



## **Context-Dependent Effects of Deer Exclusion Across Environmental and Disturbance Gradients on Galiano Island, British Columbia**

A Directed Studies and Research Project – BIOL 490J

Kateri Lawson

Student ID: V01018047

Submitted to Dr. Barbara Hawkins for review

I acknowledge that this study was conducted in the shared, unceded and traditional territories of the Hul'qumi'num-speaking First Nations Peoples and those who hold traditional rights, responsibilities, and Indigenous rights in and around what is now known as Galiano Island. I live, work and study in the traditional territories of the ləkʷəŋən and W̱SÁNEĆ peoples.

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# Introduction / Literature Review

## Galiano Island

Galiano island is part of the Gulf Islands archipelago, located in southwestern British Columbia, Canada in the shared, unceded and traditional territory of the Hul'qumi'num-speaking Coast Salish peoples. It lies within the Coastal Douglas-fir (CDF) biogeoclimatic zone, one of the most globally rare and threatened ecosystems in North America.

Occupying only 0.3% of British Columbia's total land area, the CDF zone occurs on a narrow strip of southeastern Vancouver Island, portions of the Gulf Islands, and pockets along the south coast and mainland of British Columbia (Coastal Douglas-fir Conservation Partnership [CDFCP], 2024). The zone exists in the rainshadow of Vancouver Island and the Olympic Mountains, where a unique Mediterranean-type climate of warm, dry summers and mild, wet winters creates conditions found nowhere else in Canada (MacKinnon, 2003). The CDF zone is home to the highest number of species and ecosystems at risk in British Columbia, many of which are ranked globally as imperiled or critically imperiled (CDFCP, 2024; BC Ministry of Environment, Lands and Parks [BCMELP], n.d.).

Within the CDF zone, Garry oak (*Quercus garryana*) and associated ecosystems represent some of the most diverse and imperiled habitats. These ecosystems are complex assemblages that include coastal bluff, maritime meadow, vernal pool, grassland, rock outcrop, and transitional forest ecosystems (Parks Canada Agency [PCA], 2006a). Garry oak and associated ecosystems are home to more plant species than any other terrestrial community in coastal British Columbia, with many of these species occurring nowhere else in Canada (PCA, 2006a; Garry Oak Ecosystems Recovery Team [GOERT], n.d.-a). On Galiano Island, these meadow and woodland ecosystems comprise only about 3% of the island but host an outsized concentration of biodiversity, supporting over 100 provincially-listed species at risk (Habitat Conservation Trust Foundation, 2024).

The ecological condition of the CDF zone is dire. The CDF zone has the highest road density of any biogeoclimatic zone in British Columbia, which profoundly fragments habitats (Raincoast Conservation Foundation, 2021). Approximately 75% of the human population

of BC lives in the CDF zone, and 49% of the land base within the zone has been permanently converted by human activities, creating ongoing pressures from urbanization, recreational use, and altered disturbance regimes (CDFCP, 2024). Only 37-40% of the CDF's historic forested extent actually remains forested, with approximately 17 km<sup>2</sup> defined as old growth—less than 1% of the amount that should be present in this region (CDFCP, 2024; Raincoast Conservation Foundation, 2021). Only approximately 11% of the CDF zone is protected in conservation areas, and the extent of disturbance combined with the low level of protection places the ecological integrity of the zone at high risk (CDFCP, 2024). The catastrophic loss of habitat has led to Garry oak and associated ecosystems being among the most endangered in Canada—less than 5% of the original habitat remains in a near-natural condition (GOERT, n.d.-a; PCA, 2006a). In the last 150 years, agricultural development, urbanization, and fire suppression have combined to eliminate or highly modify most of the original Garry oak savanna from southern Vancouver Island and adjacent Gulf Islands (PCA, 2006b). Over 95% of the original plant cover has already been lost, with remaining woodland patches facing mounting pressures from multiple interacting stressors, including invasive species, habitat fragmentation, and overabundant ungulate populations (PCA, 2021; PCA, 2006c).

## Columbian Black-tailed Deer

The Columbian black-tailed deer (*Odocoileus hemionus columbianus*) is a subspecies of mule deer native to the southwestern corner of British Columbia, occurring on most islands south of Rivers Inlet, including Vancouver Island and the Southern Gulf Islands, and ranging east to near the summits of the Cascade and Coast ranges (Nyberg & Janz, 1990). Black-tailed deer are distinguished from their larger, more arid-adapted inland mule deer relatives by their smaller bodies, smaller ears, and largely black tail surrounded by a smaller white rump patch (Nyberg & Janz, 1990; Shackleton, 1999). The species occurs commonly throughout their range, with populations in BC currently stable at approximately 180,000 individuals (Nyberg & Janz, 1990). Black-tailed deer require food, water, and cover to ensure survival across seasons, with habitat use varying from sea-level to sub-alpine elevations, although elevations greater than 1,000 meters are rarely used as winter habitat

(Nyberg & Janz, 1990). Columbian black-tailed deer populations can consist of either resident or migratory individuals, with average annual home range for migratory deer in the moderate snowpack zone being 1,770 ha, whereas resident deer in the same zone maintain home ranges of only 140 ha (Nyberg & Janz, 1990). On the Southern Gulf Islands, where predators have been extirpated and islands are relatively small, deer populations are largely sedentary with individuals maintaining relatively stable home ranges year-round (Harestad, 1979; Martin et al., 2011).

Columbian black-tailed deer exhibit primarily browsing behavior with marked seasonal variation in diet composition reflecting changes in nutritional quality and forage availability. During spring, deer favor areas with early green-up on low elevation areas with warm aspects on moderate to steep slopes, consuming important spring forage species including fireweed (*Chamerion angustifolium*), pearly everlasting (*Anaphalis margaritacea*), bunchberry (*Cornus canadensis*), *Rubus* species, *Vaccinium* species, willow, and many herbs and grasses (Nyberg & Janz, 1990). Summer habitat consists of areas with a suitable mix of young to old forest, with key summer forage species including fireweed, pearly everlasting, salal (*Gaultheria shallon*), *Rubus* species, *Vaccinium* species, willow, and alder (Nyberg & Janz, 1990). Although summer forage is typically greater in quantity, forage quality and variety is reduced compared to spring (Walmo, 1981). Winter represents a critical season when deer are forced from high elevation habitat to low elevation areas with south-facing, warm-aspect slopes or floodplain areas where snowpack is minimal (Nyberg & Janz, 1990). In his foundational work on southern Vancouver Island, Cowan (1945) documented that Douglas-fir (*Pseudotsuga menziesii*) foliage constituted 47% of the winter diet, with salal, Oregon grape (*Mahonia nervosa*), and arboreal lichens (*Alectoria*, *Bryoria*, and *Usnea* spp.) made available through litterfall serving as major food sources during severe winters when deep snow limits access to understory vegetation. Key winter forage species include western redcedar (*Thuja plicata*), Douglas-fir, red huckleberry (*Vaccinium parvifolium*), salal, deer fern (*Blechnum spicant*), and arboreal lichens (Cowan, 1945; Nyberg & Janz, 1990).

## Deer Population Boom

The dramatic increase in native Columbian black-tailed deer (*Odocoileus hemionus columbianus*) populations across the Gulf Islands, including Galiano Island, stems from a confluence of historical factors rooted in colonialism and ecological disruption. Prior to European settlement, these island ecosystems functioned as intensively managed food production systems by Coast Salish stewards, serving as centers of cultivation for culturally important species, most notably camas (*Camassia quamash*, *Camassia leichtlinii*), but also including bare-stem desert parsley, chocolate lily, and numerous other food and medicinal plants (Turner, 2014; Turner *et al.*, 2000). Fire was the primary tool used to maintain these productive ecosystems. Camas meadows were burned after harvesting bulbs to return nutrients to the soil and to keep meadows open for camas and other culturally-important plants (Turner, 2014). The use of fire by First Nations is thought to have allowed the oak woodlands to persist and perhaps expand on southeastern Vancouver Island, particularly in areas with deeper soil, by preventing conifer encroachment as the climate became wetter (Fuchs, 2001; Hebda & Aitkens, 1993). These carefully cultivated ecosystems also served to facilitate hunting practices by clearing the land and creating edge habitats ideal for deer foraging.

European colonization was devastating to this balance. Along with colonial settlement, fire suppression policies were introduced, and Coast Salish Peoples were prohibited from undertaking the prescribed burning practices that were integral to maintaining landscape, cultural, and physical health (Turner, 2014). The interruption of traditional land management practices and the alienation of Indigenous hunters from their traditional hunting practices following European settlement (Arnett, 2000) created the first condition for deer population expansion. The second critical factor was the systematic extirpation of natural predators. Black-tailed deer are endemic to the Southern Gulf Islands, as are wolves, cougars, and bears; however, by the late 1800s, European settlement resulted in the removal of large predators from the region (Martin *et al.*, 2011; Shackleton, 1999). Due to the near-extirpation of native predator populations from Galiano and other Gulf Islands, and decreasing human hunting pressure over the past century, local deer populations have

expanded to historically unprecedented levels (Galiano Conservancy Association [GCA], n.d.). Predation by cougars and wolves, along with hunting by First Nations and then Europeans, probably kept deer densities low historically (Darimont *et al.*, 2004; Gonzales & Arcese, 2008; MacDougall, 2008). Deer populations on islands can also be expected to have experienced periodic extinction events related to predator pressure and island size and isolation, suggesting browsing pressure has not been continuous historically (Darimont *et al.*, 2004).

The regulatory landscape governing deer hunting underwent significant shifts that further contributed to population growth. Europeans became the main agent of population control for deer via hunting until at least the late 1970s, but more recently, human hunting pressure has declined or been eliminated due to increased regulation and changing human sentiment, leading to the rapid growth of deer populations and their high abundance on many islands (Gonzales & Arcese, 2008; Martin *et al.*, 2011). In the 1970s, local residents started supporting stricter hunting regulations, banning the sport entirely on some of the islands (Arnett, 2000). Current hunting regulations specify that there is no open season for deer hunting on most Gulf Islands in Management Unit 1-1, with exceptions only for specific islands like Gabriola, Sidney, and James Islands (Government of British Columbia, 2024). These regulatory restrictions, combined with human-altered landscapes that create ideal edge habitats for deer, have enabled populations to expand unchecked.

The combined effects of these historical disruptions have been profound. Following almost two decades of research, black-tailed deer populations on the Southern Gulf Islands, including Galiano Island, are now estimated to be up to 10 times higher than they were a century ago (McComb *et al.*, 2024). Contemporary deer densities in Garry Oak Archipelago Ecosystems (GOAE) now range from 0.75 to 1.69 deer/ha (Beckett *et al.*, 2022)—significantly exceeding both the recommended ecological recovery goal of 0.1 deer/ha (Martin *et al.*, 2011) and the threshold of  $\leq 0.08$  deer/ha identified as necessary to maintain native shrub communities at least 50% as rich and diverse as those on deer-free islands (Arcese *et al.*, 2014). These densities are approximately 10 times higher than those found in predator-present locations across North America, which average 0.12 deer/ha (Beckett *et*

*al.*, 2022).

Studies on wild ungulate-community interactions have documented characteristic patterns of deer browsing that shape vegetation structure and composition, with these effects becoming particularly pronounced at high deer densities. Deer demonstrate selective foraging behavior, preferring highly palatable species such as *Rosa nutkana*, *Symphoricarpos albus*, and *Lonicera* species while avoiding unpalatable species, thereby altering competitive dynamics within plant communities (Arcese *et al.*, 2014; Cowan, 1945). Through selective browsing, deer reduce sapling and shrub density of preferred species, decreasing canopy shade and promoting the establishment of shade-tolerant understory species such as grasses, ferns, and sedges (Hanberry & Faison, 2023; Ramirez *et al.*, 2019; Rooney, 2001). Selective browsing also favors non-palatable and disturbance-resistant plant communities (Bai *et al.*, 2016; Rooney, 2001) and can effectively arrest forest succession (Ramirez *et al.*, 2019). Historical concerns about *O. h. columbianus* impeding forest regeneration following logging in Pacific Northwest coastal ecosystems (Crouch, 1976, 1979) have proven prescient, as contemporary research demonstrates that hyperabundant deer populations fundamentally alter successional trajectories. Additionally, browsing and trampling lead to soil compaction and reduced leaf litter layers, affecting invertebrate habitat and altering hydrological regimes (Pellerin *et al.*, 2010; Ramirez *et al.*, 2021a).

These vegetation changes cascade to affect wildlife communities: a study of 18 islands found that deer browsing reduced shrub cover and diversity, which in turn negatively impacted understory-nesting songbird abundances and reproductive success (Martin *et al.*, 2011). Similarly, deer presence indirectly reduced female bumblebee abundance through depletion of floral resources, with male bumblebee counts directly and significantly affected by deer presence (Beckett *et al.*, 2022). The browsing pressure not only threatens endangered and culturally significant plant species that thrived under aboriginal stewardship (Arcese *et al.*, 2014), but also fundamentally disrupts the ecological relationships between native flora and their associated wildlife communities, placing entire ecosystem assemblages at risk.

## Invasive Species

Invasive species represent one of the most severe contemporary threats to Galiano Island's ecosystems. At least 173 invasive species have been identified in Garry oak ecosystems across the region, including 4 trees, 15 shrubs, 147 herbs, 1 reptile, 6 birds, and 7 mammals (Garry Oak Ecosystems Recovery Team, 2003; ISCBC, 2024a). Invasive plant species represent a diverse assemblage of trees, shrubs, forbs, and grasses that collectively threaten native biodiversity and ecosystem function. These invasive species alter competitive dynamics, modify soil chemistry and hydrology, increase fire risk, and create conditions that favor further invasion while suppressing native plant recruitment and persistence (Cronk & Fuller, 2013).

Invasive woody species are particularly problematic in forested and transitional habitats. Scotch broom (*Cytisus scoparius*), with its bright yellow flowers and tendency to rapidly colonize open swaths of land, is perhaps the most widely recognized invasive plant within the CDF region and is particularly widespread on Galiano Island (ISCBC, 2024a). Due to its aggressive growing tendencies, Scotch broom quickly crowds out native species, with each plant living up to 25 years and dropping thousands of seeds that can remain viable for up to 30 years in the soil (ISCBC, 2024a). High-density infestations pose a severe wildfire risk due to added fuel loads and the high oil content of this plant (ISCBC, 2024a). Disturbed areas are most vulnerable to uncontrolled growth, as Scotch broom requires sunlight to establish, and these sites can be entirely taken over, leaving behind near monocultures with little chance of survival or establishment for native species (GOERT, 2002a). Beyond altering fire regimes, Scotch broom suppresses soil phosphorous availability, further disadvantaging native species (Shaben & Myers, 2010). Other invasive shrubs such as spurge-laurel (*Daphne laureola*), English holly (*Ilex aquifolium*), and Himalayan blackberry (*Rubus armeniacus*) form dense thickets that crowd out native understory species in both forested and open habitats.

Woody vines and sprawling groundcovers contribute to biodiversity loss by smothering native vegetation and creating impenetrable thickets. Himalayan blackberry (*Rubus*

*armeniacus*)—one of the 40 most invasive woody angiosperms globally and the most invasive nonnative shrub on the West Coast—forms dense canopies that severely limit understory light availability (GOERT, 2002b; Gaire *et al.*, 2015). Its competitive advantage stems from high photosynthetic efficiency, enabling vigorous vegetative growth and reproduction without typical trade-offs (Lambrecht-McDowell & Radosevich, 2005). Dense blackberry thickets reduce habitat availability for wildlife, impede forest regeneration, increase soil organic matter through litter accumulation, and create ladder fuels that heighten fire risk (Caplan & Yeakley, 2010; GOERT, 2002b). Cutleaf blackberry (*Rubus laciniatus*) exhibits similar traits, forming dense thickets with extensive woody root systems. Both species are prolific colonizers of disturbed lands, riparian corridors, pastures, and forest edges, where they clog waterways, restrict land use, and further elevate fire risk (Fryer, 2021; U.S. Forest Service, 2021). Additional groundcover invasives on Galiano, such as lesser periwinkle (*Vinca minor*) and introduced buttercups (*Ranunculus* spp.), form dense mats that suppress native herbaceous species in shaded or moist microsites.

Invasive grasses represent a particularly insidious threat to Garry oak meadow ecosystems. They may cover a combined 50–80% of the landscape, altering fire regimes, nutrient cycling, and competitive dynamics (GOERT, n.d.-b). Non-native grasses documented on Galiano Island include orchardgrass (*Dactylis glomerata*), common velvetgrass (*Holcus lanatus*), sweet vernalgrass (*Anthoxanthum odoratum*), Kentucky bluegrass (*Poa pratensis*), and several species of brome (*Bromus* spp.). Invasive grasses increase fire occurrence and frequency by creating fine fuel continuity and accumulating biomass (Balch *et al.*, 2013). Thatch accumulation from invasive grasses can exponentially reduce native forb performance and result in near-complete exclusion of many native species through light reduction, with effects far exceeding those of competition from living grass vegetation (Corbin & D'Antonio, 2004). These introduced grasses tend to form dense sods that suppress native forb establishment and accumulate thatch that alters soil moisture and temperature regimes (Pertierra *et al.*, 2023). Invasive grasses are particularly successful in disturbed sites and areas with historical agricultural use, where soil

compaction and altered nutrient availability favor their establishment over native species (Eschtruth & Battles, 2009). The dominance of non-native grasses in degraded meadow habitats creates a positive feedback loop: dense grass cover prevents native forb seedling establishment, reduces floral diversity critical for pollinators, and may facilitate further invasion by other non-native species adapted to grassland conditions (Bennett et al., 2013). As will be discussed further, the interaction between invasive species and other stressors—particularly deer herbivory—creates synergistic impacts that exceed the effects of either stressor alone.

