Evaluation of Competitive Moose-Beaver Herbivory on Isle Royale National Park

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February 04, 2022

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Executive Summary

Beavers (*Castor canadensis*) play a key role in creating aquatic habitat and sustaining aquatic biodiversity in freshwater ecosystems across North America, including in Isle Royale National Park (ISRO). The National Park Service (NPS) hypothesize that competitive pressure from moose (*Alces alces*) in ISRO will drive beavers to forage at greater distances from their lodges, which may place them at greater risk for predation and ultimately have negative implications for the park's aquatic ecosystems. Determining whether this occurs in ISRO, and if so, the degree to which it occurs, is an important research goal for NPS. The objective of this study is to identify common foraging preferences for beavers and moose and to investigate whether competition from moose leads to changes in beaver foraging behavior. Using forest structure, beaver herbivory, and moose herbivory survey data provided by NPS, we developed a predictive model forecasting beaver foraging behavior in response to moose herbivory pressure. While the literature to date supports that distance and vegetation type influence beavers' foraging preferences, our model results only found the effect of distance to water, but were inconclusive with respect to vegetation preferences and the impact of moose on beaver foraging. Output from our analysis was limited by the amount of available data, and the disjoint protocols, i.e., beaver, vegetation and moose data were collected at different locations. To better identify beaver preferences and any potential competitive effect from moose we recommend that future data collection include vegetation transects that record both beaver and moose browse data and vegetation structure, i.e., available vegetation data.

Acknowledgements

Introduction

Beavers (*Castor canadensis*) are well-known ecosystem engineers (Jones et al., 1994). By constructing impoundments and subsequently flooding the surrounding areas with slow-flowing open water (i.e. beaver ponds), beavers play a critical role in forming and maintaining heterogenous aquatic habitats (Collen & Gibson, 2000; Hood & Bayley, 2008a). The creation and maintenance of open inland waters and wetlands leads to a more biodiverse community assemblage than would otherwise occur (Moen et al., 1990).

In Isle Royale National Park (ISRO), beavers and moose (*Alces alces*) share a variety of food resources, particularly broadleaf deciduous trees like trembling aspen (Populus tremuloides) and aquatic macrophytes (Bergen et al., 2018; Tischler, 2019). National Park Service (NPS) staff hypothesize that this overlap in food resources creates competitive pressure, driving beavers to forage at greater distances from aquatic edges. Out of the water and far from their lodges, beavers are likely more susceptible to gray wolf (*Canis lupus*) predation (Gable et al., 2018). Additionally, there is concern that moose browse could create significant changes in the plant community by targeting species such as balsam fir (*Abies balsamea*), which may change the forest's successional trajectory in favor of non-preferred species such as spruce (*Picea* spp.) (Pastor et al., 1993). The magnitude of moose-beaver competition for resources in ISRO is currently unknown, but any substantial negative effect on the beaver population may in turn diminish their positive impact on ISRO's aquatic habitat and biodiversity.

Given the key role of beavers in ISRO's ecosystem, we seek to determine:

1) foraging preferences of beavers in ISRO
2) foraging preferences of moose in ISRO
3) the degree to which competitive herbivory between moose and beavers occurs

We addressed these research questions by synthesizing NPS-provided data and applying a predictive model. This report contains a summary of the data provided, data collection protocols, and the predictive model; a discussion of model results; and recommendations for future data collection and research.

Beavers as ecosystem engineers

Beavers' ecological role

Beavers build impoundments in streams, and occasionally in lakeshores, as habitat and to ensure protection from terrestrial predators (Novak, 1987). Impoundments are made from woody debris that beavers collect from trees, saplings, and shrubs (Moen et al., 1990). In areas with beavers, flooded impoundments can comprise up to 12% of the land area (Moen et al., 1990). In second to fourth order streams, beavers can influence up to 30-50% of the total stream length through dam construction (Naiman & Melillo, 1984). The damming of streams can increase stream surface area and slow stream flow velocity, creating bodies of open water in areas previously covered by dry land (Collen & Gibson, 2000). This alteration in land use and riparian characteristics influences a stream's water temperature, stratification, sedimentation, dissolved nutrient content, productivity, temporal habitat stability, local climate, and ultimately, species diversity (Collen & Gibson, 2000; Hood & Bayley, 2008a). These effects are compounded when a waterway has more than one impoundment (Collen & Gibson, 2000). Impoundments may be active with beavers, but inactive impoundments continue to affect local hydrology and ecology after beavers have left (Collen & Gibson, 2000). As a result, beavers have dramatic long-term impacts on ecosystems; for example, in a study by Remillard et al. (1987) in New York, forty years of aerial photographs showed that none of the zero previously beaver-disturbed areas returned to the original forest matrix status.

Beaver impoundments do not benefit all species. Cold-adapted fish like trout may be harmed by the temperature increases in beaver impoundments (Collen & Gibson, 2000). Beaver dams increase dissolved nutrient content and reduce water quality, which manifests in the reduction of bioindicator species in the orders

Ephemeroptera, Plecoptera, and Trichoptera (Collen & Gibson, 2000). However, the net effect of beaver on stream biodiversity is positive due to the various wetland ecosystem types that they support and the habitat provided for terrestrial and aquatic species (National Park Service, 2020).

In addition to the effects their impoundments have on their surrounding environment, beavers alter ecosystems in several ways integral to ecological structure. Beavers change the densities and relative proportions of plant species present in an area through foraging, selecting for and ultimately reducing the relative proportions of preferred forage species (Moen et al., 1990). Due to beavers' preferences for woody stems closer to the water's edge, areas with beaver activity have a higher richness of herbaceous species close to shore and a higher richness of woody species farther from shore (Brzyski & Schulte, 2009). Additionally, beavers, like many other herbivores, induce the production of unpalatable secondary metabolites in some forage species (Basey et al., 1988). In sites with active beaver foraging, juvenile aspen (*Populus* spp.) shoots have been found to have higher bark concentrations of secondary metabolites (Basey et al., 1988). Hence, through their various ecosystem impacts, beavers are appropriately regarded as "ecosystem engineers" (Jones et al., 1994).

The beaver population size in ISRO, and thereby its ecosystem impact, fluctuates as a function of factors including climate, forage availability, and predation pressure (Romanski, 2010). The National Park Service (2020) estimated that the beaver population in ISRO dramatically increased from 2012 to 2018, reaching 542 beaver colonies and approximately 5,550 to 5,600 individuals in 2018. NPS attributed this increase to a lack of predation pressure (Hoy et al., 2020).

Beavers' foraging preferences

Beavers have a wide range of food sources but prefer certain species given their nutritional characteristics, palatability, and availability (Gerwing et al., 2013). Food sources include adult trees, saplings, small shrubs, herbaceous plants, and aquatic macrophytes (Moen et al., 1990). Beavers will cut trees and shrubs at their bases and use the felled material both for food and for dam construction. Trembling aspen (*Populus tremuloides*) and willow (*Salix* spp.) are their most preferred species, along with pin cherry (Prunus pensylvanica), bigtooth aspen (*Populus grandidentata*), and beaked hazelnut (*Corylus cornuta*) (Gallant et al., 2004). In forests with higher proportions of preferred species, beavers can forage more selectively. However, in forests with higher proportions of less-preferred species, beavers are often less selective, cutting species like balsam fir (*Abies balsamea*) and other conifers (Gallant et al., 2004).

Beavers forage in a manner consistent with the central-place foraging theory (Mahoney & Stella, 2020; Raffel et al., 2009). The central-place foraging theory posits that for species that forage from a central location, there is an optimal browsing strategy based on energy spent, energy gained, and perceived predation risk during excursion, and their foraging behavior can be based on these factors (Jenkins, 1980; Raffel et al., 2009). Beavers are considered central-place foragers because they travel from and return to a central location, i.e., a beaver dam (Jenkins, 1980; Mahoney & Stella, 2020; Raffel et al., 2009). Beavers are slow-moving on land but can quickly swim away from predators like wolves, and thus rarely forage farther than 60 meters from the water's edge (Donkor & Fryxell, 1999; Gerwing et al., 2013; Moen et al., 1990). According to central-place foraging theory, beavers prefer woody stems that are nutritious, easy to transport, and close to their lodge (Donkor & Fryxell, 1999; Gerwing et al., 2013; Moen et al., 1990). However, distance traveled would depend on surrounding vegetation and on time since lodge was built, because over time, proximal preferred stems will be consumed (refs). Indeed, Moen et al. (1990) found that beavers will travel farther from the water's edge to find preferred woody species if preferred species are not available close to shore.

Past studies have found that beaver foraging preferences are also influenced by stem size; however, their preferences for stem size are complex and species-specific (Gallant et al., 2004; Mahoney & Stella, 2020; Raffel et al., 2009). Stem size determines how difficult and energy-intensive it is for beavers to fell and retrieve them; larger stems will take more time and energy to fell and may be impossible to carry, while seedlings may not be worth the energy used to leave the water (McGinley & Witham, 1985; Raffel et al., 2009). There is a consensus that beavers typically prefer trees with small to intermediate stem diameters (2-10 cm) (Gallant et al., 2004; Raffel et al., 2009; Mahoney & Stella, 2020). However, in high-quality habitat,

which is defined as areas with high proportions of preferred species (Gallant et al., 2004), beavers may travel farther from lodges to select fewer, larger trees of a preferred species, in addition to selecting primarily for small stems close to the water's edge (Gallant et al., 2004; Raffel et al., 2009). Beavers tend to collect the branches and leaves of large cut stems and bring them back to their lodges, while leaving the main trunk at the cutting site, returning for repeated feeding (Gallant et al., 2004). This behavior may be energetically economical for beavers; by repeatedly returning to large cut stems at the site of harvest, beavers reduce the time spent foraging while increasing the amount of forage available from the branches, leaves, and bark of the downed tree (Gallant et al., 2004). Additionally, in areas with a legacy of intense beaver browse, beavers may avoid small trembling aspen (*Populus tremuloides*) stems due to the presence of unpalatable defensive compounds in the bark of young individuals (Basey et al., 1988).

Moose as competitors for resources

Moose's ecological role

Like other large ungulates, moose impact ecosystem structure and function through herbivory and trampling (Persson et al., 2000). In boreal forests, their behavior can alter plant community composition, canopy structure, soil structure, decomposition rates, and nutrient cycling (Donkor & Fryxell, 1999; Pastor et al., 1988). Similar to beavers, moose browse can spur the production of secondary metabolites in plants as a defense mechanism (Bryant et al., 1991). Moose browsing pressure on preferred forage species can also alter tree growth, resulting in stunted growth forms (Taylor et al., 2020). Ultimately, moose may reduce the relative proportions of preferred forage species, and can even push forests towards the dominance of less-preferred conifer species (Persson et al., 2000). In sub-boreal forests in Wisconsin and Nova Scotia, ungulates have driven areas to succeed from mixed northern hardwood ecosystems to grass- and sedge-rich savanna ecosystems (Rooney, 2009; Taylor et al., 2020). Furthermore, the ecosystem impacts of ungulates compound with the effects of other disturbances (e.g., fire, windthrow, host-specific insect outbreaks) (Hobbs, 1996; Stritar et al., 2010).

In ISRO, the moose population and its impacts on the ecosystem are highly dynamic, dependent on factors including browse availability and predation pressure from wolves (De Jager et al., 2017). In 2019 the moose population surpassed 2000 individuals, a relative peak (Hoy et al., 2020). Moose foraging on the island has historically altered biogeochemical cycles, depressing soil nutrient content, nitrogen mineralization, cation exchange capacity, microbial activity, and net primary productivity (Pastor et al., 1993; Paulson et al., 2016). Additionally, high browse pressure has changed the plant community composition of ISRO, reducing the proportions of trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*) and promoting succession toward the dominance of less-preferred spruce (Pastor et al., 1993). Stands where spruce are dominant have lower leaf litter quality and soil nutrient availability, reinforcing spruce dominance (Bryant et al., 1991; Pastor et al., 1993).

Moose's foraging preferences

Moose are generalist herbivores that roam to forage throughout a given area (Hood & Bayley, 2008b); unlike beavers, they do not forage from a central place like a body of water. In ISRO, during the winter, the dormant twigs of balsam fir (*Abies balsamea*) comprise the most significant portion of moose diet, in addition to mountain-ash (*Sorbus americana*), birch (*Betula spp.*), willow (*Salix spp.*), and red-osier dogwood (*Cornus sericea*) (Moen et al., 1990). During the summer they prefer to strip the growing leaves of mountain-ash (*Sorbus americana*), maple (*Acer spp.*), and birch (*Betula spp.*) (Moen et al., 1990). Similar to beaver, moose show the greatest preference for aspen (*Populus* spp.) year-round (Moen et al., 1990). Aquatic macrophytes found in inland lakes and beaver ponds are an important food source for moose as well, making up 13-27% of their summer diet (Tischler et al., 2019).

Moose select for a diverse set of food resources to meet their nutritional needs (Hoy et al., 2019). Even in cases where their preferred species are relatively rare, moose will still select for these species, which may exacerbate

their rarity (Hoy et al., 2019). This behavior is referred to as negative frequency dependent foraging (Hoy et al., 2019). By foraging in a negative frequency dependent manner, moose maximize nutrition while minimizing intake of plant defense compounds like secondary metabolites (Marsh et al., 2006). Unchecked moose browse on increasingly rare species could have destabilizing effects on ISRO's food web dynamics (Charron & Hermanutz, 2017; Hoy et al., 2019). However, these effects can be moderated by processes like wolf predation and some density independent foraging behavior by the moose (Hoy et al., 2019; Lundberg et al., 1990).

