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Stem size selectivity is stronger than species preferences for beaver, a central place forager

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ABSTRACT

The North American beaver (*Castor canadensis*) is a classic ecosystem engineer, creating and expanding wetlands throughout their vast range. As important as their impacts on aquatic ecosystems, beaver as central place foragers restructure the surrounding forest community by their selective cutting of preferred woody species and size classes. These effects, which have been studied in several regions of North America, are still poorly understood within forests of the northeastern United States, where beaver populations are rebounding following regional extirpation. Here, beaver represent a key disturbance agent in a region where other drivers such as fire and timber cutting have been greatly reduced over the last century. Understanding their specific impacts on forest composition and structure is needed to manage these forests and their multiple ecosystem services.

In this context, we assessed beaver foraging preferences throughout New York's Adirondack State Park, a vast northern wooded region, to model their impacts on forest structure and composition. Across 19 sites distributed throughout the Park, beavers preferentially harvested stems < 10 cm diameter, with the 2–5 cm size class most preferred overall. Mixed-effects logistic regression models showed greater probability of harvest for stems closer to the impoundment for all species and taxonomic groups modeled, consistent with central place foraging theory. Broadleaf deciduous tree species were browsed at rates 33% greater than coniferous species, with American beech (*Fagus grandifolia*) among the most utilized species, contrary to other regions where it is typically avoided. Though stem diameter preferences and spatial gradients of foraging intensity were consistent with those found in other regions, species preferences differed greatly, suggesting that selectivity for a deciduous species expressed on the landscape is primarily a function of the size distribution of its available stems.

1. Introduction

Across North America, beaver (*Castor canadensis*) are ecosystem engineers that induce landscape-level changes in hydrology and forest structure through a combination of damming and foraging behaviors (Anderson et al., 2014; Burchsted et al., 2010; Johnston and Naiman, 1990a; Little et al., 2012; Wright et al., 2002). Besides the obvious impacts on wetlands, beaver create local, intense forest disturbances akin to patch dynamics (Wright et al., 2004), albeit with highly asymmetric effects on tree species and size classes (Raffel et al., 2009). Once nearly extirpated from the United States, beaver populations have rebounded following limitations on hunting and trapping but remain much lower than their historical levels (Call, 2014; Sandoz, 1964). As their populations and geographic range recover, it is increasingly important to understand the effects beavers have as disturbance agents in shaping the surrounding forest ecosystem (Siemer et al., 2013).

While beaver are well-known for their ability to create and enhance wetlands by impounding streams (Johnston and Naiman, 1990a), the impacts of beaver foraging on forest structure and composition is likely as important an influence to the riparian community as their dam building activities (Donkor and Fryxell, 1999; Johnston and Naiman, 1990b; Martell et al., 2006). Though aquatic vegetation represents most of their diet during the warm growing season (Bergman et al., 2018; Milligan and Humphries, 2010; Severud et al., 2013), seasonal fluctuations in availability make woody material harvested from the adjacent forest critical as an overwinter food source (Svendsen, 1980). This foraging in addition to the cutting of trees to build dams exerts a selective pressure on riparian forest communities, with distinct species and stem sizes preferred over others (Raffel et al., 2009). These behaviors have the potential to profoundly modify the structure and composition of northeastern forests, particularly with the vigorous re-establishment of beaver populations within the region.

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The variation in foraging intensity with distance from their lodges and impoundments introduces a spatial component to beaver disturbance impacts. Like other central place foragers such as nesting birds and seals, beaver select their food in order to maximize energetic value, taking into consideration the energy costs associated with searching for food, provisioning it, and bringing it back to the central cache (Müller-Schwarze and Sun, 2003; Schoener, 1979). However, while other foraging species tend to select larger food the further they are from their central place, the high energetic cost and increased predation risk of hauling woody material back to a food cache, along with the gradient of forage intensity radiating from pond and lodge locations, induce potentially complex influences on the size structure and composition of the forest in beaver-occupied landscapes (Basey and Jenkins, 1995). Studies in other biomes have shown a preference for an intermediate size class of stems ranging from 2 to 7 cm in diameter, whereas larger stems – which contain more total nutrition, but require more energy to transport and provision into smaller sections – were selected less frequently (McGinley and Whitham, 1985; Raffel et al., 2009).

Size and distance foraging patterns also interact with the variation in palatability and energy content of available woody species. Many studies show beaver to prefer deciduous trees, whose digestibility (i.e., the percentage of biomass convertible into energy by beaver) is typically greater than conifers (Fryxell and Doucet, 1991; Gallant et al., 2004). These preferences are expressed more strongly with greater distance from the impoundment, as woody species with less energetic return on investment are harvested opportunistically at the pond edge but much less so farther away. These patterns have been demonstrated repeatedly in boreal biomes (Donkor and Fryxell, 1999; Nummi and Kuuluvaine, 2013) and in various forested regions within the United States, including the Midwest (Raffel et al., 2009) and Southwest (Barela et al., 2016).

In northeastern North America, there has been little research into how these foraging preferences impact forest structure and composition, with beaver research primarily focused on stream ecosystem processes (Burchsted et al., 2010; Smith et al., 1989) and biodiversity of taxa such as wetland plants and amphibians (Karraker and Gibbs, 2009; Wright et al., 2002). However, beaver impacts may have an outsized importance in forests of the Northeast compared to other regions, due to the long stand rotation times and low disturbance regimes which characterize the region (Lorimer and White, 2003; Ziegler, 2007). Particularly in areas such as New York's Adirondack State Park, where timber harvesting is severely restricted and fire and other forest disturbances are rare, beaver serve as one of the most important disturbance agents on a landscape level (DeGraaf and Yamasaki, 2003). In this role, beaver create many local patches of early successional habitat that benefit a vast array of species, enhancing biodiversity and providing new forest and wildlife management opportunities throughout the region (Bouwes et al., 2018; McCall et al., 1996; Popescu and Gibbs, 2009; Stevens et al., 2007). Additionally, many of beaver's preferred forage species, such as early successional aspen (*Populus tremuloides*) and willow (*Salix* spp.), are of low abundance in the northeastern forest due to the region's suppressed disturbance regime. As such, it is unclear how the lack of preferred species will modify selectivity and harvest patterns, and consequently lead to distinct impacts to forest structure relative to other regions.

To investigate these questions, we surveyed beaver-impacted areas throughout New York's Adirondack State Park to identify beaver foraging preferences and impacts on forest structure associated with the region's unique forest type and disturbance regime. First, we quantified the impacts that beaver activity had on the surrounding forest, measuring variation in forest structure and canopy cover with increasing distances from beaver impoundments and occupied lakes. Second, we compared beaver selection preferences among tree species and diameter size classes to identify the most desirable browse in a biome virtually devoid of their most preferred forage material. Finally, we modeled these preferences using mixed-effect logistic regression to predict the likelihood of harvest for stems across a range of species, sizes, and distances from beaver impoundments. Understanding how beaver select their forage and the effects of these foraging preferences will aid in predicting the full impact of beaver disturbance on forest communities, as well as potential patterns of future beaver occupancy in landscapes where they are currently excluded. This information is of direct relevance in assessing forest health and predicting future ecological trajectories, as well as informing beaver management practices as beaver populations continue to recover.

2. Methods

2.1. Study area

The Adirondack Park (hereafter the Park) is a 2,400,000 ha (ha) area of mixed usage land, contained entirely within the northern hardwoods-hemlock forest (Dyer, 2006). Elevations in the region range from 37 m above sea level at the Ausable River to 5,344 m at the peak of Mount Marcy. Annual precipitation ranges from 78 cm in the northeast to 156 cm in the more mountainous regions (Ito et al., 2002), and average temperatures range from −9 °C in January to 20 °C in July (Diamond et al., 2013). The region has primarily post-glacial soils, with over half of the land area composed of glacial till (Cadwell and Schauble, 1993). Dominant forest tree species include red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), red spruce (*Picea rubens*), sugar maple (*Acer saccharum*), striped maple (*Acer pensylvanicum*), balsam fir (*Abies balsamea*), and eastern hemlock (*Tsuga canadensis*) (Smallidge and Leopold, 1994).

