# Introduction

Competitive strategies drive vegetation succession

Competition is one successional process that shapes resulting community

Competitive dominance results in key species holding space and defining ecosystem characteristics (e.g., forest succession theory, keystone species/functional groups)

Plants may exhibit different competitive advantages through alternative reproductive strategies, such as clonal reproduction or heavy seed production. Tradeoffs exist:

One competitive advantage may be at the expense of another, such as strong clonal expansion at expense of seed limitation (e.g., sp. like CALY; CITE). Or, plants may have equally strong clonal and seed reproductive capability, enabling community dominance (e.g., exotic sp.; CITE).

Species presence or introduction (succession) may be enhanced or negatively affected by parent plant: seed bank linkages and feedbacks (CITE).

Drivers of similarity between seed banks and above-ground vegetation.

Dissimilarity increases with greater time since disturbance in wetlands (Hopfensperger, 2007)

Local seed dispersal more likely, although vectors such as wind & water dispersal can carry seeds to colonize new sites.

Should one competitive strategy (seed or clonal) be removed from the population during disturbance, then recovery via succession would be influenced by the relative competitive strength of remaining propagative material. Successional outcomes may vary depending on the composition of the available propagative sources.

For example, if clonally propagative parts were removed form habitat, recovery would be obligated to reproduce by seed (or other dispersed propagules); OR, successional outcomes may be affected by the relative rate of recovery by alternative reproductive strategies. E.g., competitive seeds could take over faster than clonal regrowth from adjacent patches.

Recovery from seed requires the propagule to be dispersed from another population, and for those propagules to be retained in the site to be available during succession.

Ecosystem capacity for recovery via succession following disturbance, and grazing as a form of natural disturbance

Define resilience broadly as communities’ ability to recover following disturbance. In vegetation communities, seed/clonal strategies help post-disturbance recovery.

Disturbance intensity and duration can push a habitat beyond its capacity for recovery. One measure of resilience may be to assess whether the habitat returns to a pre-disturbance state following the removal of the disturbance agent. (Standish et al., 2014)

* 1. Some ecosystems experience regular disturbance, which may be environmental (estuaries), or from biotic interactions (grazing). Either of these can under some conditions promotes diversity/resilience/productivity (CITE). However, if disturbance is persistent or return intervals exceed recovery time, ecosystem shifts to alternate compositional or functional states (CITE).

Overstress, such as through overgrazing, would lead to reduced capacity for recovery. In the absence of predators, over-abundant populations must be excluded to allow passive recovery (cite examples from forestry/ag/riparian lit).

The Green World Hypothesis (Hairston, Smith, & Slobodkin, 1960) would posit that grazing pressure must be released as predators should take advantage of herbivore populations. However, if grazers are not limited by predation, then grazing pressure can alter site ecology and thus limit the capacity of the habitat to recover (Srivastava & Jefferies, 1996).

Interactions of different disturbance sources – some ecosystems may be highly adapted to strong disturbance if they experience disturbance of varying degrees regularly.

Estuaries, and overgrazing study context

Estuaries are ecosystems where varying degrees of natural disturbance are experienced in daily tides, seasonal storms, or over longer geomorphic timescales and processes such as marsh accretion, erosion, or subsidence (Pasternack, 2009). Estuaries around the Salish Sea along the Pacific northwest coast of North America may be spatially constrained by geography, and are often heavily impacted by human infrastructure (CITE). However, their immense habitat value to marine species such as salmonids and shorebirds is reflected in federal and international efforts for conservation and restoration (CITE).

In this region, the Canada goose (CAGO) is an introduced exotic grazer.

Describe migratory history & regional introduction (1-2 sentences), life cycle/residency (non-migratory pops., 2 sentences), grazing/grubbing behavior (2-3 sentences, focusing on rhizome removal).

Describe exclosures & passive recovery as a means of restoration (broadly). Restoration goals may be to target keystone species, or key functional groups. Native vs. exotic composition is always a concern, and the increasing social priorities placed on ethnoecological restoration cannot be overlooked.

