# Discussion – old version

Repeat sampling of vegetation communities over long time frames can inform responses to global change along with appropriate conservation management. This study examined whether plant species assemblages within a protected area in the Fraser River Estuary are characterized by the same dominant species over time, whether measures of species diversity were stable within assemblage types, and whether turnover may be driven by increasing invasive species abundance. We find 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. However, we also find that there have been substantive changes in the species composition over time, indicating that despite conservation status and broad resilience of our study region, regional pressures are influencing considerable shifts in the species composition within this habitat. Moreover, cluster analysis shows there was increasing heterogeneity of species compositional abundance between assemblages, but greater similarity of species cover abundance within each assemblage (Figure 2). Overall, these findings indicate decreased cover abundance by fewer species within each assemblage type, creating patchy but sparse assemblages within in the community.

Although the Bogbean assemblage had a high abundance of non-native *Mentha aquatica* cover, it also had the highest α-diversity, and lowest β-diversity over time. Because bogbean (*M. trifoliata*) is tolerant of saturated soils, it may be that this assemblage type is more stable and resistant to diversity loss than assemblages with better-drained soils. The Fescue assemblage had the greatest loss of α-diversity, and greatest increase in β-diversity. The overall loss of species, and greater variation in species compositional abundance between plots in this assemblage may be indicative of greater loss of resilience, and increased susceptibility to invasion. Total turnover for all assemblages was higher in 1999-2019 than 1979-1999, and largely driven by species loss (disappearance), which is concerning for total biodiversity of the habitat and may indicate increased susceptibility to invasive species (Tilman, 1999). This is especially evident by encroachment of invasive species in the Fescue and Bogbean assemblages. The Fescue assemblage has historically been defined by a non-native species (*Festuca arundinaceae*), however abundance of *Festuca arundinaceae* is being overtaken by *Phalaris arundinaceae*, or reed canary grass (RCG). This presents a management concern for Ladner Marsh, as RCG can be a monoculture-forming species (Apfelbaum & Sams, 1987), further reducing species diversity within the community. Similarly, the Bogbean assemblage is increasingly dominated by non-native *Mentha aquatica*, however this assemblage did not lose as much floristic richness as the Fescue assemblage did (Table 7, Supplemental). Increasing abundance of specific non-native species, paired with cluster analysis showing greater similarity within plots of each assemblage, supports our expectation that species loss is being driven by proliferation of non-native species.

The patterns reported here of lost plant species richness over time are reflected in global trends driven by anthropogenic stressors such as urbanization and climate change, and related risk of species homogenization (Brice, Pellerin, & Poulin, 2017; Dornelas et al., 2014). In tidal wetlands, a key climate change-related concern is sea level rise, which will lead to habitat loss through “coastal squeeze” (Torio & Chmura, 2013). Some species will be adaptable to the changing inundation regimes, and tidal marsh habitats can be resilient to climate change if land managers take action before species losses are too great (Short, et al., 2016). Maintaining diverse estuarine habitats under sea level rise important for a variety of wildlife, including migratory and resident shorebirds, and anadromous salmon populations (Chalifour et al., 2019; Finn et al., 2021; Kehoe & Martin, 2021). Understanding historical trends in species composition and assemblage heterogeneity is critical for land managers to define measures of success in restoration projects, and for conserving ecological processes. In the absence of ideal reference conditions, use of historical datasets may be used to determine ecologically meaningful benchmarks. While historical conditions can provide greater understanding of species diversity, land managers must be aware of species composition and abundance shifts, which are only possible to detect through long-term monitoring projects and resampling such as in this study.

## Study limitations

These data do not show variation in population dynamics over time, thus inferences of interannual trends in species gained/lost 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). Permanent transects were not used, thus transect relocation and plot placement may have resulted in somewhat different observations. However, bootstrapping minimum numbers of plots in each assemblage did not reveal alternative patterns, offering assurance of the general trend of species loss.

Mechanistic processes to explain changes in species composition or site factors were not tested. However, likely driving factors can be inferred to generate new tests of mechanistic changes in in community stability. Specifically: edaphic factors may be driving species selection by adaptation to saturation or drainage between assemblage patches, more strictly partitioning the diversity of species that can occupy an assemblage. Additionally, recruitment of new diverse individuals into the assemblage may be limited due to dispersal or recruitment limitation.

