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Plant community compositional stability over 40 years in a Fraser River Estuary tidal freshwater marsh

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Abstract

Long-term data sets documenting temporal changes in vegetation communities are uncommon, yet imperative for understanding trends and triggering potential conservation management interventions. For example, decreasing species diversity and increasing non-native species abundance may be indicative of decreasing community stability. We explore long-term plant community change over a 40-year period through the contribution of data collected in 2019 to two historical datasets collected in 1979 and 1999 to evaluate decadal changes in plant community biodiversity in a tidal freshwater marsh in the Fraser River Estuary in British Columbia, Canada. We examine whether characteristic plant assemblages are consistent over time, whether alpha (α) and beta (β) diversity change within and between assemblages, and whether associated indicator species change. We found that plant assemblages were characterized by the same dominant indicator species, but most other indicator species changed, and that overall α-diversity decreased while β-diversity increased. Further, we found evidence for plant assemblage homogenization through the increased abundance of non-native invasive species such as yellow flag iris (*Iris pseudacorus*) and reed canary grass (*Phalaris arundinacea*). These observations may inform concepts of habitat stability in the absence of pulse disturbance pressures, and corroborate globally observed trends of native species loss and non-native species encroachment. Our results indicate that within the Fraser River Estuary, active threat management may be necessary in areas of conservation concern in order to prevent further native species biodiversity loss.

Introduction

In a time of rapid global change, temporal shifts in plant community composition can indicate ecosystem stress response and inform conservation management interventions. Shifts in community-dominant species may be indicative of interspecific interactions such as facilitation (Bruno, 2000), succession (Butzeck et al., 2016), or cycles of population dynamics (Holling, 1973). Alternatively, changes in community-dominant species paired with loss of native species diversity and increasing abundance of non-native species may indicate loss of stability through loss of functional redundancy (Donohue et al., 2016; Tilman, 1999; Palmer et al., 1997). In turn, this may indicate reduced resistance to change or capacity to recover from disturbance, known as resilience (Tilman et al., 2006; Bai et al., 2004). Furthermore, the local loss of native species may have stronger negative impacts on regional biodiversity persistence when the regional pool of potential species is reduced or environmentally constrained (Lepš, 2004; Hanski, 1982). Characterization of plant community changes on decadal timescales contributes to observation of meaningful long-term patterns of compositional stability, and is instructive for developing hypotheses to test drivers of disturbance, especially in data-deficient, dynamic landscapes heavily impacted by anthropogenic activities such as estuaries (Underwood et al., 2000; Ovaskainen et al., 2019).

Estuaries are at the terrestrial-marine interface where hydrogeomorphic and ecological changes occur on annual, decadal, and millennial timescales (Pasternack, 2009). Estuarine habitats support high species richness, including species at risk (Kehoe et al., 2021) and are important carbon reservoirs (Gailis et al., 2021; Douglas et al., 2022). Because these ecosystems will experience accelerated change under sea

level rise, they are of increasing conservation concern (Brophy et al., 2019); understanding estuarine habitat changes and implications for habitat stability can inform global change resilience strategies. Estuaries in North America are of particular conservation importance in the Pacific Northwest (PNW) because their pathways of retreat or expansion are often spatially restricted by fjord geography (Emmett et al., 2000), whereas estuaries along the Atlantic coast may spread along expansive coastal plains. Tidal freshwater marshes are the upper reaches of estuaries dominated by riverine freshwater, and in the PNW they are particularly important as early transitional habitat along a salinity gradient for anadromous salmonids (Davis et al., 2021; Chalifour et al., 2019). The Fraser River Estuary is the largest estuary in British Columbia and of irreplaceable ecological and commercial value, yet has lost 85% of floodplain and 64% of stream habitat in the Lower Fraser watershed (Finn et al., 2021), emphasizing the need to understand the condition of remaining estuarine habitat. Estuary conservation efforts are intended to protect coastal municipalities and provide sufficient habitat for wildlife. Stability of plant communities within tidal marshes contributes to the ability of these habitats to resist change or recover from disturbance (Holling, 1973).

A barrier to understanding community stability, including within estuaries, is the lack of long-term data. In the absence of long-term monitoring, historical datasets can provide a 'snapshot' of species compositional variation over time. One such opportunity exists in the Fraser River estuary, British Columbia, Canada in an area called Ladner Marsh (Fig. 1). Despite large-scale industrialization and urbanization within the region, Ladner Marsh has escaped direct industrial development, and to the best of our knowledge has not experienced major natural or anthropogenic disturbance in the past 50 years. Two historical studies conducted in Ladner Marsh (Bradfield & Porter, 1982; Denoth & Myers, 2007) used similar methods to document floristic diversity. Bradfield & Porter (1982) tested whether species dominating the community statistically characterized distinct sub-community assemblages within the marsh. Their analysis distinguished three assemblages, each dominated by a unique species: Sedge (*Carex lyngbyei* Hornem.), Fescue (*Schedonorus arundinaceus* (Schreb., formerly *Festuca arundinacea*) Dumort., nom. cons.), and Bogbean (*Menyanthes trifoliata* L.). They postulated that edaphic factors drove assemblage distribution: that the Bogbean assemblage occurred on waterlogged soils, the Fescue assemblage on well-drained soils mostly along levees, and the Sedge assemblage along channel edges with greater inundation frequency. Twenty years later, Denoth & Myers (2007) repeated the sampling methods to test relationships between non-native purple loosestrife (*Lythrum salicaria* L.) and native Henderson's checker-mallow (*Sidalcea hendersonii* S. Watson), a threatened species. While these studies independently characterize different community metrics, these datasets provide the opportunity to repeat observations and characterize long-term plant community changes to inform inferences about habitat stability. We used three observational datasets spanning four decades to answer the following questions:

(1) Are tidal freshwater marsh assemblages characterized by the same dominant plant species over a 40-year period? In the absence of significant environmental disturbance, we expect the same species composition to dominate each assemblage as identified by Bradfield & Porter (1982).