Slightly more than a million hectares of the Park is public land managed by the New York State Department of Environmental Conservation (DEC). While hunting and trapping are seasonally permitted on these lands, timber harvests were generally prohibited on all parcels as they were incorporated into the Forest Preserve, beginning in 1885 (Terrie, 1981). Due to this management approach and the long rotation age of northern hardwood forests, there exists very little young forest in the Adirondacks, with most stands increasing in age since their incorporation into the Park (McGee et al., 2007). The Adirondacks are a unique place to study beaver, as the relative inaccessibility of the landscape may have prevented beavers from ever being truly extirpated as happened in other regions of the country (Jenkins and Busher, 1979).

2.2. Site selection and sampling design

Site selection proceeded from a data set of all bodies of water within New York State that was filtered to include only waterbodies on Wilderness and Wild Forest lands of the Adirondacks with slopes of under 20%, which is the upper limit documented for beaver occupancy in this region (Curtis and Jensen, 2004; New York State Office of Cyber Security, 2008a; 2008b; Wildland Fire Science et al., 2016). To ensure that all areas of the Park were represented, the dataset was stratified into northern, central, and southern regions, with each region then subdivided into eastern, central, and western zones. All spatial analyses were done using ArcGIS software, version 10.6 (ESRI, 2018).

Ten individual bodies of water were selected at random from each of these regions as potential study sites, and each evaluated for signs of beaver colonization using satellite images from 2015 to 2018 (Alphabet Inc, 2018). We selected for sampling those sites with signs of colonization which could reasonably be accessed, defined as being within twenty miles of a trailhead and requiring no more than two miles of off-trail navigation. In total, nineteen sites were selected and surveyed, including twelve sites along streams and seven on lakes (Fig. 1; Supplementary Materials S1).

At each surveyed waterbody, four transects were established at equidistant points along its perimeter perpendicular to the edge of water. For each transect, plot centers were located every ten meters beginning at four meters from the water body and extending until the

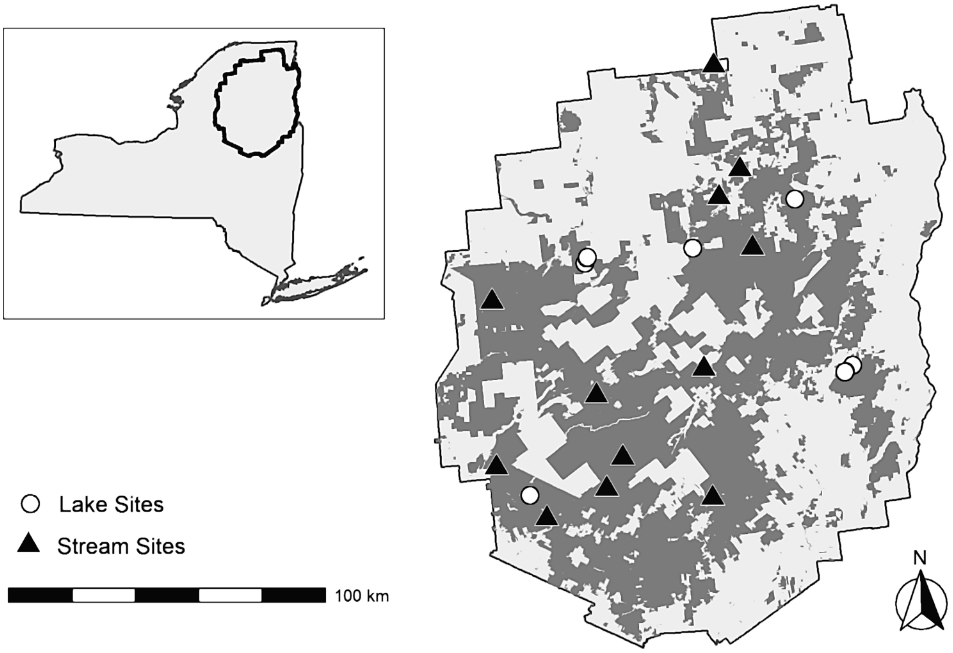


Fig. 1. Location of field sites throughout Adirondack Park of New York. Darker areas represent forest preserve lands. Inset is a map showing location of the Park within New York State.

last plot was fully outside of the forage area, defined as the land area between the impoundment edge and the furthest beaver-harvested stumps identified upslope. Canopy cover was assessed at each plot center using a spherical densiometer.

2.3. Vegetation surveys

Two concentric, fixed-area circular plots were established at each plot center. The smaller understory plots had a radius of 2 m (12.57 m^2 area), within which all live and beaver-harvested stumps ≥ 1 cm diameter were surveyed for species, diameter (measured at breast height for live stems and height of harvest for stumps), and height. Diameter was recorded in classes of 1–2 cm, 2–5 cm, 5–10 cm, and 10–15 cm, with trees of over 15 cm being measured to the nearest tenth of a centimeter. Stems less than 1 cm in diameter were not recorded for either live or dead fractions because of the difficulty in accurately detecting small harvested stems.

The larger overstory plots had a radius of 4 m (50.27 m^2 area), within which all stems over 5 cm diameter were recorded in the same manner as stems in the understory plots. All stems were also classified as either coniferous (family Pinaceae) or deciduous broadleaf (all angiosperm species). Stem identification was done conservatively, with stems whose species could not be determined classified simply as coniferous or deciduous. As coniferous species have been known to decay more slowly than deciduous trees (Tarasov and Birdsey, 2001), these species, and the rates at which they are harvested by beaver, may be somewhat overrepresented in the data.

2.4. Data analysis

Canopy cover was assessed by calculating the proportion of densiometer readings occupied by the tree canopy at each plot center along the transects. A beta regression was then fit to the data in order to determine the impact of distance from the impoundment on canopy cover, and to assess differences in canopy cover between lake and stream sites (Ferrari and Cribari-Neto, 2004; Smithson and Verkuilen, 2006). Trends in stem density, basal area, and median stem diameter with distance were compared for coniferous and deciduous stems using analysis of covariance (ANCOVA).

Stem selectivity, noted as S, was defined as the proportion of a given species harvested to the total amount of that species available (harvested plus live at a given site), so that a selectivity index value of 1 signifies that all available stems of a species were harvested and a selectivity index value of 0 means that no individuals of the species were harvested. This definition was chosen due to its straightforward calculation and prevalence in the literature (Gallant et al., 2004; Raffel et al., 2009). Additionally, Chesson's α was calculated for each species to identify which species were preferentially harvested and which were avoided (Chesson, 1978; Lechowicz, 1982). This metric, which ranges from 0 to 1, standardizes each species S (i.e., proportion harvested) by all other species present (i.e., the sum of all species' S), and can be thought of as the perceived value of a food item in relation to both its abundance and the other food types available. Chesson's α values closer to 1 and 0 indicate preferred and avoided species, respectively, out of the pool of species available (Chesson, 1978; Lechowicz, 1982). Species with an α value $> 1 / n$, where n represents the number of species available for forage at a site, were considered to be preferentially harvested, and the percentage of sites at which a species was preferentially selected was calculated for each species. Because trees varied widely in relative density and morphology, both selectivity metrics were quantified two ways, by proportion harvested of available individual stems and of available basal area in the plots.

Relationships between selectivity metrics were assessed using Kendall's τ (Knight, 1966). Additionally, the relationships between beaver foraging preferences and species dry matter digestibility, digestible energy, and digestible protein were assessed using stem digestibility data from Peterson (2018) via linear regression, as was the relationship between species selectivity and the proportion of that species having diameters between 2 and 5 cm. As digestibility data in Peterson (2018) was calculated using twigs of < 8 mm diameter, digestible energy estimates may be higher than actual amounts in beaver forage due to the increased ratio of cambium to stem volume.