## Potential mechanisms

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. *Menyanthes trifoliata* (bogbean) and *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.

Besides potential abiotic drivers of species loss, species recruitment may also be impacted. Regional pools of propagules (seeds, clonal fragments) are required to disperse into a site, and suitable conditions must exist to recruit the propagules into the population. If remnant habitats such as Ladner Marsh are locally losing species (or if the habitat is lost altogether through development), species diversity is being lost from the dispersal network , which effectively fragments the dispersal network and potentially leads to regional extinction (Deane, et al., 2017).

## Broader impacts & recommendations

Long-term monitoring is relatively rare, but necessary to inform future management and planning (Willis et al., 2007). Land management planning in anticipation of climate change, particularly sea level rise, should be cognizant of biodiversity loss. This is important at global scales (e.g., global objectives for wetland conservation outlined by the Ramsar Convention), but also at national and local conservation initiatives (e.g., meeting objectives of Canada’s Oceans Protection Plan or British Columbia’s Salmon Restoration & Innovation Fund). Understanding what tidal marsh community stability looks like within decadal timescales is useful to land managers wanting to maintain or restore shoreline communities for immediate habitat conservation or floodwater protection initiatives that will have broader resilience to sea level rise. Initiatives for tidal marsh restoration must identify some ‘reference’ condition (Hallett et al., 2016), which needs to be account for anthropogenic impacts such as biodiversity loss (Diefenderfer et al., 2011). This study is a case-in-point that the biodiversity and compositional abundance of the habitat (and thus ‘reference’ condition) in Ladner Marsh has changed over 40 years despite protected status, and revealed a decreased reference quality in 2019 compared to the original 1979 survey. It is also important to note its condition when surveyed in 1979 was undoubtedly altered from earlier compositional states, and thus not truly a reference to tidal marshes undisturbed by colonial and industrial impacts.

The main need from these results is to determine whether species loss and decreasing habitat heterogeneity is driven by loss of sediment quantity or quality (Nyman et al., 2006), and whether this is affecting the ability of native species to recruit into the community from seed or clonal propagules. If sedimentation quantity or quality is limiting positive feedback between marsh accretion and vegetation recruitment, land managers must address this by implementing sediment application programs to mimic natural sedimentation (VanZomeren, et al., 2018). A paired need is to decouple sedimentation drivers of recruitment from loss of seed or propagule diversity from the dispersal network. If sedimentation is adequate to recruit individuals, recruitment may still be limited by loss of seed or clonal propagules from the dispersal network (Erfanzadeh, et al., 2010; Rand, 2000). If this is the case, land managers must re-introduce populations of native species to existing habitats. These efforts should also be paired with restoration or creation of marsh habitat to increase dispersal connectivity throughout the estuary.

# Discussion – revised outline

We find there have been substantive changes in the 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.

* Emphasize the importance of changes as a case example of broader global trends of species homogenization, and 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*** 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 changes in invasive species cover from each assemblage. Consider the magnitude of cover, not just the % increase/decrease
   * Explain or emphasize how increasing abundance of exotic cover and homogenization of cover across assemblages leads to potential loss of functional redundancy (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: species contributing to floristic diversity are becoming more locally rare, both in terms of presence/absence and cover abundance.
   * Emphasize whether more natives/exotics were lost/gained.
     1. Point out whether species lost are generally “rare”, and whether they’re functionally different than the indicator species.
     2. Contrast with explaining whether the species gained are functionally similar to those lost.
   * Highlight that this reflects broader global trends of biodiversity loss, and unknown consequences for trophic cascades such as pollinator networks or primary production which may be creating broader instability within the ecosystem.
3. Shifts in secondary indicator species and turnover
   * Main message: lower turnover is related to greater stability, thus we should expect fewer shifts in associated indicator species in stable communities. This was not the case given our observations. (\*give examples).
     1. Higher species turnover can indicate greater invasibility (Kuiters, Kramer, Van der Hagen, & Schaminée, 2009).
   * 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.

## 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.