# Results

Three main assemblages within Ladner Marsh can be characterized by the same dominant species across all sampling periods. However, cluster analysis shows species cover is becoming more homogenous within assemblages, but more distinct between assemblages (Figure 2). While the indicator species with greater significance across each assemblage remain constant over time (*i.e.*, *Carex lyngbyei*, *Menyanthes trifoliata, Fescue arundinaceae*) and drive cluster groups, other species that significantly drive indicators of assemblages change over time (Table 1, Table 4). For example, in 1979 the indicator species defining the Sedge assemblage cluster were *C. lyngbyei, S. latifolia,* and *S. tabernaemontani*, however in 1999 the same assemblage included indicator species *C. lyngbyei, A. stolonifera,* and *I. capensis*. Thus, although *C. lyngbyei* remained the common indicator species of the assemblage cluster group, the associated indicator species had changed. Additionally, fewer indicator species were found in the Sedge and Fescue assemblages in 2019 than in 1979. For example, the Sedge assemblage was characterized by three species (including *C. lyngbyei*) in 1979 and 1999, but only by *C. lyngbyei* in 2019. The Fescue group was characterized by seven species in 1979, four species in 1999, and three species in 2019. While *Festuca arundinaceae* remained a common indicator species within the assemblage, all other indicator species changed in each observation year.

Across the entire Ladner Marsh plant community, two to three species were lost each year following the 1979 survey. Within every assemblage alpha-diversity (mean number of species per plot) decreased every observation year, while beta-diversity (variation in number of species between plots) increased each year for all assemblages. (Table 2) For example, the Sedge community suffered the least loss of species and alpha-diversity across sampling years, although beta-diversity increased as in other assemblages, indicating increasing variability (and thus increased rarity) in which species may be encountered within a given assemblage. The Fescue assemblage had the greatest loss of alpha-diversity (> 50%) between 1979 and 2019. Nearly 50% fewer plots clustered as Fescue in 2019 than in 1979, however bootstrapping 18 random plots from every sampling year showed the same trend, indicating that loss of species is not related to loss of plots (Table S5). Total magnitude of species turnover between 1999 and 2019 was ~50% in each assemblage, largely driven by greater species disappearance (loss) between 1999 and 2019 (Table 6). The greatest loss of native species richness occurred in the Fescue assemblage, while nominal gains in exotic richness were found in all assemblages (Table 7). The Fescue assemblage lost a total of 23 native species (net loss of 18 native species) between 1979 and 2019. Among the species lost from the assemblage, 12 were lost from all three assemblages (six forbs, six graminoids), or were never found in any other assemblage. Species gained include two woody species, and one each of forb, graminoid, and fern ally (*Equisetum arvense*). There was a net zero gain of exotics in the Fescue assemblage, however exotic RCG accounts for the greatest 2019 mean cover in the entire assemblage (25-50% mean cover). In the Bogbean assemblage, new exotic species include *Phalaris arundinaceae* (reed canary grass, RCG) and *Iris pseudacorus* (yellow flag iris). Within the Sedge assemblage, there was a net loss of 3 native species, and net gain of 3 exotic species, including yellow flag iris and RCG. As of 2019, these species accounted for < 25% mean cover, but may be of significant management concern.

Cover abundance of species significantly driving assemblage associations show an overall trend of decreasing cover over time (Figure 3). Notably, Fescue assemblage shows ~50% decrease in cover of characteristic exotic species *Festuca arundinaceae* between 1979 and 2019, while cover of exotic *Phalaris arundinaceae* tripled since 1999. In the Sedge assemblage both native keystone species *Carex lyngbyei* and exotic grass *Agrostis stolonifera* had decreased cover abundance from 1979-2019 (Figure 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% mean cover) by 2019 (Table 7). Similarly, in the Bogbean assemblage, cover abundance of native keystone species *Menyanthes trifoliata* had declined ~21% (50-75% mean cover) by 2019, while cover of exotic *Mentha aquatica* had increased ~385% (~25-50% mean cover). In summary, while the dominant species are maintained, their cover abundance within each assemblage is declining. Moreover, some exotic species have increased substantially in cover abundance in the Fescue and Bogbean assemblages since the original survey, indicating these assemblages are becoming increasingly occupied by exotic species.