Beaver and moose interactions

In ecosystems with both species, beavers and moose have effects on ecological structure and function that compound in some cases and neutralize each other in other cases (Hood & Bayley, 2009; Kay, 1994). Beavers and moose share preferences for some forage species, particularly trembling aspen (*Populus tremuloides*) and willow (*Salix* spp.) (Mahoney & Stella, 2020). The combined effects of beaver and moose foraging place pronounced pressure on overlapping preferred species, accelerating their declines (Hood & Bayley, 2009). Conversely, while moose negatively impact riparian habitat through herbivory, beavers counteract this impact by creating viable riparian habitat through impoundment construction (Kay, 1994).

The overlap in forage preferences (e.g., trembling aspen) between moose and beaver indicates interspecies competition for food resources, and has led to the theory that moose may competitively exclude beavers in areas with scarce food resources (Hood & Bayley, 2008b). This hypothesis was tested by Hood & Bayley (2008b) in Elk Island National Park in Alberta, Canada, where the authors observed the effects of large ungulates, including moose, on the feeding behaviors of the local beaver population. Hood & Bayley (2008b) found that while competition between the two species did not rise to the level of exclusion, there was evidence that ungulates negatively impact beavers via competition. As a result, beavers change their foraging behavior in response to ungulate browsing pressure, feeding at closer distances to ponds and cutting larger aspen stems (Hood & Bayley, 2008b). Other studies have explored the impacts of elk (*Cervus canadensis*), another ungulate with a similar functional role as moose, on the foraging behavior of beavers (Baker, 2003; Kay, 1994; Nietvelt, 2001). These studies found varying degrees of competition as a function of ungulate and beaver population levels, as well as the assortment of available browse species, highlighting the importance of site-specific context when evaluating interspecies effects (Baker, 2003; Kay, 1994; Nietvelt, 2001).

The wildlife of insular ecosystems such as ISRO are subject to greater population fluctuations due to resource overexploitation, trophic cascading, disease, and genetic deterioration (Graham et al., 2017). Additionally, anthropic impacts like climate change place further pressure on wildlife in insular ecosystems (Fisichelli et al., 2013). In ISRO, beaver and moose have cumulative effects on vegetation structure, reducing forage availability and hastening succession toward spruce stand dominance (Moen et al., 1990). As forage becomes more limited, competition between the two species for food resources will continue to grow in intensity. It is unknown how ISRO's beaver and moose populations will be affected by these pressures, given their geographic isolation and limited space.

Effects of wolf presence on beaver-moose interactions

Wolves (*Canis lupus*) are large apex predators that live in packs and defend large territories (~130-2,500 km^2) (U.S. Fish & Wildlife Service, 2020). They prey upon herbivorous mammals like moose, beavers, and hares (Hoy et al., 2020), placing top-down pressure on populations and leading to indirect effects on prey behavior like altered movement patterns and heightened vigilance (Brown et al. 1999). In the Canadian Rocky Mountains, large game made up approximately 80% of the wolves' diets (Cowan, 1947). They also supplement their diets with small game, including beavers. In one study, beavers comprised between 3% and 42% of wolf diets in Manitoba, although for one outlier wolf, beavers made up 83% of its diet (Moayeri, 2013). Further west in Alberta and British Columbia, Cowan (1947) found that small game like beaver and snowshoe hare made up 18% of wolves' diets.

Wolf predation pressure has a stabilizing effect on moose populations in ISRO (De Jager et al., 2017). In the absence of top predators, moose population densities grew to unsustainable numbers, leading to chronic overbrowsing and the disruption of forest community structure. By contrast, areas with a stable wolf population had lower moose population density and higher forage availability (De Jager et al., 2017). Although wolves are important in controlling moose populations, the presence or absence of winter forage is often more impactful on population numbers and movement patterns than wolves (Cowan, 1947; Kittle et al., 2008).

With respect to wolf-beaver interactions, research is more scarce. Some studies have posited that wolves will eat beaver more often in ice-free seasons and when beaver population density is high (>5 beavers km^2) (Gable et al., 2018). However, Cowan (1947) has speculated that beaver populations continue to increase despite wolf predation until high quality forage (i.e., Populus spp.) is no longer available.

The wolf population of ISRO has fluctuated dramatically in recent years. Since reaching a relative high of roughly 30 individuals in 2006, the island's wolf population sustained precipitous losses, hitting a dangerous low of two individuals in 2018 (Hoy et al., 2020). In response, NPS translocated 19 wolves to the park between 2018 and 2020 to restore their population (Hoy et al., 2020; National Park Service, 2021a). Since that event, ISRO's wolves have shown signs of rebound, with the birth of wolf pups and reemergence of social organization (Christensen, 2021).

The impacts of wolves on ISRO's beaver and moose populations, and their interspecies interactions, is highly dynamic. As the wolf population approached extirpation in 2018, both beaver and moose populations grew (Hoy et al., 2020). It is unclear how the wolf population's rebound will impact beavers and moose. Additionally, some have hypothesized that high beaver density could exacerbate wolf predation on ungulates by increasing wolf pup survival during low ungulate density years (Gable et al., 2018).

Analysis of existing data

Habitat Use and Forest Structure protocol

In 2018, Michigan Technological University (MTU) created a protocol for NPS to examine the extent and potential impacts of competitive herbivory between moose and beaver in ISRO . The purpose of the 2018 protocol was to collect foraging data during a period of low wolf predation and high beaver activity (2012-2018) and then to subsequently collect data as wolves are reintroduced (Hoy et al., 2018). The specific objectives of this protocol were:

i. Assess the presence of beaver in areas with moose present to determine dietary overlap.

ii. Assess beaver-preferred forest products where moose and beaver are present to evaluate browse pressure versus species availability.

iii. Assess size and availability of beaver-preferred species from aquatic edge to provide probably length of residence.

iv. Assess distance beavers travel from aquatic edges to obtain preferred species to estimate predation risk.

v. Assess effects of moose herbivory to species preferred by both moose and beaver to evaluate current and future exclusion of species availability as food for each herbivore.

A key component of this protocol is forest structure and composition, which provides the context from which the beavers choose their preferred diet. Additionally, beaver foraging data were collected along active beaver trails, including both the species foraged and the distance from the aquatic edge of each cut. Researchers trained by MTU scientists collected data using this protocol during September 2019 and 2020. The data resulting from this protocol were used in this study.

Data collection to date

NPS provided two datasets that were collected using the 2018 protocol. These are hereafter referred to as "Habitat Use" and "Forest Structure". Habitat Use quantifies and qualifies foraging patterns of beaver in ISRO (Hoy et al., 2018), while Forest Structure quantifies and qualifies ISRO's vegetation profile, as well as moose browse intensity on stems uncut by beavers (Tourville et al., 2018).

To collect the Habitat Use data, researchers first identified aquatic sites around the island with active beaver ponds. At each site, they identified the two most active beaver trails originating from the water's edge, established transects on those trails, and logged start and end coordinates. Researchers tallied the number of beaver-cut stems within two meters on either side of the transect, broken up by the following categories: species, diameter class, distance category, and fresh or old cut. The diameter class categories range from integers 1 - 4, where 1 = <5cm, 2 = 5-10cm, 3 = 10-20cm, and 4 = 20+ cm. The distance categories range from integers 1 - 6, where 1 = 0-2.5m, 2 = 2.5-5m, 3 = 5-10m, 4 = 10-20m, 5 = 20-40m, and 6 = 40-60m. Shorter beaver trails did not use all distance categories.

To collect the Forest Structure data, researchers established sites around the ISRO trail system and established two 60-meter straight-line transects per site. Each transect originates either from the aquatic edge of a beaver impoundment or from a park trail, and is perpendicular to the edge or trail. Starting GPS coordinates, length, and bearing of each transect were recorded. Researchers identified every tree or sapling within two meters on both sides of the transect within various distance intervals from the transect starting point. These distance categories range from integers 1 - 5, where 1 = 0-10m, 2 = 20-25m, 3 = 30-35m, 4 = 40-45m, and 5 = 55-60m. Individuals were classified as either a tree or sapling. Trees were defined as woody stems with a diameter at breast height (DBH) greater than or equal to 10 cm and height greater than or equal to 1.5 meters. Saplings were defined as woody stems with a DBH below 10 cm and height less than 1.5 meters. For each tree, researchers recorded species, position along transect, distance from the transect tape, DBH, status dead or alive, and Accumulated Browse Index (ABI), a unitless metric that will be described below. For each sapling, they recorded species, position along transect, distance from the transect tape, basal diameter, height, status dead or alive, ABI, and bites taken/available.

Accumulated Browse Index (ABI) is a unitless classification of the impact severity that moose browse has had on tree or sapling growth, using a scale of integers between 0-3. An ABI of 0 refers to an individual with a growth pattern unimpacted by moose browse. An ABI of 3 refers to an individual severely impacted by moose browse. This measurement can be used as an estimation of historical moose browse intensity on trees and saplings.
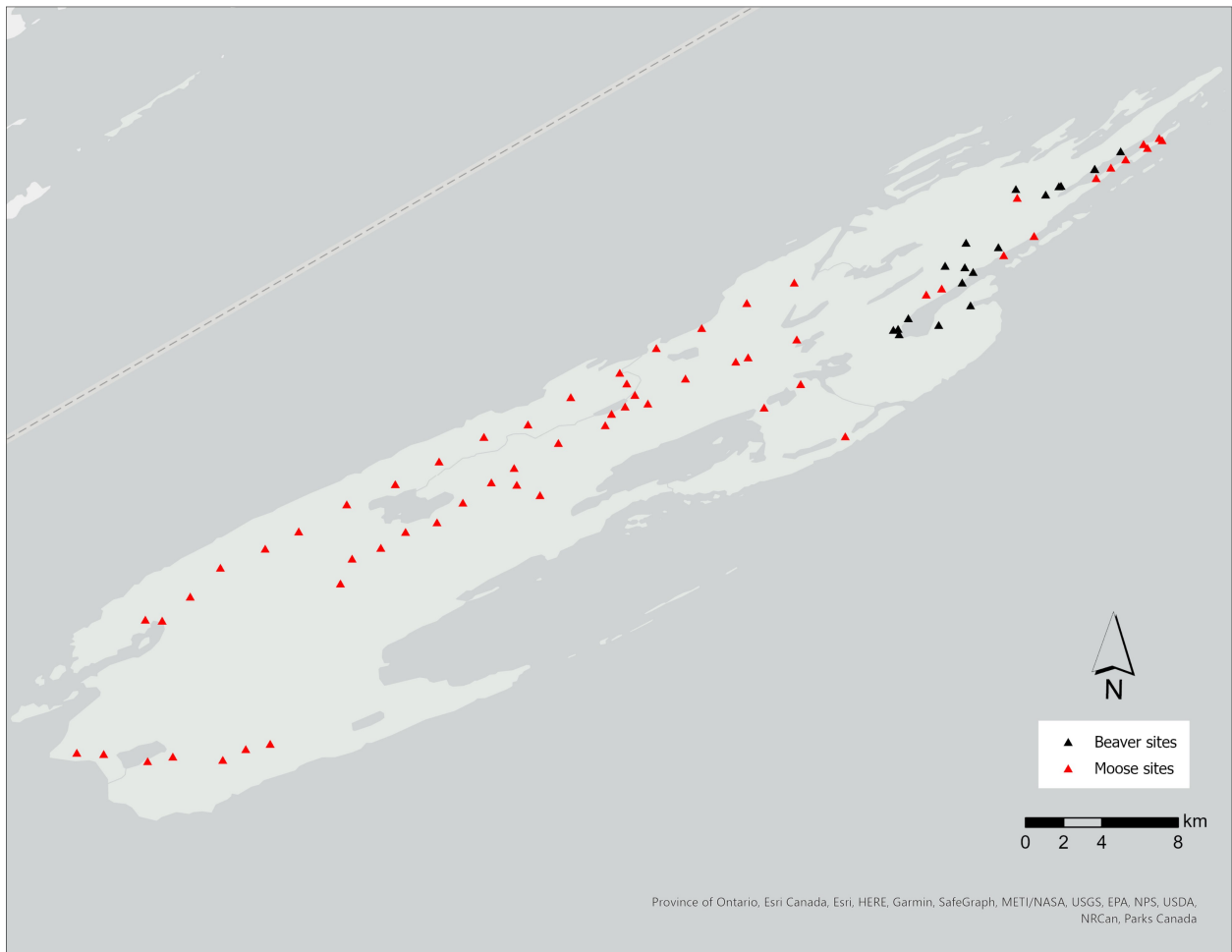
Figure 1: Map of ISRO surveys. Forest Structure data surveying vegetation composition and moose browse were collected at all moose sites (red) and some beaver sites (black). Habitat Use data surveying beaver browse were collected at beaver sites only.

