consistently represented in the analysis over time. For example, the Sedge and Fescue assemblages had the greatest losses of assemblage indicator species. The Fescue assemblage included six indicator species in 1979, but only three in 2019, while the Sedge assemblage had three species in 1979, but only one in 2019. In both assemblages, the only species that remained the same ‘indicators’ were the defining species *Carex lyngbyei* (sedge), and *Festuca arundinaceae*, (fescue). However, in the Fescue assemblage RCG (*Phalaris arundinaceae*) has replaced *F. arundinaceae* as the most significant indicator species.

The identity of the shifting indicator species may offer clues to changing abiotic conditions or functional traits. For example, the indicator species analysis for the Sedge assemblage in 1979 included indicators of highly saturated soils (*Sagittaria latifolia, Schoenoplectus tabernaemontani*), but in 1999 the assemblage indicators included species tolerant of drier conditions (*Agrostis stolonifera, Impatiens capensis*). Alternatively, if the shifts in assemblage indicator species do not readily point to functional traits or abiotic factors, they may be more indicative of the likelihood of high interannual variability in the assemblage or broader community despite the perennial life history of many of the species. For example, the number of indicator species for the Bogbean assemblage varied across time, with 6, 10, and 6 species in 1979, 1999, and 2019, respectively. In the Fescue assemblage, woody willow species *Salix lasiandra* was an indicator species in 1979, and therefore one might expect a succession of riparian fringe over time. By 1999 the species was no longer a significant indicator species, which either suggests a long-term shift in environmental factors making the habitat less hospitable to willow (such as encroachment of RCG), or that environmental factors shift so frequently that indicator species will shift accordingly on faster timescales.

The turnover of secondary indicator species may simply represent dynamic trends in compositional abundance. However, greater homogeneity of cover abundance within assemblages, and greater compositional abundance distinction between assemblages may result directly from overall loss of native floristic richness. These trends of high turnover and loss of richness may indicate greater susceptibility to invasion (Kuiters, *et al.*, 2009), and thus a loss of resistance over time to exotic species encroachment.

## Potential mechanisms

We propose several interacting mechanisms are likely responsible for the observed changes. These mechanisms include fragmentation of remnant tidal wetlands (loss of native propagules) and increased exotic abundance from municipal and agricultural settlement (introduction of exotic propagules), combined with altered sedimentation processes and resulting edaphic conditions.

Local colonization and extinction dependent on the local, but also regional propagule pool. At the local scale, if secondary species are becoming rarer due to local extinction, this results in loss of local propagative inputs to the habitat. However, local native species loss may be rescued by dispersal through regional aquatic networks. Yet if similar habitats within the estuarine ecosystem are lost to the point where distance between patches exceeds propagule dispersal distance (cite), then species colonization within the ecosystem is rare or lost. Similarly, if exotic species are more prevalent throughout the regional dispersal network, then there is a greater chance of exotic species introduction over native within a local marsh community. Ladner Marsh was described as being high in floristic diversity (Bradfield & Porter, 1982). We found this site is losing total species diversity, and becoming homogenized in terms of species cover. This indicates that a source of native propagules is being lost in the Fraser River Estuary dispersal network, and/or abundance of exotic propagules are more readily available, and thus more competitive in the environment. As exotic species increase in presence and abundance, they co-opt space and resources, increasing stress upon the native ecosystem. This stress feedback loop further shifts community composition and function, and over time consequential abiotic shifts may be altering the seed recruitment niches to favor exotics and limit native species recruitment (Lane, 2022). This reflects a general trend of exotic species’ competitive advantage in disturbed systems, and represents ongoing press disturbance by anthropogenic impacts with cumulative ecosystem effects.

