# Discussion – revised outline

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. The 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. Homogenization of **cover** abundance ***between*** (across) assemblages (cluster analysis), and increasing **cover** of exotic species
   * Main message: dominant species cover is becoming more dominant at the expense of cover of ‘rare’ species, sharpening the contrast in compositional abundance between assemblages.
     1. Exemplify how within-assemblage cover is more dissimilar (partitioned assemblages), and more similar cover within assemblages (homogenization).
        + If using the term ‘dominant,’ explain which contribute to homogenization (and thus definition of ‘dominant).
     2. Exemplify overall changes in native/exotic species cover from each assemblage. Consider the magnitude of cover, not just the % increase/decrease
        + Bogbean: ~385% increase in exotic M. aquatica cover since 1979 (25-50% mean plot cover in 2019), and introduction of exotic yellow flag iris (up to 25% 2019 mean plot cover) since 1979.
        + Fescue: ~1430% increase in exotic PHAR cover since 1979 (25-50% of 2019 mean plot cover)
        + Sedge: ~48% and 102% increase in exotic Lythrum salicaria and Festuca arundinaceae, respectively (< 25% in 2019 mean plot cover), and ~870% increase in native S. lasiandra cover since 1979 (< 25% in 2019 mean plot cover) -> woody link to edaphic changes. Meanwhile, assemblage-defining sp. decreased ~35% from 50-75% mean cover (1979) to 25-50% mean cover (2019).
        + Blue-listed species SIHE had ~46% decrease in fescue assemblage, but ~143% increase in sedge (< 25% mean plot cover) -> conservation implications/opportunities?
   * Fig. S5b: although mean exotic cover is not increasing substantially (actually decreasing in bogbean), the ratio of native to exotic is decreasing, resulting in greater proportional cover abundance of exotic species. This contributes to homogenization of cover between assemblages, and leads to potential loss of functional redundancy both between and within assemblages (transition to next paragraph).
2. Loss of total diversity and increasing beta **diversity** (increasing rarity of secondary species cover ***within*** assemblages) leads to biodiversity loss, and potential loss of functional redundancy within the assemblage.

Main message: native species contributing to floristic diversity are being lost, both in terms of presence/absence and cover abundance.

* + 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)
    1. Point out whether native species lost are generally “rare”, and whether they’re functionally different than the indicator species.
       - 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. Net 0 gain of exotics, however exotic RCG accounts for the greatest 2019 mean cover in the entire assemblage (25-50%).
    2. Contrast with explaining whether the species gained are functionally similar to those lost.
       - Bogbean: Overall, net gain of 1 native species and 3 exotic species. New native species gained include woody *Salix* sp., and cattail (*Typha latifolia*), which are different from species lost [how]. New exotic species include RCG and 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).
       - Sedge: Overall, 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 again are of significant mgmt. concern.
  + Highlight that this reflects broader global trends of biodiversity loss paired with exotic invasion, and unknown consequences for propagule dispersal networks, trophic cascades such as pollinator networks or primary production, which may be creating broader instability within the Fraser River Estuary ecosystem.

1. Shifts in secondary indicator species and turnover

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 as ‘indicators’ were the defining species *Carex lyngbyei* (sedge), and *Festuca arundinaceae*, (fescue).

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 wetland indicator species (*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, or that environmental factors shift so frequently that indicator species will shift accordingly on faster timescales.