## Historical Agriculture

Agricultural settlement on Galiano Island began in the mid-19th century following the 1858 Fraser River Gold Rush, when British families sent sons to the Gulf Islands to learn farming, leading the island to become known as “Little England” (Grant, 2014). Early settlers found the island’s soils poor and water scarce, so farming shifted toward fishing, hunting, sheep grazing, and small-scale orcharding (Gulf Islands Guide, 2009). Pioneer farm settlements were established in areas such as Plumper Pass (now Active Pass), though poor soil quality limited the extent of agriculture compared to nearby Salt Spring Island (Galiano Museum Society, 2023).

Sheep grazing was practiced historically on portions of Galiano Island and intensively on neighbouring islands such as Portland and Prevost. Across the Southern Gulf Islands, British, Hawaiian (Kanaka), and other European settlers cleared forests for orchards and livestock grazing (Gulf Islands Guide, 2009; Koppel, 1995). Portland Island, for example, supported intensive sheep farming from the 1880s until feral sheep were removed in 1980; however, understory vegetation remained sparse for decades due to persistent deer browsing (Gulf Islands National Park, 2015). In contrast, the removal of deer in recent years has allowed a marked recovery of native understory vegetation, illustrating both the persistence and potential reversibility of grazing impacts.

Agricultural legacies continue to shape ecological conditions long after livestock removal. Livestock trampling compacts soils by decreasing macroporosity and infiltration,

increasing surface runoff, and altering hydrological processes (Cui *et al.*, 2005; Jordon, 2021; McDowell *et al.*, 2003). Studies document substantial increases in soil penetration resistance following grazing—for example, up to  $1.59 \pm 0.17$  MPa in formerly grazed areas (McKenzie *et al.*, 2017). Soil compaction and altered hydrology can persist for decades. Grazing also reshaped plant communities by selectively removing palatable species, damaging vegetation, and promoting competitive advantages for disturbance-tolerant and invasive plants (Semmartin *et al.*, 2010). Widespread overgrazing by domestic livestock—and later by feral sheep, feral goats, horses, cattle, and introduced rabbits—contributed to the dominance of non-native species in many areas (ISCBC, 2024b).

These agricultural legacies interact with contemporary ecological pressures, particularly chronic overbrowsing by hyperabundant deer populations, to inhibit recovery and in some cases push ecosystems toward alternative stable states dominated by unpalatable or invasive species. On sites where both historical grazing and current deer browsing occur, restoration may be especially challenging due to the combined long-term soil impacts and continued suppression of native plant recruitment.

## Historical Forestry

On Galiano Island, industrial forestry has left some of the most significant and persistent ecological legacies. For much of the 20th century, approximately half of the island was owned by the forestry company MacMillan Bloedel (Galiano Island Historical Society [GIHS], n.d.). Beginning in the 1960s, the company was granted logging rights that facilitated extensive clear-cutting across the island, which in turn generated substantial community opposition (MacMillan Bloedel Ltd. v. Galiano Island Trust Committee, 2002; GIHS, n.d.). Major portions of the island were logged in the 1970s and 1980s, often without replanting, contributing to widespread forest loss and habitat simplification (Huggins, 2022; Glavin, 2002).

Although Galiano appears heavily forested today due to recent conservation and stewardship efforts, much of this forest cover consists of dense, even-aged Douglas-fir plantations that regenerated following commercial logging. These simplified plantations

lack the structural and compositional complexity characteristic of mature Coastal Douglas-fir (CDF) forests (Huggins, 2022). Remaining old and mature forest patches are now embedded within large areas of these plantation stands, which are only 30–70 years old and provide limited ecological connectivity between older forest remnants (Huggins, 2022). Many of the remaining mature forests were also high-graded—selectively harvested to remove the most valuable timber—leaving stands depleted of keystone species and with limited natural regeneration potential (Huggins, 2022).

The ecological impacts of these forestry practices endure to the present. Plantation forests exhibit reduced understory diversity, simplified structure, altered soil conditions, and modified hydrology relative to historical forest conditions. These legacies constrain the recovery of native species and ecosystem functions and interact with contemporary stressors such as invasive species and deer overbrowsing. Nonetheless, restoration efforts led by the Galiano Conservancy Association demonstrate that plantation forests can be transitioned toward more functionally diverse ecosystems through active structural and ecological restoration (Huggins, 2022).

## Cumulative Anthropogenic Pressures

The convergence of these pressures—habitat loss, fragmentation, fire suppression, invasive species, historical logging and livestock disturbance, and hyperabundant *O. hemionus columbianus* populations—places Galiano Island's remaining CDF and Garry oak ecosystems at critical risk. Previous studies on Galiano Island and neighbouring islands have documented severe cascading impacts from hyperabundant deer across multiple trophic levels. Across 66 sites on 35 islands, native and culturally significant shrub cover, richness, and diversity were 52–85% lower at sites with deer compared to deer-free sites, with the steepest declines occurring even at low deer densities below 0.08 deer/ha (Arcese et al., 2014). Palatable plant species cover was 92% lower where deer were abundant (Arcese et al., 2014), and native plant species richness utilized by pollinators was 67% lower on browsed versus unbrowsed islands (Beckett et al., 2022).

As deer selectively browse palatable native species while avoiding unpalatable invasives, invasive plants have a competitive advantage and their spread is accelerated (Blossey *et al.*, 2017; Bourg *et al.*, 2017). Disturbance and herbivory interact to facilitate invasive species establishment, with browsing reducing native plant competitive ability and creating opportunities for invasion in disturbed areas (Eschtruth & Battles, 2009). In heavily browsed areas, the native plant community may be so depleted that even nominally unpalatable invasive species such as Scotch broom provide critical resources; for example, Scotch broom flowers support pollinator populations on islands where native floral resources have been eliminated by deer browsing, despite reducing pollination success of some native Garry oak-associated plant species (Beckett *et al.*, 2022; Muir & Vamosi, 2015).

Emerging research suggests that the impacts of deer herbivory may be particularly severe in ecosystems already compromised by other anthropogenic stressors, with evidence pointing to synergistic rather than simply additive effects. A large-scale analysis of 33 national parks across the eastern United States found that sites with both high deer densities and invasive plant cover exhibited the most severe regeneration failures, with interactive effects creating compounding impacts on native plant recruitment and long-term forest structure (Miller *et al.*, 2023). Experimental work has further demonstrated that deer exclusion and invasive plant removal produce interactive effects on native plant recovery, with the greatest understory diversity and native species cover occurring only when both stressors are addressed simultaneously (Bourg *et al.*, 2017). This synergy appears to operate through multiple mechanisms: deer browsing reduces native plant competitive ability and creates disturbance-mediated opportunities for invasive establishment (Eschtruth & Battles, 2009), while selective consumption of palatable natives over unpalatable exotics further reinforces invasive dominance (Blossey *et al.*, 2017; Bourg *et al.*, 2017).

Beyond invasive species, deer herbivory interacts with a broader suite of anthropogenic stressors including climate change, habitat fragmentation, and legacy effects of historical land use. Climate warming has emerged as a primary driver of deer range expansion at

northern latitudes, with white-tailed deer expanding their range in western Canada due to milder winters and altered snow conditions, while land use changes play a secondary role (Dawe *et al.*, 2014). This climate-driven expansion is particularly concerning for ecosystems like the Gulf Islands that historically supported lower deer densities. Habitat fragmentation further complicates deer impacts by creating edge effects and altering spatial patterns of herbivory pressure across landscapes (Ramirez *et al.*, 2021b). Long-term studies have demonstrated that deer herbivory can explain substantial regional shifts in plant community composition even when controlling for succession, habitat fragmentation, climate change, and nitrogen deposition, with local deer impacts accounting for 41% of variance in 50-year regional changes (Frerker *et al.*, 2014). The development of indicator approaches that can capture these cumulative impacts in the presence of multiple associated stressors has become increasingly important for effective conservation monitoring (Blossey *et al.*, 2017).

The relative importance of deer herbivory versus other stressors may vary considerably across ecosystems and successional stages. Research conducted specifically in Gulf Islands Garry oak ecosystems has demonstrated that deer herbivory can be a more limiting factor than interspecific competition for both seedling establishment and established native plant growth (Gonzales & Arcese, 2008), challenging management approaches that prioritize invasive species removal over herbivore control. Furthermore, historical concerns about *O. hemionus columbianus* impeding forest regeneration following logging in Pacific Northwest coastal ecosystems (Crouch, 1976) suggest that browsing pressure has been a persistent impediment to ecosystem rehabilitation in disturbed forests for decades. These compounding effects have critical implications for reforestation and restoration efforts: a meta-analysis of deer herbivory mitigation strategies in temperate hardwood forests found that unprotected planted seedlings experienced significantly reduced survival and growth, with browsing impacts varying substantially across species based on palatability (Redick & Jacobs, 2020). The challenge for conservation organizations like the GCA is not only managing deer populations but also developing adaptive strategies that account for how

browsing pressure interacts with site-specific conditions and regional-scale stressors to determine restoration success.

Despite growing recognition that multiple stressors interact to shape plant community trajectories, the extent to which site-specific factors such as microclimate, soil conditions, and historical degradation gradients mediate deer impacts on plant community composition remains poorly understood. Rapid assessment methods that can capture deer browsing intensity across heterogeneous landscapes—such as the AVID (Assessing Vegetation Impacts from Deer) protocol, which evaluates browsing damage on hardwood regeneration—are increasingly important for informing adaptive management decisions (Curtis *et al.*, 2021). However, effectively measuring forest degradation and recovery requires multi-scale ecological integrity indicators that can integrate the cumulative impacts of deer herbivory with other anthropogenic pressures (DellaSala *et al.*, 2025). This knowledge gap is particularly critical for endangered Coastal Douglas-fir and Garry oak ecosystems on the Gulf Islands, where conservation managers require practical frameworks for assessing ecological condition, prioritizing intervention sites, and evaluating the effectiveness of integrated management strategies that address both deer populations and co-occurring stressors.

## Galiano Conservancy Association

Established in 1989 as a community-based land acquisition, management and conservation organization, the Galiano Conservancy Association (GCA) is one of British Columbia's oldest community-based land trusts (Community Conservation Research Network, n.d.; Galiano Conservancy Association [GCA], n.d.). As one of BC's first land trusts, the Conservancy owns or has covenants on 1,000 acres of environmentally sensitive properties on Galiano and has contributed to the protection of 2,000 acres on Galiano Island. Over more than three decades, the GCA has evolved from a land acquisition organization into a comprehensive conservation leader engaged in ecological restoration, environmental education, and sustainable living demonstration. The organization conducts extensive long-term biological monitoring and has grown to take on

a broader range of activities than traditional conservation organizations, including the stewardship and restoration of ecosystems degraded through intensive logging operations, as well as efforts to educate the public and raise awareness of sustainable human relationships with the natural world (GCA, n.d.). The Conservancy has received international recognition for its innovative approaches to ecological restoration.

The GCA's restoration work is centered at the Millard Learning Centre, a 144 hectare property on the midwest coast of Galiano Island acquired in 2012 to serve as a hub for ecological education and applied research in sustainable living (GCA, n.d.). The site functions as a "living laboratory" for ecological restoration, sustainable food production, and small-scale renewable energy generation, featuring a native plant nursery, permaculture demonstration sites, and the Nuts'a'maat Forage Forest—a collaborative project with Coast Salish communities. The organization's approach to conservation explicitly recognizes the intertwined nature of ecological and cultural restoration, embracing the history of human habitation by documenting it, incorporating it into educational programming, and refashioning it in contemporary ways such as establishing food forests on earlier agricultural land (Community Conservation Research Network, n.d.). Recent conservation acquisitions include 4.2 hectares of coastal Douglas-fir forest and sensitive Garry oak bluff habitat neighboring the existing Mt. Sutil Nature Sanctuary—the GCA's first land acquisition—establishing Mt. Sutil as a priority site for conserving rare Garry oak and associated ecosystems (Habitat Conservation Trust Foundation, 2024).

Central to the GCA's restoration challenges is managing the impact of hyperabundant black-tailed deer populations on ecosystem recovery. In alignment with their goal of achieving long-term ecosystem recovery and reconciliation in a unique island landscape shaped by cumulative historical impacts, the GCA has established a network of paired deer exclosures and open monitoring plots across the Millard Learning Centre and Mt. Sutil to support ongoing restoration and conservation efforts. These sites span a gradient of microclimatic conditions and historical disturbance regimes, including areas affected by logging, paddocks and browsing by free range domestic sheep, drainage modifications, compaction from roads, and pollution. Preliminary observations and photographic

monitoring suggest striking variation in how deer browsing affects vegetation between sites: some paired plots show minimal differences between exclosed and open areas, while others exhibit stark contrasts in vegetation composition and structure. This variation raises critical questions about the context-dependency of deer impacts and the factors that may confer resilience or vulnerability to browsing pressure.

## Study rationale

This study examines how browsing pressure from overabundant *O. hemionus columbianus* affects plant community composition across sites with varying degrees of historical ecological disturbance. Specifically, plant community characteristics—including successional stage, native species richness and cover, and invasive species richness and cover—between deer exclosures and their paired open plots, while accounting for site-level differences in disturbance history and soil moisture regime. I hypothesize that browsing by *O. hemionus columbianus* exerts greater downward pressure on plant communities in historically disturbed ecosystems compared to less disturbed sites, potentially creating alternative stable states that prevent recovery of native plant communities. By elucidating the interactive effects of deer herbivory and site condition on plant community dynamics, this research will contribute to the analytical framework for monitoring the deer exclosures installed by the Galiano Conservancy Association.

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## Methods

### Study Area

This study was conducted at the Millard Learning Centre on Galiano Island, British Columbia, Canada (49.41°N, 124.64°W), operated by the Galiano Conservancy Association. The site lies within the Coastal Douglas-fir biogeoclimatic zone (BC Ministry of Forests and Range & BC Ministry of Environment, 2010), a globally rare ecosystem characterized by a Mediterranean-type climate with mild, wet winters (mean annual

precipitation: 1020 mm) and dry summers (BC Ministry of Environment, Lands and Parks, n.d.). Steep island topography creates cool, moist valley bottoms that contrast with drier upper slopes.

Five paired monitoring sites established between 2019 and 2021 were included in this study: Mill Site, Nuts'a'maat Forage Forest (hereafter "Forage Forest"), Trincomali Bluffs (hereafter "Bluffs"), Camas Seep, and Fuelwood Forest. These sites span a gradient of historic anthropogenic disturbance (scores 0–18). Elevations range from approximately 60–130 m and encompass a variety of forest conditions, including mature coastal Douglas-fir (*Pseudotsuga menziesii*) and arbutus (*Arbutus menziesii*) stands, regenerating clearcuts, active restoration areas, and sensitive seep habitats supporting native wildflower communities.

Hyperabundant native black-tailed deer exert substantial browsing pressure throughout the study area (Cote *et al.*, 2004; Martin *et al.*, 2011). Historical land use varied among sites and included selective to clearcut logging (2002–2012), sheep paddocks and free-range livestock browsing, a wood mill, ecological restoration (initiated 2013), and more than a century of cumulative anthropogenic disturbance (GCA, 2022). This variation contributed to the disturbance gradient used in the analysis.

Each site, excluding Mill Site, consisted of paired 10 m × 10 m monitoring plots: a deer-excluded plot within a permanent ungulate enclosure (2.4-m wire-mesh fencing installed between 2013–2021 by the GCA) and an adjacent open control plot accessible to deer. Mill Site contained two enclosures (established in 2013 and 2021) and one open plot. Deer enclosures are an established and effective method for isolating herbivory effects on vegetation communities across diverse forest conditions (Curtis *et al.*, 2021; Redick & Jacobs, 2020).

Three additional paired plots were excluded from this study: two located on Mount Sutil, which lay outside the defined ecological and geographic scope, and the North Marsh site at the Millard Learning Centre, where enclosure and open plots exhibited minimal ecological divergence.

Vegetation surveys were conducted within this monitoring framework to assess the influence of deer browsing and historic disturbance on understory plant communities.

## Field Sampling

Vegetation was surveyed in late summer 2025 at all 11 included plots (five paired sites, plus Mill Site with two exclosures and one open plot). Within each plot, three 1 m × 1 m quadrats were established at randomly selected locations, yielding a set of 33 quadrats. Random coordinate pairs within each plot boundary were generated using an online random number generator and approximated in the field. Field data collection was conducted with assistance, while all subsequent data entry, processing, and analysis were completed by the author.