(2) Are assemblages characterized by similar indicator plant species? If not, which species gained or lost are associated with changes within each assemblage? We expect that increasing abundance of non-native species over time would result in a greater net loss of native species.

(3) Is the mean species diversity (α-diversity) and variation (β-diversity) within and between assemblages constant between the three sampling periods (1979, 1999, 2019)? If the plant community is stable, we expect little change in α-diversity and β-diversity.

Methods

The Fraser River is the largest watershed catchment in British Columbia, covering one quarter of the province (Finn et al., 2021). The current extent of the Fraser River Estuary spans 2,814 ha, one-third of which lies within the South Arm Marshes Wildlife Management Area, which was formally protected in 1991 (Schaefer, 2004) (Fig. 1B). Ladner Marsh occupies approximately 100 ha within the South Arm Marshes, bounded to the east by urban and industrial development and to the west by the Fraser River (Fig. 1). Plant species common to these habitats are generally herbaceous, and the community is largely dominated by sedges and rushes with some salinity tolerance, and a diversity of herbaceous flowering species (hereafter, forbs). This publication will reference dates the data were collected, rather than publication dates of the corresponding studies.

Our main goal was to sample the vegetation in a representative way to allow comparison with the datasets collected in 1979 (Bradfield & Porter, 1982) and 1999 (Denoth & Myers, 2007). Because Bradfield & Porter (1982) wanted to assess whether statistical analysis verified visual estimation of species associations, the sampling conducted in 1979 introduces a bias to statistically confirm patterns identified by subjective visual assessment. Denoth and Myers (2007) sought to relocate plots sampled by Bradfield & Porter (1982). In 2019 we sought to sample vegetation in as close a manner as the original 1979 survey, which does not eliminate bias from previous sampling designs. However, within the context of this sampling design we can make comparisons of changes in floristic diversity and compositional abundance.

No permanent markers were left in Ladner Marsh, so precise transects assessed by Bradfield & Porter (1982) or Denoth & Myers (2007) were not identifiable in 2019. Transect endpoints were approximated within an estimated ~ 5 m by overlaying Fig. 1 in Bradfield & Porter's 1982 publication (Fig. 1C) on a georeferenced basemap, aligning prominent features such as tidal channel tributary junctions, marking GPS locations in Avenza Maps (Avenza Systems Inc., Ontario, Canada, v. 3.2), and finding these points in the field. Transect "Q" (n = 7 plots) was omitted in 1999 and 2019 due to inaccessibility through riparian forest with a dense understory of non-native Himalayan blackberry (*Rubus armeniacus* Focke); these plots from 1979 were not surveyed in 1999, and are not included in the present analyses. An additional 18 plots surveyed in 1979 and 1999 were also omitted in 2019 because of overgrowth of riparian fringe, widening of tidal channels, or variation in transect placement (Table S1). Despite these decisions to

exclude plots, Kopecký & Macek (2015) have demonstrated that uncertainty of plot location does not produce unreliable evidence of plant community changes on decadal timescales.

Along each transect, we noted patchy species assemblages dominated by one or two species. We defined 'dominance' as a species having more than 50% cover within the patchy assemblage (Fig. 2). If patches extended along more than 10 m of transect length, or no dominant species could be determined, we sampled every 10 m of transect length; we did not consider patches adjacent to the transect. Each plot was comprised of a 1 m^2 quadrat centered over the transect to survey species composition and cover abundance within the center of the species-dominated patch, or every 10 m of transect length, whichever distance was shorter (Fig. 2D). No patches were so small that the 1 m^2 plot was less than 1 m from the boundary of the next patch. To record species compositional abundance, we identified all species with ≥ 50% of their foliage-producing basal stems within the plot boundary; overhanging foliage from basal stems outside the plot were not considered. For clonally reproducing species (e.g., *Carex lyngbyei*), we did not attempt to distinguish stems or ramets from whole plants. Aerial plot cover was estimated by modified Braun-Blanquet cover classes [0 = (0%), 1 = (< 25%), 2 = (25–50%), 3 = (50–75%), and 4 = (> 75%)].

Taxonomy

For all sampling years, observation of vascular plant species was conducted in early summer when species are identifiable by sexual reproductive traits, but before senescence (approx. June – July). In all datasets, most plants were identified to species according to Hitchcock & Cronquist (1973), although a few were identified at higher taxonomic levels due to insufficient identifying characteristics (n = 6 to genus, n = 2 to Family; see Table S7). To account for changes in nomenclature revision over time, all datasets were harmonized to use the most recently accepted species name as reported in the PLANTS Database of the United States Department of Agriculture, Natural Resources Conservation Science [USDA NRCS]. For example, in the instance of *Agrostis* species, we assumed *Agrostis alba* L. identified in 1979 and 1999 was synonymous with *Agrostis stolonifera* L. in 2019. All species and their synonymous nomenclature from prior data collection years are available in Supplemental Table S7.

Analyses

All analyses were performed in R v. 4.2.1 (R Core Team, 2022). We performed cluster analysis on species compositional abundance at the plot scale for each dataset. We used Euclidean distance as the measure of plot dissimilarity ("stats," R Core Team) to facilitate direct comparisons to results produced by Bradfield & Porter (1982). Following (Legendre & Legendre, 2012), we also performed cluster analysis using Bray-Curtis dissimilarity to compare with Euclidean distance and found no meaningful difference in results from the two distance measures. For each dataset, three main clusters were identified (termed "assemblages"), and species indicator analysis was used to determine which species' compositional abundance characterized each assemblage ("indicspecies,"R package De Cáceres & Jansen, 2016). Indicator Value (IndVal) association indices between species and clustered assemblages were calculated

using an abundance-based point biserial correlation coefficient (multipatt func = “r.g”), and significance of associations was tested by permutational analysis (Dufrêne & Legendre, 1997). All species’ mean cover abundance is summarized in Table S6.