We analyzed more fine-scale patterns of beavers' forage preferences using mixed-effect logistic regression to model probability of stem harvest by beaver as a function of stem diameter (in cm) and distance (in m) from the impoundment, with site as a random effect in order to account for potential differences in other available forage. Separate models were developed for the full data set, coniferous and deciduous groupings (hereafter referred to as "stem groupings"), and the six most prevalent species with at least twenty-five harvested stems. In these models, stem diameter was included as a continuous variable using the midpoint of each stem class (e.g., 1.5 cm for the 1–2 cm size class, 3.5 cm for the 2–5 cm size class, etc.). For this variable, we tested diameter (D) as both a linear and quadratic polynomial factor (i.e., $D + D^2$) to account for potential non-linear relationships in beavers' stem size preferences. The use of a quadratic term is biologically appropriate, as it can describe the scaling of the potential time and energy costs of browsing and hauling larger diameter food items to their energetic gains, as per Central Place Foraging theory (Schoener, 1979). For a stem of a given length, costs can be represented as a function of the stem's basal area, which scales to the square of the diameter ($A = \pi * [D/2]^2$), whereas the energetic gain derived from its nutritious cambium distributed around the stem's circumference scales to diameter as a linear function ($C = \pi * D$). Models for individual tree species used distance as a linear factor, whereas the three stem groupings used log-transformed distance to satisfy model residual assumptions.

A total of eight models with different combinations of predictors were compared for each analysis of stem groupings and for individual tree species (Supplementary Materials S2). Candidate models were ranked using the Akaike Information Criterion (AIC), with the model with the lowest AIC value selected as the best model. We considered models having ΔAIC ≤4 to have substantial empirical support (Akaike, 1974; Burnham and Anderson, 2004). Model goodness-of-fit was also assessed using the c-statistic for the area under the receiver operating characteristic (ROC) curve (Austin and Steyerberg, 2012). Model variants for which the parameter optimization algorithm did not converge were not included in these assessments.

Data analyses were performed in R version 3.4.4 (R Core Team, 2018), utilizing the pROC (Robin et al., 2011) and betareg (Cribari-Neto and Zeileis, 2010) packages.

3. Results

3.1. Forest structure and composition

A total of 1,491 stems >1 cm dbh were measured within 189 plots established along 74 transects at 19 sites. There were 22 unique woody species included within the 2 m understory plots, with species richness averaging 8 ± 0.9 per site (range 1–17 species). Red spruce had the highest density of all sampled species, with 1171 stems ha^{-1} and 18.96 $\text{m}^2\ \text{ha}^{-1}$ basal area (Table 1).

Canopy closure decreased significantly with proximity to the edge of water ($z_{1,185} = 3.05$, $p = 0.002$), with impounded stream sites having significantly lower canopy closure than lakes ($z_{1,185} = -3.28$, $p = 0.001$). Canopy closure along lakes was 15–20% greater up to ca. 35 m from the edge of water, and there was no significant interaction between site type and distance ($z_{1,185} = 0.246$, $p = 0.12$) (Fig. 2).

Forest structure also varied with distance from the impoundment (Fig. 3), with different patterns for conifers and deciduous species and, in the case of stem density, between water body types. For density of live stems, there was a significant interaction effect between stem grouping, waterbody type, and distance from the impoundment ($F_{7,20} = 10.21$, $R^2 = 0.70$, $p < 0.001$). Deciduous stem density was highest at close proximity to stream impoundments, while coniferous density was generally lower and equivalent between stream and lake sites (Fig. 3). Median stem diameter varied significantly with distance from the impoundment, stem grouping, and waterbody type ($F_{3,225} = 12.71$, $R^2 = 0.13$, $p < 0.001$). The median diameter of coniferous stems was relatively uniform across all these factors, whereas the median diameter of deciduous stems increased until 24 m away from the impoundment and then decreased, with this effect more pronounced at lake sites than along streams (Fig. 3). Distance from the impoundment did not significantly influence basal area ($F_{3,10} = 3.10$, $p = 0.076$).

3.2. Beaver selectivity across tree species

Patterns in selectivity, measured as both the proportion of available stems harvested and Chesson's α for a given site, varied greatly among tree species (Table 2). Across all species occurring at three or more sites, mean stem S and α were highest for speckled alder (S = 0.653 ± 0.128, α = 0.693 ± 0.110), striped maple (S = 0.575 ± 0.236, α = 0.199 ± 0.102), and red maple (S = 0.457 ± 0.123, α = 0.171 ± 0.050). Mean basal area S and α were similar to the stem level rankings, with speckled alder (S = 0.703 ± 0.120, α = 0.867 ± 0.084), striped maple (S = 0.589 ± 0.241, α = 0.237 ± 0.107), and American beech (S = 0.236 ± 0.125, α = 0.227 ± 0.140) being the proportionally most selected species. Of all the species, only speckled alder and striped maple had high (60–89%) α selectivity for both stems and basal area across a large proportion of sites where it was present (Table 2). Most species had greater S on a stem-wise basis than by basal area, indicating that smaller stems were more desirable. Rankings of S and α were highly correlated, with basal area selectivity rankings having a stronger correlation than those for stem selectivity (Stem $\tau = 0.721$, $p < 0.001$; Basal area $\tau = 0.840$, $p < 0.001$).

We investigated how well species preferences correlated with species-specific nutritional data from a study of moose browse preferences throughout the Adirondacks (Peterson, 2018). Averages of summer and winter dry matter digestibility (percent mass), digestible energy (kcal/g), and digestible protein (g/100 g feed) from Peterson (2018) were available for ten species included in our study: balsam fir, black cherry, quaking aspen, sugar maple, yellow birch, paper birch, fire cherry, red maple, American beech, and striped maple. Comparing our selectivity metrics with stem nutrition data, there was no significant relationship between any selectivity metric (S and α on a stem-wide and basal area basis) and dry matter digestibility, digestible energy, or digestible protein. For the six species with preference metrics in common between the studies, selectivity (S) was highly correlated with the similar Ivlev ratio in Peterson (2018) at R = 0.79, but Chesson's α for both studies were uncorrelated (R = 0.05).

3.3. Beaver selectivity by stem size and distance

For the pooled data across all species and sites, there were distinct spatial and stem size patterns for harvested stems, live trees, and selectivity (Fig. 4). The majority of harvested stems were less than 5 cm in diameter, with the relative proportion of harvested stems belonging to the 2–5 cm size class increasing with distance from the impoundment from 40.6% at 4 m to 62.5% at 34 m (Fig. 4a). The proportion of harvested stems <2 cm decreased with distance from the impoundment, decreasing from 35.8% of all harvested stems at 4 m from the impoundment to 0% of harvested stems at 34 m. In contrast, the proportion of harvested stems composed of larger size classes did not vary greatly with distance, with 5–10 cm stems making up 14.3–37.5% of those harvested, and stems >10 cm comprising 0–3.5% of all harvested stems (Fig. 4a). The size distributions of live stems (i.e., those not utilized by beaver) were comparable, ranging from 5.5 to 33.8% across all size classes, and did not vary systematically with distance from the impoundment (Fig. 4b). The selectivity index, which scales the number of stems harvested by those available at each distance, showed a strong interaction between stem size and proximity to the pond edge (Fig. 4c). S values for all size classes were greatest closest to the shore, with selectivity highest for stems ≤ 5 cm and decreasing with increasing stem diameter. Selectivity decreased with pond distance for all size classes except 2–5 cm, which remained high up to 34 m away.

When considering spatial and size-based beaver preference patterns among species and subgroups of the data, stem selectivity decreased monotonically with increasing distance from the impoundment (Fig. 5).

Table 1
Sample sizes, median stem diameter, and the proportion of stems within the 2–5 cm size class for all species identified within the 2 m understory plots on a per-hectare basis.