Our main objective for this study was to understand surface seed bank and above-ground vegetation composition at discrete stages of recovery since grazing disturbance and grazing exclusion in two estuaries in the Salish Sea. Traditional succession models would say the most competitive species will increasingly dominate the plant community as time since disturbance increases. This would particularly be the case in a clonal ecosystem, where recovery is driven by species spreading clonally from adjacent undisturbed sites. If succession is happening the we expect:

1. Above-ground vegetation in recently disturbed sites will be highly similar to seed inputs than older disturbance vegetation similarity to seed, or reference vegetation similarity to seed
2. Above-ground vegetation at older disturbance sites will be more similar to reference vegetation than recently disturbed (regardless of seed inputs)
3. Alternatively, novel disturbance and novel seed inputs lead to alternative succession pathways, where new competitors from seed inputs derail the "slow encroachment" of the clonal dominant from the neighboring intact site.

From a conservation and land management perspective, we should be cognizant of long-term grazing impacts on recovery of plant communities and the implications for alternate successional trajectories. This is especially the case in ecosystems that already experience natural and anthropogenic disturbance, such as estuaries, and wetlands more broadly.

# Methods

## Study area & site history

* Site descriptions of Little Qualicum and Nanaimo River Estuaries as Wildlife Management Areas (map).
* Grazing exclosure history
  + Wooden fencing was iteratively installed (cite GoMIES?) to physically prevent Canada geese from grazing vegetation, hereafter referred to as ‘exclosures.’
    - Exclosures were placed opportunistically along channel edges where intensive herbivory was observed to protect remnant marsh platform from further degradation.
  + Ongong restoration strategies have afforded observation of recovery timepoints 1 and 10 years post-grazing exclusion in two different estuaries (Table 1).
    - Exclosure sites were selected to represent comparable starting conditions of disturbance within the exclosures; undisturbed and grubbed sites are not protected by an exclosure.

Table . Grazing disturbance conditions in the Little Qualicum River and Nanaimo Estuaries resulted in conversion of vegetated marsh to partially or fully grubbed mudflats; exclosures were installed to prevent further degradation into the marsh platform. Each disturbance category n = 4 for each estuary.

|  |  |  |  |
| --- | --- | --- | --- |
| **Estuary** | **Time Since Disturbance** | **Disturbance condition** | **Revegetation status** |
| Little Qualicum, Nanaimo | 0 years (recent grubbing disturbance) | Grubbed | No transplants; ruderal vegetation exists |
| Nanaimo | 1-year post-grazing/grubbing disturbance | Partially grubbed | No transplants; vegetation recovery from remnant and adjacent vegetation |
| Little Qualicum | 10 years post-grazing/grubbing disturbance | Partially grubbed | No transplants; vegetation recovery from remnant and adjacent vegetation |
| Little Qualicum, Nanaimo | No known grazing disturbance | Undisturbed | No manipulations |

## Sampling methods

### Vegetation sampling

Vegetation sampling was conducted once in mid-July, 2021. Two 1 m2 vegetation plots were placed within the exclosures (sites, n = 4 per estuary), at least 1 m from the bank edge and any exclosure boundary, and at least 3 m apart within the exclosure. Quadrats were placed so that the plot edge nearest creek was parallel to the bank.

All vascular species were identified according Hitchcock and Cronquist (1973), and currently accepted nomenclature standardized according to the PLANTS Database of the United States Department of Agriculture, Natural Resources Conservation Science [USDA NRCS]. Species were considered in the plot if at least half of their basal stem(s) were inside the quadrat boundary; overhanging vegetation was not considered. Aerial vegetated cover to the nearest 3 % (1/32 m2) was recorded. For any species present with less than 3 % cover, species were assigned 2% cover if > 20 individuals were present, 1 % cover if 2-20 individuals were present, and 0.1% cover for single individuals. Bare ground was estimated as the remainder of the plot area not covered by above-ground vegetation. Any plots with > 100% cover were standardized relative to 100%. To characterize plant structure, species were assigned to a height category tall (> 1 m), medium (50-100 cm), or short (< 50 cm) based on their maximum reported height in the Illustrated Flora of British Columbia (Douglas, Meidinger, & Pojar, 1998).