Vegetation classification

We assigned a vegetation classification type to each distance interval along the transects of both the Habitat Use and Forest Structure data (Fig. 2). We did this to classify beaver preferences and moose preferences on their own, and to examine their spatial relationship. To do this, we used land cover classification data created by NPS, per the USGS-NPS Vegetation Mapping Program (National Park Service, 2000). In this program, NPS classified the land cover of ISRO into 52 vegetation types using field surveys and expert knowledge photo-interpretation based on the shape, size, tone (color or black and white), shadow, pattern, and texture of the vegetation from an aerial shot. Using Esri's ArcGIS Pro v2.8.2, we plotted and spatially joined each transect with the vegetation classification layer, and assigned a vegetation type to each distance interval along the transects. Some vegetation types were associated with both Habitat Use and Forest Structure transect intervals, while other vegetation types were only associated with either Habitat Use or Forest Structure transects. Additionally, some transects contain multiple vegetation types along its length, at different distance intervals. Vegetation types with Habitat Use or Forest Structure observations are listed in Table 1.
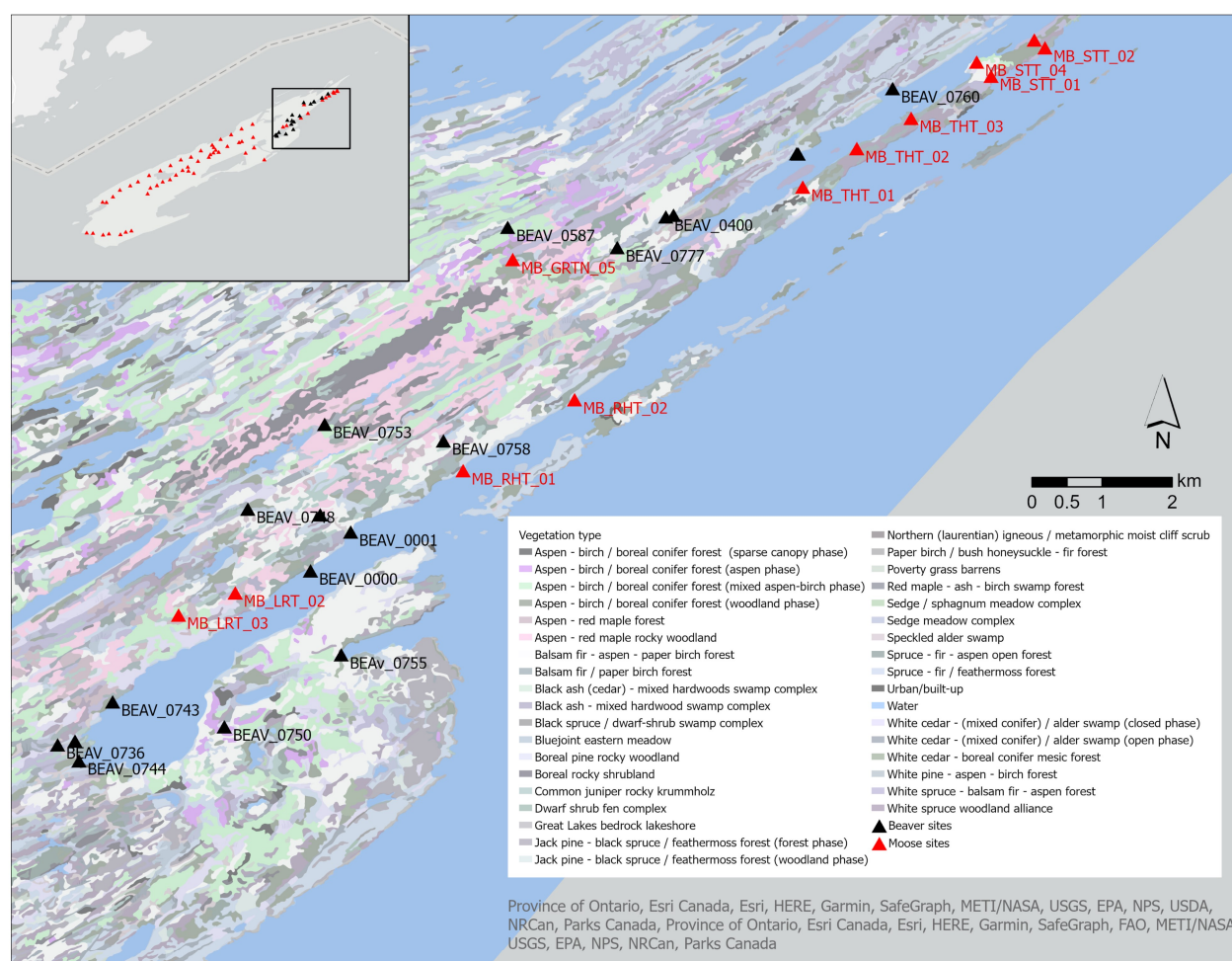

Figure 2: Fine-scaled USGS-NPS vegetation classification with all beaver sites shown.

Table 1. Number of stems observed during Habitat Use and Forest Structure surveys throughout ISRO.

Vegetation type	Habitat Use	Forest Structure
Aspen - birch / boreal conifer forest (aspen phase)	13	78

Vegetation type	Habitat Use	Forest Structure
Aspen - birch / boreal conifer forest (mixed aspen-birch phase)		535
Aspen - birch / boreal conifer forest (sparse canopy phase)		254
Aspen - birch / boreal conifer forest (woodland phase)	27	299
Aspen - birch / sugar maple - mixed hardwoods forest (paper birch phase)		213
Aspen - red maple forest	7	
Aspen - red maple rocky woodland	32	63
Balsam fir - aspen - paper birch forest	24	676
Balsam fir / paper birch forest	9	705
Black ash (cedar) - mixed hardwoods swamp complex		6
Black ash - mixed hardwood swamp complex	22	
Bluejoint eastern meadow	1	33
Boreal pine rocky woodland		82
Boreal rocky shrubland	10	118
Jack pine - black spruce / feathermoss forest (woodland phase)		116
Maple - yellow birch - northern hardwoods forest (sugar maple phase)		221
Paper birch / bush honeysuckle - fir forest		295
Poverty grass barrens	18	129
Sedge meadow complex	6	12
Speckled alder swamp	25	116
Spruce - fir - aspen open forest	32	48
Spruce - fir / feathermoss forest	35	152
Spruce - fir and sugar maple - yellow birch mosaic		38
White cedar - (mixed conifer) / alder swamp (closed phase)	52	157
White cedar - (mixed conifer) / alder swamp (open phase)		19
White spruce woodland alliance	14	300
Yellow birch - (spruce) forest		53

Data summaries

We used R (R Core Team, 2021), and the packages 'recode' (Wickham, 2021) and 'readxl' (Wickham and Bryan, 2019), to estimate beaver browsing behavior using the Habitat Use dataset. The principal metric used to quantify beaver browse is the number of beaver-cut stems. We analyzed the distributions of beaver-cut stems among vegetation types, species, distance intervals, and diameter classes. Because distance intervals had varying lengths (e.g. 2.5-5m followed by 5-10m), we normalized the counts of beaver-cut stems per distance interval by area (cuts/m^2), and used the normalized values in some analyses.

We also used R (R Core Team, 2021), and the packages 'recode' (Wickham, 2021) and 'readxl' (Wickham and Bryan, 2019), to estimate moose browsing behavior and vegetation structure using the Forest Structure dataset. Forest Structure data were collected throughout the island at moose and beaver sites, and the following results are a reflection of this. The principal metric used to quantify moose browse is the Accumulated Browse Index (ABI) (Tourville et al., 2018). A second metric, an estimation of the number of 5cm x 5cm moose bites taken and the number of 5cm x 5cm moose bites available, was collected for each sapling, but not for trees. We therefore only use ABI in this analysis. Average ABI values were calculated based on vegetation type, species, and DBH. Tables and graphs were created using all surveyed data.

Pilot analysis

In a preliminary analysis, we explored the relationship between beaver cuts and other variables that may have influenced beaver behavior. We created a generalized linear model (Fig. 3), where beaver cuts (*ln*) were estimated as a function of vegetation type, to reflect any preferences as a function of the vegetation

type; distance to water (by vegetation type), to account for safer activity closer to water; number of stems available, to reflect actual usage of vegetation, and of moose browsing to account for any competitive effects between the two species. Moose browsing was included as the mean ABI value for that vegetation type (summed trees and sapling estimates), thus a proxy for actual browsing for each vegetation type (Table 3).
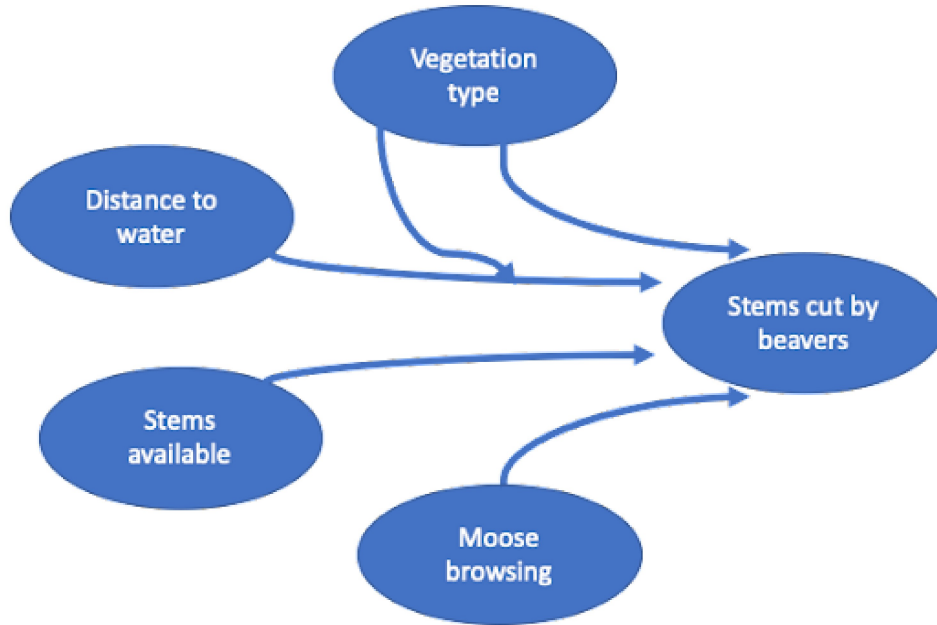

Figure 3: Conceptual diagram of a generalized linear model predicting stems cut by beavers.

Results and recommendations

Beaver preferences

Most beaver cuts are in the "White cedar - (mixed conifer) / alder swamp (closed phase)", "Spruce - fir - aspen open forest", and "Aspen - birch / boreal conifer forest (woodland phase)" classes (Fig. 4). "White cedar - (mixed conifer) / alder swamp (closed phase)" includes 16.5% of total beaver cuts observed on the transects, showing that many beaver sites are located in or around swampy, inundated areas. "Spruce - fir - aspen open forest" and "Aspen - birch / boreal conifer forest (woodland phase)" include 10.9% and 10.6% of total cuts, respectively. This indicates that beavers prefer areas in or within a safe distance of mixed broadleaf-needleleaf forests with aspen.

While Forest Structure data were collected throughout the island, Habitat Use data were collected mostly on the northeast side of the island, and is thus only a subsample of all beaver impoundments in ISRO. It could be possible that the "White cedar - (mixed conifer) / alder swamp (closed phase)" vegetation type is more common in this area, and that the surface area of each vegetation class influences the possible number of cuts. Only 8% of the total land surface area of ISRO is classified as "White cedar - (mixed conifer) / alder swamp (closed phase)" despite having the largest share of total stems cut.

Throughout all vegetation types, beavers browsed trembling aspen (*Populus tremuloides*) the most, comprising one-third (34.2%) of total cuts. Grey alder (*Alnus incana*) comprises 17.0% of cuts, which is in agreement with the observation that the highest number of cuts were made in an alder swamp vegetation class. Data show that beavers cut fewer white spruce and mountain maple.