Community diversity calculations for each year of observation followed Whittaker (1975), with α-diversity calculated as the mean number of species per plot within an observation year and assemblage, and β-diversity calculated as the total number of species within the assemblage divided by α-diversity. These calculations were also performed on all data recorded for each observation year to generate community-wide measures of diversity. Community turnover for each assemblage was measured using the “codyn” R package (Hallett et al., 2016). Total species turnover (total magnitude of change), species gained (appearances), and species lost (disappearances) were calculated as a percent change for each assemblage between 1979–1999, and 1999–2019. Total turnover was calculated as a ratio of the absolute value of species gained and lost to the total number of species observed in both timepoints.

During analyses, both Euclidean and Bray-Curtis distances were used to assess the effect of distance measure on results; cluster analysis figures and indicator species using Bray-Curtis distance are available in supplementals Fig. S1 and Table S2, respectively. To address inconsistent numbers of plots grouped into assemblages each year, diversity metrics were bootstrapped 10 times using the minimum number of plots observed in an assemblage each year (n = 18) (Table S3).

Results

Three main assemblages identified by cluster analysis, characterized by the same dominant indicator species – Sedge (*Carex lyngbyei*), Fescue (*Schedonorus arundinaceus*), and Bogbean (*Menyanthes trifoliata*) – were evident across all sampling periods (Fig. 3). Overall dendrogram structures were similar for 1979 and 1999, but two main vegetation changes were evident in the 2019 dendrogram, notably, an increased homogenization of assemblages (i.e., shorter dendrogram branch lengths within cluster groups, and longer branch lengths between cluster groups), and a switch from a stronger Bogbean-Sedge connection 1979 and 1999 to a stronger Fescue-Bogbean connection in 2019 (Fig. 3).

While the three assemblage indicator species remained constant over time, changes were evident in other species with significant indicator values (Table 2). For example, in 1979 the indicator species defining the Sedge assemblage cluster were *C. lyngbyei, Sagittaria latifolia* Wiild., and *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla. In 1999, however, the same assemblage included indicator species *C. lyngbyei*, and *Impatiens capensis* Meerb. By 2019, *C. lyngbyei* was the only indicator for this assemblage. Similarly, *S. arundinaceus* remained a common indicator species within the Fescue assemblage, but the assemblage lost four out of seven total indicator species between 1979–2019. While the identities of the remaining indicator species changed, there was no strong trend of changes in clade, or potential difference for changes in ecological function based on a qualitative review of changing species identity.

Across the entire Ladner Marsh plant community, two to three species were lost from each sampling year following the 1979 survey (Table S6). Within every assemblage α-diversity (mean number of species per

plot) decreased every observation year, while β-diversity (ratio of total species in the assemblage to α-diversity) increased each year for all assemblages (Table 1). For example, the Sedge community suffered the least loss of species and α-diversity across sampling years, although β-diversity increased as in other assemblages, indicating increasing variability in which species may be encountered within a given assemblage. The Fescue assemblage had the greatest loss of α-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 was not related to loss of plots (Table S3). 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 S4).

The greatest loss of native species richness occurred in the Fescue assemblage, while gains in non-native richness were found in all assemblages (Fig. S2). The Fescue assemblage had a net loss of 17 native species between 1979 and 2019 (Table S5). Among the species lost from the Fescue 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* L.). There was a net loss of one non-native species in the Fescue assemblage, however non-native invasive *Phalaris arundinacea* (reed canary grass) accounts for the greatest 2019 mean cover in the entire assemblage (25–50% mean cover, Table S5). In the Bogbean assemblage, the net gain of two non-native species included *P. arundinacea* and *Iris pseudacorus* L. (yellow flag iris). Within the Sedge assemblage, there was a net loss of two native species, and net gain of two non-native species, including *P. arundinacea* and *I. pseudacorus*. As of 2019, these species accounted for ≤ 25% mean cover, but may be of significant management concern (Fig. 4).

Assemblage-defining indicator species showed an overall trend of decreasing cover over time (Fig. 4). Notably, in the Fescue assemblage, the cover class of non-native indicator *S. arundinaceus* fell from a mean of ~ 1.5 to ~ 0.75 from 1979–2019, while the mean cover class of non-native *P. arundinacea* tripled from 1999–2019. In the Sedge assemblage native indicator sedge species *C. lyngbyei* decreased cover abundance from 1979–2019 (Fig. 4), stepping down from a mean cover class value of 3 (50–75% cover) to 2 (25–50% cover) between 1979–2019. Meanwhile, non-native species *L. salicaria* and *S. arundinaceus* increased in their mean cover abundance, although both species remained in the same mean cover class (≤ 25% mean cover) by 2019. Similarly, in the Bogbean assemblage, cover abundance of native species *M. trifoliata* declined from a mean cover class of 4 (> 75%) to 3 (50–75% mean cover) by 2019, while cover of non-native *Mentha aquatica* L. increased from a mean cover class of 0.4 in 1979 (Table S5) to a mean cover class of ~ 2 (~ 25–50% mean cover) by 2019 (Fig. 4, Table S5).