	Density (stems ha^{-1})			Basal Area (m^{2}ha^{-1})			Stem Diameter	
Common Name	Live Stems	Harvested Stems	Total Stems	Live Stems	Harvested Stems	Total Stems	Median DBH (cm)	Proportion in 2–5 cm
All Species	4,501	2,130	6,631	73.79	4.34	78.12	7.5	0.255
American Beech	299	303	602	4.92	0.51	5.43	3.5	0.259
American Elm	46	38	84	0.03	0.04	0.06	2.5	0.450
Balsam Fir	855	59	914	9.67	0.16	9.83	7.5	0.189
Beaked Hazelnut	8	4	13	0.00	0.00	0.00	1.5	0.000
Black Birch	4	67	72	0.00	0.08	0.08	3.5	0.941
Black Cherry	8	0	8	0.04	0.00	0.04	7.5	0.000
Black Spruce	34	0	34	0.46	0.00	0.46	12.5	0.125
Blue Beech	0	55	55	0.00	0.27	0.27	7.5	0.000
Eastern Hemlock	408	13	421	14.78	0.04	14.82	12.5	0.100
Eastern Tamarack	55	0	55	0.41	0.00	0.41	7.5	0.000
Fire Cherry	29	13	42	0.28	0.04	0.32	7.5	0.100
Paper Birch	76	34	109	1.87	0.10	1.97	3.5	0.231
Quaking Aspen	4	0	4	0.28	0.00	0.28	29.1	0.000
Red Maple	181	219	400	7.62	0.39	8.01	7.5	0.211
Red Spruce	1,171	46	1,217	18.96	0.09	19.05	7.5	0.152
Speckled Alder	813	838	1,650	0.64	0.60	1.23	3.5	0.452
Striped Maple	25	67	93	0.08	0.16	0.24	5.5	0.409
Sugar Maple	34	8	42	0.95	0.02	0.97	7.5	0.000
White Ash	21	13	34	0.16	0.04	0.20	7.5	0.125
White Cedar	118	34	152	3.09	0.34	3.43	12.5	0.111
White Pine	67	21	88	3.43	0.32	3.75	18.4	0.000
Yellow Birch	232	278	509	6.04	1.07	7.11	7.5	0.182

This was the case for deciduous and coniferous stem groupings, and for all individual species considered except for red maple, which had the smallest sample size out of those analyzed separately (Table 1) and was influenced by high densities in several distal plots. Unlike with distance, size-based selectivity patterns did not vary monotonically with stem diameter; the. The 2–5 cm diameter class had the highest proportions selected compared to stems both smaller (1–2 cm) and all classes larger (Fig. 5). This was the case across all stems and for all stem groupings and species considered except for yellow birch, red maple, and red spruce, which had monotonically decreasing selectivity with increased stem diameter. Mean species selectivity across all sites had a strong linear relationship with the proportion of all stems of a species that were in the 2–5 cm diameter class ($F_{1,9} = 15.95$, $R^2 = 0.60$, $p = 0.003$; Tables 1 and 2).

3.4. Selectivity models

Comparison of mixed-effect logistic models predicting the probability of harvest indicated that stem diameter and distance from the impoundment were significant predictors for all groups and species analyzed, with some differences in interaction effects (Table 3; Supplementary Materials S3). Selectivity decreased significantly with distance and diameter in the best models for all groups and species (Table 3; Fig. 6). The best models for the overall and deciduous stem groups, along with American beech and balsam fir included a quadratic term for diameter, indicating a modal response with intermediate (2–5 cm) size classes as most preferred (Table 3; Fig. 6). For the conifer stem grouping and all other species except for speckled alder, the quadratic diameter term was included in the second-best models, which had $\Delta AIC < 2$ and were equivalent to the best models. The goodness of fit (ROC c-statistic) for best models was 0.92 for all stems combined, 0.92 for deciduous stems, and 0.91 for coniferous stems. The goodness of fit of the individual species models was at least as high as for the pooled datasets, with c scores ranging from 0.92 to 0.98.

4. Discussion

This study documents a complex pattern of beaver foraging within the mixed deciduous and coniferous forests throughout the Adirondacks that varies according to distance from impoundments, tree species, and

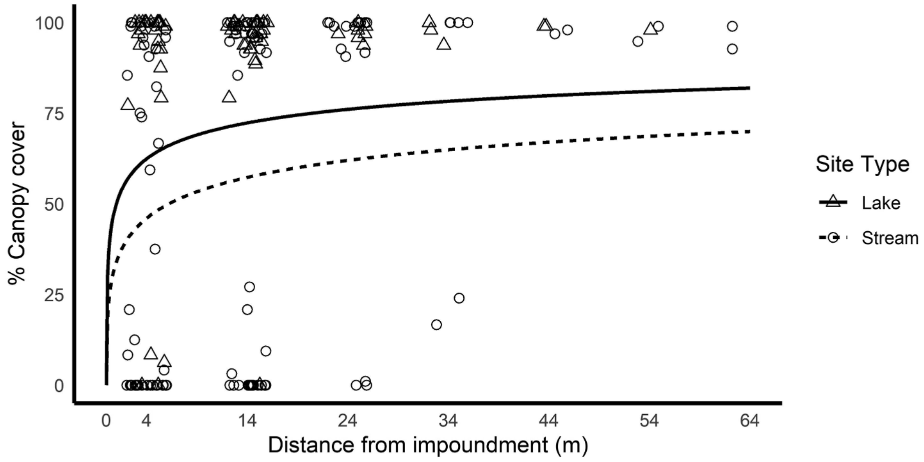


Fig. 2. Percent canopy closure as a function of distance from impoundment. Stream and lake sites were measured and modeled separately. Open triangles and circles represent field measurements at lake and stream sites, respectively; points were jittered for better viewing. Model predictions as a function of distance are also shown for lakes (solid line) and streams (dashed line).