These summaries are an estimation of beaver foraging behavior in ISRO and provide insight on their preferred species. However, it is difficult to confidently determine their preferred choices without knowing the nearby
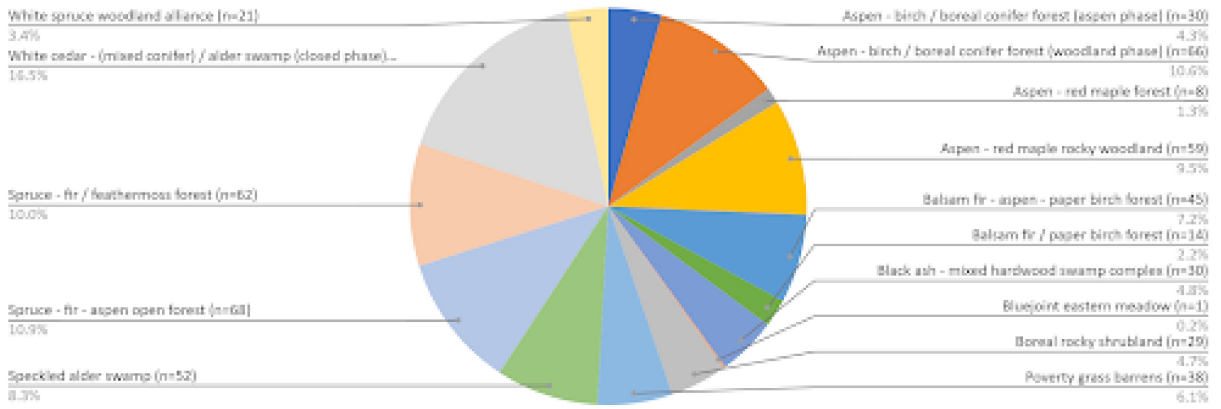
Figure 4: Beaver activity (no. cuts per sq. m) in each vegetation class. Cuts stems include both saplings and trees
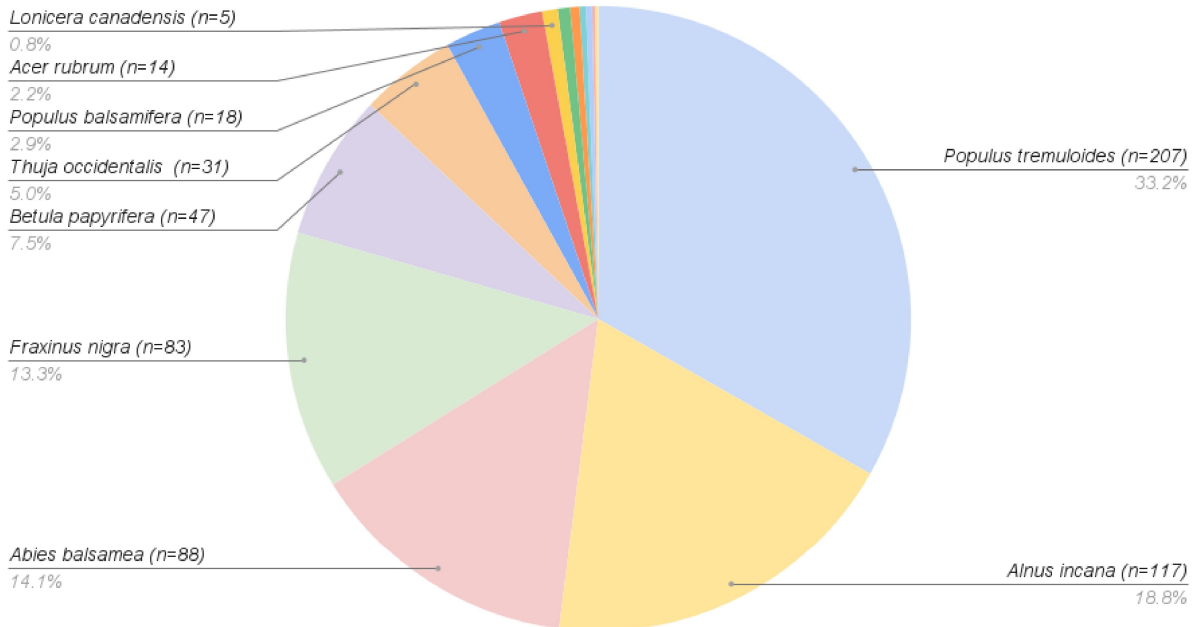

Figure 5: Proportion beaver cuts by species, n=626.

14

available species. Without nearby Forest Structure data, we cannot tell whether a species was seldom cut because it is a rare species or because beavers actively selected against it. For example, it is possible that mountain maple (*Acer spicatum*) is palatable to beavers due to its similarity with red maple (*Acer rubrum*), but is hardly selected for because it isn't common near impoundments.
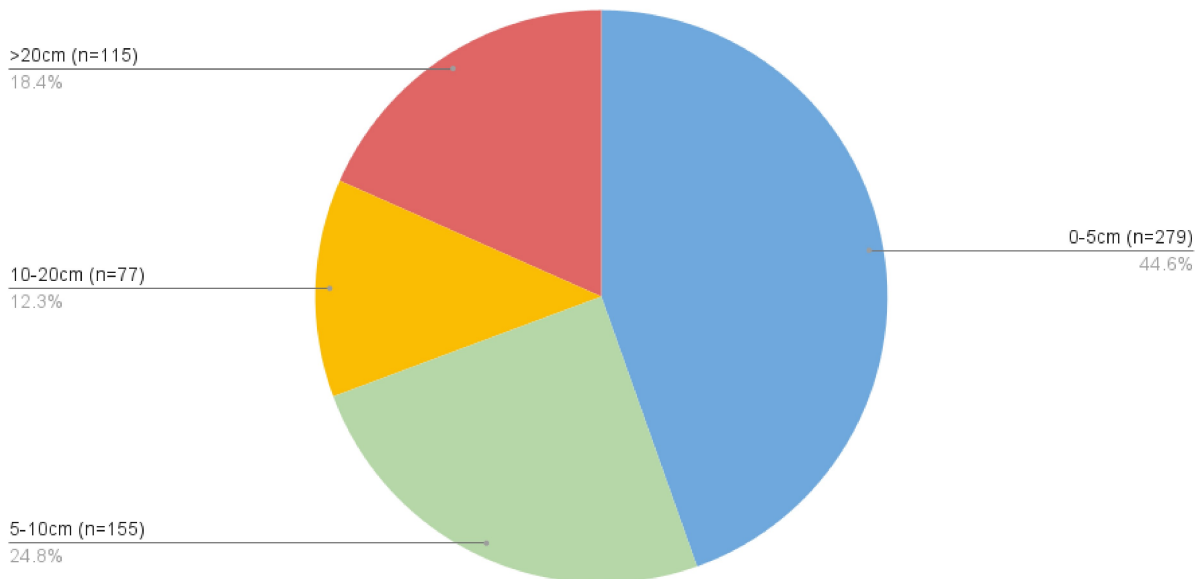

Figure 6: Proportion of beaver-cut stems by diameter class (cm), n=626

Table 2. Beaver-cut stem density in each distance interval, for all vegetation classes.

Distance interval (m)	Mean cuts/m^2
0-2.5	0.283 ± 0.251
2.5-5	0.176 ± 0.128
5-10	0.101 ± 0.082
10-20	0.049 ± 0.044
20-40	0.026 ± 0.019
40-60	0.027 ± 0.020

Most cuts were observed within 2.5m of the water's edge (Table 2; 0.283±0.251 cuts/m^2), and were under 5 cm in diameter (Fig. 6). This is consistent with the central place foraging theory. These observations are also consistent with other studies that found beavers prefer aspen, select for small- to mid-sized (2-10cm diameter) stems, and forage within a short distance of water (Gallant et al., 2004; Mahoney & Stella, 2020; Raffel et al., 2009). However, the distribution of plant species and stem sizes along beaver trails is mostly unknown, because most Habitat Use data does not have associated Forest Structure data collected on the same transects. Thus, it is unknown whether these foraging patterns (Table 2; Fig. 4, 5, 6) are truly due to beaver preference, or are simply a reflection of the distribution of species growth (e.g. *Alnus incana* near water's edge).

Further, beaver browse preference may not rely on only one of these summarized characteristics—it is most likely that characteristics (e.g., distance from water and species) are correlated and vary by vegetation type. Figure 6 is an example of how all characteristics including species, diameter, and distance from water interplay in the "Aspen-birch/boreal conifer forest" vegetation type. Additional figures showing beaver browse relationships with species, size, and distance are available in Appendix 4 for each of the vegetation types where available vegetation data were collected.
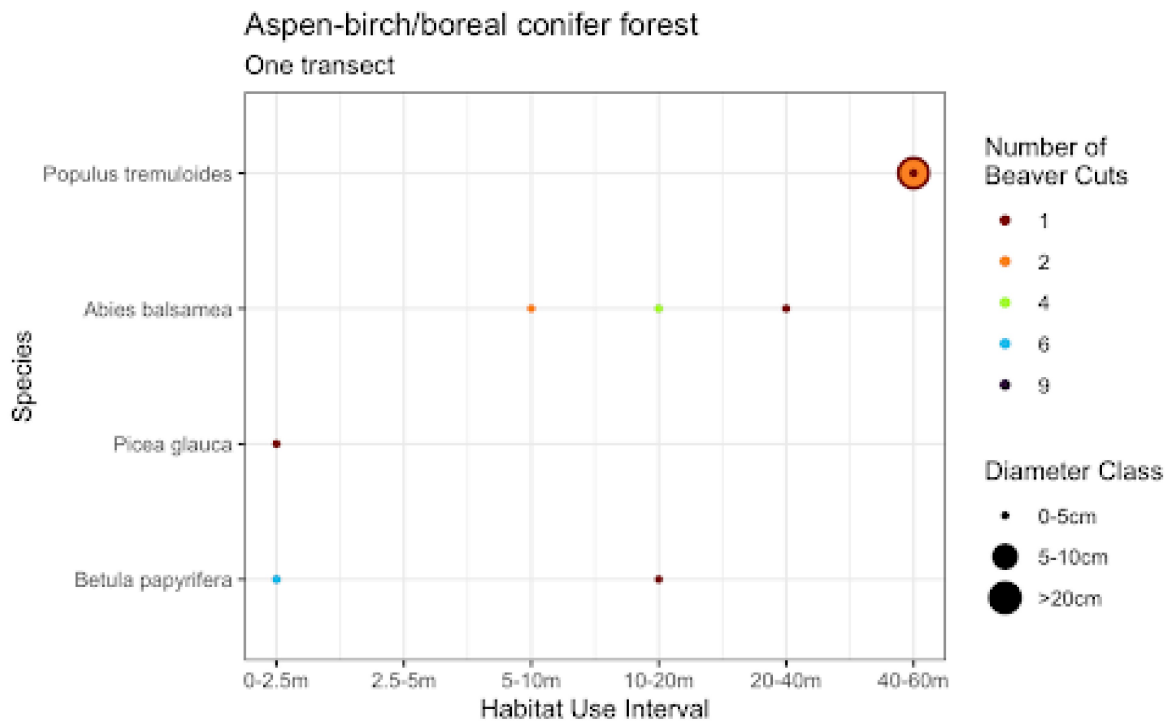
Figure 7: Number and approximate size of trees cut by beavers by distance and species. A slight linear relationship is seen between distance and species. Future investigation of the relationship between available browse and browse selection per vegetation class is indicated as a possible next step.

Moose preferences

Moose browsing activity in ISRO is not uniformly distributed among different vegetation types (Table 3), and may not be correlated like beavers and swampy vegetation types (Fig. 4). We used all Forest Structure samples throughout ISRO for these summaries to provide a robust summary of preference. Moose browsed the "Aspen - red maple rocky woodland" vegetation type the most, with a mean ABI of 1.89±0.064 (Table 3), and browsed "White cedar - (mixed conifer) / alder swamp (open phase)" vegetation type the least, with a mean ABI of 0.474±0.140.

Table 3. Moose browse severity per vegetation type.

Vegetation type	n	Mean ABI
Aspen - red maple rocky woodland	83	1.89 ± 0.064
Yellow birch - (spruce) forest	53	1.66 ± 0.093
Paper birch / bush honeysuckle - fir forest	305	1.48 ± 0.047
Aspen - birch / boreal conifer forest (sparse canopy phase)	280	1.38 ± 0.052
Aspen - birch / sugar maple - mixed hardwoods forest (paper birch phase)	252	1.36 ± 0.051
Maple - yellow birch - northern hardwoods forest (sugar maple phase)	258	1.32 ± 0.050
Boreal rocky shrubland	118	1.26 ± 0.052
Spruce - fir / feathermoss forest	202	1.23 ± 0.066
Aspen - birch / boreal conifer forest (mixed aspen-birch phase)	598	1.18 ± 0.040
Poverty grass barrens	147	1.14 ± 0.092
Spruce - fir - aspen open forest	65	1.13 ± 0.082
White cedar - (mixed conifer) / alder swamp (closed phase)	241	1.11 ± 0.081
Bluejoint eastern meadow	35	1.10 ± 0.051
Aspen - birch / boreal conifer forest (woodland phase)	331	1.05 ± 0.046
Spruce - fir and sugar maple - yellow birch mosaic	40	1.03 ± 0.171
Speckled alder swamp	167	0.922 ± 0.075
White spruce woodland alliance	469	0.906 ± 0.048
Jack pine - black spruce / feathermoss forest (woodland phase)	156	0.836 ± 0.067
Aspen - birch / boreal conifer forest (aspen phase)	139	0.821 ± 0.075
Balsam fir - aspen - paper birch forest	773	0.800 ± 0.029
Sedge meadow complex	18	0.750 ± 0.218
Boreal pine rocky woodland	95	0.683 ± 0.077
Black ash (cedar) - mixed hardwoods swamp complex	6	0.667 ± 0.211
Balsam fir / paper birch forest	847	0.570 ± 0.025
White cedar - (mixed conifer) / alder swamp (open phase)	22	0.474 ± 0.140

Excluding species with low sample sizes (less than 30 recorded individuals), *Populus tremuloides* had the highest mean ABI (1.52±0.047), *Sorbus decora* had the second highest (1.42±0.075), and *Acer saccharum* had the third highest (1.36±0.020) (Table 4). *Abies balsamea*, the most numerous species in the surveyed forests, had a mean ABI of 0.90±0.017.

Table 4. Counts and mean Accumulated Browse Index for each species. Average ABI in the model are vegetation type estimates.

Species	n browsed	n observed	Proportion browsed	Mean ABI
Abies balsamea	1384	1963	0.71	0.90 ± 0.0017
Acer rubrum	8	14	0.57	0.71 ± 0.194
Acer saccharum	1154	1278	0.90	1.36 ± 0.020
Acer spicatum	56	68	0.82	1.04 ± 0.080
Alnus incana	1	1	1.00	2.00
Betula alleghaniensis	11	13	0.85	1.00 ± 0.160

Species	n browsed	n observed	Proportion browsed	Mean ABI
Betula papyrifera	142	250	0.57	0.90 ± 0.057
Cornus sericea	3	3	1.00	1.00 ± 0.00
Crataegus spp.	1	1	1.00	1.00
Fraxinus nigra	71	125	0.57	0.75 ± 0.068
Picea glauca	50	266	0.19	0.23 ± 0.032
Picea mariana	1	3	0.33	0.33 ± 0.033
Pinus banksiana	0	1	0.00	0.00
Pinus resinosa	0	1	0.00	1.00
Pinus strobus	1	3	0.33	0.33 ± 0.033
Populus balsamifera	1	2	0.50	1.50 ± 1.50
Populus tremuloides	394	496	0.79	1.52 ± 0.047
Quercus rubra	7	8	0.88	1.13 ± 0.227
Sorbus americana	5	5	1.00	1.40 ± 0.245
Sorbus decora	89	99	0.90	1.42 ± 0.075
Thuja occidentalis	53	203	0.26	0.34 ± 0.047
Viburnum edule	3	3	1.00	1.00 ± 0.00

Although being the species with the third highest average ABI, *Acer saccharum* was the species with the highest browsed proportion (Table 4; 0.90). This suggests that even though a smaller proportion of *Populus tremuloides* individuals were browsed (0.79), *Populus tremuloides* stems still exhibited signs of higher browsing pressure. However, it is worth noting that the number of stems counted per species varies. *Acer saccharum* (n=1278) was observed over twice as often as *Populus tremuloides* (n=496) and is thus more available.