Table 1

Between 1979 and 2019, 8 fewer plots and 5 fewer species were observed, resulting in lower α-diversity and greater β-diversity. For each assemblage type, Bogbean is the only assemblage to proportionally gain plots between 1979 and 2019, while the Fescue and Sedge assemblages lost plots. Plot loss did not appear to have an effect on diversity components, as tested by bootstrapping a minimum of 18 plots per assemblage each year (Table S3)

	Plot-level components		Diversity components		
Assemblage	**No. plots**	**No. species**	**α diversity**	**α diversity sd**	**β diversity**
Sedge					
1979	34	36	8.7	2.5	3.9
1999	31	35	8.3	2.0	4.2
2019	28	34	7.9	2.7	4.3
Fescue					
1979	29	45	10.8	3.9	4.2
1999	33	41	9.7	4.0	4.2
2019	18	27	5.8	2.8	4.6
Bogbean					
1979	19	30	10.8	3.6	2.8
1999	18	36	11.5	2.9	3.1
2019	28	34	10.5	1.9	3.3
Total					
1979	82	48	10.0	3.4	4.8
1999	82	45	9.6	3.3	4.7
2019	74	44	9.4	3.0	4.7

Table 2

Species significantly driving cluster groups (Euclidean distance) include the same dominant species in each assemblage type (Sedge by *Carex lyngbyei*, Fescue by *Schedonorus arundinaceus*, Bogbean by *Menyanthes trifoliata*). Indicator species significantly defining the assemblage reported for $p < 0.05$

	1979		**1999**		**2019**	
Cluster Group Name	Species	p-value	Species	p-value	Species	p-value
"Sedge"	*Carex lyngbyei*	< 0.01	*Carex lyngbyei*	< 0.01	*Carex lyngbyei*	< 0.01
	Sagittaria latifolia	< 0.01	*Impatiens capensis*	0.01		
	Schoenoplectus tabernaemontani	< 0.01				
"Fescue"	*Schedonorus arundinaceus*	< 0.01	*Poa palustris*	< 0.01	*Phalaris arundinacea*	< 0.01
	Salix lasiandra	< 0.01	*Schedonorus arundinaceus*	< 0.01	*Schedonorus arundinaceus*	< 0.01
	Equisetum palustre	< 0.01	*Trifolium wormskioldii*	< 0.01	*Equisetum fluviatile*	0.01
	Lathyrus palustris	< 0.01	*Bidens cernua*	< 0.01		
	Sidalcea hendersonii	0.01				
	Hordeum brachyantherum	0.02				
	Deschampsia caespitosa	0.05				
"Bogbean"	*Menyanthes trifoliata*	< 0.01	*Mentha aquatica*	< 0.01	*Menyanthes trifoliata*	< 0.01
	Myosotis scorpioides	< 0.01	*Menyanthes trifoliata*	< 0.01	*Mentha aquatica*	< 0.01
	Bidens cernua	< 0.01	Grass (unidentified)	< 0.01	*Lysimachia thyrsiflora*	< 0.01
	Lythrum salicaria	< 0.01	*Lythrum salicaria*	< 0.01	*Galium trifidum*	< 0.01
	Equisetum fluviatile	0.01	*Juncus articulatus*	< 0.01	*Myosotis scorpioides*	0.01
	Lysimachia thyrsiflora	0.01	*Equisetum fluviatile*	< 0.01	*Juncus articulatus*	0.02

1979	1999	2019
	Myosotis scorpioides	< 0.01
	Eleocharis palustris	0.02
	Equisetum variegatum	0.04
	Deschampsia caespitosa	0.03

Discussion

Despite its status as a Wildlife Management Area and general resilience of the Fraser River tidal marsh ecosystem we found substantive changes in species composition over a 40-year time-frame, potentially indicating broader-scale processes affected by regional pressures. The three species most significantly characterizing the three 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 disturbance. We observed a decline of native species richness accompanied by an increased richness and abundance of non-native species, including invasive non-native species. Of greater concern is our observation of the homogenization of cover abundance within assemblages, and overall loss of indicator species for the Sedge and Fescue assemblages. Increasing abundance of non-native species within each assemblage is likely driving the greater similarity within assemblages (homogenization) and greater dissimilarity between assemblages, as shown by cluster analysis (Fig. 3). While addition of non-native species can contribute to greater biodiversity (Sagoff, 2005), the homogenization of plant communities (especially by dominance of non-native invasive species) leads to lower diversity overall (Houlahan & Findlay, 2004), which in turn may lead to lower functional redundancy and potential for reduced ecosystem stability (de Bello et al., 2021).

The changing identity of species or functional traits in an assemblage may offer clues to shifting abiotic conditions within or between assemblages (Waller et al., 2020). One functional group to note were the woody species, as their traits convey different structural habitat qualities than herbaceous species. Willow (*Salix lucida* Muhl.) 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 competitive encroachment of non-native invasive reed canary grass (*Phalaris arundinacea*), making the Fescue assemblage less hospitable to willow recruitment. Alternatively, this could indicate that environmental conditions are becoming more similar between the two assemblages, as evidenced by the clustering of the Fescue and Sedge groups on the same branch in the 2019 dendrogram (Fig. 3). The indicator species analysis for the Sedge assemblage in 1979 included plants tolerant of highly saturated soils (*Sagittaria latifolia, Schoenoplectus tabernaemontani*), but in 1999 the assemblage indicators included species less tolerant of aquatic or constantly saturated soils (*Impatiens capensis*) (Table 2).

In contrast, the turnover of indicator species may simply represent variation in species compositional abundance in each sampling year, despite being a perennial-dominated community. For example, the Bogbean assemblage, was indicated largely by unique forbs in 1979 and 2019, and an even mix of unique forbs and graminoids in 1999 (Table 2). It is harder to attribute replacement of forb indicator species to potential woody riparian succession in the Bogbean assemblage as in the Sedge and Fescue assemblages. The indicator graminoid species found only in 1999 in the Bogbean assemblage (excluding an unknown grass identified only to family) are all native wetland species commonly found in brackish estuarine marshes in the Pacific Northwest of North America. Rather than indicating altered abiotic conditions, their inclusion as indicator species may represent population dynamics of short-lived perennials such as dispersal and recruitment. Thus, we propose two potential alternative explanations for the observed changes in floristic composition observed in the different assemblages: greater compositional abundance of woody species or species tolerant of drier conditions could be indicative of channel morphology processes limiting bank topography suitable for aquatic emergent plants, or sedimentation feedback processes increasing elevation of the marsh platform relative to tidal inundation. Alternatively, population dynamics may be operating independently of abiotic conditions, or have different outcomes depending on edaphic conditions in each assemblage. Testing how life histories (e.g., species longevity) offer competitive advantage in the context of changing abiotic conditions would be a valuable long-term addition to general interactions of competition and edaphic factors. These interactions would present a valuable experimental test of competitive advantage or how edaphic conditions drive the dominance of native vs. non-native species in tidal wetlands.