A key abiotic driver of tidal marsh development includes sediment deposition that allows plant communities to compensate for changing inundation rates due to sea level rise (Marijnissen, et al., 2020). Sediment delivered by river transport is trapped by vegetation, creating a feedback loop of rising tidal marsh platforms, increased vegetation growth, and increased sediment trapping capacity (Corenblit et al., 2015; Peteet et al., 2018). In their 1982 publication, Bradfield and Porter proposed assemblage occurrence was largely driven by edaphic factors, with the Bogbean assemblage occurring in poorly drained areas, Sedge assemblage occurring in regularly flooded and drained areas, and Fescue assemblage along slightly elevated channel edges. Native *Menyanthes trifoliata* (bogbean) and exotic *Mentha aquatica* are highly adapted to aquatic or poorly drained habitats, and the increased prevalence of plots clustered in the Bogbean assemblage within Ladner Marsh may be indicative of changing edaphic factors such as sediment starvation or marsh subsidence (Mendelssohn & Kuhn, 2003; Nyman, Walters, et al., 2006). Conversely, in 1979 the Sedge assemblage was characterized by indicator species tolerant of highly saturated conditions, but by 2019 the assemblage included species more tolerant of drier conditions. These contrasting changes may indicate assemblage-specific patterns of subsidence and sediment deposition driven by vegetation structure or physical settling processes during sediment deposition.

Loss of sediment within the Lower Fraser River reaches is driven by a combination of factors, such as increased impervious cover, bank dyking or armoring, and channel dredging (Atkins, et al., 2016). Disentangling explicit sediment dynamics and causes for loss or changes in deposition of sediment over time would be difficult, however effects from these processes could lead to patchier distribution of saturated and well-draining areas within the marsh. Edaphic shifts resulting in more saturated areas would likely drive the increased prevalence of Bogbean assemblage, and may also be driving disappearance of species across all assemblages, as fewer species are able to tolerate increasingly saturated conditions. Similarly, areas receiving more sediment would accrete in elevation, and may also be more likely to receive exotic propagules within the distributed sediment. Thus, these processes may be altering the recruitment niche for clonal and seed propagules (Lane, 2022), which may favor species tolerant to the changing soil conditions (e.g., reed canary grass).

## Limitations & opportunities

While these data have shown coarse trends through time, we cannot account for interannual variation in compositional abundance trends. However, this snapshot of long-term trends may be used to refine future questions such as identifying whether abiotic drivers, recruitment potential, or assemblage-scale conservation of species diversity convey greater susceptibility or resistance to invasion and loss of native species diversity. We observed that while the Bogbean assemblage showed an increasing abundance of exotic *Mentha aquatica*, it retained cover abundance and increased richness of native species. Thus, although the assemblage is being invaded, homogenization and loss of diversity may be happening more slowly than in other assemblages. These trends may yield further insights to how abiotic processes mitigate or facilitate competitive pre-emption of space and propagule recruitment to prevent loss of species diversity.

Ecosystem stressors such as sediment loss, propagule loss, and competitive strategies are likely interacting, resulting in loss of species diversity and facilitating spread of invasive species. Disentangling explicit causes would be no easy task, however experimentally testing effects of sediment loading on species-specific clonal or seed recruitment would prove valuable for understanding best practices to shift the plant community towards functionally desired compositional states.

## Applications

Despite our knowledge to the contrary, we often erroneously assume “no direct anthropogenic disturbance” suffices to conserve an ecologically appropriate reference state (cite). However, the biodiversity loss described here presents real concerns for the resilience of this important community, and highlights negative impacts in unmanaged ecosystems thought to be relatively pristine. Most importantly: active management will be needed to maintain ecologically desired species composition in the face of climate change. These active management decisions will necessitate understanding native species loss through experimental adaptive management of hydro-geomorphological drivers, dispersal networks, and recruitment strategies.

These findings yet again confirm that contemporary “reference” sites are not sufficient benchmarks for restoration success (Shackelford, et al., 2021). Despite Ladner Marsh’s status as a protected wetland and legacy of little anthropogenic disturbance, its plant community is succumbing to cumulative pressures that reduce its quality as a reference condition. Therefore, as land managers consider restoration outcomes resilient to climate change in coastal wetlands, they must necessarily look beyond contemporary remnants of historic ecosystems to design models and functional ecological targets.

## Recommendations

If we are to prioritize conservation of functional coastal wetlands that include a significant representation of native species, we must seek new ways to actively manage habitats such as Ladner Marsh through mechanical control of invasive species (e.g., stands of reed canary grass), combined with experimental management practices using sediment application and/or native species planting to enhance ecosystem processes within remnant marsh habitats.

This active management process also presents a timely and necessary opportunity to engage with First Nations to revive traditional management practices: working with traditional knowledge holders may yield deeper understanding of plant community function and habitat stability, which would enhance ecosystem resilience and potentially lead to positive effects on salmonid populations while contributing to reconciliation between Indigenous and colonial cultures.