* + Main message: overall losses in 2o indicators, and changes within those indicator species.
    1. Greatest loss of secondary indicator species in sedge and fescue assemblages. Bogbean is exception, although also has high invasion of exotic mint.
       - Here, if bogbean has lower richness turnover, does axiom of higher turnover = higher invasibility hold??
    2. Strength of indicator sp decreases over time,
       - ex, CALY’s indicator value drops every year, as does the strength of the 2 (different) assoc sp in 1979-1999; no assoc sp in 2019.
       - Or, in fescue, there is (1) 50% loss of floristic richness of 2o indicator species, and (2) exchange of one exotic indicsp (FEAR) for another (RCG). (3) strength of indval decreases over time regardless of species identity, indicating weaker signals of community dominant sp. This, combined with increasing strength of RCG indval, may indicate a loss of resistance to invasion within the assemblage.
         1. In 2019 fescue, RCG accounts for ~ 25% of plot mean cover (up 1400% since 1979, S7), while 26 native species have suffered 90-100% loss of cover, and only replaced with 8 new species or increasing abundance, each of which account for < 25% of mean plot cover
       - However, alternative trend in Bogbean – indval for METR, MYSC, MEAQ (99-19 only) always strong, but variable, over time, and no trend of losing 2o indicspecies overall (79-19)
  + Integrate previous themes of homogenization & biodiversity loss by talking about shifting secondary indicator species as shifts in functional traits within the assemblage, and indicate loss of resistance to increasing exotic species encroachment.
    1. ~~Higher species turnover can indicate greater invasibility~~ (Kuiters, Kramer, Van der Hagen, & Schaminée, 2009).

## Potential mechanisms

Several interacting mechanisms such as 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/edaphic conditions are likely responsible for the observed changes.

* + Local colonization/extinction dependent on the local but also regional propagule pool.
    1. Local: if secondary species are becoming rarer due to local extinction, this results in loss of local propagative inputs to the habitat.
    2. Regional: 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.
       - 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/or more competitive in the environment.
  + Increasing exotic species are co-opting space and resources while shifts in edaphic factors may be altering the recruitment and occupancy niches to favor exotics and limit native species recruitment (Lane, 2022). This reflects a general trend of exotic species’ competitive advantage in disturbed systems (\*emphasize press disturbance of anthropogenic impacts and cumulatively ecosystem effects).
  + Sediment dynamics paragraph (copied below from original Disc.)

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). 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 of sediment over time would be difficult, however effects from these processes would lead to more saturated patches within the marsh. Edaphic shifts 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.

* + - * Elaborate how this alters the recruitment niche for clonal and seed propagules (Lane, 2022), which may favor species tolerant to saturated soils (e.g., reed canary grass).

## Limitations & opportunities

These data do not show variation in short-term population dynamics over time, thus inferences of interannual trends in species turnover cannot be explicitly made. However, this snapshot is useful for observing coarse patterns of species shifts, and can be used to refine future questions such as identifying whether high-diversity assemblages, such as the Bogbean assemblage, may be more resistant to invasive species (and thus more stable).

* Describe somewhat lower indicators of homogenization in the bogbean assemblage (actual increase in richness; lower beta-diversity than other assemblages; comparable cluster dissimilarity over time of species cover abundance within assemblage) - give examples of species and abiotic conditions that may drive this slower homogenization.
  + Caveat is that the assemblage is still being invaded by water mint, so the assemblage is not immune; main takeaway is that homogenization/loss of diversity may just happening slower than in other assemblages. Opportunity is to examine whether population dynamics (e.g., spatial preemption) or abiotic conditions (e.g., more saturated soils) are preventing diversity loss.

Ecosystem stressors such as sediment loss, propagule loss, and marsh platform subsidence 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.

* “managers don’t know whether species loss is just stochastic attrition without an external source of propagules, OR if it’s a sedimentation issue. It’s not a flaw that you didn’t answer that question (it wasn’t your question), but it’s a good way to finish up (by pointing out that the driver is unknown, and it makes management actions unknown), if you want to end with management themes.”

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 in coastal wetlands, they must necessarily look beyond contemporary remnants of historic ecosystems to design models and functional ecological targets.

## Recommendations

* + Intro stated that understanding community composition changes can inform management intervention, therefore, close with a call for intervention to actively manage this WMA through mechanical control of invasive species (e.g., stands of reed canary grass), combined with experimental management using sediment application and/or native species planting to enhance ecosystem processes within remnant marsh habitats.
  + This active management process would be a prime 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.