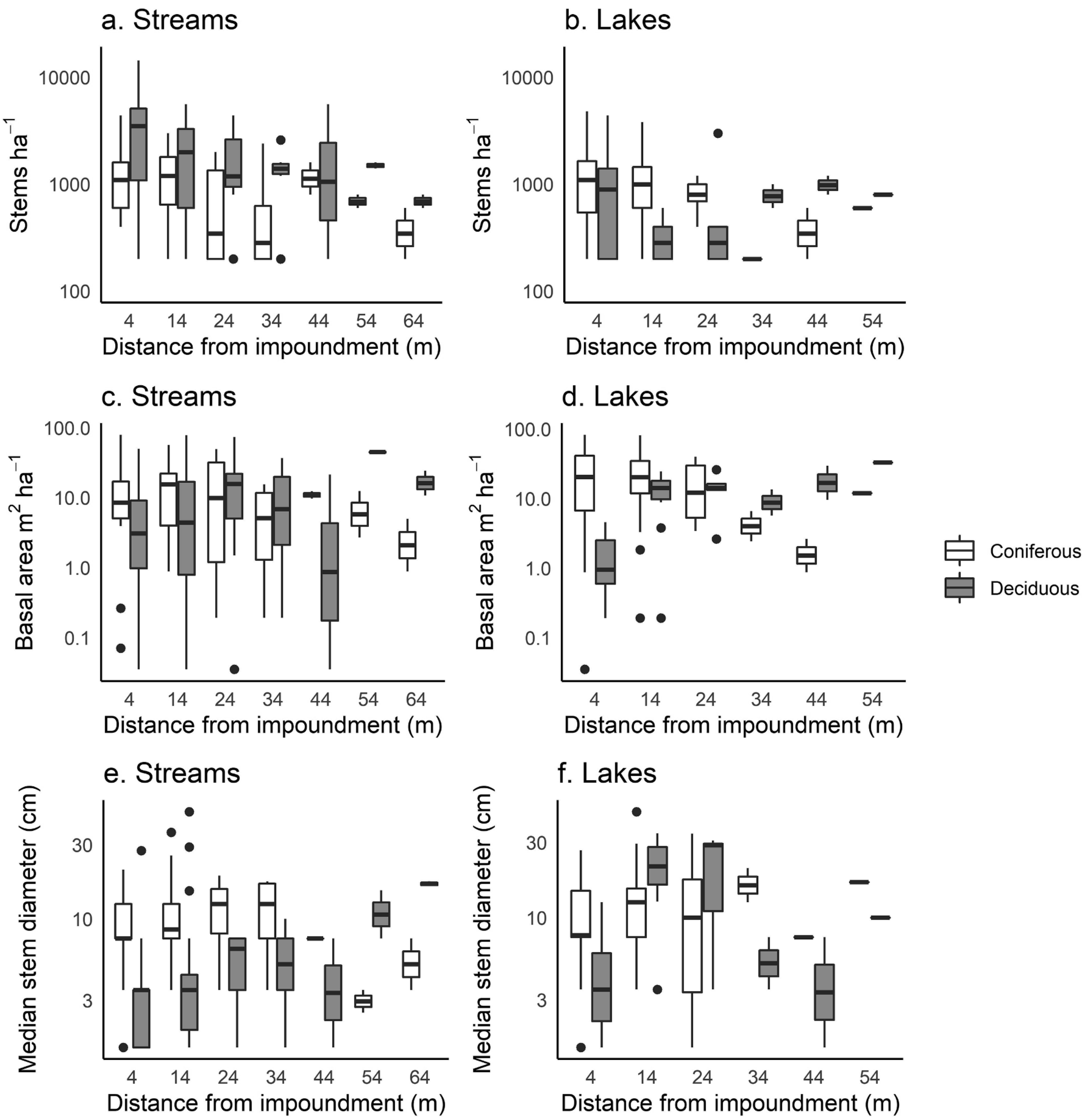


Fig. 3. Plot-based estimates of tree density (stems ha^{-1}; panels a, b), basal area (m^2 ha^{-1}; panels c, d), and median stem diameter (cm; panels e, f) for streams (panels a, c, e) and lakes (panels b, d, f) with increasing distance from impoundments.

Table 2

Selectivity metrics for all species occurring at three or more sites, including number of sites with the species present, selectivity (S) and Chesson's α values, and the percentage of sites where a species was preferred (having an α greater than 1/*n*, where *n* is the number of species present at a site). All metrics were calculated on both a stem count and basal area basis. Species that were preferred at substantially more than 50% of sites can be considered widely preferred, and those much below 50% can be considered avoided species, with more opportunistically-harvested species in between. S and α values represent the mean values and standard errors for all sites with the species present. Species in bold are included in selectivity models due to prevalence in our dataset and the literature.

		Stem Counts (stems ha^{-1})			Basal Area (m^2 ha^{-1})		
Common Name	Number of Sites	S	α	% Preferred	S	α	% Preferred
Speckled Alder	9	0.653 (0.128)	0.693 (0.110)	88.9%	0.703 (0.120)	0.867 (0.084)	88.9%
Striped Maple	5	0.575 (0.236)	0.199 (0.102)	60.0%	0.589 (0.241)	0.237 (0.107)	60.0%
Red Maple	9	0.457 (0.123)	0.171 (0.050)	55.6%	0.186 (0.110)	0.099 (0.052)	33.3%
American Beech	7	0.427 (0.093)	0.245 (0.100)	71.4%	0.236 (0.125)	0.227 (0.140)	28.6%
Paper Birch	4	0.330 (0.166)	0.371 (0.218)	75.0%	0.050 (0.027)	0.345 (0.230)	50.0%
Yellow Birch	6	0.265 (0.102)	0.102 (0.036)	50.0%	0.094 (0.070)	0.034 (0.017)	16.7%
Sugar Maple	3	0.214 (0.149)	0.081 (0.068)	33.3%	0.010 (0.009)	0.009 (0.009)	0.0%
White Pine	4	0.156 (0.156)	0.078 (0.078)	25.0%	0.000 (0.000)	0.000 (0.000)	0.0%
Balsam Fir	16	0.071 (0.026)	0.113 (0.058)	12.5%	0.031 (0.021)	0.117 (0.077)	12.5%
Red Spruce	14	0.064 (0.030)	0.060 (0.031)	21.4%	0.008 (0.004)	0.016 (0.011)	0.0%
Eastern Hemlock	7	0.014 (0.009)	0.006 (0.004)	0.0%	0.002 (0.002)	0.006 (0.006)	0.0%

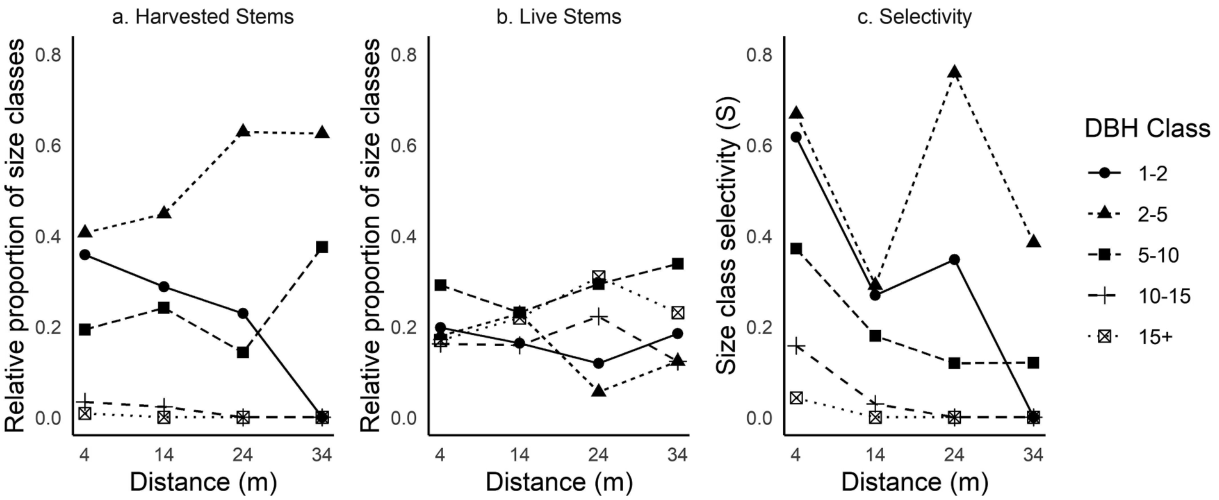


Fig. 4. Relative proportions of harvested (a) and live stems (b) for five diameter classes within plots centered at various distances between 4 and 34 m from the impoundment edge. Panel (c) shows selectivity index values for the same data, calculated as the ratio of harvested stems to the total number available (harvested plus live). Data from all sites were pooled for all calculations.

especially stem size. Beaver foraging strongly influences canopy closure and forest structure, with changes most pronounced closest to the impoundment. Non-linear variation in selectivity across a range of stem sizes strongly suggests that beaver are highly selective, rather than opportunistic, foragers. While the stem size range most selected by beaver is consistent with that observed in other regions, relative preferences among woody species diverged considerably, and are not correlated with variation in nutrition data available for the region. Mixed-effect logistic models of harvest probability based on stem size and distance from ponds were good fits to the empirical data, demonstrating strong preferences for intermediate-sized stems located closer to the impoundment. These results support predictions of both central place foraging theory and expectations of size-based optimal energy returns (Fryxell and Doucet, 1991; McGinley and Whitham, 1985; Schoener, 1979).

4.1. Lakes versus stream impoundments

A notable result of this this study is the contrast in beaver impacts on riparian forest structure along lake shores versus stream environments. Canopy openness was significantly higher along streams compared to lake shores, and substantial differences extended >35 m from the impoundment edge. Additionally, stream environments had significantly more deciduous stems at distances <35 m from the impoundment than lakes, while deciduous stems at lake sites generally had larger stem diameters than those along streams. These differences may be the result of selective beaver foraging, with deciduous species assuming smaller and shrubbier forms due to beaver harvesting as has been observed in other studies (Harrison, 2011; McGinley and Whitham, 1985).