### Surface seed bank sampling & germination

Two surface seed bank samples were taken from each plot (n = 16 per disturbance condition in each estuary) in summer (July 2020), fall (October 2020), and spring (March 2021). A 10 cm diameter handheld bulb planter (e.g., [Husky 9 in. stainless Steel Bulb Planter, Home Depot, USA](https://www.homedepot.com/p/Husky-9-in-Stainless-Steel-Bulb-Planter-GD210314/317436441)) was used to excise sediment 1 cm deep to capture the surface seed bank. Vegetative roots, rhizomes, or other viable rooted material were removed before placing sample in a plastic zipper bag. All surface seed bank samples from the same estuary and disturbance condition were then homogenized in a clean bucket with 100 mL dechlorinated water. Samples were hand-sifted for any remaining root, rhizome, or vegetative material, then homogenized sample was transferred to a clean plastic zipper bag. Summer and fall 2020 samples were stored at 4o C for approx. 12 weeks to simulate overwinter cold stratification to release seed dormancy (CITE); samples collected in the spring of 2021 underwent natural winter conditions and were not subjected to cold stratification.

Germination trials were conducted under greenhouse conditions with 15 hr daylength at ~ 20o C. Seedling pots (9 cm x 13 cm x 5.7 cm (depth), BRAND) were filled with moist, sterile potting media (Sunshine Mix No. 4, Sun Gro Horticulture, Agawam, MA, United States). Pots were placed in solid cache trays and constantly bottom-watered with municipal tap water.

Seed bank samples were sown by pouring 75 mL sediment over the top of each seedling pot (n = 8 per estuary and disturbance condition) while constantly agitating the homogenized seed bank sample. Seeds were allowed to germinate for 5 weeks, at which time all individuals were counted and removed. The seedling trays were observed for any further germination for another 7-10 days, at which time the samples were discarded. Any species that could not be identified were labelled and transplanted into 38 P plug trays (BRAND) with the same growing media and growing conditions until a positive identification could be made. Representative specimens used to confirm seedling identification were pressed and made available as herbaria.

## Analysis

We fit generalized linear models (package) to test significant differences in vegetation and surface seed bank response between disturbance categories.

We used non-metric multidimensional scaling (NMDS, package) to visualize similarity in species compositional relative abundance between surface seed banks and above ground vegetation.

# Results

*Expectations:*

1. *Above-ground vegetation in recently disturbed sites will be highly similar to seed inputs than older disturbance vegetation similarity to seed, or reference vegetation similarity to seed*
2. *Above-ground vegetation at older disturbance sites will be more similar to reference vegetation than recently disturbed (regardless of seed inputs)*
3. *Alternatively, novel disturbance and novel seed inputs lead to alternative succession pathways, where new competitors from seed inputs derail the "slow encroachment" of the clonal dominant from the neighboring intact site.*

* General summary results:
  + X species from Y genera were found in above-ground vegetation, and X/Y in the surface seed bank (Supplemental table)