Within each quadrat, all vascular plant species were recorded and two variables were measured for each: (1) percent cover and (2) maximum height. Percent cover was visually estimated using a 0–10 cover class scale (0 = 0%, 1 = 1–10%, ..., 10 = 91–100%) (Bonham *et al.*, 2004), based on vertical ground projection and excluding mature tree canopy cover, as canopy vegetation was assumed to be unaffected by deer browsing. Cover classes were later converted to midpoint values for analyses (e.g., class 1 = 5%, class 2 = 15%).

Maximum height was measured to the nearest millimetre using a tape measure, recording the averages of the three tallest individuals of each species within the quadrat.

Species were identified in the field using *Plants of the Pacific Northwest Coast* (Pojar & MacKinnon, 1994) and verified using the iNaturalist app platform (iNaturalist.org, accessed 2025). Specimens that could not be identified in the field were photographed for later identification. Some grass species that remained unidentified were recorded as “unknown”—included in total richness and cover, but were excluded from native/invasive classifications. Measurements from the three quadrats within each plot were averaged to generate plot-level values for all analyses.

## Relative Disturbance Scale

Historic anthropogenic disturbance was quantified using a cumulative disturbance index adapted from existing frameworks (Hill *et al.*, 2002; Gann *et al.*, 2019; Lomnický *et al.*, 2019). Each plot received scores across six disturbance categories: logging intensity (0–6), soil disturbance (0–6), pollution/contamination risk (0–4), hydrological alteration (0–3), presence of roads/infrastructure (0–3), and historic agricultural use (0–3). Scores were modified based on time since disturbance (recent <20 years: +1; moderate 20–50 years: 0; old >100 years: –1) and restoration activity (none: 0; minimal: –1; moderate: –2; intensive: –3) (Gann *et al.*, 2019; DellaSala *et al.*, 2025). The final disturbance score represented the sum of all categories, ranging from 0–18 (see Table 1, Figure 1). All disturbance scoring and classification procedures were conducted by the author. Detailed criteria and site-level scores are provided in Appendix Table C and Table D.

Table 1. Summary table of site disturbance scores

Site	Mill Site enclosure (1)	Mill Site enclosure (2)	Mill Site open	Forage Forest enclosure	Forage Forest open	Bluffs enclosure	Bluffs open	Camas Seep enclosure	Camas Seep open	Fuelwood Forest enclosure	Fuelwood Forest open
Disturbance Score	17	17	18	10	12	3	4	0	1	9	10

## Microclimate - Soil Moisture

Soil moisture was quantified gravimetrically as a base-line to determine site-level differences. Soil was collected at ~7.5 cm depth using a hori-hori knife, sealed in plastic bags, and weighed to determine wet mass. Samples were oven-dried at 60°C to constant mass and reweighed to determine dry mass. Gravimetric water content was calculated as:

$$\text{Soil moisture (\%)} = \frac{\text{wet mass} - \text{dry mass}}{\text{dry mass}} \times 100.$$

## Species Richness, Percent Cover, and Diversity

Plant community composition was quantified in each paired deer-exclusion and open plot using measurements of species richness, percent cover, and diversity. For every plot, all vascular plant species were identified to the lowest possible taxonomic level and classified as native, invasive, or unknown. Species richness was calculated as the total number of unique taxa per plot and further partitioned into native and invasive richness.

Percent cover estimates were recorded for each species using visual cover classes and converted to mid-point values for analysis. Total vegetation cover and the proportional contribution of native, invasive, and unknown species were calculated for each plot.

To assess community diversity, both the Shannon diversity index ( $H'$ ) and the Gini–Simpson index ( $1 - D$ ) were calculated in Excel for each plot using species-level proportional cover values. Shannon diversity was calculated as

$$H' = - \sum_{i=1}^S p_i \ln (p_i),$$

and Gini–Simpson diversity as

$$1 - D = 1 - \sum_{i=1}^S p_i^2,$$

where  $p_i$  represents the relative cover of species  $i$  within a plot. All richness, cover, and diversity metrics were summarized in a comparative table and visualized using bar charts to illustrate treatment-level differences across sites.

## Community Composition

Differences in community composition between deer-excluded and open plots were assessed using permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity matrices. Models included treatment (exclosure vs. open) and plot pair as a blocking factor. Interaction terms (treatment  $\times$  soil moisture, treatment  $\times$

disturbance score) were tested in separate models. Site identity was included as a blocking factor. All PERMANOVAs used 999 permutations with sequential testing. Analyses were performed in Rstudio version 4.4.2 using the vegan package (v. 2.6-4).

## Species Cover and Richness

Effects of deer exclusion, historic disturbance, and their interaction on invasive cover, native cover, and successional composition were assessed using linear mixed-effects models (LMMs) with plot pair as a random intercept. Species richness (native, invasive, and total) was analysed using generalized linear mixed models (GLMMs) with Poisson errors and log links. Models were fit using lme4, with inference based on Satterthwaite's approximation (LMMs; lmerTest) or Wald z-tests (GLMMs). Model assumptions were evaluated using residual diagnostics and checks for overdispersion. Singular fits were retained to preserve consistent model structure.

## Successional Stage Analysis

Successional stage ratios were calculated as early-successional cover (grasses + herbs) divided by late-successional cover (trees + shrubs + lianas). Effects of treatment, disturbance score, and their interaction were tested using LMMs with plot pair as a random intercept.

## Plant Height

Average plant height was analysed separately for five growth forms (trees, shrubs, lianas, herbs, grasses). Models included treatment, disturbance score, and their interaction as fixed effects, with plot pair as a random intercept. All analyses were conducted in Rstudio version 4.4.2 using lme4, lmerTest, glmmTMB, and vegan. Significance was assessed at  $\alpha = 0.05$ , with marginal significance defined as  $0.05 < p < 0.10$ .

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# Analysis

## Overview of Analytical Approach

Results are presented in seven parts: (1) anecdotal analyses of each plot pair (2) species cover, richness, and diversity indices, (3) community composition responses to deer browsing, soil moisture, and historical degradation; (4) invasive and native cover responses to browsing and degradation; (5) species richness responses by nativity; (6) successional composition response; (7) plant height response. All models included plot pair as a random intercept unless otherwise stated. Species with unknown status (invasive or native) were included in total vegetation cover and richness, but were otherwise excluded from the analysis. A summary table of p-values and standard deviations is included in the Appendix (Tables E, F1, and F2).

## 1. Anecdotal Analysis

### 1.1 Mill Site

The Mill Site received the highest disturbance score (17 for exclosures, 18 for open plot) and served historically as the operational center for Campbell's logging business from 1958 to 2012, with associated industrial contamination, soil compaction, and vegetation removal (Duncan & Warren, 2020). Located closest to the main road and Millard Learning Centre entrance, the site also experienced light sheep grazing during earlier agricultural use. Prior to restoration, staff described the mill site as being in especially degraded condition, with contaminated soils, pollutants, abandoned machinery, and burn piles of cedar up to 15 feet high (Duncan & Warren, 2020).

This site has been the focus of active ecological restoration since 2013, including soil decompaction, native plantings, deer exclosures, and individual plant caging—representing standard restoration practices employed by the Galiano Conservancy Association. The monitoring framework established in 2019 includes two exclosures with contrasting histories and one open control plot. Exclosure 1 was fenced immediately following restoration treatments in 2013, providing nearly a decade of deer exclusion prior to data collection beginning in 2019. Exclosure 2 was initially maintained as an open plot

with scattered caged native plantings but was incorporated into an expanded fenced area in late summer 2021. A new open control plot was established adjacent to Exclosure 2 in summer 2022 to serve as an ongoing comparison.

Vegetation structure differs markedly between treatments. Within exclosures, overhead canopy casts approximately 70% shade on the understory, and both exclosure plots exhibit dense coverage of trailing blackberry (*Rubus ursinus*). In contrast, the open plot maintains a much more open canopy with greater herb assemblage and fewer *Rubus ursinus* individuals. A planted bitter cherry (*Prunus emarginata*) with individual deer fencing within the open plot showed visible browse damage. Plant community composition differs notably between Exclosure 1 (protected since 2013), Exclosure 2 (protected since 2021), and the open plot (never protected).

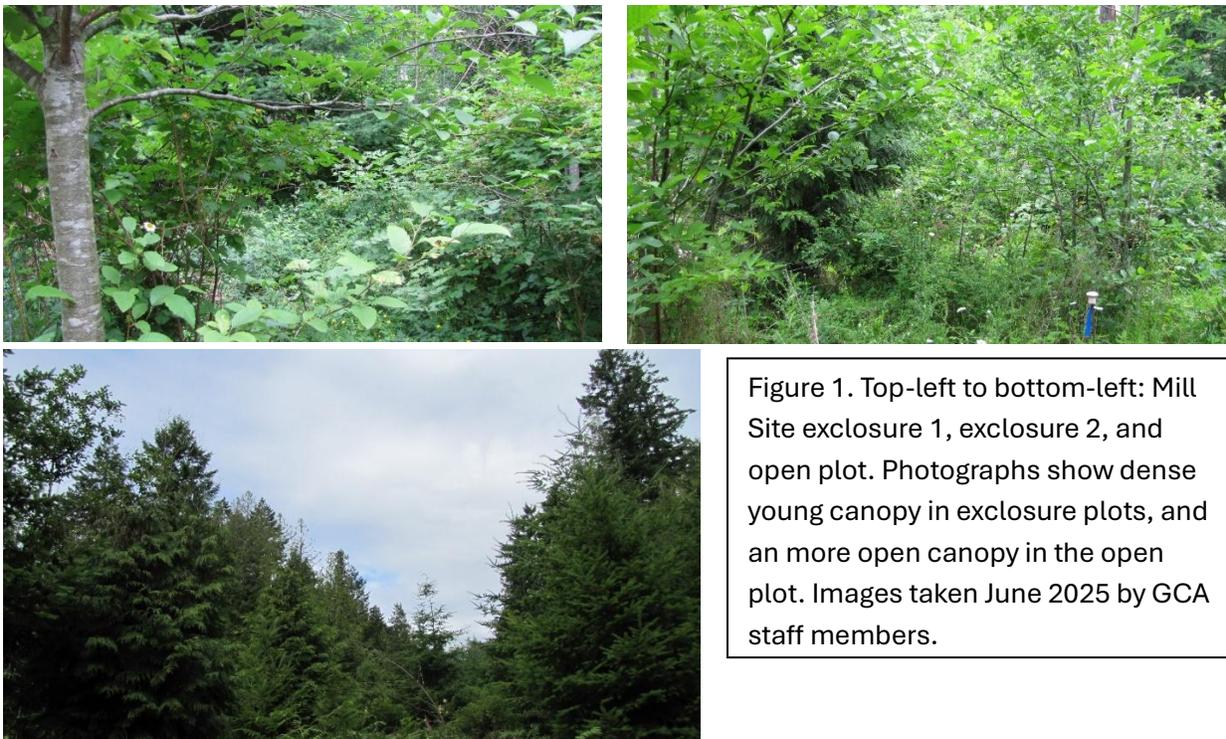


Figure 1. Top-left to bottom-left: Mill Site exclosure 1, exclosure 2, and open plot. Photographs show dense young canopy in exclosure plots, and an more open canopy in the open plot. Images taken June 2025 by GCA staff members.

## 1.2 Nuts'a'maat Forage Forest

The Nuts'a'maat Forage Forest site experienced clearcut logging between 2002 and 2012, with one old-growth cedar tree remaining as evidence of the pre-logging forest. A gravel road separates the paired monitoring plots, which straddle opposing sides of a ridge with

contrasting aspects. This plot was established in 2019 to determine deer impacts on regenerating clearcut ecosystems that retained native shrub cover following harvest.

The exclosure plot, situated on a northeast-facing slope, is incorporated within the larger Nuts'a'maat Forage Forest fenceline—a collaborative restoration project designed in consultation with Penelakut Nation elders Auggie Sylvester and Karen Charlie to create a learning and foraging space featuring edible, medicinal, and culturally significant plants (Duncan & Warren, 2020). The site was chosen specifically because healthy cover of native shrubs and forbs were retained following logging operations. Restoration activities within the exclosure have been relatively non-intensive, limited to invasive species removal and deer fencing installation, with vegetation otherwise allowed to develop naturally without active planting. The open plot occupies a southwest-facing slope on the opposite side of the same ridge, experiencing different microclimatic conditions than its paired exclosure.

Both plots are dominated by tall native shrubs and ferns, creating dense understory vegetation. The exclosure plot exhibits slightly more visible ground layer compared to the open plot, which had a dominance of salal (*Gaultheria shallon*). Notably, oceanspray (*Holodiscus discolor*) was observed within the exclosure but absent from the open plot. Additionally, deer bedding sites were observed immediately adjacent to the open plot boundaries, and a deer trail provided the primary access route to the site, demonstrating intensive deer use of the area.

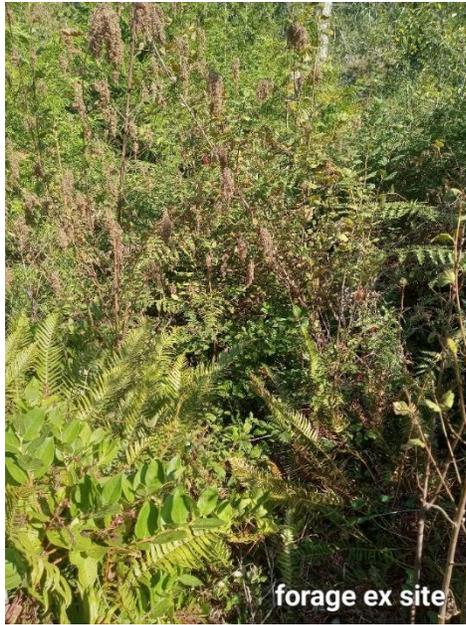


Figure 2. Top left to bottom right: Forage Forest exclusion, exclusion sampling quadrat, open plot, and open sampling quadrat. Images demonstrate dense shrubbery and low species diversity characteristic of this plot pair. Pictures taken September 13, 2025.

### 1.3 Trincomali Bluffs

The Trincomali Bluffs site is located along the Cormorant Cliff loop trail at the Millard Learning Centre and was established in 2019 to determine deer impacts on mature dry coastal forest ecosystems. The site was selected as reasonably representative of the semi-open Douglas-fir (*Pseudotsuga menziesii*) and arbutus (*Arbutus menziesii*) forests occurring along the 2 km MLC coastline, though the study plots may be slightly more

shaded than similar forests located closer to the cliff edges. Historical disturbance at this site includes selective logging many years ago and free-range sheep grazing that ceased 5-10 years prior to plot establishment, contributing to a moderate disturbance score.

Both plots consist mostly of native understory vegetation beneath a canopy exceeding 50% native tree cover. The overhead canopy creates a dark understory environment where moss, leaf mulch, and boulders collectively occupy more than 50% of ground cover.

Ongoing Scotch broom (*Cytisus scoparius*) removal occurs in both enclosure and open plots as part of invasive species management efforts, though the overall plant community remains dominated by native species.

Tree regeneration patterns differ markedly between treatments, providing clear evidence of deer browsing impacts on forest succession. Within the enclosure, 8 Douglas-fir seedlings and 5 arbutus seedlings were observed, indicating successful natural regeneration under protected conditions. In contrast, only a single Douglas-fir seedling was observed in the open plot.



Figure 3. Trincomalli bluffs enclosure (left) and adjacent open plot (right). Images show partial sun coming through the canopy and open ground. Pictures taken September 12, 2025.

## 1.4 Camas Seep

The Camas Seep site received the lowest disturbance scores (0 for enclosure, 1 for open plot), reflecting minimal historical anthropogenic impact despite some free-range sheep grazing in the past. Located above a cove at the southeast corner of the Millard Learning Centre, this plot was established in 2021 to determine deer impacts on a sensitive seepage site supporting diverse native wildflower communities. The site was specifically chosen for its abundance of native herbaceous species in an open forest ecosystem, including camas (*Camassia* spp.), death camas (*Toxicoscordion venenosum*), sea blush (*Plectritis congesta*), chocolate lily (*Fritillaria affinis*), monkeyflower (*Erythranthe* spp.), and field chickweed (*Cerastium arvense*)—many of which are culturally significant species that historically thrived under Coast Salish stewardship.

The site exhibits characteristic features of a seepage ecosystem, with rocky, exposed ground and moss creating a patchy substrate matrix. Moss, tree fall debris, and exposed boulders collectively occupy up to 30% of ground cover, creating heterogeneous microsite conditions that support the diverse wildflower assemblage. The plots contain a mix of native and introduced species, with ongoing Scotch broom (*Cytisus scoparius*) removal occurring in both enclosure and open plots as part of invasive species management. Vegetation structure differs noticeably between treatments despite the site's minimal disturbance history. The enclosure plot exhibits visually much higher presence of trailing blackberry (*Rubus ursinus*) compared to the open plot, suggesting that deer browsing pressure selectively reduces this palatable native shrub even in relatively pristine seepage habitats.



Figure 4. Top-left to bottom-right: Camas Seep enclosure, enclosure sampling quadrat, open plot, and open sampling quadrat. The images show greater shrub density in the enclosure plot and grass density in the open plot. Pictures taken September 25, 2025.