The increased relative intensity of harvest along beaver-occupied streams compared to lakes may reflect the need for dam building material in addition to forage, and may increase the impact on preferred deciduous species along streams, resulting in the observed differences in stem density and diameter between waterbody types. Additionally, the greater perimeter of lakes relative to river impoundments affords beavers comparatively safe water transit to a larger amount of forage area, potentially allowing for more diffuse and less severe foraging impacts along lakeshore areas (Raffel et al., 2009). Furthermore, the flooding and wetland expansion associated with the damming of streams often create a larger and more intense forest disturbance compared to lake shores, though the impacts vary depending upon site topography, soil type, and land use history (Burchsted et al., 2010; Little et al., 2012; Nummi and Kuuluvaine, 2013). Long-term inundation of forest stands will kill most flood-intolerant trees, converting riparian forests into wetlands. As these flooding impacts may be minimal or absent in lake environments (Collen and Gibson, 2000), the canopy impacts documented along lakes may more directly result from beaver foraging rather than the compounded forest disturbances of flooding, wetland expansion, and tree harvesting present along dammed streams.

4.2. Distance and size-based selectivity patterns

Almost all tree species had a higher selectivity value on a stem basis than by basal area, suggesting that beavers preferentially harvest smaller stems when available, and leave larger stems intact. Over 95% of harvested stems were <10 cm in diameter, and the strongest preference was for intermediate-sized stems of 2–5 cm, which were consistently selected deeper into the forest (Figs. 4 and 5). Stems in the range of 1–2 cm were harvested in decreasing proportions with distance away from the impoundment, whereas stems of all size classes > 5 cm had lower levels of harvest overall and were decreasingly selected at greater distances according to the proportion available (Figs. 4 and 5).

These findings are in line with central place foraging theory (Fryxell and Doucet, 1991; Jenkins, 1980; McGinley and Whitham, 1985; Schoener, 1979), which predicts size selectivity to be non-linear due to the increased energetic costs of hauling and provisioning larger stems, in addition to the increased risk of predation. If predation risk were the sole factor driving foraging patterns, we would expect that selected tree sizes should decrease monotonically with greater distance from the shore (i.e., safety), as the time and effort required to browse and haul large trees farther from the impoundment increase the exposure risk to predators. On the other hand, if central place foraging considerations strongly influenced stem selection, either additionally or alternatively to predation risk, optimal foraging behavior predicts that the harvested tree size distributions should reflect their potential energetic gains. As shown by Schoener (1979), who defined energy gain as the ratio of foraging energy minus provisioning costs divided by provisioning and handling time, this ratio decreases with distance because of increasing provisioning cost for larger stems. However, the gains are nonlinear with respect to prey size (or stem diameter in the case of browsers) because the greater energetic return of larger items is counterbalanced by increased handling and provisioning costs with further increases in

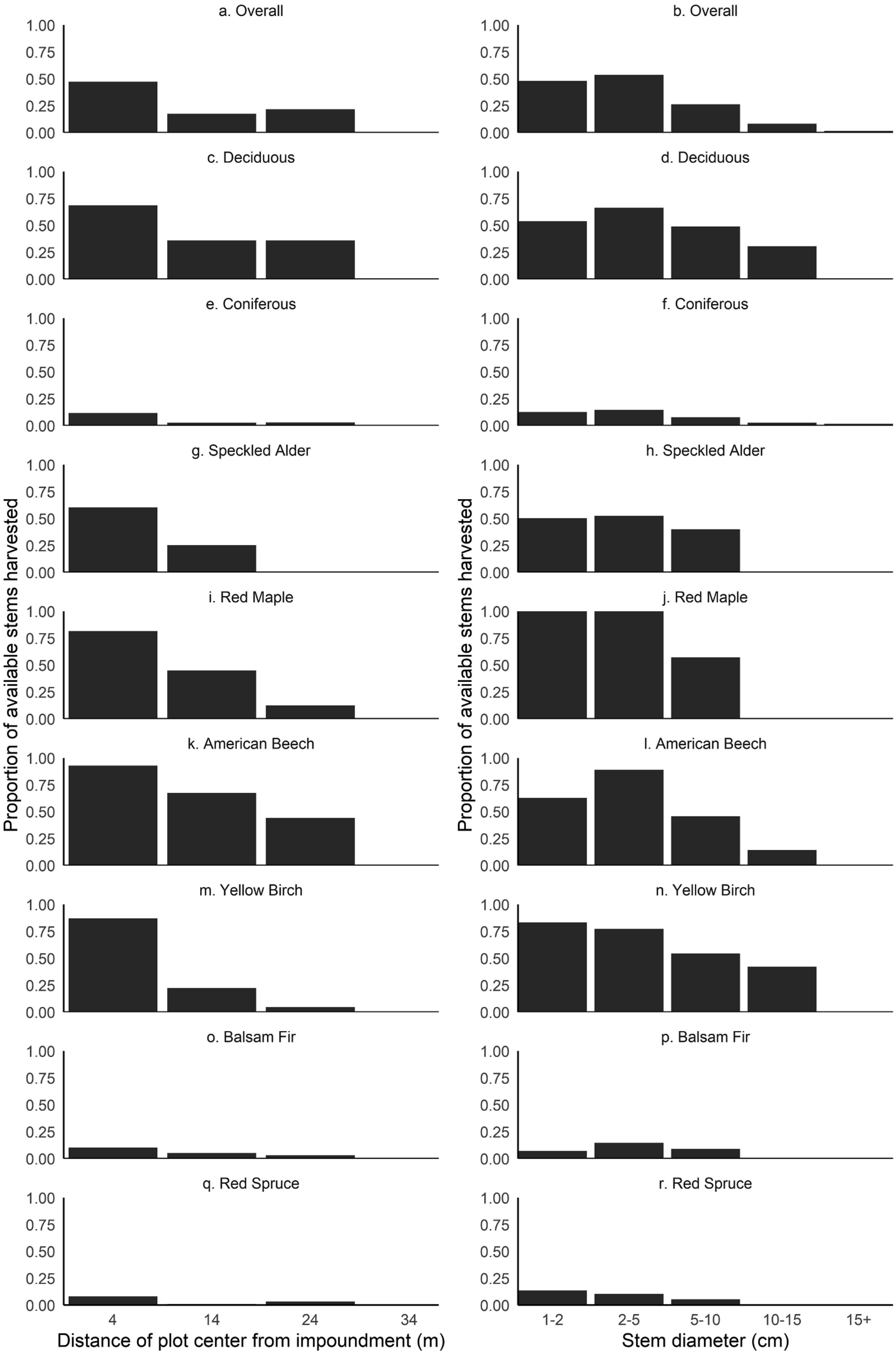


Fig. 5. Proportion of available stems harvested for various woody plant groups and species as a function of distance from impoundment (left) and as a function of each diameter class (right). Selectivity was computed from the survey data as the ratio of stems harvested to the total available, which was the sum of live stems plus harvested stumps. Selectivity values were computed for all stems (panels a and b), deciduous species only (c and d), coniferous only (e and f), and six of the most common species surveyed (panels g to r), arranged in order of decreasing selectivity (Table 2).

size. Specifically in the case of beaver, we would expect a non-linear, modal relationship for tree stem diameter (D) *sensu* Schoener (1979) because of the way that the energetic value of a stem, located in the thin cambium and bark sheath, scales linearly with stem circumference whereas the costs (e.g., weight and provisioning energy, gnawing and hauling time) scale with the stem's basal area.

Notably, this non-linear trend in beaver size preferences has been observed in other studies within the Adirondacks (Harrison, 2011), other regions of North America (McGinley and Whitham, 1985; Woodard, 1994), and in regions where beaver have been introduced as

Table 3
Model selection criteria and parameter coefficients for best generalized linear (logistic) mixed models for probability of stem harvest by beaver. Coefficient standard errors are reported in parentheses. Site was included as a random factor in all models. Distance from the edge of the impoundment (m) was log-transformed in the overall, deciduous, and coniferous models. Column names include *k* for number of model parameters, ΔAIC for the difference in Akaike Information Criteria from the best model, and ROC for receiver operating characteristic curve, a measure of model fit. For each response, all candidate models with ΔAIC ≤ 4, plus the null model, are shown. Model variants are listed in Supplemental Materials S2.