Moose browsing pressure was highest for stems with a DBH of 5 cm or less (Table 6). The average DBH for individuals with a severe browse index (ABI=3) is 2.17 cm, whereas stems with no apparent browse (ABI=0) were on average 7.85 cm DBH (Table 6). This negative relationship was consistent throughout all ABI classes. These findings provide evidence suggesting that moose in ISRO prefer to browse smaller stems. However, this could simply be a reflection of confounding factors such as preferred species having smaller diameters in ISRO. To support this supposition, we found that observed Populus tremuloides stems had a mean DBH of 4.24±6.93cm and Acer saccharum had a mean DBH of 2.70±5.18cm, two of the most preferred species, as compared to less preferred species (e.g., Pinus strobus). Likewise, smaller stems may simply be more prevalent due to forest structure and stand densities throughout ISRO (i.e. rule of thinning; see Appendix 5).

Table 5. Mean DBH per ABI class for all standing stems.

ABI	n	Mean DBH (cm)
0	1411	7.89 ± 8.92
1	2182	3.77 ± 5.39
2	1005	2.31 ± 3.60
3	261	2.17 ± 2.12

Generalized linear model results

Our data summaries above found that both moose and beaver heavily browse small 0-5cm DBH stems and Populus tremuloides, not necessarily mutually inclusively. This would support the hypothesis of competitive herbivory between moose and beaver. Our pilot analysis of all beaver transects representing vegetation types shared by moose and beaver confirm this negative interaction, although results were not statistically significant (Fig. 8). This is probably due to the lack of replication, but it still shows how the different covariates included were associated with beaver activity (Fig. 8-9). Beaver activity was similar among

vegetation types (Fig. 8), although they tended to use some types more than others. As expected, the best predictor of beaver cuts was distance to water, with decreasing activity as distance to shore increased (Fig. 9). Although not statistically significant, the number of stems cut was positively associated with stem density, indicating beavers are more active in areas of higher tree density (coefficient mean[95%CI]: 1.58[-0.37,3.79]). We also found a statistically non-significant, negative association between moose ABI and beaver cuts when accounting for all other variables (coefficient mean[95%CI]: -1.88[-6.02,0.9]; Fig. 9).
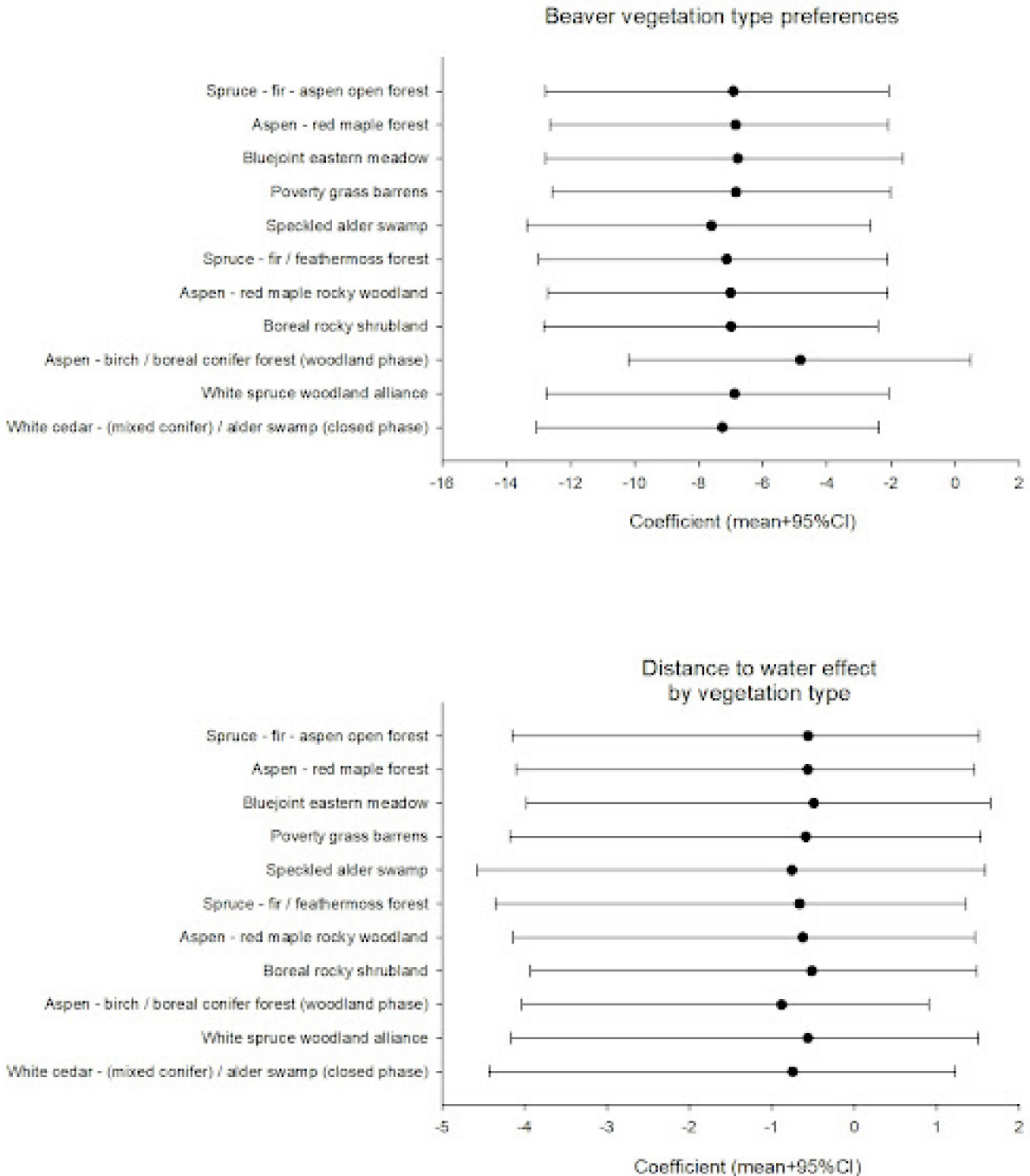
Figure 8: Effect of vegetation type and distance from water on beaver activity.
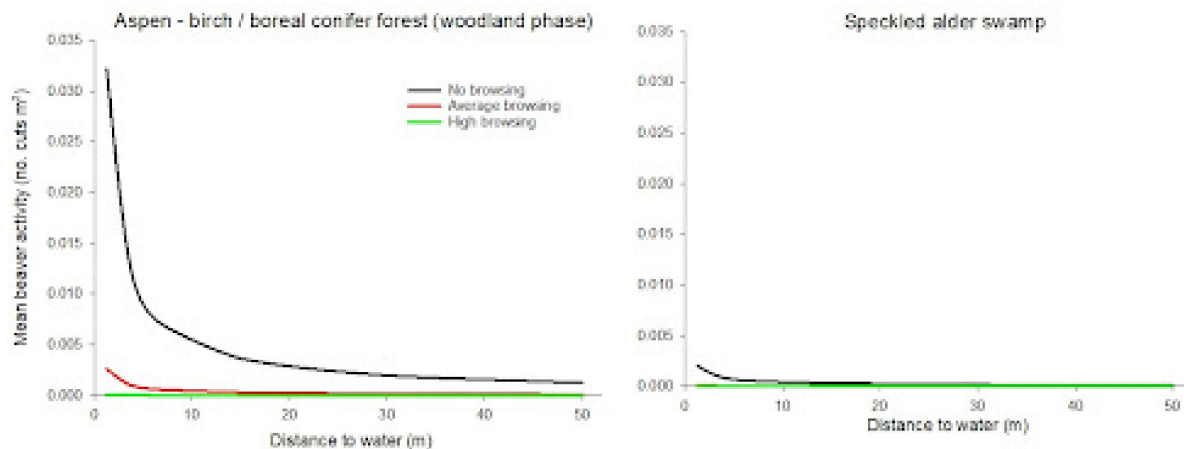
Figure 9: Predicted beaver activity (cuts per sq. m) based on moose browse severity for the vegetation type with highest beaver activity (left panel) and the one with the lowest beaver activity (right panel). Graphs for all vegetation types are included in Appendix 2.

Recommendations

To accurately assess beaver preferences and potential competition with moose, beaver activity, moose browsing and vegetation structure should be systematically and simultaneously assessed in every transect across all vegetation types surrounding ponds. Furthermore, vegetation and browsing surrounding the pond should be recorded along control transects to better assess beaver preferences. The Forest Structure data provides a robust summary of moose browse because of the distribution of sample sites throughout ISRO and the characteristics of stems recorded. However, it is difficult to assess beavers' preferences and possible competitive herbivory without knowing what food items are available. Thus, there is the need for control transects. Only by assessing moose browse in both the Habitat Use and control transects will researchers be able to quantify the impact of moose on beaver activity. There are several instances within the provided database that show Forest Structure and Habitat Use transects sharing the same starting point, but the bearing, distance intervals, and thus the vegetation classes may not be consistent. With Habitat Use and Forest Structure sampling procedures carried out on the same transect, NPS could remedy this.

We recommend that transects should start at the water's edge and run on beaver trails per the Habitat Use sampling procedure. Replicate control transects are to be conducted away from beaver trails. Recording the vegetation type per the USGS-NPS Vegetation Mapping Program is optional, but may prove significant in statistical analysis (National Park Service, 2000). Replicate transects in the same vegetation class would allow researchers to be able to assess if beavers are selecting particular vegetation types or areas with different moose browsing (starting at the water's edge, Fig. 10). Control transects do not need to follow active or inactive beaver trails, and can thus be a straight line transect. Researchers should record all stems (trees, saplings, seedlings, shrubs) within a discretionary perpendicular distance (e.g. 1, 2, 5m on each side) of the transect tape (this gives stem density—normalizing stems by area is necessary if distance intervals are not equal in length). If uncut shrubs are present, they should be recorded with a start and stop distance along the transect tape to quantify shrub diameter.
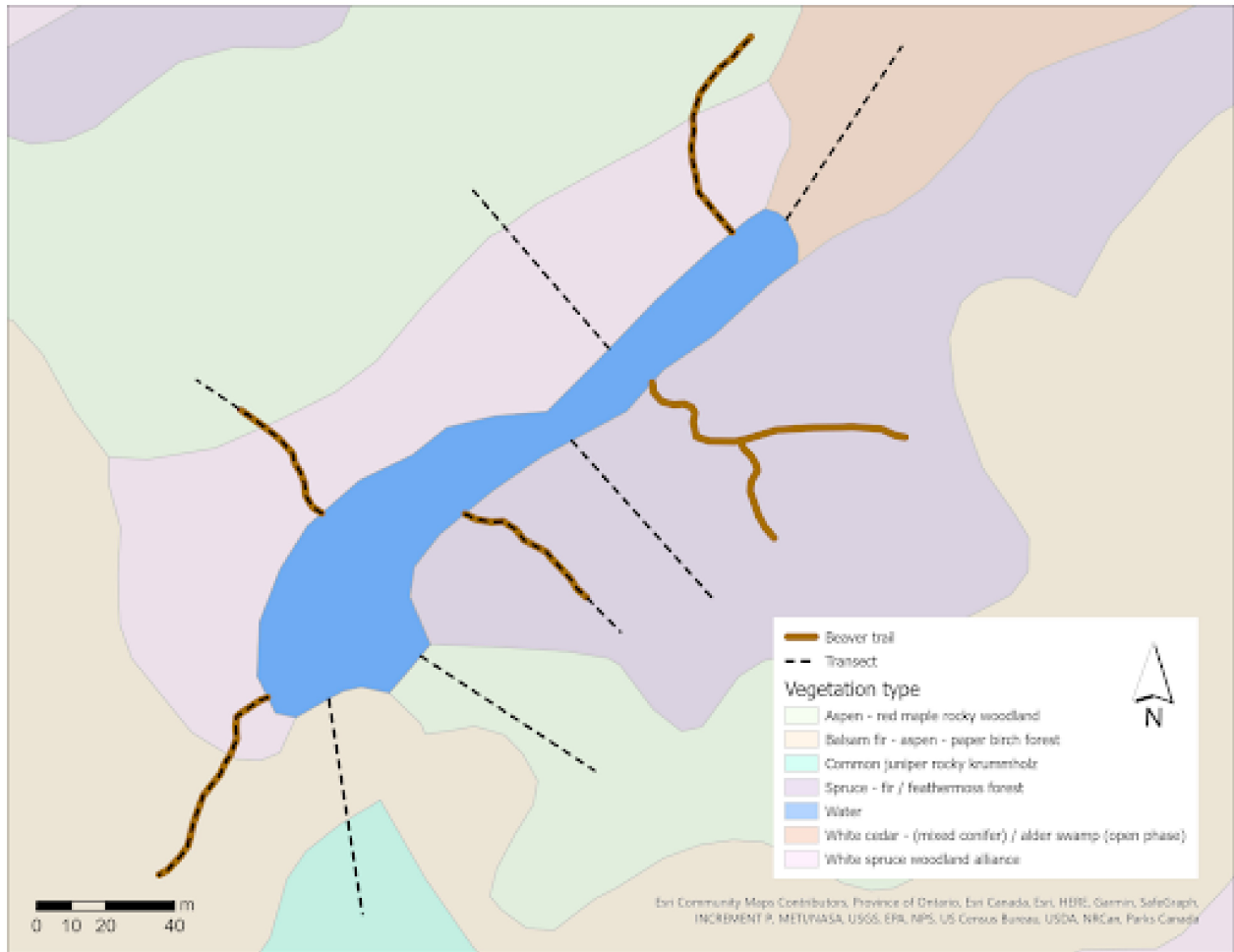
Figure 10: Proposed sampling procedure for site BEAV_0758.