Greater homogeneity of cover abundance within assemblages, and greater distinction in compositional abundance between assemblages, may result from overall loss of native floristic richness. Across all assemblages in Ladner Marsh 1979–2019, we found one to two fewer native species, while β-diversity increased. This would indicate that rare (infrequently found) species are becoming more locally rare, which contributes to the loss of heterogeneous cover abundance and increased β-diversity observed at the plot scale. More concerning is the net loss of five perennial graminoid and forb species over the study period (Table S6), as this potentially represents a loss of functional redundancy. This species loss from the observed datasets may not represent species loss from the entire Ladner Marsh Wildlife Management Area, however the net species loss from the dataset, along with the addition of three non-native species to the datasets, poses concern for potential of species loss from the habitat over time.

Plant biodiversity loss may reduce the dense root networks to trap sediment in the marsh platform and seasonal pollinator value of forbs, although these contributions by the species lost in Ladner Marsh have not been quantified. Regardless of whether the loss is due to turnover or shifting abiotic conditions, trends of lost native plant species richness may indicate greater susceptibility to invasion (Kuiters, *et al.*, 2009), and thus a loss of resistance to non-native species encroachment over time. This can be evidenced by the decreasing ratio of native to non-native cover across Ladner Marsh 1979–2019 (Fig. S2), although few species (native or non-native) represent the majority of cover within the assemblage (Table S5). Non-native species of significant management concern (e.g., *P. arundinacea*, *I. pseudacorus*))

were ≤ 25% mean plot cover in 2019, however these species are notorious for spreading to the point of near-exclusion of other species (especially natives) (Apfelbaum & Sams, 1987; Sinks et al., 2021).

Mechanisms, Synthesis & Recommendations

Non-native species invasion and native species loss may lead to instability in native populations through fragmented or lost propagule dispersal networks, potentially leading to ecosystem instability through altered trophic cascades, especially when top-down trophic interactions are also lost from the ecosystem (Duffy, 2003). Disentangling explicit effects of abiotic processes of sedimentation, propagule dispersal, or propagule recruitment from other biotic interactions would be no easy task in a tidal ecosystem; however, experimentally testing optimal recruitment niches of species-specific propagules (e.g., Lane, 2022) could prove valuable for understanding best practices to maintain at-risk populations or test community function.

Optimal abiotic conditions for the recruitment and spatial occupancy of native or non-native species may largely be driven by soil characteristics and related sedimentation processes. Sedimentary changes such as sediment starvation or subsidence would result in more saturated areas, which would likely drive the increased prevalence of saturated conditions favored by the 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 non-native propagules within the distributed sediment. While Ladner Marsh has largely escaped direct natural (e.g., scouring tidal surge) and anthropogenic disturbance (e.g., industrial development), it is subject to continuous pressures resulting from modifications throughout the Fraser River Estuary. Cumulative effects of altered water, sediment, and nutrient regimes impacting the lower reaches of the Fraser River can alter competitive dynamics of plant communities (Dethier & Hacker, 2005; Flores-Moreno et al., 2016), and promote the dominance of invasive species (Green & Galatowitsch, 2002; Woo & Zedler, 2002; Zedler & Kercher, 2004). In turn, this may facilitate dispersal and recruitment of non-native species and potentially limit the dispersal and recruitment of native species because propagule pools are dependent on local and regional proximity. If similar habitats within tidal estuarine ecosystems 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 (but see Stewart et al., 2022). Alternatively, if non-native species are more prevalent throughout the regional dispersal network, then there is a greater chance of non-native species introduction within a local marsh community (Briski et al., 2012). Thus, abiotic shifts may be altering the seed recruitment niches which may restrict recruitment of native species diversity, while dispersal networks may be delivering disproportionately more seed of non-native, invasive species.

A common (mis)assumption is that “undisturbed” protected areas such as Ladner Marsh represent ecologically appropriate reference states (e.g., Stoddard, et al., 2006, and citations therein). Our findings illustrate how, in a heavily impacted region (Finn et al., 2021), compositional states have likely shifted from recent (< 100 years) historical references, yet may still contribute value as an example of potential ecological benchmarks for restoration success (Shackelford, et al., 2021). However, the designation of

Ladner Marsh as a Wildlife Management Area is likely insufficient to protect the habitat from large-scale environmental stressors in the Fraser River Estuary, such as nutrient enrichment. We suggest that the plant community changes described here should alert land managers not only to what species diversity might be targeted in conservation practice, but also to how reference sites may have changed with respect to non-native, invasive encroachment during the span of 20–40 years. We strongly advocate for the development of long-term vegetation monitoring to inform non-native invasive species management occurring in this and similar WMAs (see also Stewart, Hood, and Martin, 2023).

If we are to prioritize conservation of functional coastal wetlands that include a significant representation of native species, we must seek new ways to manage habitats such as the Ladner Marsh. Active management may be required to maintain ecologically-desired species composition in the wake of environmental change, and should be informed by ongoing experimentation into the role of hydrogeomorphologic drivers, dispersal networks, recruitment strategies, disturbance, and invasive species management to achieve this goal. In so doing, practitioners may enhance ecosystem processes within remnant coastal wetland habitats. This active management process also presents a timely and necessary opportunity in the Pacific Northwest of North America to engage with First Nations to revive traditional management practices in tidal wetlands, such as select mechanical disturbance (Turner, 2014): working with traditional knowledge holders in these ecosystems may yield deeper understanding of plant community function and habitat stability, which would enhance ecosystem resilience and potentially lead to positive effects on regionally important salmonid and shorebird populations while contributing to reconciliation between Indigenous and colonial cultures.