### 1.5 Fuelwood Forest

The Fuelwood Forest site was established in 2019 to determine deer impacts on young, semi-open Douglas-fir forest ecosystems with developing understory structure. Located

within the Phase 1 Chrystal Creek watershed restoration area at the Millard Learning Centre, the site exemplifies young regenerating forest with sufficient light infiltration to support understory development. The plots contain a mix of native and introduced species reflecting the area's long disturbance history spanning more than a century.

The site's complex disturbance trajectory began with clearcutting approximately 100 years ago, followed by natural Douglas-fir regeneration beginning about 60 years ago, and selective thinning with a chain hoist within the last five years. More recently, the site supported a sheep paddock with livestock present until 2016. In winter 2021-2022, the original 10 m × 10 m deer enclosure was disassembled when the plot was incorporated into a larger fenced area for Phase 1 of the Chrystal Creek watershed restoration project, providing continued protection from deer browsing within an expanded restoration context.

Understory composition differs dramatically between treatments. The open plot is dominated by Oregon grape (*Berberis nervosa*), while the enclosure maintains a much more open, grassy understory structure. Most notably, 16 arbutus (*Arbutus menziesii*) seedlings were observed in the enclosure plot, whereas no tree seedlings were found in the open plot. This absence of tree regeneration in the open plot, combined with the prevalence of Oregon grape, represents a marked difference in vegetation structure and composition between deer-accessible and deer-excluded areas at this site.



Figure 5. Top-left to bottom-right: Fuelwood forest exclosure, exclosure sampling quadrat, open plot, and open sampling quadrat. Images show more open, grassy groundcover and presence of young *Arbutus* tree in the exclosure, and dense covering of *Berberis nervosa* in the open plot. Pictures taken September 13, 2025



## 2. Species cover, richness, and diversity indices

Patterns of species richness, percent cover, and diversity varied among sites and between deer-excluded and open plots (Table 2; Figures 1–2). Across most sites, open plots supported higher invasive species richness and cover, while exclosures tended to support

either higher native species richness, higher native percent cover, or higher overall community diversity, though these effects were site-specific.

## 2.1 Species Richness

Total species richness ranged from 6 to 17 species per plot, with no consistent directional effect of exclosures across all sites (Table 2). However, invasive richness was generally higher in open plots, with the Mill Site Open plot showing the highest invasive richness (9 species; Figure 6). The exception was the Fuelwood Forest site, where the exclosure contained more invasive species (2 vs. 3 in the open plot). Native species richness showed no consistent trend, varying strongly by site: for example, Bluffs exclosure and open plots both contained 10 native species, whereas the Mill Site plots varied widely (3–8 native species). These mixed patterns suggest that deer exclusion alone does not uniformly increase native richness but does tend to limit the accumulation of invasive species, particularly in more disturbed or early-successional sites.

Table 2. Plant community metrics for paired deer exclosure and open plots across five study sites

Site	Species Richness	Total Vegetation % cover	Invasive Richness	Invasive % Cover	Native Richness	Native % Cover	Shannon diversity index H'	Gini-Simpson diversity index (1-D)
Mill Site Exclosure (1)	7	75	4	20	3	55	1.389715	0.613333
Mill Site Exclosure (2)	10	100	4	20	5	75	1.842189	0.755
Mill Site Open	17	95	9	55	8	40	2.770974	0.930748
Forage Forest Exclosure	6	110	0	0	6	110	1.760237	0.822314
Forage Forest Open	6	90	1	5	5	85	1.584323	0.759259
Bluffs Exclosure	11	85	1	5	10	80	2.251595	0.878893

Bluffs Open	11	65	1	5	10	60	2.311423	0.887574
Camas Seep Exclosure	10	80	3	15	7	65	2.06365	0.835938
Camas Seep Open	15	95	5	45	10	50	2.520903	0.891967
Fuelwood Forest Exclosure	9	95	2	15	5	55	2.000507	0.842105
Fuelwood Forest Open	6	100	3	10	3	85	0.964695	0.352978

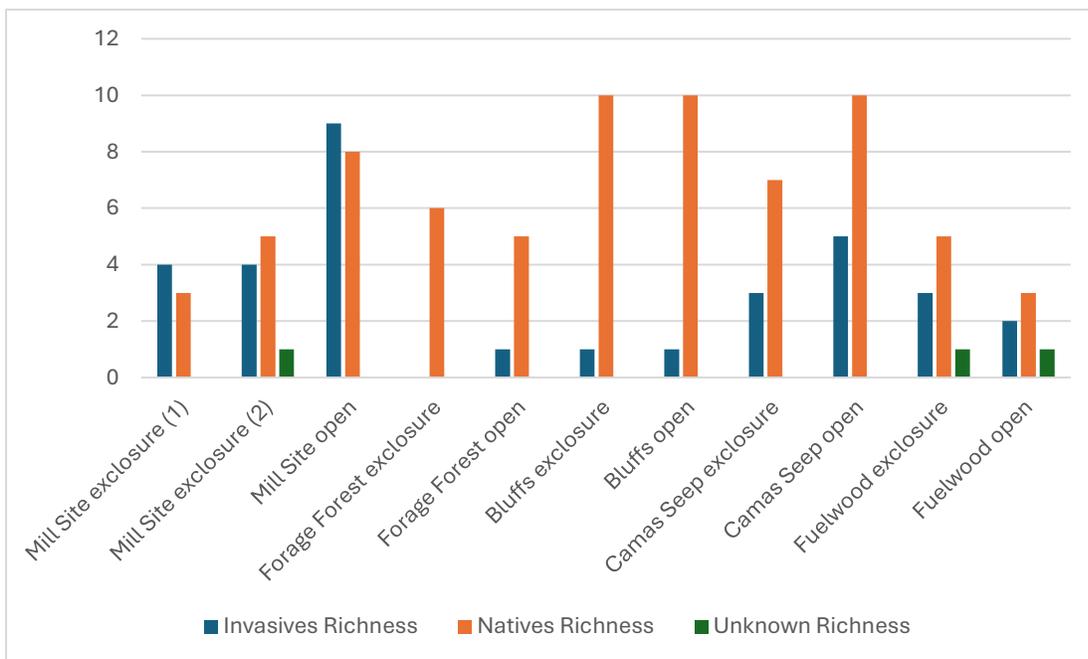


Figure 6. Richness of invasive, native, and unknown plant species recorded across paired deer-excluded and open plots at five at the Millard Learning Centre. Bars show total species richness within each plot type, illustrating a trend in increases in invasive species richness in open plots, excluding the Fuelwood Forest site, which had a greater invasives richness in the exclosure plot, and the Bluffs site, in which there was no difference. Native species richness was variable across sites.

## 2.2 Vegetation percent cover

Patterns in vegetation cover were more consistent than richness. With the exception of the Fuelwood Forest site, open plots had a greater proportion of invasive species cover than adjacent exclosures (Figure 7). Mill Site Open displayed the highest invasive cover (55%), followed by Camas Seep Open (45%). In contrast, invasive cover in exclosure plots was typically much lower (0–25%). Native percent cover was generally higher in exclosures—most notably at the Forage Forest site, where the exclosure was composed entirely of native vegetation (110% cover with layering). These trends indicate that deer exclusion is associated with higher structural dominance of native plants, even when native richness does not strongly differ. The Fuelwood Forest site again represented an exception: both plots had high native cover, but the exclosure also exhibited substantial unknown cover, complicating interpretation.

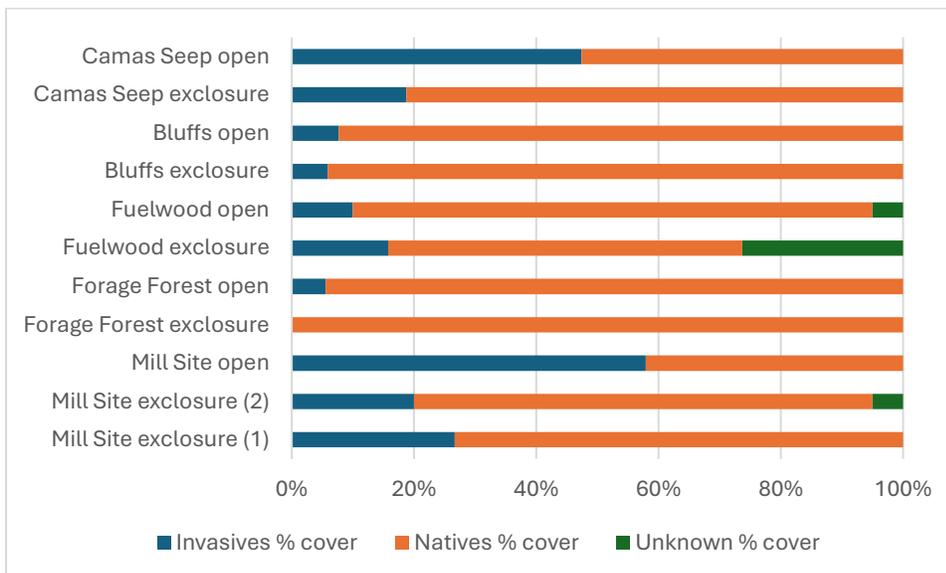


Figure 7. Relative proportions of native, invasive, and unknown plant cover by treatment (exclosure vs. open) and site. Sites are ordered from highest to lowest disturbance scores. Excluding the Fuelwood Forest, open sites tended toward having higher ratios of invasive species percent cover than their adjacent exclosed sites.

## 2.3 Diversity Indices

Both Shannon and Gini–Simpson diversity indices reflected the combined effects of richness and cover distribution. Open plots typically exhibited higher diversity values, driven by their higher total richness and more even mix of native and invasive species. Mill Site Open displayed the highest Shannon diversity ( $H' = 2.77$ ) and one of the highest Gini–Simpson values ( $1 - D = 0.93$ ). Exclosure plots showed moderate diversity values, with lower  $H'$  and  $1 - D$  in cases where native species strongly dominated the community (e.g., Forage Forest Exclosure). In several sites (e.g., Bluffs), diversity indices were similar between treatments, indicating comparable community structure despite differences in herbivory pressure.

## 3. Plant Community Composition (PERMANOVA and NMDS)

### 3.1. Deer browsing effects on plant community composition

Plant community composition differed marginally between deer-excluded and browsed plots (PERMANOVA:  $F_{1,8} = 1.67$ ,  $R^2 = 0.295$ ,  $p = 0.054$ ; Figure 8). Treatment (exclosure and open) explained 29.5% of the variation after accounting for plot pair. The moderate effect size suggests ecologically meaningful divergence between communities despite limited statistical power from the small sample size (5 plot pairs;  $n = 11$ ).

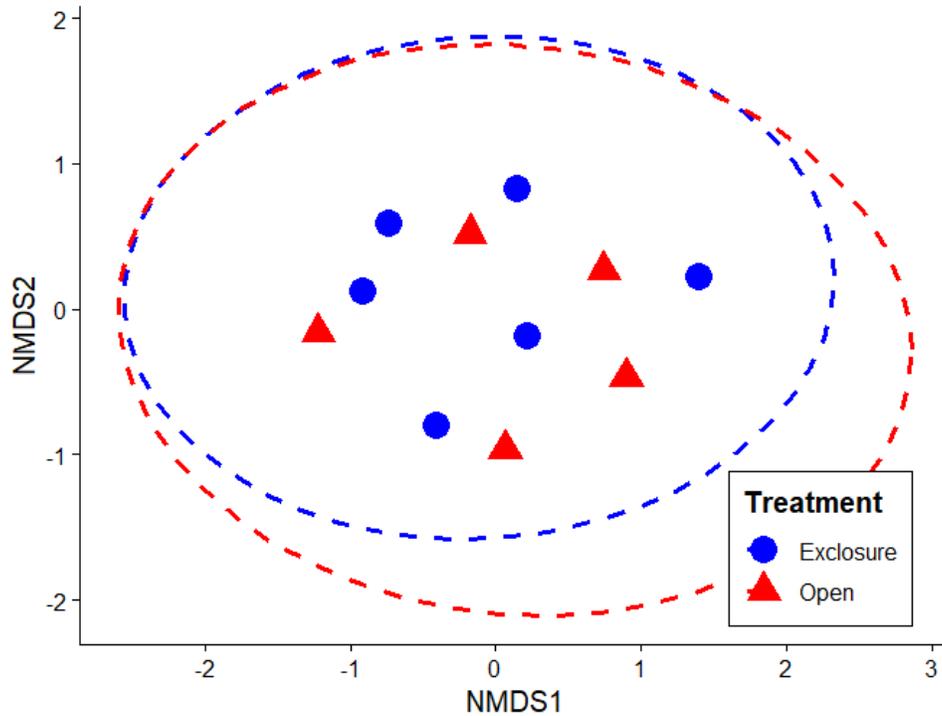


Figure 8. Non-metric multidimensional scaling (NMDS) ordination of plant community composition based on Bray-Curtis dissimilarity. Blue circles represent deer-excluded exclosures; red triangles represent browsed open plots. Shaded ellipses show 95% confidence regions for each treatment. 2D stress = [0.095].

### 3.2. Interactive effects of deer browsing and soil moisture

Soil moisture was the strongest predictor of species composition (PERMANOVA:  $R^2 = 0.168$ ,  $F = 3.88$ ,  $p = 0.001$ ). Deer browsing had a marginal effect ( $R^2 = 0.077$ ,  $F = 1.77$ ,  $p = 0.093$ ), but browsing effects did not vary across the soil moisture gradient (treatment  $\times$  moisture:  $R^2 = 0.044$ ,  $F = 1.01$ ,  $p = 0.457$ ). This indicates that browsing impacts were consistent across wet and dry sites.

### Plant Community Composition Across Soil Moisture Gradient

NMDS ordination based on Bray-Curtis dissimilarity | Stress = 0.095

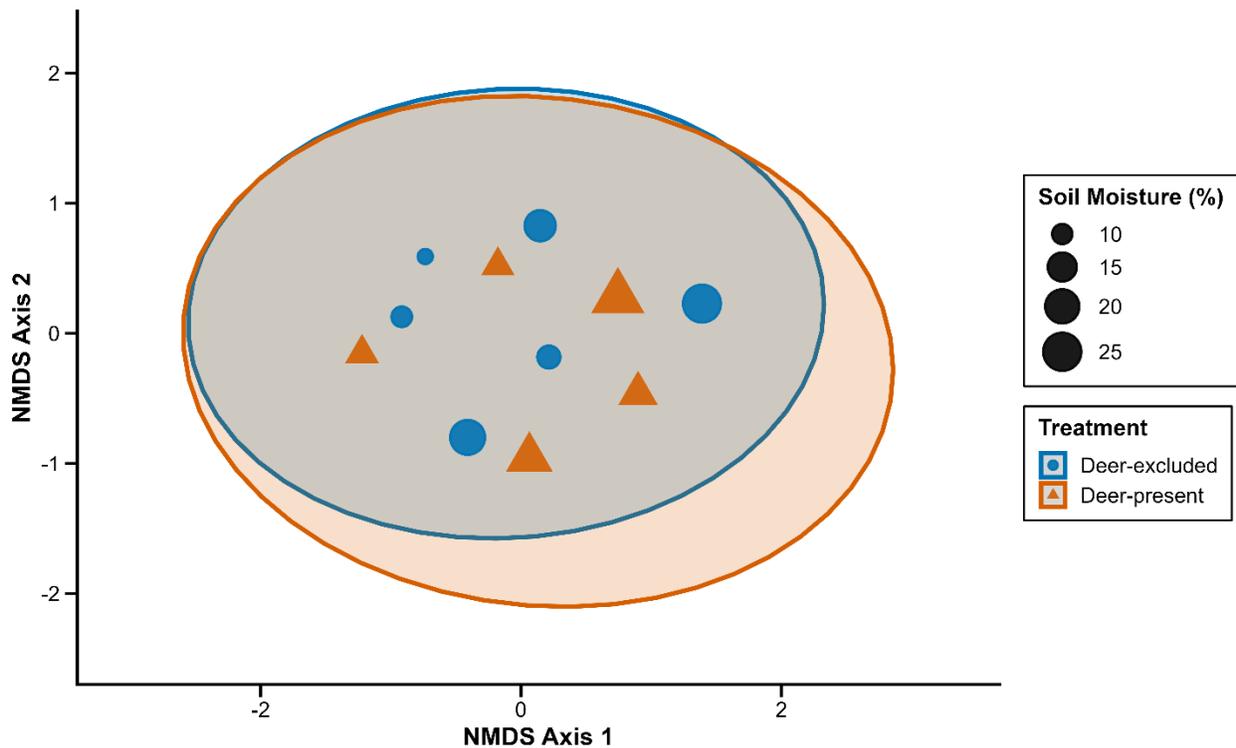


Figure 9. NMDS ordination of plant community composition in relation to deer browsing and soil moisture. Ordination based on Bray-Curtis dissimilarity. Points represent individual plots colored by treatment (blue circles = deer-excluded exclosures; orange triangles = deer-accessible open plots), with point size scaled to soil moisture percentage. Dashed lines connect paired plots. Ellipses show 95% confidence regions for each treatment. 2D stress = 0.095. PERMANOVA results reported in text; permutations restricted within plot pairs ( $n = 999$ ).