For each cut and uncut stem within a transect, researchers should record:

i. The species identity. If a stem can only be identified to the genus, then its genus is recorded. NULL is used if completely unidentifiable.

ii. Whether the stem is a tree, sapling, seedling, or shrub (Hoy, Peterson, & Vucetich, 2018; Tourville et al., 2018).

iii. The distance from the water's edge (similar to POS_ON, see Appendix 6) for each cut stem (including planted stems and felled logs) and each standing stem.

iv. Distance interval, using a uniform distance interval classification system like the one used in the Habitat Use protocol:

1 = 0-2.5m

2 = 2.5-5m

3 = 5-10m

4 = 10-20m

5 = 20-40m

6 = 40-60m

v. Diameter, using a uniform diameter classification system like the one used in the Habitat Use protocol:

1 = 0-5cm

2 = 5-10cm

3 = 10-20cm

4 = >20cm

Diameter classification is assigned based on the height of harvest for cut stems and at breast height for uncut stems (Mahoney & Stella, 2020). Measuring exact diameter measurements is optional.

vi. The ABI (0-3) for all uncut stems (trees, saplings, shrubs) to quantify moose browsing pressure.

If transects of beaver trails and available vegetation take place during different seasons, we recommend marking the start of the trail so that the vegetation survey can begin in the exact spot and in the exact direction as the trail survey.

These recommendations quantify beaver browse, moose browse, and available vegetation that they choose from. Following this procedure, NPS scientists will have a robust, spatially overlapping herbivory dataset. Each row in this database is one observed stem that is cut or uncut, with information about species, tree/sapling/shrub, distance, DBH, ABI, and vegetation class, and will have come from the same transect. Cut stems continue to describe beaver foraging behavior and preferences. Uncut stems categorized by ABI continue to describe moose browse, but also show what beavers have not chosen in the same area. By using the same transects, these measurements will be readily comparable and provide significant insight on competitive herbivory between beaver and moose in ISRO. This will provide the appropriate data for the analysis of past beaver browsing preference, an integral part of the analysis of competitive herbivory between moose and beaver.

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Appendix

Appendix 1. Model Code

```
model{


for(i in 1:119){

Densall[i]~dpois(DO[i])C(0,)
CUT_h[i]~dpois(do[i])C(0,)

DO[i]<-exp(alpha[VegType[i]]+beta[VegType[i]]*log(dist[i])+gam*(ABItress[i]
        +ABIsaplings[i])+lam*densityall[i])

}

#priors

    gam~dnorm(0,0.0001)
    lam~dnorm(0,0.000)


for(i in 1:11){
    alpha[i]~dnorm(A,tau[1])
    beta[i]~dnorm(0,tau[2])
    }

  A~dnorm(1,0.1)
  B~dnorm(0,0.001)

for(i in 1:2){
tau[i]<-1/var[i]
var[i]~dunif(0,10)
}
}#end model
```
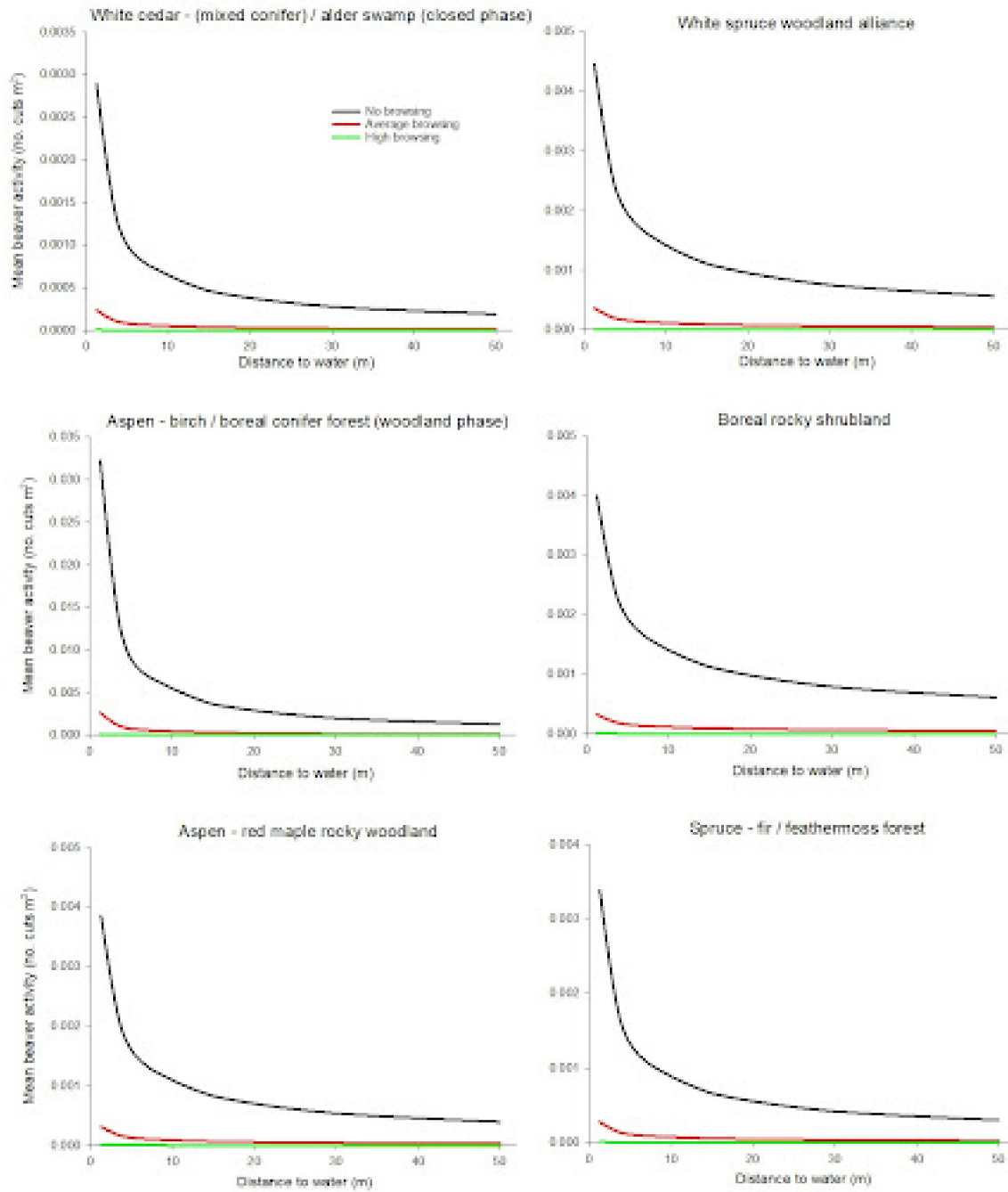
Appendix 2: Beaver cut outcomes for each vegetation type by moose browse influence

Speckled alder swamp

Mean beaver activity (no. cuts m^2)
Distance to water (m)

No browsing
Average browsing
High browsing

Poverty grass barrens

Bluejoint eastern meadow

Aspen - red maple forest

Spruce - fir - aspen open forest
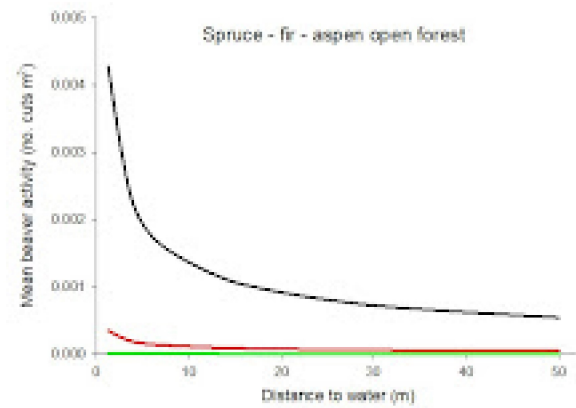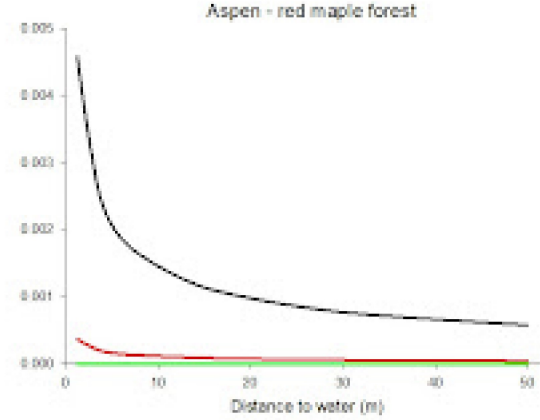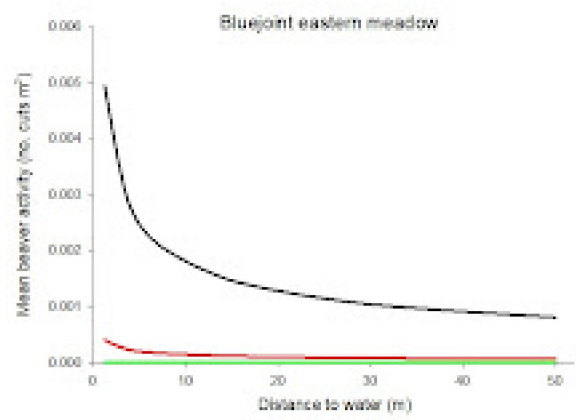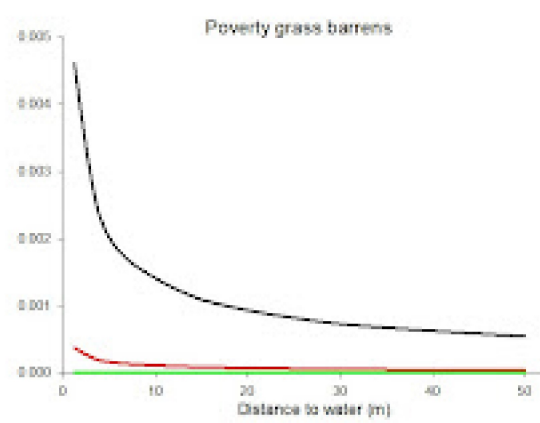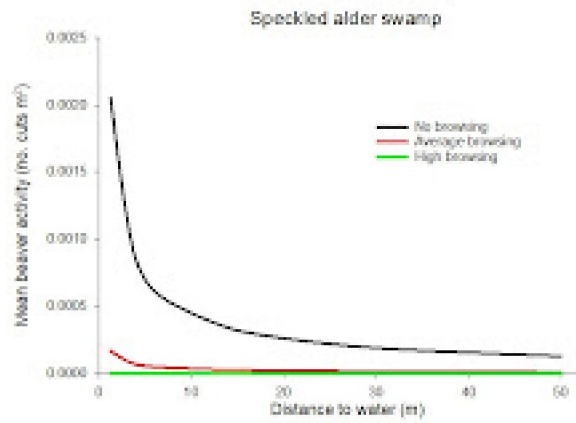
Appendix 3: Parameter values with 95% confidence intervals.