Declarations

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Competing interests

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

Author contributions

Study conception, 2019 data collection, and analysis were undertaken by Stefanie L. Lane. Original (1979) study concept comparing plant assemblages, data collection, and analysis were performed or overseen by Gary E. Bradfield. Madlen Denoth contributed data collected in 1999. Nancy A. Shackelford

assisted with theoretical framework and manuscript revision. Manuscript was drafted by Stefanie L. Lane; Gary E. Bradfield, Nancy A. Shackelford, and Tara G. Martin commented 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 (https://github.com/stefanielane/CommunityStability.git), or via Dryad (https://doi.org/10.5061/dryad.r7sqv9sh8)

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Figures

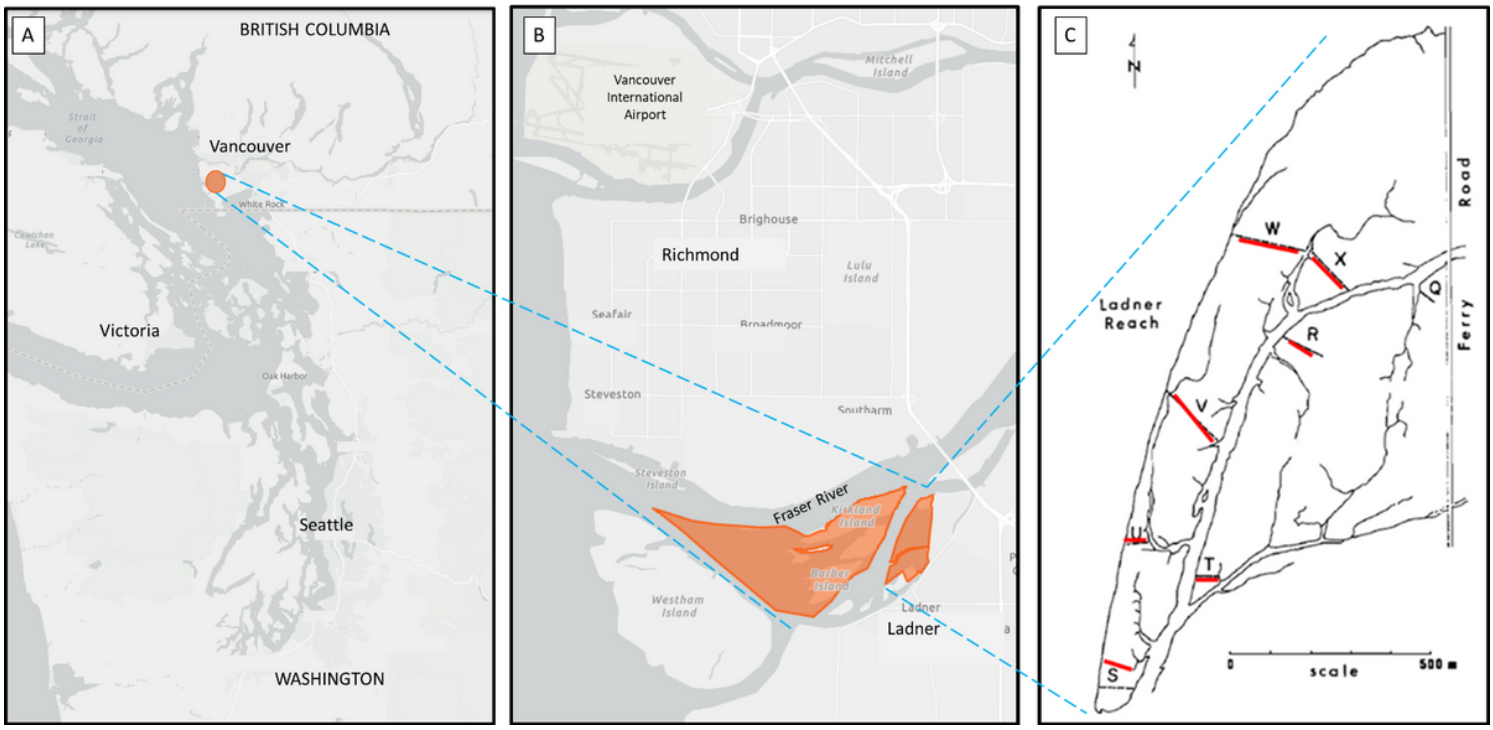


Figure 1

Study area location and sampling design. (A) Regional location of the Fraser River Estuary in southwestern British Columbia, Canada, (B) South Arm Marshes Wildlife Management Area (highlighted in orange), (C) Ladner Marsh with overlay of 2019 transect locations (shown in red) on original transect map from Bradfield and Porter (1982). Base maps (A, B) generated by iMap published by the B. C. Conservation Data Center (Victoria, BC, Canada, https://maps.gov.bc.ca/ess/hm/imap4m).