### 3.3. Interactive effects of deer browsing and historical disturbance on species composition

Deer browsing showed a marginal effect on plant community composition (PERMANOVA:  $R^2 = 0.077$ ,  $F_{1,7} = 0.79$ ,  $p = 0.063$ ), explaining 7.7% of compositional variation. Historical degradation score was not a significant predictor ( $R^2 = 0.199$ ,  $F_{1,7} = 2.04$ ,  $p = 0.208$ ), nor was there a significant treatment  $\times$  degradation interaction ( $R^2 = 0.044$ ,  $F_{1,7} = 0.45$ ,  $p = 0.458$ ), indicating that browsing effects on community composition did not vary across the degradation gradient. The majority of compositional variation (68%) remained unexplained by the model.

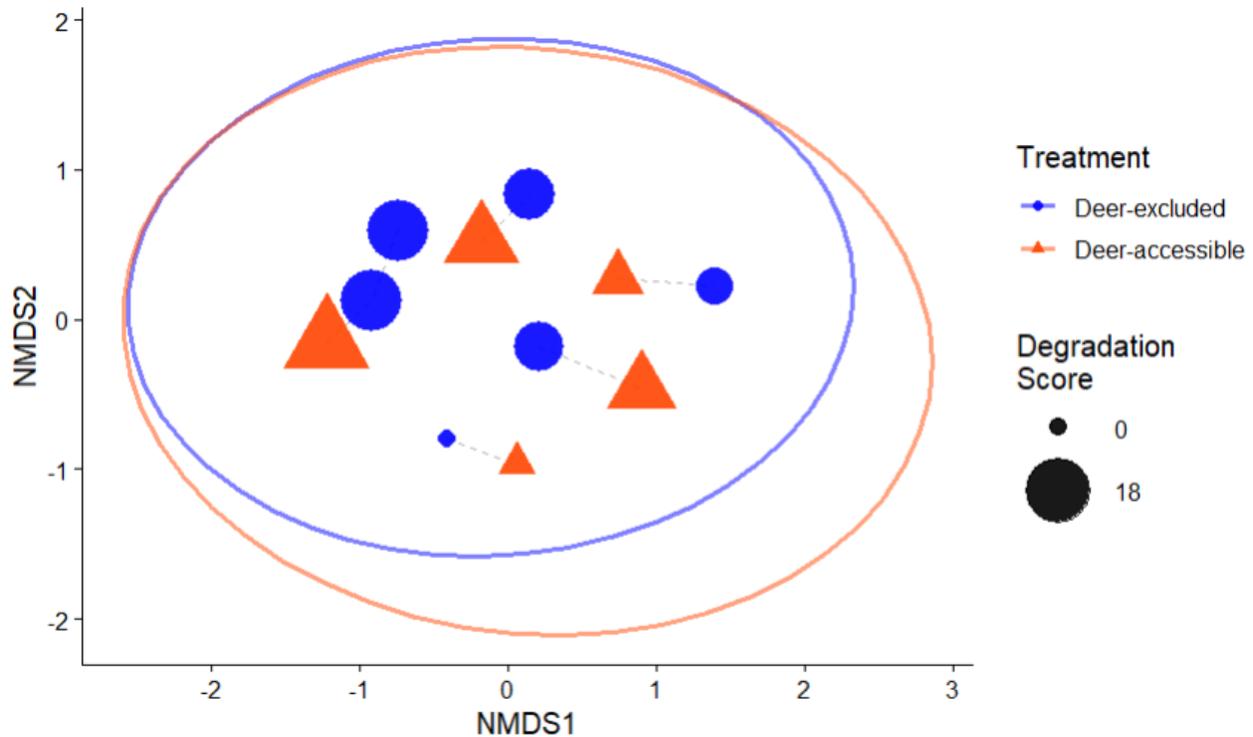


Figure 10. NMDS ordination of plant community composition based on Bray-Curtis dissimilarity. Points represent individual plots colored by treatment (blue circles = deer-excluded exclosures; orange triangles = deer-accessible open plots), with point size scaled to historical degradation score. Dashed lines connect paired exclosure-open plots at the same site. Ellipses show 95% confidence regions for each treatment. Two-dimensional NMDS stress = 0.095. Permutations restricted within plot pairs ( $n = 999$ ).

## 4. Effect of deer browsing on native and invasive plant cover across disturbance gradients

### 4.1. Native plant cover

Native cover did not differ significantly between treatments (open plots:  $-9.583 \pm 19.48885$ ;  $p = 0.648$ ) and showed no effect of disturbance ( $\beta = 0.085 \pm 1.64852$ ;  $p = 0.961$ ). The interaction was not significant ( $\beta = -0.16 \pm 1.77245$ ;  $p = 0.932$ ), indicating deer effects on native cover did not vary along the disturbance gradient. Within-site variation (residual variance = 321.9, residual SD = 17.94%) exceeded between-site variation (variance =

242.6, SD = 15.58%), indicating that local plot-level factors and treatment effects contributed substantially to native cover variation beyond site-level differences.

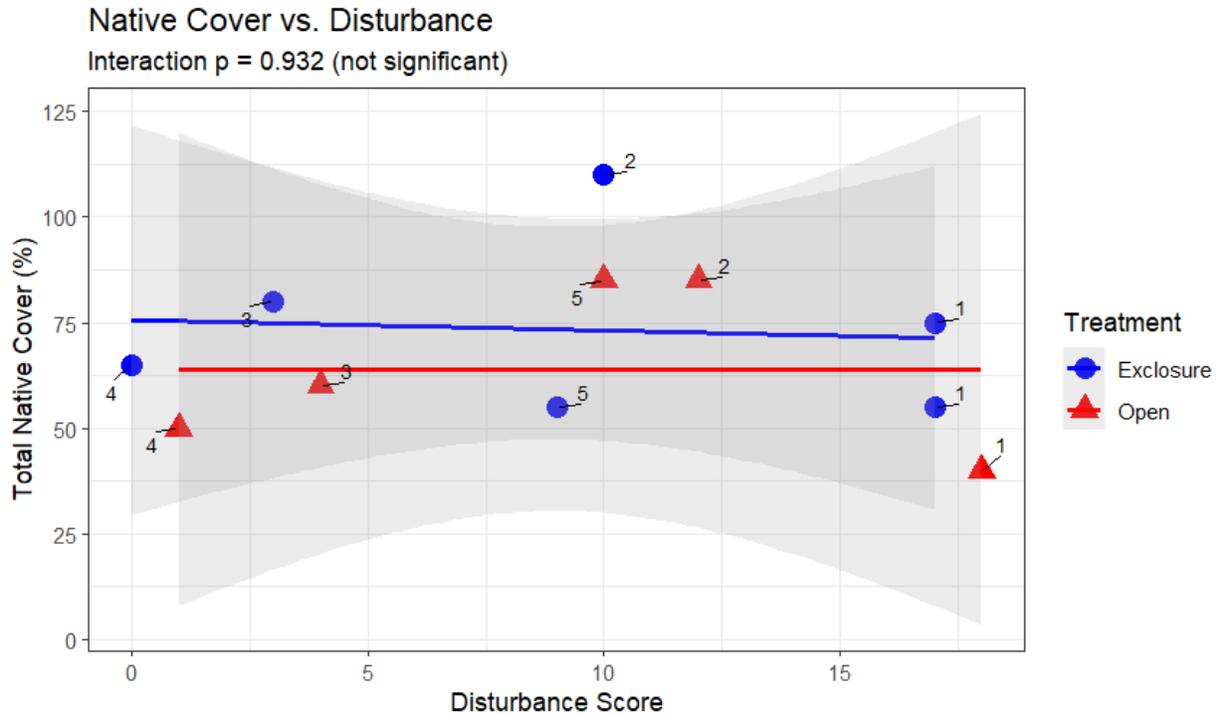


Figure 11. Relationship between total native plant cover and historical disturbance score in deer-excluded (blue circles) and browsed (red triangles) plots. Points represent individual plots labeled by site ID. Lines show linear model predictions with 95% confidence intervals (shaded regions). Native cover showed no significant differences between treatments ( $p = 0.648$ ) or across the disturbance gradient (interaction  $p = 0.932$ ), suggesting high natural variability masked detection of browsing effects on native plant abundance.

#### 4.2. Invasive plant cover

Invasive plant cover did not differ significantly between treatments ( $\beta = 7.956 \pm 14.2246$ ;  $p = 0.605$ ) and showed no relationship with disturbance ( $\beta = 0.153 \pm 1.3664$ ;  $p = 0.917$ ). The interaction was not significant ( $\beta = 0.595 \pm 1.2932$ ;  $p = 0.669$ ). Between-site variation was substantial (variance = 203.5, SD = 14.26%), exceeding within-site variation (variance = 171, residual SD = 13.08%), indicating that site-specific factors beyond browsing and disturbance strongly influenced invasive plant establishment.

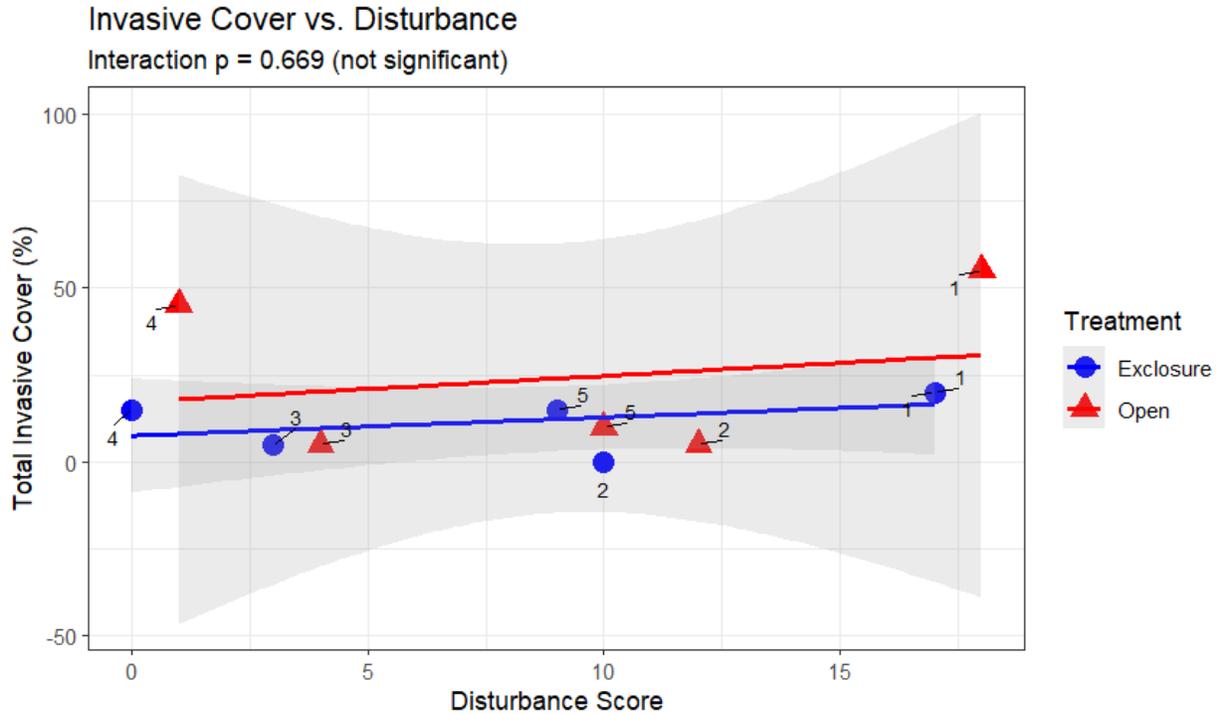


Figure 12. Relationship between total invasive plant cover and historical disturbance score in deer-excluded (blue circles) and browsed (red triangles) plots. Points represent individual plots labeled by site ID. Lines show linear model predictions with 95% confidence intervals (shaded regions).

## 5. Species Richness Across Disturbance Gradient

### 5.1. Native species richness

Native species richness did not differ significantly between deer-excluded exclosures and open plots (GLMM:  $\beta = 0.074 \pm 0.38107$ ,  $z = 0.19$ ,  $p = 0.846$ ). There was a marginal negative relationship between disturbance score and native richness ( $\beta = -0.044 \pm 0.02641$ ,  $z = -1.68$ ,  $p = 0.093$ ), suggesting that more disturbed sites tended to have slightly lower native richness. The treatment  $\times$  disturbance interaction was not significant ( $\beta = 0.013 \pm 0.06165$ ,  $z = 0.33$ ,  $p = 0.739$ ), indicating that browsing effects on native richness did not vary across the degradation gradient. The random effect of plot pair explained negligible variation (variance =  $1.615 \times 10^{-10}$ ,  $SD = 1.271 \times 10^{-5}$ ) suggesting minimal site-to-site variation in richness beyond the measured predictors.

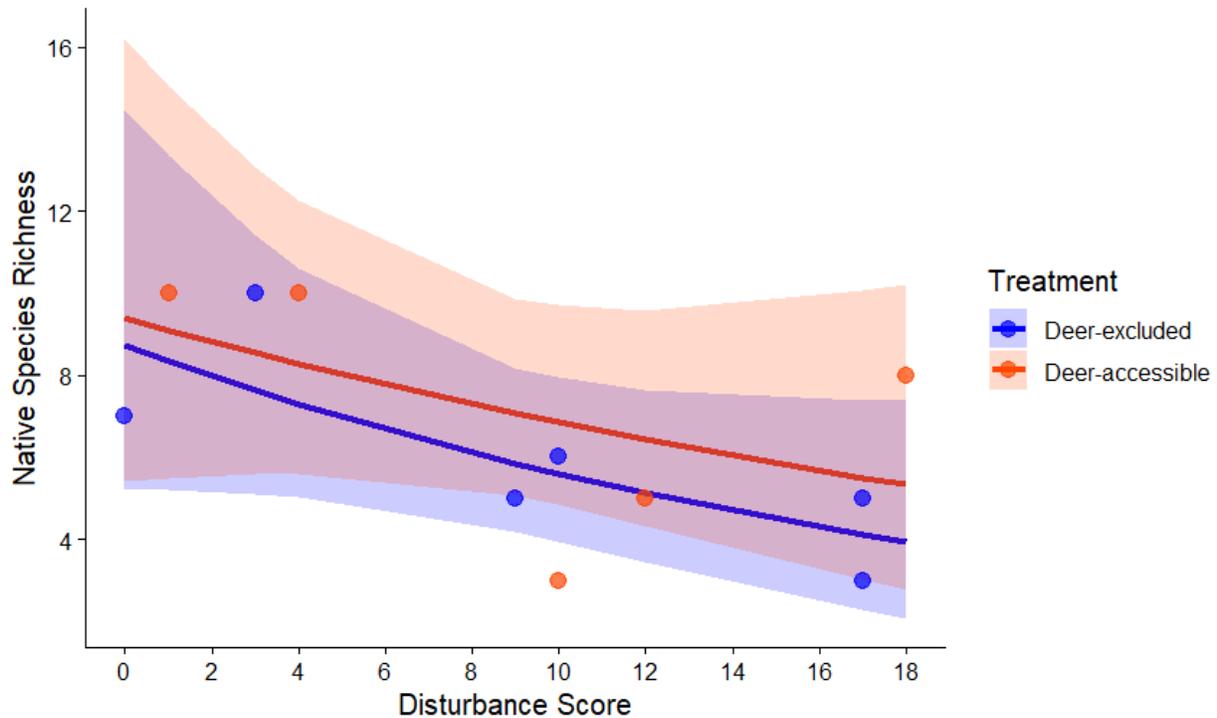


Figure 13. Native species richness in relation to deer browsing and historical degradation. Points represent individual plots colored by treatment (blue = deer-excluded exclosures; orange = deer-accessible open plots). Lines show predicted richness from a generalized linear mixed model with 95% confidence intervals (shaded regions). Native richness did not differ significantly between treatments ( $p = 0.846$ ) but showed a marginal negative trend with degradation score ( $p = 0.093$ ). The treatment  $\times$  degradation interaction was not significant ( $p = 0.739$ ).

## 5.2. Invasive species richness

Invasive species richness was not significantly affected by deer browsing (GLMM:  $\beta = 0.357 \pm 0.678$ ,  $z = 0.527$ ,  $p = 0.598$ ), degradation score ( $\beta = 0.027 \pm 0.062$ ,  $z = 0.446$ ,  $p = 0.656$ ), or their interaction ( $\beta = 0.022 \pm 0.052$ ,  $z = 0.418$ ,  $p = 0.676$ ). The random effect of plot pair showed moderate between-site variation (variance = 0.380, SD = 0.616), suggesting that factors beyond browsing and historical degradation influence invasive species establishment at different sites.