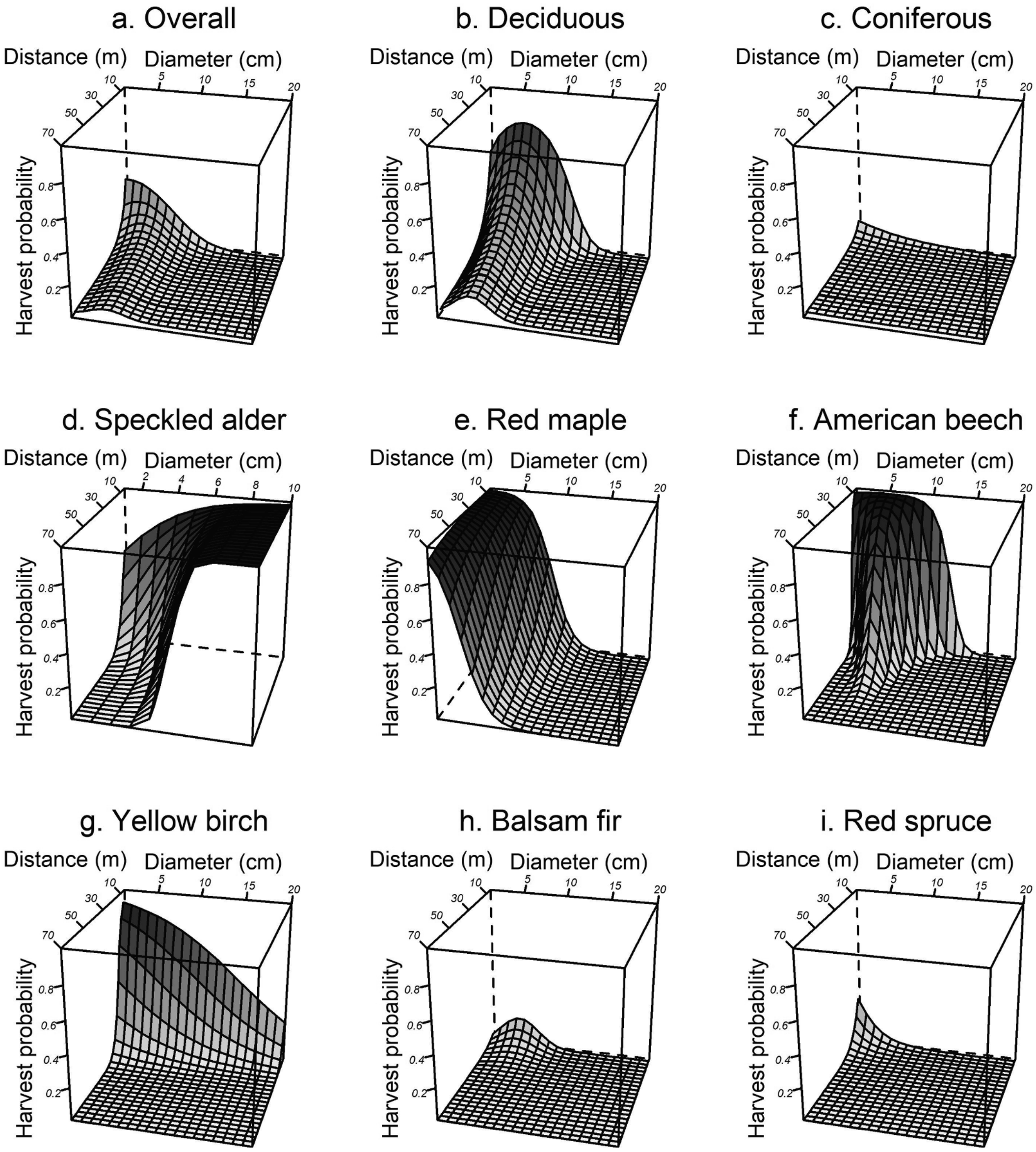
Model Rankings						Coefficients (and SE) for Effects on Stem Harvest Probability						
Model Variant	*k*	ΔAIC	Akaike Weight	Cumulative Weight	ROC	Intercept	Site	Distance	Diameter	Diameter^2	Distance : Diameter	Distance : Diameter^2
Overall												
#8	7	0	1	1	0.92	4.45 (0.80)	1.96	-2.48 (0.37)	-1.04 (0.25)	0.08 (0.02)	0.57 (0.17)	-0.05 (0.02)
Null model	2	467.1	0	1	0.80	-1.40 (0.37)	1.55					
Deciduous												
#8	7	0	0.98	0.98	0.92	3.91 (1.16)	2.46	-2.08 (0.49)	-0.03 (0.42)	0.02 (0.04)	0.33 (0.22)	-0.04 (0.02)
Null model	2	313	0	1	0.78	-0.05 (0.42)	1.63					
Coniferous												
#5	4	0	0.412	0.412	0.91	0.84 (0.92)	1.72	-1.31 (0.35)	-0.18 (0.04)			
#7	5	0.1	0.392	0.804	0.92	1.22 (0.96)	1.75	-1.35 (0.35)	-0.26 (0.07)	0.003 (0.001)		
#6	5	1.5	0.196	1	0.91	0.30 (1.19)	1.74	-1.02 (0.53)	-0.10 (0.13)		-0.05 (0.07)	
Null model	2	50	0	1	0.83	-3.37 (0.46)	1.32					
American Beech												
#8	7	0	0.923	0.923	0.97	9.31 (4.09)	3.74	-0.83 (0.34)	-0.97 (1.16)	0.08 (0.09)	0.24 (0.12)	-0.02 (0.01)
Null model	2	102	0	1	0.65	-0.07 (0.32)	0.61					
Yellow Birch												
#5	4	0	0.441	0.441	0.96	4.93 (0.90)	0.00	-0.30 (0.06)	-0.19 (0.07)			
#7	5	0.9	0.277	0.718	0.96	3.91 (1.38)	0.00	-0.31 (0.06)	0.09 (0.38)	-0.02 (0.03)		
#6	5	1.4	0.222	0.941	0.96	5.51 (1.17)	0.00	-0.38 (0.10)	-0.26 (0.11)		0.01 (0.01)	
Null model	2	100.2	0	1	0.58	-0.52 (0.67)	0.69					
Red Maple												
#5	4	0	0.66	0.66	0.97	7.36 (2.02)	0.00	-0.06 (0.02)	-0.82 (0.26)			
#7	5	1.9	0.261	0.92	0.97	6.28 (3.54)	0.00	-0.06 (0.02)	-0.41 (1.28)	-0.04 (0.11)		
Null model	2	67	0	1	0.83	-0.09 (0.69)	1.75					
Speckled Alder												
#6	5	0	0.415	0.415	0.92	1.88 (1.27)	3.06	-0.27 (0.10)	0.21 (0.19)		0.04 (0.03)	
#5	4	0.2	0.366	0.781	0.92	1.11 (1.14)	3.01	-0.14 (0.04)	0.45 (0.11)			
#7	5	2.1	0.143	0.923	0.92	0.99 (1.31)	3.04	-0.15 (0.04)	0.56 (0.36)	-0.01 (0.04)		
#8	7	3.4	0.074	0.998	0.92	1.42 (0.002)	3.03	-0.24 (0.002)	0.59 (0.002)	-0.05 (0.002)	0.02 (0.002)	0.003 (0.001)
Null model	2	23.9	0	1	0.89	1.31 (0.98)	2.68					
Balsam Fir												
#7	5	0	0.601	0.601	0.94	-2.69 (2.50)	1.91	-0.14 (0.07)	0.99 (1.01)	-0.11 (0.10)		
#5	4	2.6	0.166	0.767	0.93	0.52 (1.14)	1.76	-0.14 (0.07)	-0.32 (0.11)			
#3	4	3	0.134	0.901	0.94	-4.41 (2.23)	1.63		1.06 (0.93)	-0.11 (0.09)		
Null model	2	18.5	0	1	0.84	-2.89 (0.48)	0.96					
Red Spruce												
#5	4	0	0.418	0.418	0.98	0.93 (1.71)	3.08	-0.18 (0.09)	-0.52 (0.22)			
#7	5	0.2	0.374	0.791	0.98	-1.25 (2.90)	3.76	-0.20 (0.11)	0.55 (1.14)	-0.10 (0.11)		
#6	5	1.6	0.184	0.975	0.98	1.37 (1.86)	3.06	-0.23 (0.13)	-0.62 (0.28)		0.01 (0.02)	
Null model	2	24.1	0	1	0.88	-3.74 (0.67)	1.37					

an invasive species (Silva and Saavedra, 2008). This consistent intermediate size preference across biomes is independent of the different regional pools of woody plant species available, and thus is strongly suggestive of beaver as a central place forager that optimizes energetic gains across a range of available stem sizes.