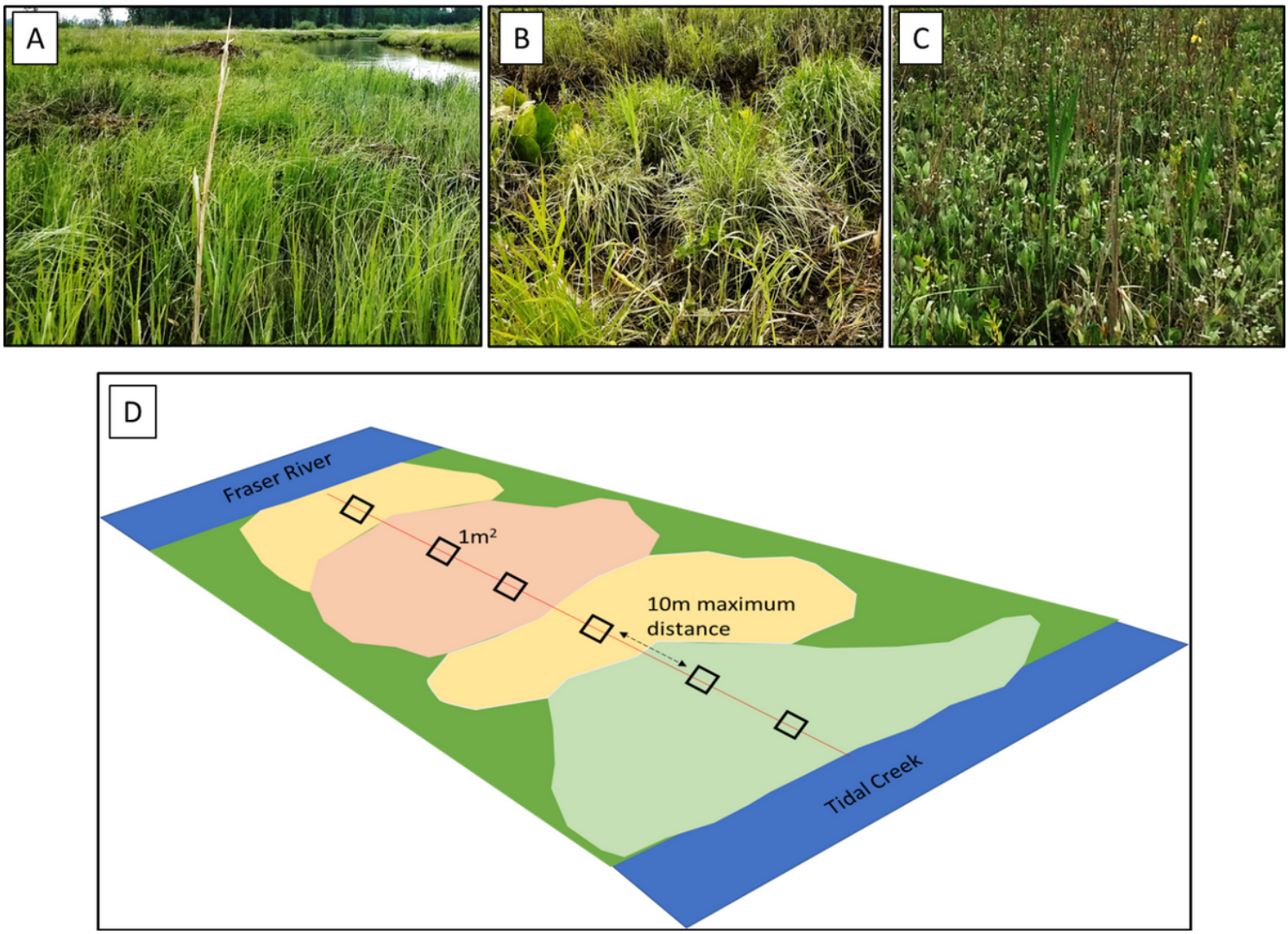


Figure 2

Dominant community vegetation characteristics observed in the (A) Sedge, (B) Fescue), and (C) Bogbean assemblages. (D) illustration of semi-systematic plot placement along transect bisecting different vegetation patches.