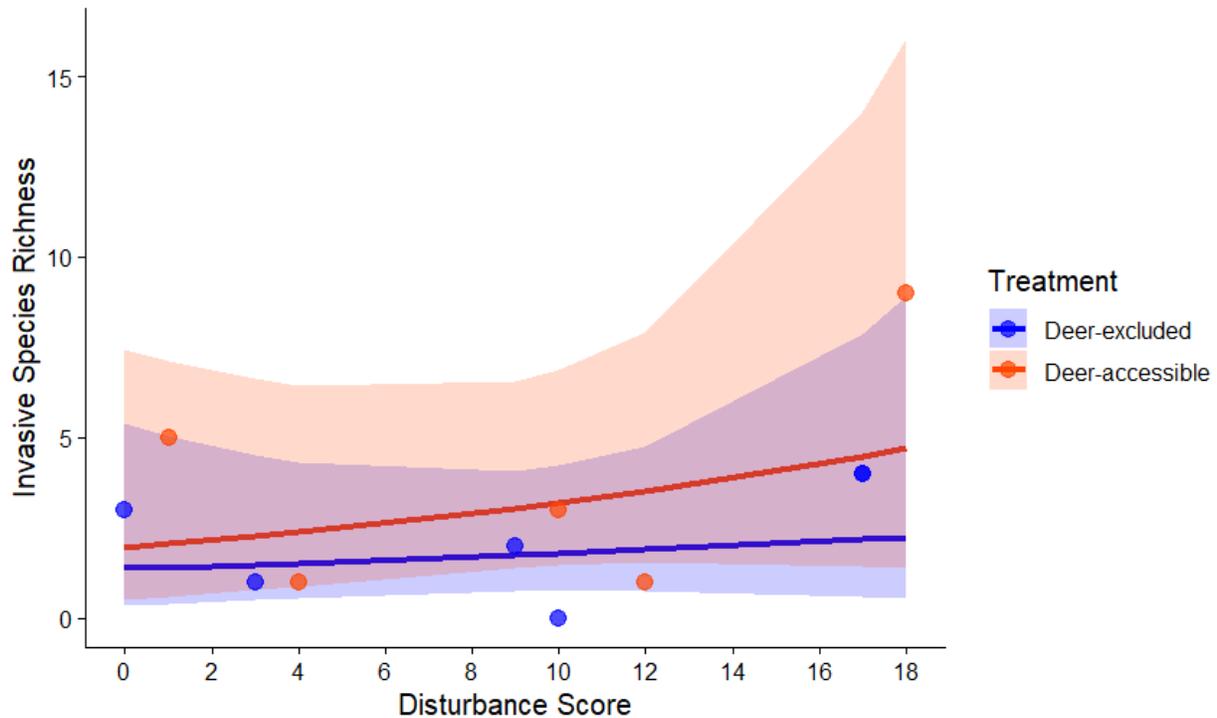


Figure 14. Invasive species richness showed no response to deer browsing or degradation. Individual plots colored by treatment (blue = deer-excluded exclosures; orange = deer-accessible open plots). Lines represent Poisson GLMM predictions with 95% confidence intervals. Neither browsing ( $p = 0.598$ ), disturbance ( $p = 0.656$ ), nor their interaction ( $p = 0.676$ ) significantly predicted invasive richness.

### 5.3. Overall species richness across treatments and disturbance

Total species richness (native + invasive + unknown) did not differ significantly between deer-excluded exclosures and open plots (GLMM:  $\beta = 0.103 \pm 0.330$ ,  $z = 0.311$ ,  $p = 0.756$ ), nor was it affected by degradation score ( $\beta = -0.018 \pm 0.024$ ,  $z = -0.725$ ,  $p = 0.468$ ) or their interaction ( $\beta = 0.019 \pm 0.030$ ,  $z = 0.623$ ,  $p = 0.533$ ). The random effect of plot pair showed minimal between-site variation (variance = 0.022, SD = 0.150), indicating sites were similar in total richness once treatment and degradation were accounted for.

## 6. Successional Composition (Early : Late cover ratios)

Early successional cover (grasses + herbs) did not differ significantly between deer-excluded exclosures and open plots (linear mixed model:  $\beta = 7.446 \pm 20.214$ ,  $t = 0.368$ ,  $p = 0.724$ ), nor was it affected by degradation score ( $\beta = -0.720 \pm 1.192$ ,  $t = -0.604$ ,  $p = 0.565$ ) or their interaction ( $\beta = 0.220 \pm 1.833$ ,  $t = 0.120$ ,  $p = 0.908$ ). Similarly, late successional cover (trees + shrubs) showed no significant response to deer browsing ( $\beta = -8.462 \pm 18.661$ ,  $t = -0.453$ ,  $p = 0.664$ ), disturbance score ( $\beta = 1.379 \pm 1.101$ ,  $t = 1.253$ ,  $p = 0.250$ ), or their interaction ( $\beta = -0.101 \pm 1.692$ ,  $t = -0.060$ ,  $p = 0.954$ ). Both models showed negligible between-site variation (variance < 0.001) but substantial within-site variation (residual SD = 18.67% for early cover, 17.24% for late cover), indicating high local heterogeneity in successional stage composition independent of treatment or disturbance history.

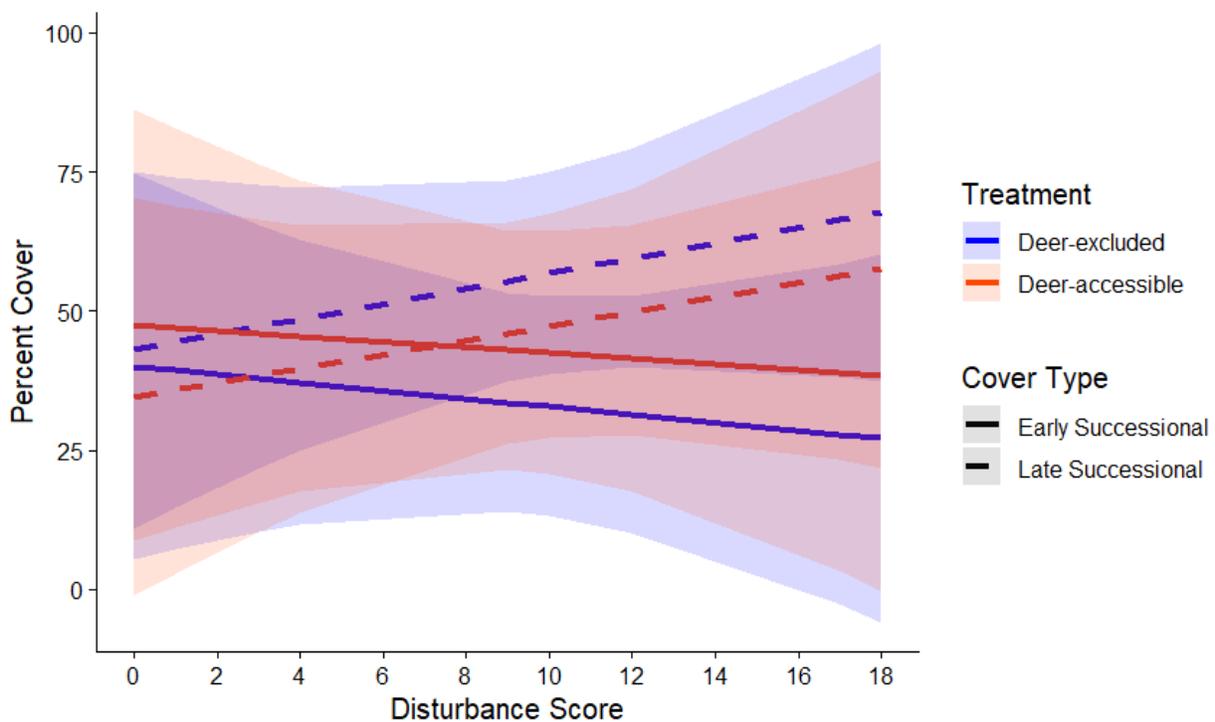


Figure 15. Early vs. late successional cover across treatments and degradation gradient. Solid lines represent early successional cover (grasses + herbs) and dashed lines represent late successional cover (trees + shrubs), colored by treatment (blue = deer-excluded exclosures; orange = deer-accessible open plots). Lines show predicted values from linear mixed models with 95% confidence intervals (shaded regions). Early successional cover was not significantly affected by treatment ( $p = 0.724$ ) or degradation ( $p = 0.565$ ). Late successional cover was also unaffected by treatment ( $p = 0.664$ ) or degradation ( $p = 0.250$ ).

## 7. Plant Height by Growth Form

Average plant height responses to deer browsing and degradation varied by growth form (Table F in Appendix, Figure 16).

Trees showed a significant treatment  $\times$  degradation interaction ( $\beta = -5.100 \pm 1.718$ ,  $t = -2.968$ ,  $p = 0.040$ ), with tree height increasing with degradation score in open plots ( $\beta = 7.464 \pm 2.364$ ,  $t = 3.158$ ,  $p = 0.040$ ) but less so in exclosures. Between-site variation (SD = 27.69 cm) exceeded within-site variation (SD = 17.35 cm), indicating that site identity influenced tree height beyond treatment effects.

Shrubs showed no significant effects of browsing ( $\beta = -30.639 \pm 41.328$ ,  $t = -0.741$ ,  $p = 0.499$ ), degradation ( $\beta = -1.190 \pm 3.776$ ,  $t = -0.315$ ,  $p = 0.768$ ), or their interaction ( $\beta = 2.827 \pm 3.758$ ,  $t = 0.752$ ,  $p = 0.494$ ). Between-site (SD = 38.09 cm) and within-site (SD = 38.02 cm) variation were nearly equal, suggesting shrub height was highly variable both among and within sites.

Lianas were unaffected by browsing ( $\beta = 3.053 \pm 19.047$ ,  $t = 0.160$ ,  $p = 0.880$ ), degradation ( $\beta = 2.062 \pm 3.201$ ,  $t = 0.644$ ,  $p = 0.561$ ), or their interaction ( $\beta = -1.473 \pm 1.715$ ,  $t = -0.859$ ,  $p = 0.439$ ). Liana height showed the highest between-site variation (SD = 40.05 cm) relative to within-site variation (SD = 17.30 cm), indicating strong site-specific effects.

Herbs exhibited a significant treatment  $\times$  degradation interaction ( $\beta = 3.857 \pm 1.330$ ,  $t = 2.900$ ,  $p = 0.045$ ), with herbs taller in exclosures at low degradation sites, but this effect diminished with increasing degradation. High between-site variation (SD = 33.85 cm) compared to within-site variation (SD = 13.42 cm) suggested herb height was strongly site-dependent.

Grasses/sedges showed no significant responses to browsing ( $\beta = 4.784 \pm 28.921$ ,  $t = 0.165$ ,  $p = 0.873$ ), degradation ( $\beta = -1.682 \pm 1.706$ ,  $t = -0.986$ ,  $p = 0.357$ ), or their interaction ( $\beta = 1.553 \pm 2.622$ ,  $t = 0.592$ ,  $p = 0.572$ ). Between-site variation was negligible (variance < 0.001), with all variation occurring within sites (SD = 26.72 cm).

Overall, deer browsing influenced plant height in a growth-form-specific manner, with significant interactive effects emerging only in trees and herbs.

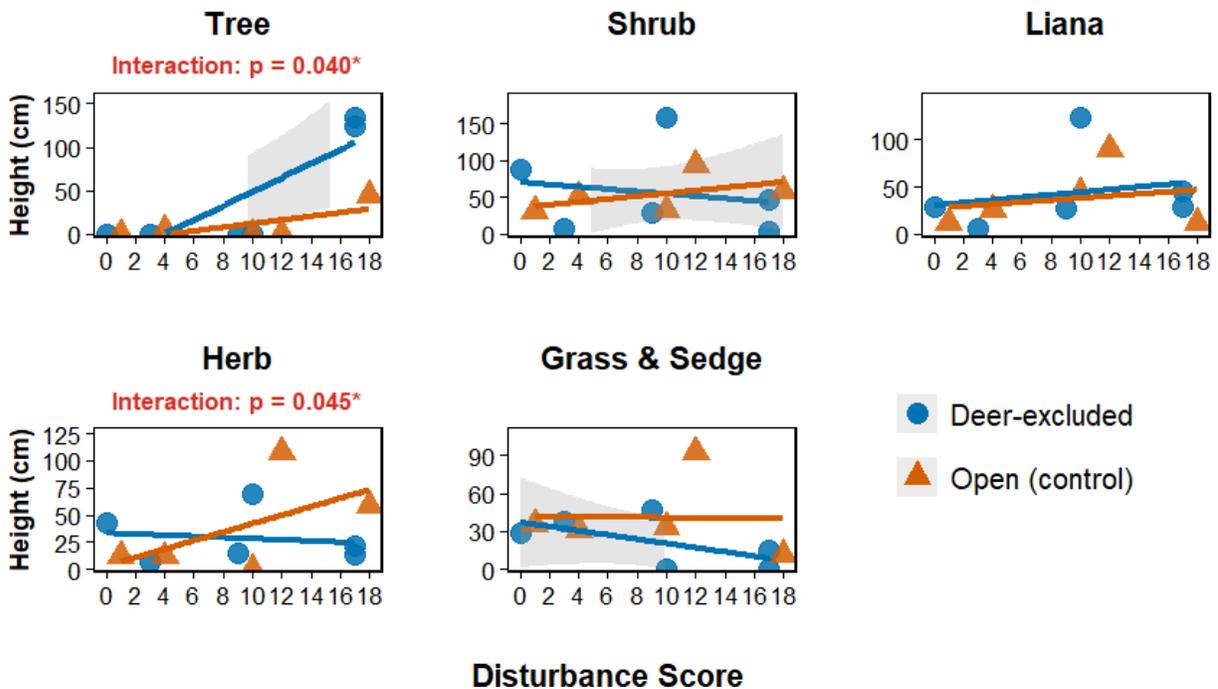


Figure 16. Average plant height by growth form in relation to deer exclusion and historical degradation. Points represent individual plots (blue circles = deer-excluded exclosures, orange triangles = open control plots with deer present). Lines show linear model predictions with 95% confidence intervals (shaded regions). Tree and herb heights showed significant deer exclusion  $\times$  degradation interactions (indicated by red asterisks; tree:  $\beta = -5.10 \pm 2.39$  cm,  $p = 0.040$ ; herb:  $\beta = 3.86 \pm 1.82$  cm,  $p = 0.045$ ). Shrub, grass, and liana heights showed no significant treatment, disturbance, or interaction effects. Separate linear mixed-effects models were fit for each growth form with plot pair as random intercept ( $n = 11$  plots from 5 paired sites).

## Discussion

This study examined how deer browsing and historical anthropogenic disturbance interact to shape plant community composition across five paired monitoring sites on Galiano Island, British Columbia. The study sites occur within the Coastal Douglas-fir

biogeoclimatic zone, a globally rare and critically endangered ecosystem that has been reduced to less than 5% of its original extent due to land conversion, fragmentation, and altered ecological processes (Fuchs, 2001; Coastal Douglas-fir Conservation Partnership, 2024). While formal statistical analyses revealed marginal effects of deer exclusion on overall community composition ( $p = 0.054$ ) and no significant effects on many response variables, field observations consistently revealed stark differences between exclosed and open plots that were not captured by the quantitative data. This disconnect between anecdotal observations and statistical results reflects the fundamental challenge of detecting treatment effects amid high site-level heterogeneity with limited replication, and suggests that future research should examine each site individually rather than pooling data across environmentally distinct locations.

## Integrating Field Observations with Statistical Results

### **Mill Site: Where Disturbance Overwhelms Browsing Effects**

Field observations at the Mill Site revealed dramatic differences between treatments that statistical analyses struggled to capture. Dense *Rubus ursinus* dominance in both exclosures contrasted sharply with the herb-rich and visibly browsed open plot. These visual differences aligned with the quantitative data showing the Mill Site open plot had the highest invasive species richness (9 species) and cover (55%) among all sites, along with the highest diversity indices (Shannon  $H' = 2.77$ , Gini-Simpson  $1-D = 0.93$ ). The striking contrast between Exclosure 1 (protected since 2013, 3 native species, 55% native cover) and Exclosure 2 (protected since 2021, 5 native species, 75% native cover) versus the open plot (8 native species, 40% native cover) illustrated time-since-exclusion effects, though the small sample size ( $n = 3$  plots) precluded formal temporal analysis.

The Mill Site, with the highest disturbance scores (17–18), exemplifies how severe historical degradation continues to structure vegetation communities even after a decade of restoration interventions. The observed patterns align with findings from Eschtruth and Battles (2009), who demonstrated that disturbance and deer herbivory interact synergistically to facilitate invasive plant establishment, with invasion risk highest where multiple facilitating conditions co-occur. The elevated diversity in the open plot reflects

invasion-driven evenness rather than ecological health—a critical nuance when interpreting diversity metrics in herbivore-impacted systems. Blossey *et al.* (2017) emphasize that traditional deer impact assessments often fail to consider how herbivory interacts with other disturbances, leading to incomplete understanding of ecosystem degradation. The Mill Site demonstrates this principle: deer exclusion promotes native shrub recovery, but long-term restoration trajectories remain strongly constrained by legacy industrial contamination, soil compaction from historical pasture use (Cui *et al.*, 2005; Jordon, 2021; McDowell *et al.*, 2003), and altered hydrology. The observed shade differences suggest that browsing indirectly shapes light environments, which in turn influences understory community assembly, though this may also result from greater tree density in the enclosure plots. This indirect effect may be as important as direct consumption in determining plant community structure, consistent with broader patterns of black-tailed deer impacts on forest regeneration in coastal British Columbia documented since the mid-20th century (Cowan, 1945; Crouch, 1976, 1979).