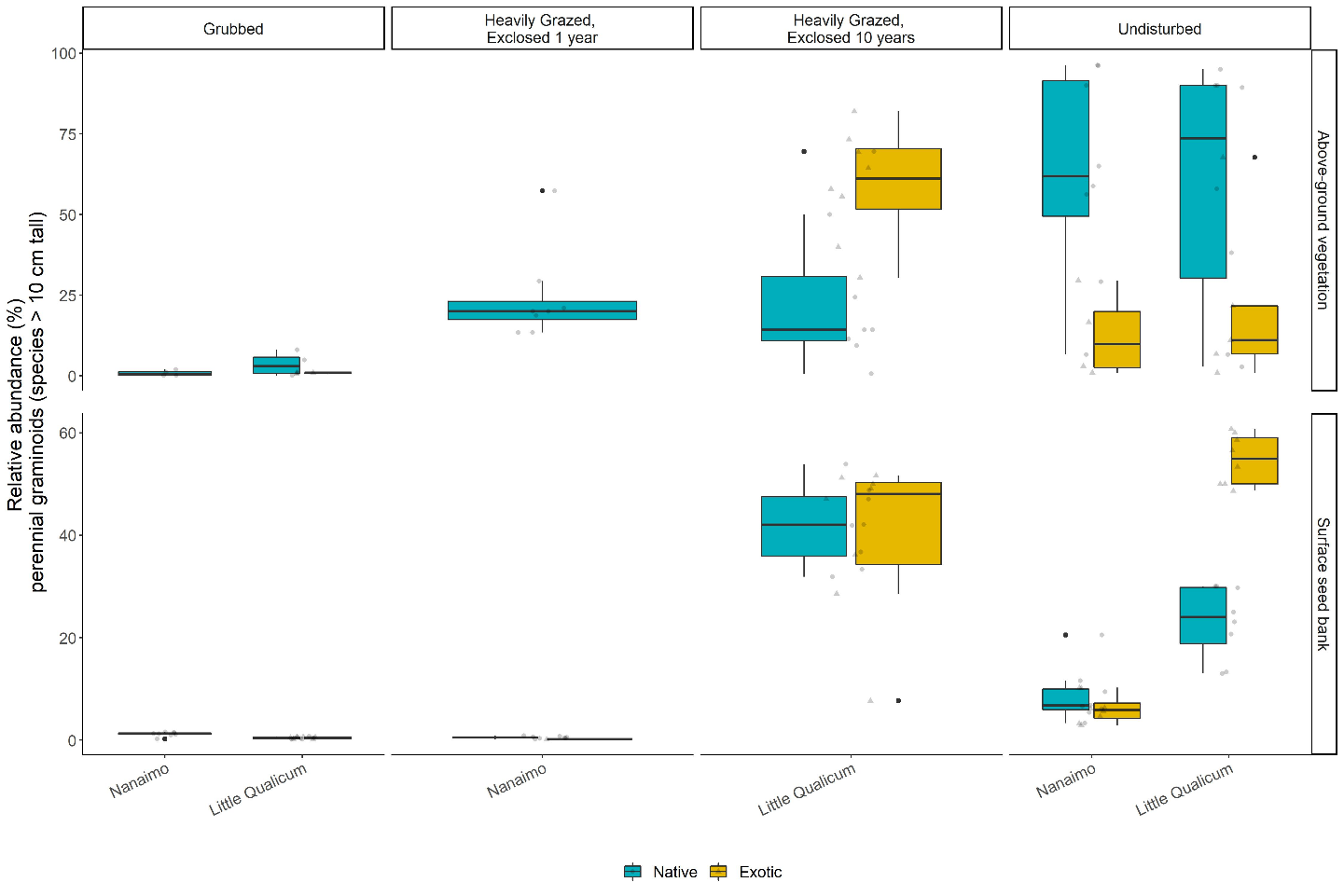


Figure . Above-ground cover abundance of key functional group ‘perennial graminoids’ is not significantly different from undisturbed (reference) sites after 10 years. However, this above-ground cover is dominated by exotic graminoid species. Moreover, seed bank abundance of tall, perennial graminoids is significantly higher in 10-year old exclosures compared to other disturbance conditions, including undisturbed (reference) sites. Notably, there is nearly equal abundance of exotic and native graminoid seed in 10-year old exclosures, and significantly greater representation of exotic than native graminoid seed in undisturbed sites in Little Qualicum Estuary.