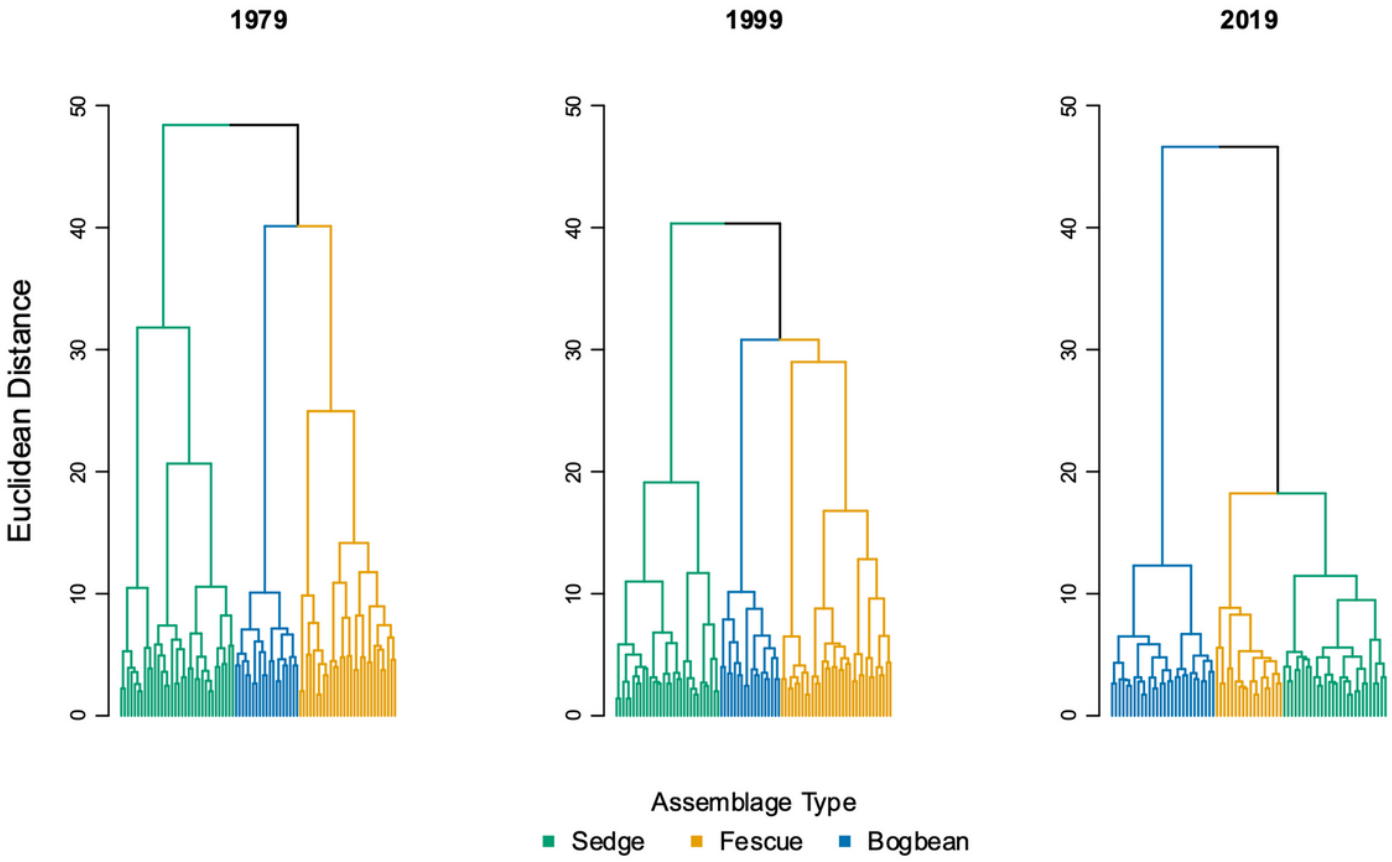


Figure 3

Species cover abundance becomes more dissimilar in each assemblage over time, as shown by greater Euclidean distance between assemblage types. Note clusters of the Sedge and Fescue assemblages are more similar in 2019

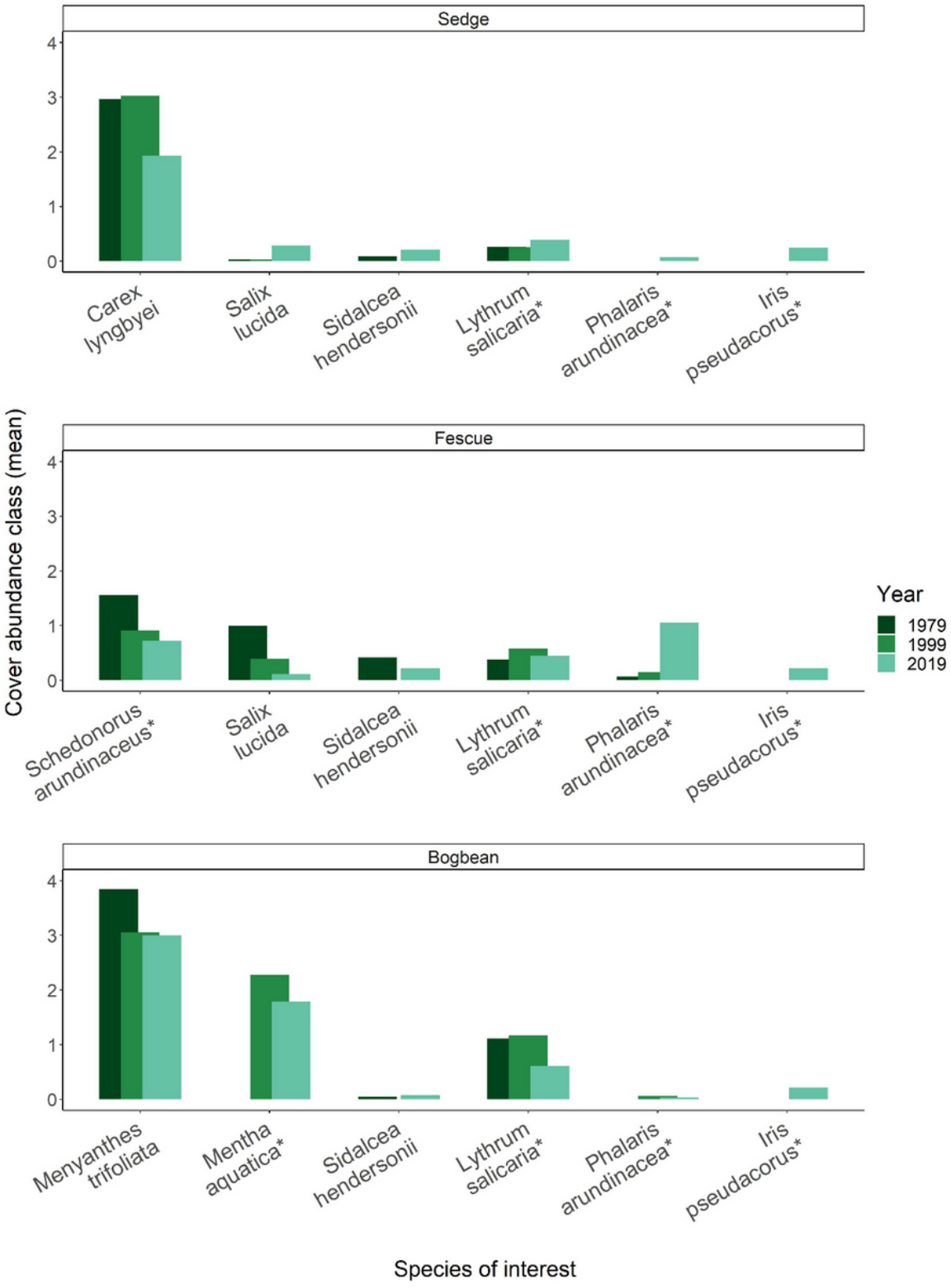


Figure 4

Changes in mean cover abundance (cover classes) for select significant indicator species (*Carex lyngbyei, Schedonorus arundinaceus, Menyanthes trifoliata*), the most-abundant woody species (*Salix lucida*), and native/non-native species of local management interest (*Sidalcea hendersonii, Lythrum salicaria, Phalaris arundinacea, Iris pseudacorus*). Non-native species denoted by asterisk (*). Significant indicator species within each assemblage have decreased in abundance over time, while several non-

native species have increased in cover abundance since 1979. Cover classes are: [1] = < 25%, [2] = 25-50%, [3] = 51-75%, [4] = >75% above-ground vegetated cover.

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