#### **Nuts'a'maat Forage Forest: Aspect and Proximity to Deer Activity**

Field observations at the Forage Forest revealed stark compositional differences between the northeast-facing enclosure and southwest-facing open plot. The presence of *Holodiscus discolor* in the enclosure but complete absence from the open plot demonstrated selective browsing impacts. Deer bedding sites immediately adjacent to the open plot and a deer trail providing primary access to the site indicated intensive local deer use that likely explained the reduced shrub diversity observed in the field. The enclosure's slightly more visible ground layer contrasted with the open plot's *Gaultheria shallon* dominance, suggesting browsing-mediated shifts in competitive dynamics.

The quantitative data showed both plots maintained high native cover (110% in enclosure with layering, 85% in open plot) and relatively low invasive richness (0 species in enclosure, 1 in open plot), but these metrics masked the compositional differences observed in the field. The Forage Forest enclosure exhibited the lowest diversity indices (Shannon  $H' = 1.76$ ) among all enclosures due to dominance by a few native fern and shrub species, while the open plot showed similar diversity ( $H' = 1.58$ ). This pattern illustrates how diversity metrics

can fail to capture ecologically meaningful differences—the enclosure supported culturally important species absent from the open plot, yet both had comparable diversity scores. Brault *et al.* (2023) found that browsing intensity on target plants varied significantly depending on the composition and structure of surrounding vegetation, with areas containing diverse palatable understory plants experiencing reduced browsing pressure due to alternative forage availability. The documented deer bedding sites and intensive trail use at the Forage Forest open plot illustrate this spatial heterogeneity of herbivore impacts within landscapes (Ramirez *et al.*, 2021b). Despite moderate disturbance history (clearcut logging followed by limited restoration interventions, disturbance scores 10–12), both plots maintained dense native fern and shrub cover, demonstrating that legacy clearcut sites can retain resilient native understories when seedbanks persist. However, browsing still fundamentally altered species presence and absence, particularly for palatable shrubs.

### **Trincomali Bluffs: Regeneration Failure Despite Native Dominance**

The Bluffs presented perhaps the clearest anecdotal evidence of deer impacts: 13 seedlings (8 *P. menziesii*, 5 *A. menziesii*) in the enclosure versus only 1 *P. menziesii* seedling in the open plot represented a dramatic difference in natural regeneration. This striking field observation was not directly analyzed in the formal statistical models, as seedling counts were not included as a response variable in the linear mixed models examining cover, richness, or height. The dark understory environment created by >50% canopy cover, combined with moss, leaf mulch, and boulders occupying >50% of ground cover, made the complete absence of tree recruitment in browsed areas visually striking.

The quantitative data showed both plots had identical species composition patterns: 11 total species each, 10 native species each, 1 invasive species each, with similar total cover (85% vs 65%) and nearly identical diversity indices (Shannon  $H'$  = 2.25 vs 2.31, Gini–Simpson 1-D = 0.88). These metrics suggested minimal browsing impact, yet the seedling pattern told a completely different story about long-term forest regeneration trajectories. This disconnect exemplifies how standard vegetation metrics can fail to capture the most ecologically consequential browsing effects.

The Trincomali Bluffs, characterized by low disturbance scores (3–4) and mature coastal Douglas-fir–arbutus forest structure, demonstrated that deer browsing can limit natural regeneration even in relatively intact ecosystems. Both plots were predominantly native-dominated, indicating that low-disturbance dry coastal forests maintain native understory structure despite historical selective logging and livestock grazing. These patterns align with regional findings from Martin *et al.* (2011), who documented that deer impacts on tree regeneration are particularly severe in mature Gulf Islands forests, where seedlings are especially vulnerable to browsing in shaded understory conditions. The large canopy cover and light-limited forest floor at the Bluffs mean that competition for light, rather than competition with invasive species, drives understory composition. Redick and Jacobs (2020) demonstrated in their meta-analysis that browsing effects on forest regeneration are more severe at higher deer densities and vary among tree species based on palatability, with physical exclusion through fencing consistently the most effective mitigation strategy across diverse forest types. Long-term studies have shown that deer browsing can fundamentally alter forest successional trajectories and structural development over decadal timescales (Ramirez *et al.*, 2019, 2021a).

The Bluffs exemplify how browsing pressure suppresses successional processes and potentially alters long-term forest structure, even when overall native dominance is maintained and standard diversity metrics show minimal differences between treatments. Importantly, invasive species management efforts (*C. scoparius* removal) did not differ between treatments, reinforcing that observed regeneration differences can be confidently attributed to browsing rather than confounding management activities.

### **Camas Seep: Subtle Shifts in Near-Pristine Conditions**

Field observations at the Camas Seep revealed "visually much higher presence" of *Rubus ursinus* in the enclosure compared to the open plot, indicating preferential browsing of this palatable native shrub even in the least disturbed site (disturbance scores 0–1). The heterogeneous microhabitat structure—rocky exposed ground, moss mats, tree fall debris, and boulders collectively occupying ~30% of ground cover—created naturally patchy

conditions that supported diverse wildflower assemblages. Despite this minimal disturbance history, browsing pressure still noticeably altered vegetation structure. The quantitative data showed the open plot had higher total richness (15 vs 10 species), higher invasive richness (5 vs 3 species), and substantially higher invasive cover (45% vs 15%), though lower native cover (50% vs 65%). The open plot also exhibited higher diversity (Shannon  $H' = 2.52$  vs  $2.06$ ), again illustrating invasion-driven diversity inflation. However, these metrics did not capture the field-observed selectivity of browsing on *Rubus ursinus* or the diverse forb assemblage that included culturally significant plants like camas (*Camassia* spp.), death camas (*Toxicoscordion venenosum*), sea blush (*Plectritis congesta*), chocolate lily (*Fritillaria affinis*), monkeyflower (*Erythranthe* spp.), and field chickweed (*Cerastium arvense*) that have been observed in previous surveys in early summer.

The Camas Seep demonstrates that browsing impacts persist even in near-pristine habitats where anthropogenic disturbance history is minimal. This pattern is consistent with findings by Arcese *et al.* (2014), who demonstrated that deer density strongly predicts reductions in plant species richness, shrub cover, and aboriginal food value across the Gulf Islands and San Juan archipelago. The site's rich wildflower assemblages highlight both cultural and ecological significance, as many seep-associated species are traditional Indigenous food and medicinal plants (Turner, 2014). Critically, both the exclosure and open plot exhibited relatively low invasive species cover compared to more disturbed sites, reinforcing that deer herbivory, rather than disturbance history or propagule pressure, is the primary ecological driver at this location. Gonzales and Arcese (2008) found in Gulf Islands Garry oak meadows that deer herbivory was a stronger limiting factor than interspecific competition for both native seedling establishment and established plant growth, challenging assumptions that competition primarily drives invasion dynamics in these systems.

The Camas Seep open plot was identified as an outlier in successional composition analyses due to unusually high grass cover (though this was not formally quantified in the successional ratio models due to null results), potentially reflecting the susceptibility of

wet meadow systems to competitive exclusion by grasses and forbs under persistent browsing pressure that reduces shrub recruitment.

### **Fuelwood Forest: Complete Regeneration Exclusion**

The most dramatic field observation at the Fuelwood Forest was the presence of 16 *A. menziesii* seedlings in the enclosure versus complete absence (0 seedlings) in the open plot. This absolute difference in tree recruitment demonstrated that browsing completely prevents woody regeneration at this site, yet this observation was not captured in the formal height analyses because those seedlings were not included in the randomly selected quadrats used for statistical sampling. The open plot's visual dominance by Oregon grape (*Berberis nervosa*) contrasted sharply with the enclosure's much more open, grassy understory structure, reflecting fundamentally different vegetation trajectories under browsing versus exclusion.

The quantitative data showed lower total richness in the open plot (6 vs 9 species) and lower native richness (3 vs 5 native species), though both plots had high total cover (100% each). Invasive richness and cover were actually slightly higher in the enclosure (2 species, 15% cover) than the open plot (3 species, 10% cover), making the Fuelwood Forest an outlier in invasion patterns. However, the open plot exhibited extremely low diversity (Shannon  $H' = 0.96$ , Gini-Simpson  $1-D = 0.35$ ) compared to the enclosure ( $H' = 2.00$ ,  $1-D = 0.84$ ), reflecting near-monoculture conditions dominated by *B. nervosa*. These metrics captured some of the browsing effect, but did not convey the complete absence of tree regeneration observed in the field or the structural differences in understory composition. The Fuelwood Forest, with moderate disturbance scores (9–10), exhibited a complex disturbance history including sequential clearcutting (~100 years ago), natural regeneration (~60 years ago), selective thinning (<5 years prior), livestock grazing (until 2016), and recent incorporation into the Phase 1 Chrystal Creek watershed restoration area. Despite this layered land-use legacy, the stark contrast in tree seedling presence demonstrates that browsing completely prevents tree recruitment, consistent with patterns observed across multiple restoration contexts (Crouch, 1976; Miller *et al.*, 2023).

The open plot's dominance by *B. nervosa* suggests establishment of a browsing-tolerant understory that may inhibit regeneration under continuous herbivory through competitive suppression of more palatable species. Conversely, the enclosure's grassy understory indicates increased light penetration and reduced shrub dominance, potentially reflecting both browsing release and structural differences in canopy development following fence installation. Interestingly, the Fuelwood Forest was an outlier in invasive species patterns, showing higher invasive richness in the enclosure than the open plot—likely reflecting site-specific conditions that favour the recruitment of non-palatable species, such as *B. nervosa*, in the open site, shading out invasive herbs and grasses.

Despite moderate disturbance scores, the enclosure functioned as a recovery hotspot, with accelerated structural diversification evident in tree recruitment that was completely absent in browsed areas. This pattern suggests that restoration fencing is especially important in young, regenerating forests where deer can completely collapse early-successional trajectories by eliminating palatable woody seedlings before canopy establishment.

## General Patterns: Reconciling Field Observations with Statistical Analyses

### **Multivariate Community Composition: Marginal Significance Masking Real Patterns**

Permutational multivariate analysis revealed a marginal but ecologically meaningful effect of deer exclusion on plant community composition (PERMANOVA:  $F_{1,8} = 1.67$ ,  $R^2 = 0.295$ ,  $p = 0.054$ ). While this result narrowly missed conventional statistical significance, the moderate effect size indicates that browsing explains nearly 30% of compositional variation after accounting for plot pairing—a substantial proportion in community ecology where multiple interacting factors shape species assemblages. The NMDS ordination showed partial but clear separation between enclosure and open plots (stress = 0.095), with enclosure communities trending toward more native-dominated compositions while open plots harbored higher proportions of invasive and browse-tolerant species.

This marginal statistical result stands in contrast to the consistently striking visual differences observed in the field across all five sites: dense native shrub dominance in

exclosures versus herb-rich or browse-tolerant understories in open plots (Mill Site), presence versus absence of culturally important species (Forage Forest), 13-fold differences in seedling recruitment (Bluffs), higher *R. ursinus* abundance under protection (Mill Site and Camas Seep), and tree regeneration failure in browsed areas (Fuelwood Forest). The disconnect between field observations and statistical significance reflects the fundamental challenge of exclosure research: high site-level environmental heterogeneity overwhelms treatment effects when sample sizes are small.

The limited statistical power likely reflects the small sample size ( $n = 5$  plot pairs) combined with high environmental heterogeneity among sites. Bai *et al.* (2016) demonstrated in Japanese temperate forests that deer herbivory influences plant community assembly by altering competitive interactions and functional diversity, selectively removing palatable species with specific trait combinations and thereby shifting community composition toward unpalatable, disturbance-tolerant species. This functional filtering mechanism clearly operates at the Galiano sites based on field observations—the selective presence of *Holodiscus discolor* in the Forage Forest exclosure, the *R. ursinus* dominance differences at Mill Site and Camas Seep, and the *B. nervosa* monoculture at Fuelwood Forest open plot all demonstrate preferential browsing—but detection in formal statistical models requires larger sample sizes or longer time series to overcome site-level variability. The consistency of browsing effects across North American systems—from Pacific Northwest coastal forests (Crouch, 1979; Nyberg & Janz, 1990) to eastern deciduous forests (Rooney, 2001; Frerker *et al.*, 2014)—suggests that the marginal significance observed in this study reflects genuine ecological patterns constrained by sampling limitations rather than absence of effects.

### **Environmental Gradients Overwhelming Treatment Effects**

Soil moisture emerged as the strongest single predictor of community composition (PERMANOVA:  $R^2 = 0.168$ ,  $F = 3.88$ ,  $p = 0.001$ ), with site identity explaining even more variation ( $R^2 = 0.581$ ). These results underscore that abiotic gradients and inherent environmental differences among locations are primary drivers of species sorting, while deer browsing contributes a smaller but consistent effect ( $R^2 = 0.077$ ,  $F = 1.77$ ,  $p = 0.093$ ).

Critically, no significant browsing × moisture interaction was detected ( $R^2 = 0.044$ ,  $F = 1.01$ ,  $p = 0.457$ ), indicating that deer effects on community composition are consistent across the moisture gradient. Wet and dry sites differ strongly in species composition, but deer push communities along similar trajectories—toward more invasive or browse-tolerant assemblages—regardless of moisture regime.

Similarly, historical disturbance showed a marginal effect on community structure ( $R^2 = 0.199$ ,  $F_{1,7} = 2.04$ ,  $p = 0.208$ ), but no browsing × disturbance interaction was detected ( $R^2 = 0.044$ ,  $F_{1,7} = 0.45$ ,  $p = 0.458$ ). Both factors influence composition independently rather than synergistically. This finding contrasts with expectations from Bourg *et al.* (2017), who found interactive rather than additive effects of deer exclusion and invasive plant removal on native plant recovery in deciduous forests. The absence of interaction effects in the Galiano study may reflect several possibilities: (1) browsing pressure is uniformly high across all sites regardless of disturbance history, as suggested by evidence of intensive deer use at all locations including deer trails, bedding sites, and browse damage; (2) invaded and disturbed sites are more strongly shaped by historical legacies than by contemporary browsing, as demonstrated by the Mill Site's potential soil contamination issues and Fuelwood Forest's century-long disturbance trajectory; or (3) the small sample size, at a time of year when many annuals have died back and perennials have gone into senescence, limited power to detect interactions that may exist at finer spatial scales. Additionally, the disturbance gradient at the Millard Learning Centre encompasses diverse disturbance types—from industrial mill contamination to selective logging to livestock grazing—each with distinct ecological legacies that may interact differently with herbivory (DellaSala *et al.*, 2025).

Pellerin *et al.* (2006) documented in peatlands on Anticosti Island that chronic deer pressure led to altered species composition favoring unpalatable and disturbance-tolerant plants, with effects persisting over multiple decades. Their findings emphasize that deer impacts can vary across habitat types and moisture regimes, with trampling effects particularly severe in wetland systems. The Camas Seep results, showing altered shrub dominance in a seepage zone, are consistent with this pattern of moisture-mediated

browsing impacts, even though statistical interactions were not detected across the full site gradient.

### **Species Richness and Cover: High Variance Obscuring Treatment Signals**

Native species richness, invasive species richness, total richness, native cover, and invasive cover showed no significant differences between exclosure and open plots in the formal mixed-effects models. However, the raw data revealed clear directional patterns: invasive richness was higher in open plots at 4 of 5 sites (Mill Site: 9 vs 4 species, Camas Seep: 5 vs 3 species, Forage Forest: 1 vs 0 species, Bluffs: 1 vs 1 species), with only Fuelwood Forest showing the opposite pattern (3 vs 2 species). Native cover was higher in exclosures at most sites (Forage Forest: 110% vs 85%, Mill Site Exclosure 2: 75% vs 40%, Bluffs: 80% vs 60%, Camas Seep: 65% vs 50%), though the Fuelwood Forest again showed minimal difference (55% vs 85%). These consistent directional trends across sites were overwhelmed by high variance when pooled in statistical models (native cover: within-site SD = 17.94%, between-site SD = 15.58%; invasive cover: within-site SD = 13.08%, between-site SD = 14.26%), resulting in null results.

The marginal negative relationship between disturbance score and native richness (GLMM:  $\beta = -0.044$ ,  $z = -1.68$ ,  $p = 0.093$ ) suggests that more disturbed sites tended to have lower native richness, though this pattern did not reach conventional significance. The raw data supported this trend: Mill Site (disturbance 17-18) had 3-8 native species across plots, while Camas Seep (disturbance 0-1) had 7-10 native species. Over the observed disturbance range (0–18), historical land-use intensity could substantially reduce native diversity, indicating that legacy effects remain strong determinants of contemporary species richness.

The lack of consistent richness responses to deer exclusion in statistical models reinforces that richness alone may not be the most sensitive indicator of herbivory effects in these systems (Côté *et al.*, 2004), particularly when treatment effects are directionally consistent but overwhelmed by site heterogeneity. Site context—including microclimate, disturbance history, seedbank composition, and surrounding vegetation—appears to exert stronger control over species richness than browsing pressure in formal models. However, field

observations suggest that native species responses to herbivory are highly species-specific rather than affecting richness uniformly: deer selectively browse *Holodiscus discolor* (present in Forage Forest enclosure, absent in open plot), prefer *Rubus ursinus* over browse-tolerant species, and completely exclude tree seedlings from open plots while leaving unpalatable invasives like *Geranium robertianum* and *Vinca major* to establish. Black-tailed deer exhibit selective foraging based on plant palatability, nutritional content, and seasonal availability (Cowan, 1945; Shackleton, 1999), meaning browsing impacts vary among plant species and functional groups rather than uniformly reducing all native plants.