Code:

```r
f <- read.csv('significance.csv')
f <- as.data.frame(f)

ggplot(f, aes(x=f$mean, y=f$X))+
  geom_point()+
  geom_errorbar(aes(xmin=f$lower, xmax=f$upper), width=0.2)+
  geom_vline(xintercept=0)+
  theme(axis.ticks.y=element_blank(),
        axis.title.x=element_blank(),
        axis.title.y=element_blank(),
        legend.position="none")
```

Appendix 4: Beaver consumtion preference for species, diameter, and distance

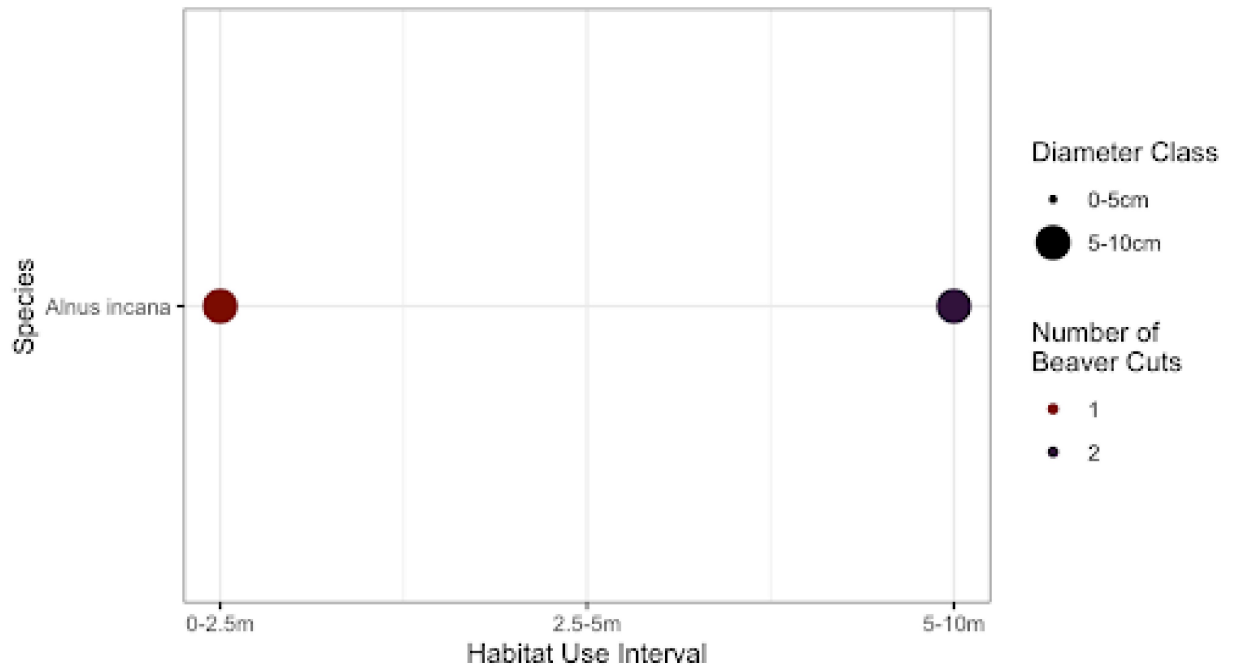By vegetation type, for each transect with available browse data
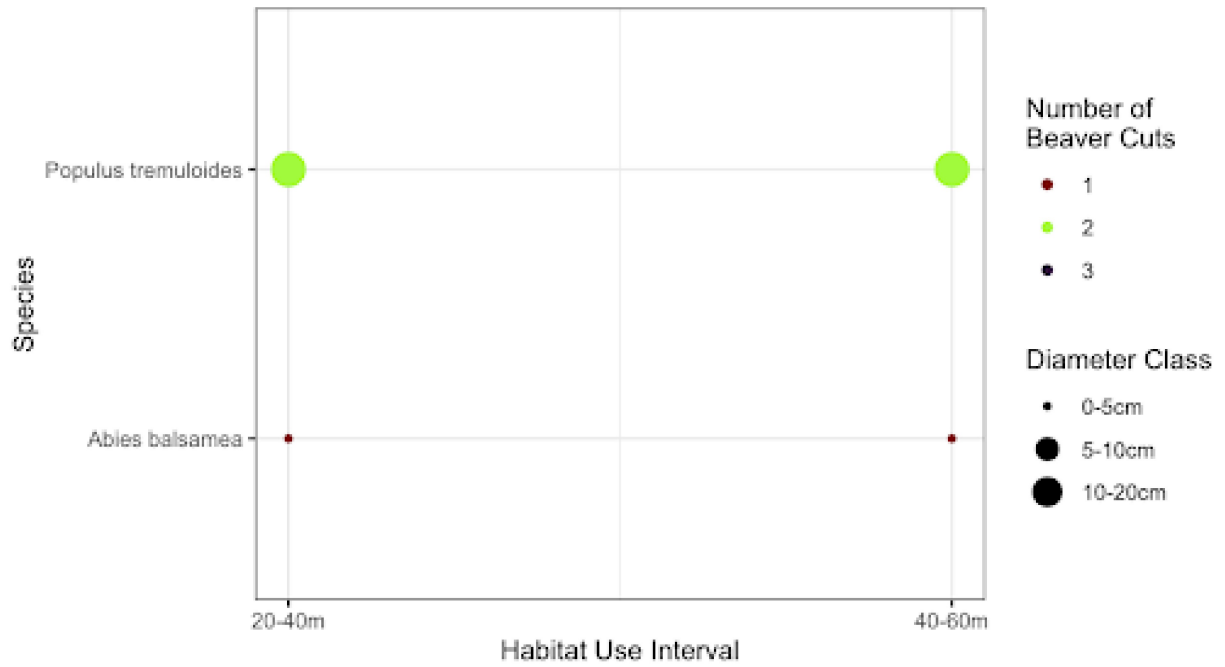
Poverty Grass Barrens
Part of one transect

Number of
Beaver Cuts

● 2

Diameter Class
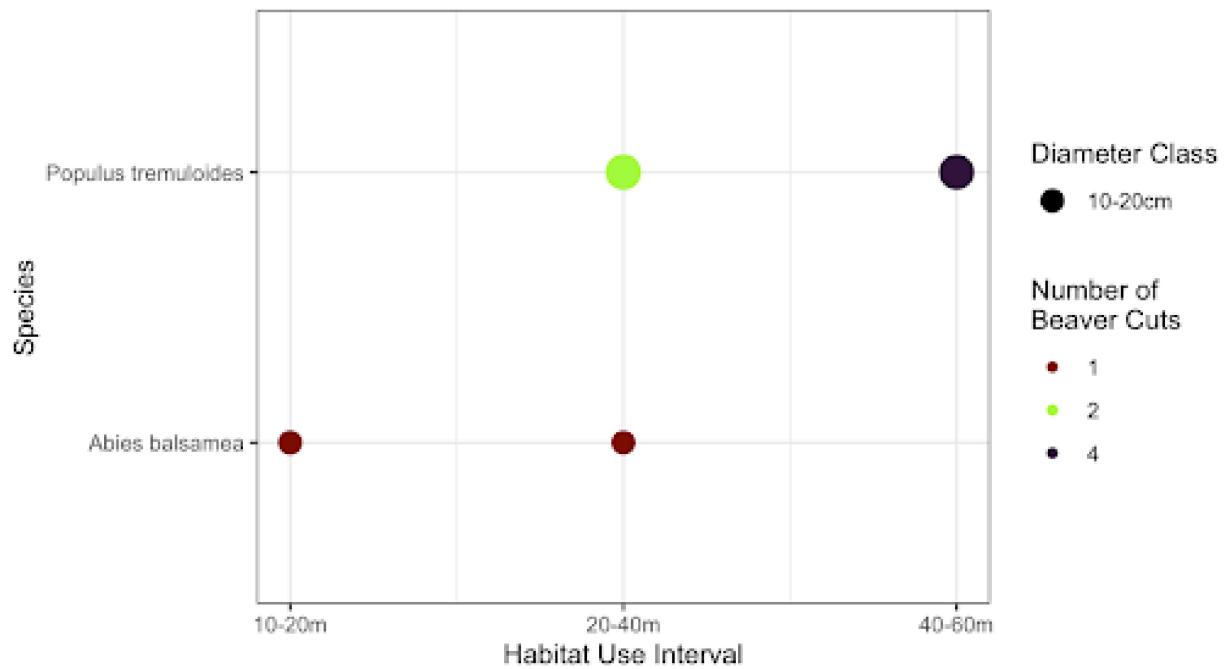
● >20cm

Species

Populus tremuloides

Habitat Use Interval

40-60m
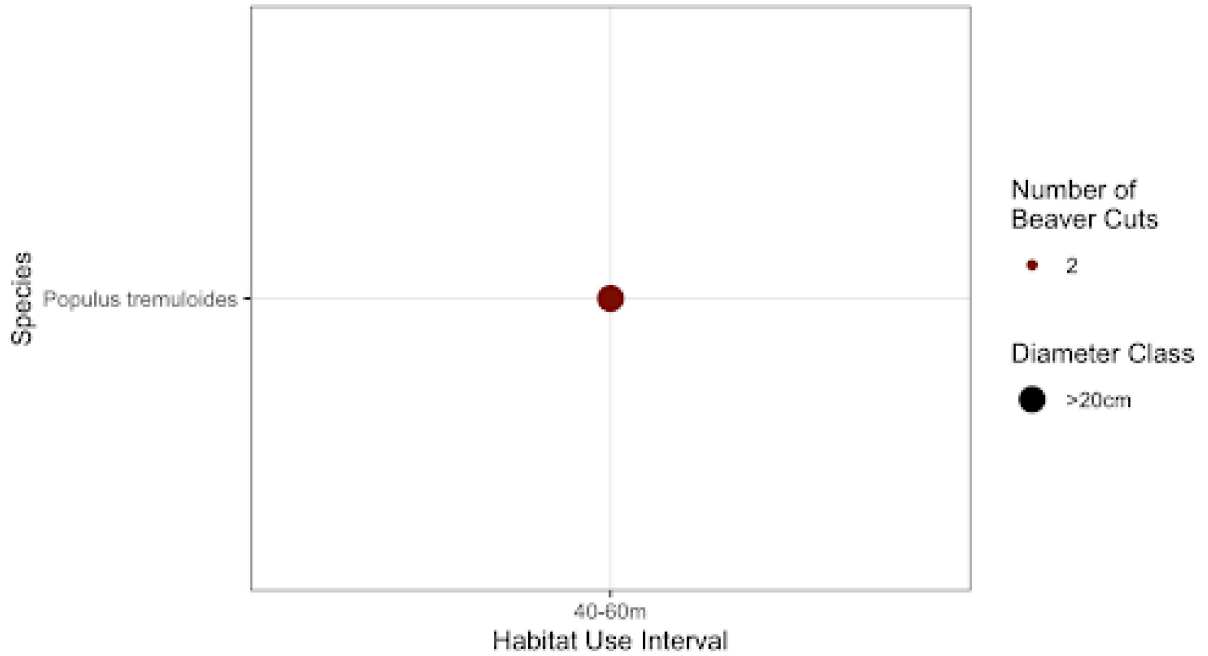
Speckled Alder Swamp
Part of one transect

Diameter Class

· 0-5cm

● 5-10cm

Number of
Beaver Cuts

· 1

· 2

Species

Alnus incana

Habitat Use Interval

0-2.5m   2.5-5m   5-10m

Spruce - fir - aspen open forest
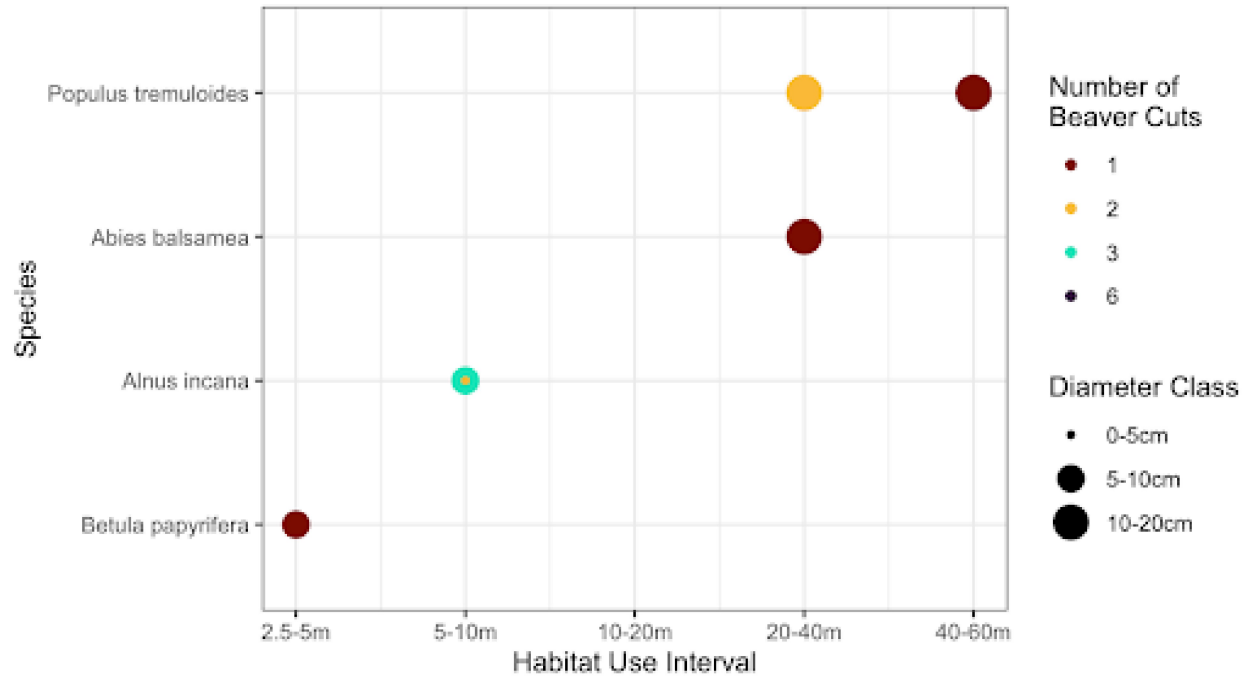
Two transects