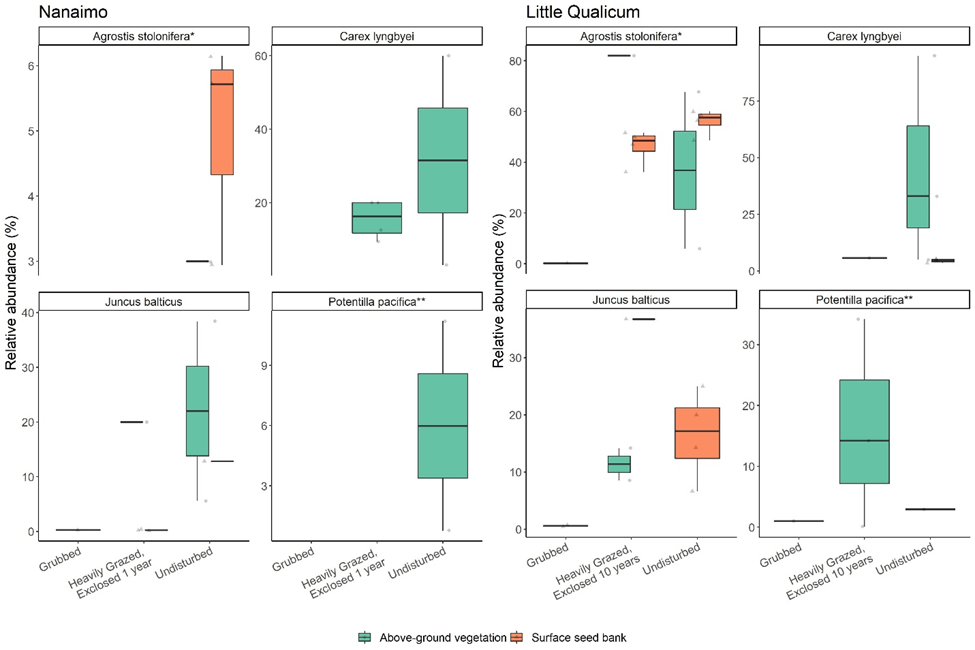


Figure . Seed limitation of keystone species Carex lyngbyei results in overall lower representation in the seed bank compared to other competitive dominant species. Notably, seed of this species is absent in undisturbed sites in Nanaimo River Estuary, and nearly so in undisturbed and 10-year old exclosure sites in the Little Qualicum Estuary, indicating strong reliance on clonal reproductive strategies. Exotic species denoted by (\*), culturally significant species denoted by (\*\*). Note y-axis scale freely varies by species.