The absence of detectable invasive cover differences between treatments in formal models ( $\beta = 7.956$ ,  $p = 0.605$ ), despite raw data showing higher invasive cover in open plots at most sites (Mill Site: 55% vs 20%, Camas Seep: 45% vs 15%), suggests that percent cover may be less sensitive than compositional metrics for detecting browsing effects when variance is high. Many invasive species on Galiano are browse-tolerant or unpalatable, meaning browsing pressure does not reduce their biomass even if it influences their establishment or spread. Additionally, high spatial variance driven by heterogeneous microhabitats (moss mats, boulders, tree fall debris occupying 30-50% of ground cover at some sites) reduces statistical power to detect treatment effects at the plot scale. These findings support the use of multivariate and richness-based analyses, which captured browsing effects more clearly than univariate cover models, and highlight that deer exclusion alone may not reduce invasive plant biomass without integrated management (removal, native planting, monitoring).

### **Diversity Indices: When High Diversity Signals Degradation**

Open plots generally exhibited higher Shannon and Gini–Simpson diversity indices than enclosures in the raw data (Mill Site:  $H' = 2.77$  vs 1.39-1.84 in enclosures; Camas Seep:  $H' = 2.52$  vs 2.06), but this pattern reflects invasion-driven evenness rather than ecological improvement. High diversity in open plots resulted from the mixture of native and invasive species, creating more even abundance distributions across species. In contrast, enclosures often showed lower diversity due to native species dominance—fewer species

overall, but ecologically desirable community structure for restoration objectives. This counterintuitive pattern, where the most degraded and invaded plot (Mill Site Open) showed the highest diversity, demonstrates the critical importance of interpreting diversity metrics in ecological context rather than assuming higher diversity equals better ecosystem condition.

This pattern—where browsed areas exhibit higher diversity—has been documented in other deer exclosure studies. Bai *et al.* (2016) found that deer browsing increased species richness and diversity in Japanese forest floors by selectively removing dominant species and creating more even abundance distributions, even though the resulting communities were functionally degraded. Their study explicitly demonstrated that "species richness and diversity were higher in the control plot" exposed to deer browsing compared to exclosures, mirroring the patterns observed at Galiano. Similarly, a nine-year deer density experiment in Japan found that high deer density combined with logging decreased Simpson's diversity index scores, but the mechanisms involved increased cover of unpalatable species rather than simple species loss (Hino *et al.*, 2023). These findings illustrate that diversity indices can produce misleading conclusions when invasive or disturbance-tolerant species inflate species evenness.

The Mill Site open plot exemplified this pattern, showing the highest diversity among all plots (Shannon  $H' = 2.77$ , Gini–Simpson  $1-D = 0.93$ ) due to high disturbance and invasion creating a classic invasion-driven diversity peak. This phenomenon relates to the broader "invasion paradox" in ecology, where positive relationships between native and exotic richness have been documented at landscape scales, often driven by shared environmental factors that promote both native and invasive species (Fridley *et al.*, 2007; Peng *et al.*, 2019). At the plot scale examined in this study, the mixture of natives and invaders in browsed plots created high evenness—a key component of diversity indices—but this evenness reflects historical disturbance and browsing-mediated community restructuring rather than ecosystem health. Conversely, the Forage Forest exclosure showed low diversity ( $H' = 1.76$ ,  $1-D = 0.82$ ) despite high native cover (110%), reflecting

dominance by a few native fern and shrub species that reduced evenness but created desirable native-dominated structure.

These results emphasize that diversity indices alone can be misleading in herbivore-impacted systems and should be interpreted alongside compositional and functional metrics (Vellend *et al.*, 2017). A meta-analysis of white-tailed deer impacts across North American forests noted that "richness and evenness are varying in opposite directions" in many deer exclosure studies, potentially masking strong provenance differences between native and invasive species (Habeck & Schultz, 2015). Higher diversity does not necessarily indicate ecological health when that diversity is inflated by invasive species establishment and the suppression of competitive dominant natives. This distinction is critical for restoration planning: success should be measured by native community recovery and functional integrity rather than raw diversity metrics that weigh native and invasive species equally.

### **Successional Composition and Height: Growth-Form-Specific Responses**

Successional stage ratios (early-successional herbs and grasses divided by late-successional trees, shrubs, and lianas) showed no significant effects of deer exclusion ( $\beta = 7.446$ ,  $p = 0.724$ ), disturbance history ( $\beta = -0.720$ ,  $p = 0.565$ ), or their interaction ( $\beta = 0.220$ ,  $p = 0.908$ ). This null result suggests that browsing pressure is not currently the main driver of early versus late-successional dominance in formal analyses, though field observations revealed dramatic differences in woody regeneration. The complete absence of tree seedlings in open plots at Fuelwood Forest and Bluffs, contrasted with 16 and 13 seedlings respectively in exclosures, represents clear browsing suppression of late-successional recruitment that was not captured by the successional ratio models. High within-site variability (residual SD = 18.67% for early cover, 17.24% for late cover) overwhelmed treatment signals, suggesting successional dynamics operate at very fine spatial scales driven by microsite differences. The absence of treatment effects in models may also indicate that recovery from browsing is slow, that herbaceous layers compensate for browsing impacts on woody species, or that five years of exclosure age is insufficient to shift successional trajectories measured as cover ratios. Long-term monitoring is needed

because successional shifts occur slowly and may require over a decade to detect browsing-related changes in vegetation cover metrics.

However, plant height analyses revealed growth-form-specific browsing effects that partially aligned with field observations. Trees showed a significant treatment  $\times$  disturbance interaction ( $\beta = -5.100$ ,  $p = 0.040$ ), with tree height increasing with degradation score in open plots ( $\beta = 7.464$ ,  $p = 0.040$ ) but less so in exclosures. This counterintuitive pattern—where trees were taller in more degraded open plots—likely reflects sampling artifacts rather than biological patterns. The 16 *A. menziesii* seedlings observed in the Fuelwood Forest exclosure were not included in the randomly selected quadrats used for statistical height measurements, meaning the statistical model did not capture the most dramatic regeneration differences. The pattern may also reflect selective survival of a few unpalatable or mature trees in degraded open sites, while the exclosures support abundant but younger seedlings that are shorter on average. In exclosures, the treatment effect was weaker, suggesting that exclosures buffer against degradation-driven height differences.

Herbs showed a significant treatment  $\times$  disturbance interaction ( $\beta = 3.857$ ,  $p = 0.045$ ), with herbs taller in exclosures at low degradation sites, but this exclosure benefit diminished at more degraded sites. This pattern aligns with field observations of more diverse herb assemblages in exclosures at relatively undisturbed sites like Camas Seep, but suggests that at highly disturbed sites like Mill Site, degradation constraints (reduced soil fertility, competition with grasses, lower herbaceous species richness) limit herb growth even when browsing is removed. The lack of significant effects for shrubs ( $\beta = -30.639$ ,  $p = 0.499$ ), grasses ( $\beta = 4.784$ ,  $p = 0.873$ ), and lianas ( $\beta = 3.053$ ,  $p = 0.880$ ) suggests these growth forms are resistant or tolerant to browsing, or that their height is controlled by abiotic factors (moisture, light) rather than herbivory. Many shrubs and sedges compensate structurally after browsing through basal resprouting, masking treatment effects on height measurements. These growth-form-specific patterns indicate that browsing effects are not uniform across vegetation and highlight the importance of targeting tree and herb layers in

restoration monitoring, though even these metrics may miss critical regeneration patterns when sampling does not specifically target seedling cohorts.

## Study Limitations: The Challenge of Detecting Known Effects

The fundamental limitation of this study was the mismatch between strong anecdotal evidence of browsing effects and weak statistical signals. Field observations consistently revealed stark differences between exclosed and open plots—dense native shrub dominance versus browse-tolerant understories, presence versus absence of culturally important species, order-of-magnitude differences in seedling recruitment, and complete regeneration failure in browsed areas. Yet formal statistical analyses found marginal or non-significant effects for most response variables. This disconnect does not indicate absence of ecological effects but rather reflects three critical methodological constraints:

- **Insufficient replication within and among sites.** With only three 1 m × 1 m quadrats per plot and one paired plot per location, statistical power was limited to detect treatment effects given the high environmental heterogeneity among sites. The most dramatic field observations—16 *A. menziesii* seedlings in Fuelwood Forest exclosure versus 0 in the open plot, 13 seedlings in Bluffs exclosure versus 1 in the open plot—were not directly captured by the statistical models because seedling counts were not included as response variables and the random quadrat sampling missed these cohorts. This sampling limitation meant that the most ecologically consequential browsing impacts (complete prevention of tree regeneration) were documented anecdotally but not quantified statistically.
- **Visual estimation bias.** An additional methodological limitation was the use of visual estimation for percent cover rather than more objective photographic or image analysis techniques. While Bonham *et al.* (2004) validated visual cover estimation as efficient and sufficiently accurate when standardized protocols are followed, research has increasingly demonstrated that visual estimation is prone to observer bias and can be less consistent than photographic methods. Studies comparing visual estimates with digital image analysis have found that visual assessment often overestimates percent cover and exhibits higher coefficients of

variation, particularly in complex vegetation communities (Luscier *et al.*, 2006; Olmstead & Wample, 2008). Object-based image analysis (OBIA) can achieve 80-96% classification accuracy with strong Kappa index agreement values (Luscier *et al.*, 2006), while photographic analysis has been shown to correspond highly with in situ assessments while reducing observer subjectivity (Yu & Guo, 2021). The single-observer approach used in this study reduces inter-observer variability but does not eliminate the inherent subjectivity of visual estimation. The monitoring systems in place at the Galiano Conservancy Association benefit from incorporating photosphere photography as well as close-range digital photography with standardized camera angles and image analysis software to objectively quantify percent cover, reduce measurement error, and enable retrospective reanalysis as methods improve.

- **Site heterogeneity overwhelming treatment effects.** Site-level differences in abiotic factors—including soil moisture, aspect, slope position, canopy cover, and proximity to deer habitat—naturally structure plant community composition independent of browsing or disturbance effects. These environmental gradients likely drove much of the observed variation, as evidenced by soil moisture ( $R^2 = 0.168$ ) and site identity ( $R^2 = 0.581$ ) explaining more compositional variance than deer exclusion ( $R^2 = 0.077$ ) in PERMANOVA models. Pooling data across environmentally distinct sites may have been inappropriate, as the assumption of comparable baseline conditions was violated. Each site represents a unique combination of microclimate, disturbance history, seedbank composition, invasive propagule pressure, and deer use intensity—factors that interact to produce highly context-dependent vegetation responses.

Recent research has increasingly recognized that deer exclusion effects are highly variable and context-dependent. A 20-year exclusion study on Haida Gwaii demonstrated that while deer exclusion increased plant richness and cover, it also "unveiled" abiotic filtering by soil moisture and fertility that had previously been masked by uniform browsing pressure (Chollet *et al.*, 2021). The authors emphasized that results from their long-term exclusion

experiment "provided results not entirely in agreement with those observed at more broader and more realistic spatial and/or temporal scales," highlighting the challenge of extrapolating from paired-plot designs to landscape-level patterns. Similarly, Sabo *et al.* (2017) found that deer-mediated environmental changes compounded direct herbivory effects, with deer exclusion altering not just species composition but also the functional relationships between vegetation and environmental gradients.

The importance of site heterogeneity is further illustrated by contrasting results across study systems. In a Connecticut suburban forest, 15 years of deer exclusion produced complex, life-form-specific responses, with site heterogeneity remaining "an important driver of vegetation dynamics" even after long-term treatment (Faison *et al.*, 2016).

Critically, this study found higher native and exotic richness in browsed plots at fine spatial scales—a pattern opposite to typical expectations—demonstrating that deer effects depend strongly on local environmental context and vegetation structure. A German forest study found no changes in plant diversity or composition after five years of deer exclusion, despite detecting structural changes in vegetation height and heterogeneity (Bucher *et al.*, 2021). In contrast, studies in areas with extreme deer overabundance often detect strong compositional shifts even with shorter enclosure ages.

A meta-analysis of white-tailed deer impacts concluded that deer effects are "significant, but not ubiquitous across all components of the forest understorey plant community," with considerable variation depending on study design, forest type, and regional context (Habeck & Schultz, 2015). Côté *et al.* (2004) noted that "the problem of confounding site factors (such as productivity) that themselves affect deer densities or responses to herbivory" remains a persistent challenge in enclosure research. Morrison and Woldemariam (2022) found species-specific metabolomic and growth responses to deer exclusion that varied with plant functional traits, demonstrating that plant responses to deer removal operate through multiple pathways including altered soil conditions, competitive dynamics, and species-specific palatability.

**Recommendation for future research.** Future research should examine each paired plot individually, using site-specific analysis to account for unique environmental contexts,

disturbance legacies, and deer use patterns. This approach would enable more nuanced interpretation of browsing effects and restoration trajectories without forcing comparisons across fundamentally different ecological conditions. Long-term monitoring at individual sites would also better capture successional dynamics and recovery rates that vary with time-since-exclosure establishment. The Galiano study's findings—particularly the strong site identity effects, the absence of browsing × environment interactions, and the disconnect between field observations and pooled statistical analyses—support this recommendation for site-specific rather than pooled analytical frameworks in future deer impact research.

## Implications for Restoration and Management

Despite limited statistical significance for many response variables, the consistent field observations and directional trends across metrics suggest that deer browsing exerts ecologically meaningful effects on plant communities at the Millard Learning Centre. The most robust finding—evident both anecdotally and in the raw data—is that deer exclusion facilitates tree seedling recruitment and alters native versus invasive community structure. Complete regeneration failure in open plots at multiple sites (Fuelwood Forest: 16 vs 0 arbutus seedlings; Bluffs: 13 vs 1 seedlings) has critical implications for forest regeneration and long-term community structure, as browsing pressure effectively eliminates the next palatable native tree and shrub generation regardless of site conditions (Miller *et al.*, 2023). Restoration efforts should prioritize deer exclusion in areas where tree regeneration is a management goal, particularly in young regenerating forests (e.g., Fuelwood Forest) and cultural restoration sites (e.g., Nuts'a'maat Forage Forest) where specific native species like *Holodiscus discolor* are targets. However, exclosures alone are insufficient to address invasive species establishment, especially at highly disturbed sites like the Mill Site where legacy effects create persistent invasion pressure. Integrated management combining deer exclusion, invasive species removal, and active native planting is necessary to overcome the compounded effects of browsing and disturbance (Bourg *et al.*, 2017; Eschtruth & Battles, 2009).

The strong influence of historical disturbance on native richness and community composition indicates that prioritizing low-disturbance or recovering areas may yield better outcomes than focusing solely on herbivore management at severely degraded sites. At locations like the Mill Site, soil remediation and hydrological restoration may be prerequisites for meaningful vegetation recovery, even with deer excluded. Conversely, near-pristine sites like the Camas Seep may respond strongly to deer management alone, as disturbance legacies do not limit recovery potential.

Finally, the framework of Hanberry and Faison (2023), who reframe deer herbivory as a natural disturbance regime with associated ecological and socioeconomic trade-offs, provides perspective for interpreting these results. Black-tailed deer (*Odocoileus hemionus columbianus*) are native to Galiano Island and the broader Gulf Islands archipelago (Shackleton, 1999), but contemporary densities likely exceed historical levels due to predator extirpation and limited hunting pressure (Darimont *et al.*, 2004). The loss of apex predators and altered Indigenous burning practices (Hebda & Aitkens, 1993) have fundamentally changed the disturbance regime that shaped these ecosystems for millennia. The browsed communities in open plots represent an anthropogenically altered disturbance regime rather than simply degraded conditions. Restoration targets should acknowledge this complexity, recognizing that exclosure communities represent one potential trajectory (toward pre-disturbance structure) while open communities represent an alternative stable state shaped by overabundant herbivores (MacDougall, 2008). Management decisions must balance ecological restoration goals with cultural values, economic constraints, and the socioecological context of deer populations in the Gulf Islands.

## Conclusion

This study demonstrates that deer browsing influences plant community composition on Galiano Island through multiple pathways—selective removal of palatable species, complete prevention of tree regeneration, and facilitation of invasion in disturbed areas—but these effects are highly context-dependent and mediated by site-specific

environmental conditions and disturbance histories. Field observations consistently revealed stark differences between exclosed and open plots that formal statistical analyses struggled to capture due to small sample sizes and high site heterogeneity. The disconnect between anecdotal evidence and statistical significance does not indicate absence of ecological effects but rather highlights fundamental challenges in exclosure research design when environmental gradients are strong and replication is limited. The substantial variation among sites in vegetation responses to deer exclusion—from complete regeneration exclosure at Fuelwood Forest and Bluffs, to selective browsing of culturally important species at Forage Forest and Camas Seep, to invasion-driven diversity peaks at Mill Site—argues against pooled analyses in future research, instead favoring site-specific investigations that account for unique microclimatic, historical, and ecological contexts. Effective restoration in these systems requires integrated management addressing both deer herbivory and legacy disturbance effects, with strategies tailored to the specific conditions and recovery potential of each location.

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