# Discussion

Despite conservation status and broad resilience of this ecosystem we found there have been substantive changes in species composition over time, potentially indicating broader-scale processes affected by regional pressures. We found the three species most significantly characterizing the three main plant assemblages, Sedge, Fescue and Bogbean, have remained the same over the past 40 years, supporting our expectation that these characteristic species should not change in the absence of significant environmental disturbance. Also, in line with our expectations, we observed a decline of native species richness accompanied by an increased richness and abundance of exotic species. This has led to homogenization of cover abundance within assemblages, greater dissimilarity between assemblages, and 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.

The biodiversity loss of native species richness could potentially indicate loss of functional redundancy (and thus resilience) within the assemblage or marsh community as a whole, although many species gained and lost between years were comparable in terms of generalized plant function. That is, the exchange of one perennial graminoid or forb species for another may not result in community-wide functional changes. One functional group to note were the woody species gained and lost, as woody species traits convey different structural habitat qualities than herbaceous species. Willow (*Salix* sp.) was most prevalent in the Fescue assemblage in 1979, but was most abundant in the Sedge assemblage in 2019. This could suggest long-term shifts in edaphic factors and/or the subsequent encroachment of exotic reed canary grass (“RCG,” *Phalaris arundinaceae*), making the Fescue assemblage less hospitable to willow. The identity of the shifting indicator species may also 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*). *[that’s all, folks?]* The turnover of secondary indicator species may simply represent high interannual variation in species compositional abundance, despite being a perennial-dominated community. 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. Over time the ratio of native to exotic cover within assemblages declined, although few species (native or exotic) represent the majority of cover within the assemblage (Figure 5b). Exotic species of local management concern (e.g., RCG, yellow flag iris (*Iris pseudacorus*)) were < 25% mean plot cover in 2019, however these species are notorious for quickly spreading to the point of near-exclusion of other species (especially natives) (Apfelbaum & Sams, 1987; Sinks et al., 2021).

Loss of sediment within estuaries including the Fraser River Estuary is driven by a combination of factors, such as increased impervious cover, bank dyking or armoring, and channel dredging (Atkins et al., 2016). Sedimentary changes such as sediment starvation or subsidence would result in more saturated areas, which would likely drive the increased prevalence of Bogbean assemblage (Mendelssohn & Kuhn, 2003). Alternatively, positive feedbacks between vegetation and sedimentation could support areas of marsh accretion (Nyman et al., 2006), which may also be more likely to receive exotic propagules within the distributed sediment. Whether or not seed propagules are present would depend on local and regional propagule pools. If similar habitats within the estuarine ecosystem are lost to the point where distance between patches exceeds propagule dispersal distance (Shi, et al., 2020), 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. Abiotic shifts may be altering the seed recruitment niches to favor exotics and limit native species recruitment (Lane, 2022), while dispersal networks may be delivering disproportionately more exotic species seed. 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.

## Synthesis & Recommendations

Species invasion and native species loss may increase ecosystem instability through fragmented or lost propagule dispersal networks, and result in altered trophic cascades such as pollinator networks or primary production. These changes will have implications for endangered species, such as *Sidalcea hendersonii*, a species of special concern under the Canadian Species at Risk Act found in Ladner Marsh. It is difficult to say whether abiotic conditions or encroaching exotic species such as RCG were responsible for its shift in greatest cover abundance from the Fescue (1979) to Sedge (2019) assemblage. Disentangling explicit impacts of sedimentary, dispersal, or recruitment processes would be no easy task, however experimentally testing effects of sediment loading on species-specific clonal or seed propagule recruitment could prove valuable for understanding best practices to maintain populations or community function.

Despite our knowledge to the contrary, practitioners often erroneously assume no direct anthropogenic disturbance suffices to conserve an ecologically appropriate reference state (e.g., Stoddard, et al., 2006, and citations therein). These findings yet again confirm that contemporary “reference” sites are not sufficient benchmarks for restoration success (Shackelford, et al., 2021). The biodiversity loss described here presents real concerns for this community, and highlights negative trends in unmanaged ecosystems thought to be relatively pristine. Most importantly: active management informed by experimental testing of hydrogeomorphologic drivers, dispersal networks, and recruitment strategies will be needed to maintain ecologically desired species composition in the face of climate change. 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, 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, such as select mechanical disturbance (Turner, 2014): 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.