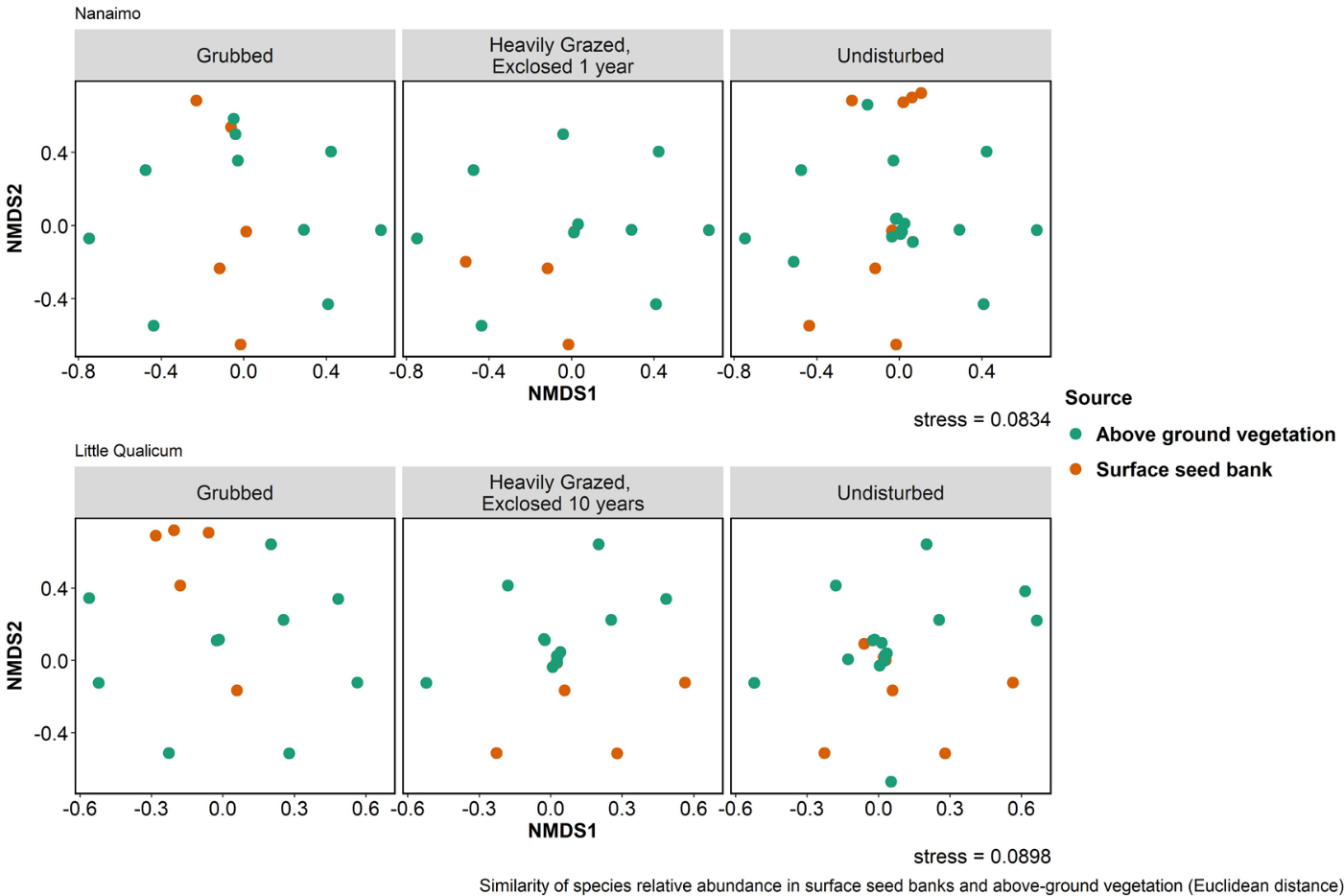


Figure . Species relative abundance had greatest similarity between above-ground vegetation and surface seed banks in grubbed and undisturbed sites, and greatest dissimilarity in both exclosures (1 and 10 years post-grazing exclusion).

# Discussion

1. Does the system recover? Explain why expectations were or weren’t met.
   1. Functional groups have recovered, however compositional quality has changed.
      1. Clonal and seed competitive advantage of exotic grass leads to novel composition after disturbance.
   2. Seed inputs are most similar in grubbed and undisturbed sites. This contradicts our expectations of high similarity in older and reference sites. However, this also shows that native seeds of desired functional groups are not dispersed or retained in grubbed sites, thus their recovery is obliged to proceed from clonal strategy.
2. Broader implication: what does this mean about succession & recovery?
   1. Loss of native species during recovery, especially in seed bank, points to “ecological memory loss” following disturbance.
      1. Highest risk for species loss may be for seed-limited species. If disturbance removes clonally reproductive above-ground vegetation, then there are no (or very few) reproductive propagules left in the system, and regional dispersal is required to revitalize the population.
      2. Would like to include a case example of above point: streambank clover (*Trifolium wormskioldii*) was a species of significant cultural importance (and thus likely historically abundant in estuaries, yet is now locally rare as a plant, and entirely absent from the seed bank.
   2. What does the species or functional identity/abundance mean (e.g., dominance of exotic Agrostis vs. native Carex)?
      1. Expand on concepts of species identity altering ecosystem function (even if functionally/cladistically similar), especially C or N contributions/sequestration (Waller et al., 2020).
   3. Extrapolate implications for other systems with other press disturbance types, especially anthropogenic stressors (e.g., general wetland/riparian invasion).
      1. Local or regional dispersal limitations cannot rescue native populations if local seed or clonal competitive pressure from exotic species is greater. That is, this trend of both native species loss *and* increasing exotic cover is exacerbated by each species’ competitive dispersal and recruitment strategies.
      2. Seed-limited species that rely on clonal reproduction may be at greatest risk for being out-competed if the competitor(s) have greater seed and clonal reproductive rates.
3. Management applications & opportunities
   1. Passive restoration may be insufficient for recovery of species with a primarily clonal reproductive strategy, especially when exotic species with competitive reproductive advantage of both seed and clonal strategies are present. In these cases, active restoration through transplanting should be prioritized in ecosystems affected by these types of disturbance.
   2. Opportunities exist: if disturbance denudes a habitat, this effectively creates a ‘blank slate’ for restoration where land managers can choose specific restoration states (CITE). Besides ecosystem function, ethnoecological restoration opportunities could exist. In the PNW, this could be restoration of culinary root gardens (Turner, 2014).