Spruce - fir / feathermoss forests
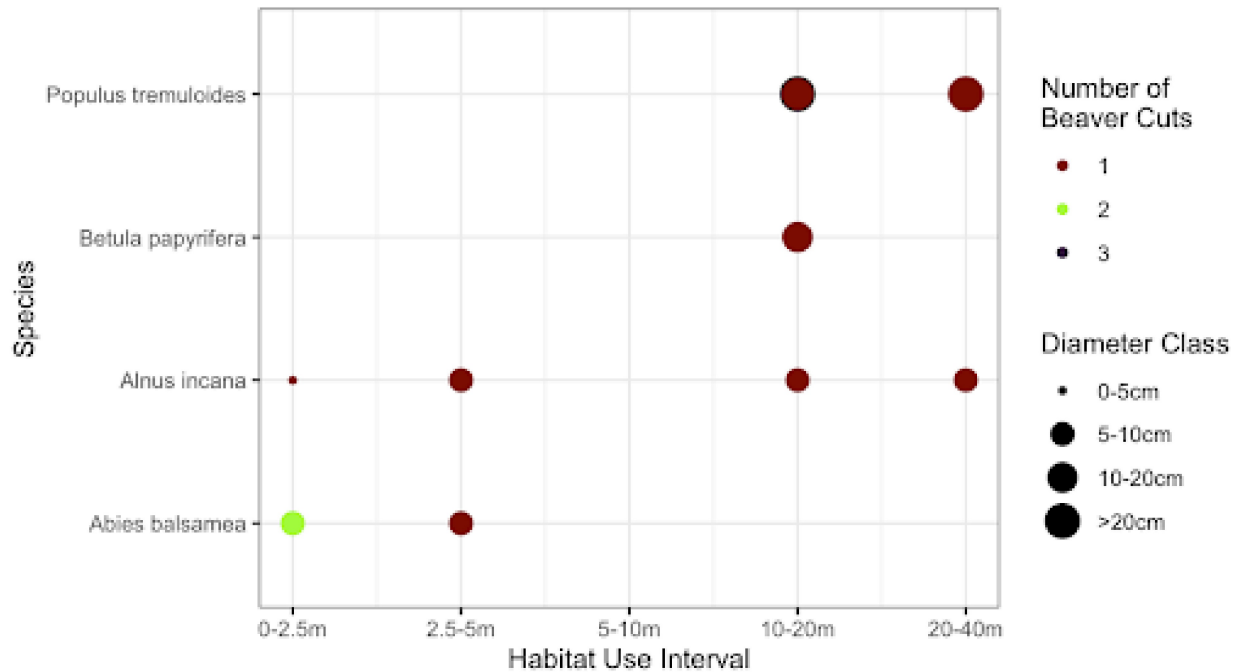
Parts of two transects

White cedar - (mixed conifer) / alder swamp (closed phase)
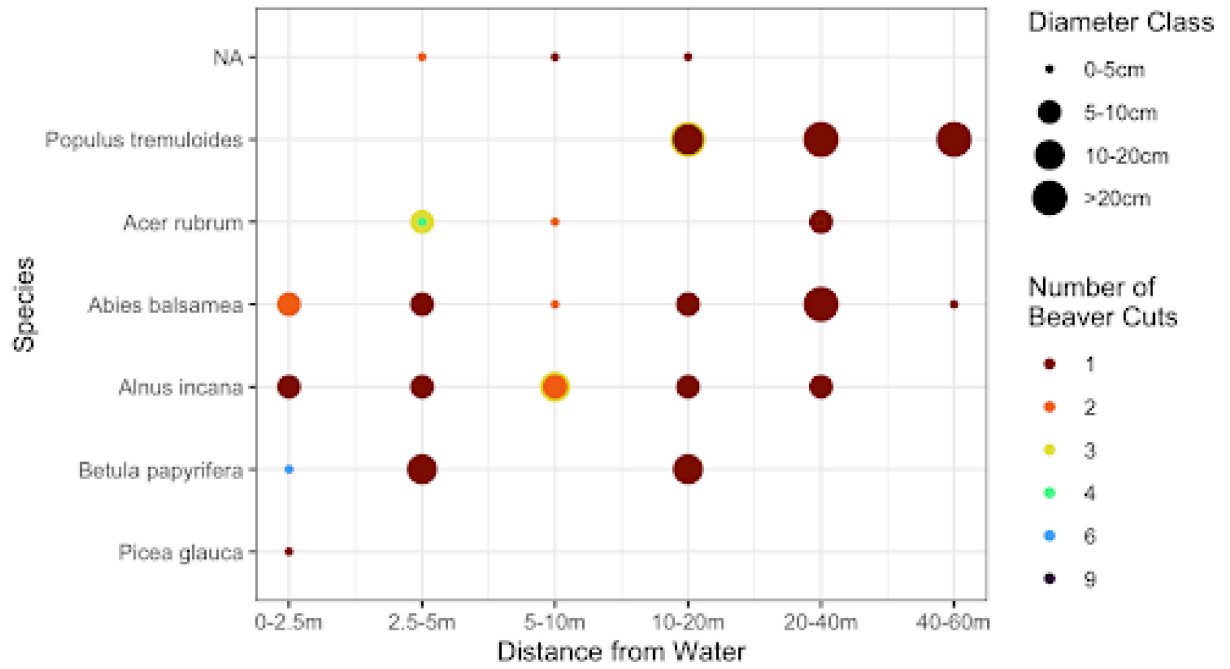## One+ transect

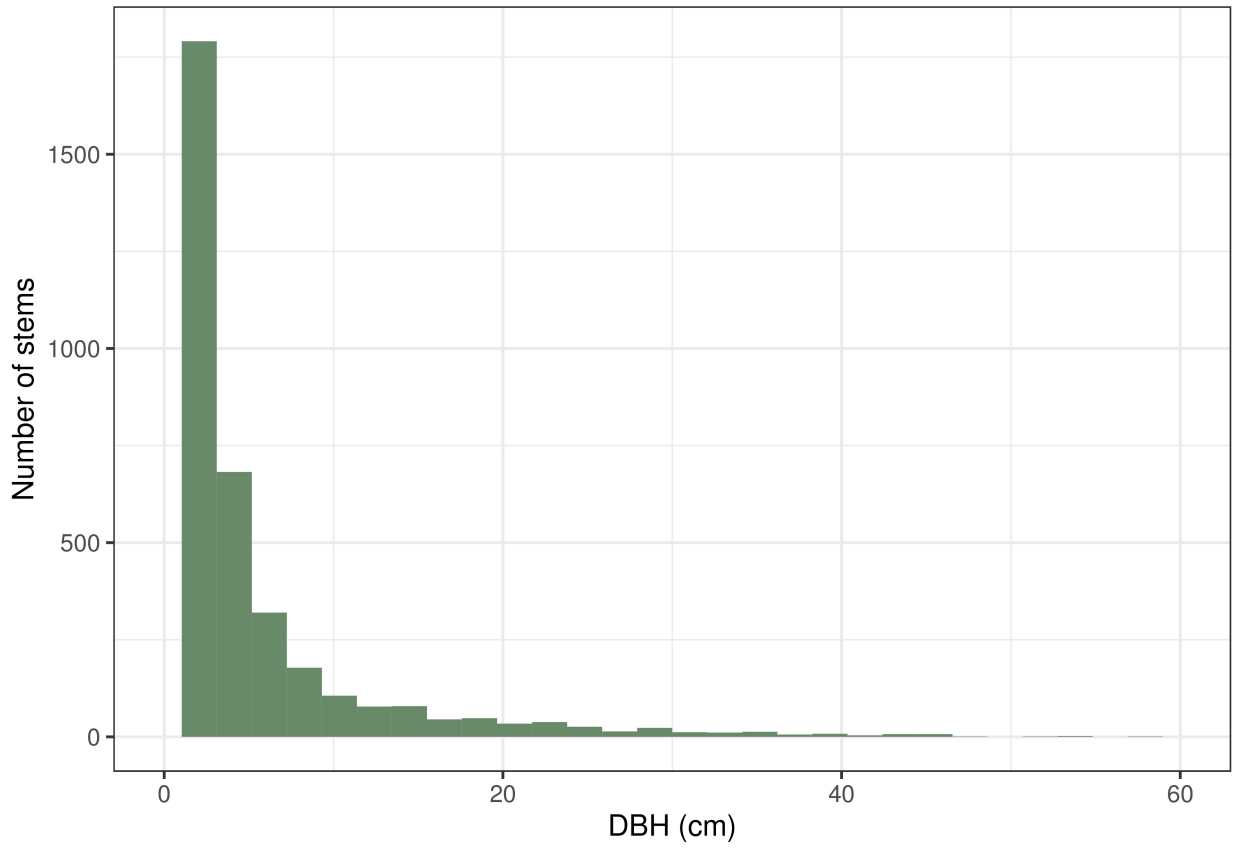# White spruce woodland alliance
Two transects

Beaver Preferences in Specific Vegetation Types
Available Browse, Nine Transects

Appendix 5: Sizes (DBH) of all standing tree and sapling stems observed in ISRO.

Appendix 6: Data dictionary

Name	Unit	Data type	Description	Valid entries	Notes
SITE_ID		unique descriptor	Site identifier	BEAVER_0000, etc.	
START_DATE		date	Day the transect started	MM-DD-YYYY	
END_DATE		date	Day the transect ended	MM-DD-YYYY	
PROTOCOL_NAME		categorical	Identifies which sampling protocol is used	beaver, moose	
PROTOCOL_VERSION		ordinal	Protocol version	1	
TRANSECT_TYPE		categorical	Denotes the type of transect. Forest structure observes standing trees and their browse. Habitat use observes beaver cuts. A and B are replicates.	FSA, FSB, HUA, HUB	
TRANSECT_TYPE_DESC		categorical	A description of the transect type	Forest Structure A, Forest Structure B, Habitat Use A, Habitat Use B	
TransectDate		date	Day of data	MM-DD-YYYY	
BEARING	degrees	discrete	360°		
START_X	meters	geographic	Longitude		
START_Y	meters	geographic	Latitude		
ZONE		geographic	UTM zone identity	16	
DATUM		geographic	Geographical frame of reference	NAD83	
HAB_USE_INTERVAL		ordinal	Distance from water interval index	1-6	Used only for beaver data
SAPLING_TREES_INTERVAL		ordinal	Distance interval from transect start	1-5	Only used for moose; missing data
INTERVAL_DESC	meters	categorical	Distance interval descriptors, from water or trail's edge	Beaver: 0-2.5, 2.5-5,5-10,10-20,20-40,40-60; Moose: 0-10,20-25,30-35,40-45,55-60	Different interval indices for beaver and moose

Name	Unit	Data type	Description	Valid entries	Notes
SPP_CODE		unique descriptor	Short code for woody species identity	ABBA, etc.	Reference Tourville et al., (2018)
SPECIES		unique descriptor	Woody species identity	*Abies balsamea*, etc.	
DIAM_CLASS		ordinal	Indexed intervals of woody stem diameter	0,1,2,3	Beaver data only
DIAM_CLASS_DESCRIPTION	cm	categorical	Description of woody stem diameter	0-5, 5-10, 10-20, >20	Beaver data only
BROWSE_STATUS		categorical	Fresh or old beaver cut	1,2,999	NA=999
BROWSE_STATUS_DESC		categorical	Description of BROWSE_STATUS	Fresh cut, old cut, NULL	
NUMBER	cut stems	Cut stems	numerical	The number of stems cut by beaver in a given distance interval	≥ 0
DIRECTION		boolean	Denotes if the observations were taken on the right or the left of the transect tape	L, R	Moose data only
POS_ON	meters	numerical	Denotes the distance from the beginning of the transect tape	≥ 0	Moose data only
POS_FROM	meters	numerical	Denotes the perpendicular distance the observation is from the transect tape	≥ 0	Moose data only
DEAD		boolean	Describes the status of the stem	TURE, FALSE	
DBH	centimeters	numerical	Diameter of woody stem at breast height	≥ 0	Only recorded for standing trees
BROWSE_AVAILABLE		boolean	Denotes if the woody stem has browse available for moose	TRUE, FALSE	Only recorded for standing, not saplings

Name	Unit	Data type	Description	Valid entries	Notes
ABI		ordinal	Accumulated Browse Index	0, 1, 2, 3, 999	Moose data only; applies to trees, saplings, and shrubs
ABI_DESCRIPTION		categorical	Description of ABI numbers	No browse, light browse, moderate browse, heavy browse, NULL	
BEAVER_CUT		boolean	Presence of beaver browse near moose browse observations	TRUE, FALSE	Applies to observations of standing trees and saplings
BASAL	centimeters	numerical	Basal diameter of a woody stem	≥ 0	Moose data only; recorded for saplings
HEIGHT	meters				Moose data only; recorded for saplings and shrubs
BITES_TAKEN	bites	numeric	The estimated number of moose bites taken from a woody stem	≥ 0	Moose data only; saplings only; defined as an area 5x5cm

Name	Unit	Data type	Description	Valid entries	Notes
BITES_AVAIL	bites	numeric	The estimated number of moose bites available on a woody stem	≥ 0	Moose data only; saplings only; defined as an area 5x5cm
HARE_BROWSE		boolean	Presence of snowshoe hare browse	TRUE, FALSE	
FURTHEST_CUT_SPP		unique descriptor	The species identity of the farthest cut woody stem from the start of a transect	*Abies balsamea*, etc.	
FURTHEST_CUT_DIAM		numerical	The DBH of the farthest cut woody stem from the start of a transect	≥ 0	
MAX_FORAGE	meter	numerical	The maximum number of stems cut at a site	≥ 0	
MAX_DIST_X	meter	geographic	X coordinate for farthest cut stem in a transect	≥ 0	
MAX_DIST_Y	meter	geographic	Y coordinate for farthest cut stem in a transect	≥ 0	
PROPORTION_SURVEYED	%	proportion	The proportion of the site that was surveyed	0-100	
PERCENT_CANOPY	%	proportion	The proportion of a 1 m^2 plot with canopy cover	0-100	
PERCENT_COVER	%	proportion		0-100	The proportion of a 1 m^2 plot with vegetation on the ground
NOTES		text	Additional information and context		
DPL		categorical	Stage of data quality control	Raw, ?	