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# Supplemental

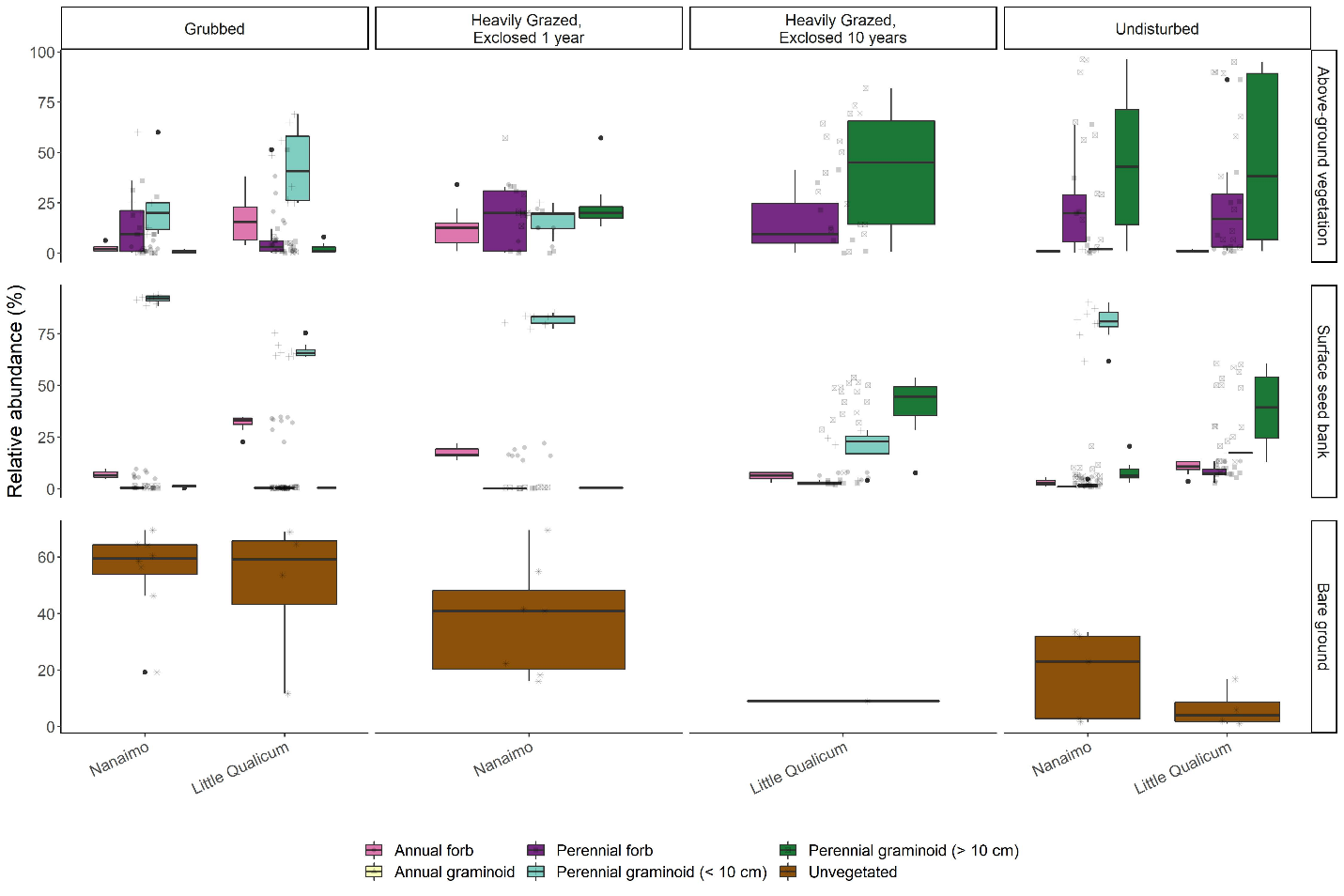


Figure . Recently grubbed and 1-year-old exclosures are dominated by > 50% mean cover of bare ground, with species relative abundance dominated by short perennial graminoid Eleocharis parvula and forbs in both above-ground vegetation and surface seed bank. After 1 year of exclosure, all plant functional groups have similar dominance in above ground vegetation, but surface seed banks do not show increased representation from perennial forbs or perennial graminoids > 10 cm. Bare ground significantly decreases after 10 years of exclosure, while relative abundance of perennial graminoids (> 10 cm) significantly increases in both above-ground vegetation and surface seed banks, not significantly different from undisturbed sites.