4.3. *Species selectivity patterns*

In this study and many others reported elsewhere, beaver foraged overwhelmingly on deciduous species and actively avoided conifers, which are known for their poor palatability (Tables 1 and 2). However, a surprising finding from this study was the high utilization of tree species which are generally considered to be avoided in other forested regions. As there exists very little early-successional forest in the Adirondacks, due both to the long natural stand rotations in northeastern forests and the Adirondack State Park's status as the largest and best protected area of public lands in the eastern United States (Lorimer and White, 2003), many species believed to be preferred by beaver in other regions were absent from or marginal in this study. In particular, quaking aspen – believed to be one of the most highly preferred species in other regions (Donkor and Fryxell, 1999; Fryxell and Doucet, 1993, 1991; Johnston and Naiman, 1990b) – was almost entirely absent from our study sites, likely due to its shade intolerance and tendency to colonize disturbed habitats (Ziegler, 2007). As previous explanations of beaver species preferences have centered on the varying digestible energy content of different tree species, we would expect to see beaver preferentially harvest species which are selected for only opportunistically in other regions, a trend borne out by the relatively high selection rates of speckled alder, red maple, and paper birch (Table 2). However, we would not expect to see otherwise avoided species be harvested preferentially if selection preferences were solely a function of average digestible energy content, yet American beech – previously found to be avoided in studies from Central Ohio (Raffel et al., 2009) – was one of the most strongly preferred species in this study.

Past studies within the Adirondacks have found similar high preferences for American beech, with Harrison (2011) identifying beech as the second most strongly selected-for species at beaver impoundments within a research forest in the Central Adirondacks. One key difference in beech ecology between this region and the Midwest is the presence of beech bark disease (*Neonectria* spp.), which has radically altered the tree's size distribution by killing off most large trees and causing a proliferation of beech sprouts measuring less than 5 cm in diameter



a. Overall b. Deciduous c. Coniferous

d. Speckled alder e. Red maple f. American beech

g. Yellow birch h. Balsam fir i. Red spruce

Fig. 6. Predicted stem harvest probability from the best models as a function of stem diameter and distance from impoundment. The response surfaces represent each of the best models for all stems (a), deciduous species only (b), coniferous only (c), and six of the most common species in the forest surveys (d–i). Higher Z-axis values and darker shading represent higher probability of harvest. The best models for overall stems, deciduous, American beech, and balsam fir include a quadratic term for stem diameter, indicating a nonlinear modal pattern and preference for intermediate stem sizes. As no speckled alder stems > 10 cm were identified in the field, the diameter axis for this species ranges from 0 to 10 cm.

(Cale et al., 2017). During the period (in the year 2000) when Raffel et al (2009) were collecting their data, beech bark disease had not yet spread to Ohio (Morin et al., 2007), meaning the beech available to beaver in that study were likely larger on average than those available in the aftermath forest of the Adirondacks (Houston, 1975). Given that species selection has a strong linear relationship to the proportion of stems in the ideal 2–5 cm size class ($R^2 = 0.60$), we believe that the difference in beech selection rates between midwestern studies and the present one can be largely explained by differences in the size distributions available to beavers.

Indeed, we propose that beaver species preferences overall can be largely explained as a function of the size distribution available for each of those species. Beaver have previously been found to preferentially select early successional species (Gallant et al., 2004), which typically have higher numbers of young seedlings and saplings that grow faster than their late successional neighbors, resulting in a high proportion of stems in the ideal forage size range. Additionally, beaver are known to preferentially harvest aspen and willow (*Salix* spp.) where available, two species noted for their root sprouts following browsing or mechanical damage. The high density of these root sprouts will cause these species to present a more desirable size distribution, similar to the impacts of beech bark disease on the American beech, allowing beaver to browse areas repeatedly on short rotations. Indeed, much of the browsing documented along beaver ponds in the Central Adirondacks has been in perpetual 'beech gardens' that show signs of repeat harvesting over the course of many years (Harrison, 2011). These strong feedback effects on terrestrial forest structure reinforce beaver's role as an ecosystem engineer in aquatic environments (Burchsted et al., 2010).

Previous studies have focused on digestible energy content to explain beavers' species preferences, with some success at predicting selection in experimental settings using stems of a uniform size (Doucet and Fryxell, 1993; Fryxell and Doucet, 1993) or of varying sizes all less than 5 cm (Fryxell and Doucet, 1991). However, we were not able to find any relationship between species selectivity and digestible energy content, digestible protein, or dry matter digestibility using values from Peterson (2018). As a result, it seems likely that variation in tree species digestible energy content is not highly determinative of beaver foraging preferences in real-world settings, where perhaps optimal stem size ranges are more limiting across available food choices. We suggest that species selectivity for deciduous species is primarily a function of the size distribution of available stems, with nutritional content and digestibility a potential secondary factor.

4.4. Landscape-level and management implications

Beaver forage intensity and preferences can have large impacts across the landscape. Beaver harvesting has been shown to reduce forest stem density and basal area by as much as 43% over the span of six years (Johnston and Naiman, 1990b), and to dramatically reduce the abundance of preferentially harvested species (Hall, 1960), resulting in distinct plant assemblages at beaver-impacted sites compared to the surrounding forest. As beaver are central place foragers, these impacts are largely constrained to the riparian perimeter of beaver ponds, but can extend up to 80 m into the forest (Harrison, 2011; Johnston, 2017; McGinley and Whitham, 1985). Within this zone, beaver create greater light penetration to the forest floor, higher seedling regeneration and sprouting from browsed stumps (Harrison, 2011) and increased horizontal structural diversity (Alza, 2014). Similarly, our study finds beaver to have outsized impacts on forest structure, increasing stem density and reducing canopy cover within the riparian zone. In low-disturbance systems such as the Adirondacks and more broadly throughout the northern forest biome, these beaver-created forest gaps serve as an important source of early-successional forest for species at all trophic levels, resulting in increased species richness across the landscape, and better habitat and browse quality for wildlife (Alza, 2014; Johnston, 2017; Peterson, 2018; Wright et al., 2002). The continued expansion of beaver populations throughout their former eastern range increases early-successional habitat where it is most limiting, and presents a valuable opportunity for reinforcing management actions to reestablish disturbance processes and young stands in the Adirondacks and similar forests throughout the region (Alza, 2014; Johnston, 2017; Wright et al., 2002). Our results suggest that promoting beaver re-establishment throughout its historical range would increase forest structural diversity at a landscape scale, and consequently benefit wildlife species that are dependent on forested wetlands and early successional habitat. Thus encouraging beaver presence in northeastern North America, where it is compatible with human settlement and infrastructure, could complement the cross-continental success story of partnering with beaver in restoring degraded streams throughout the water-limited West (Pollock et al., 2018).

5. Conclusion

As ecosystem engineers, beavers exert considerable control over their riparian environment through a combination of their foraging and dam-building behaviors. As beavers continue to recolonize their historic range, it is important for ecologists and land managers to be able to predict the impacts these activities may have on forest structure and composition in the future. This study shows that trends in canopy closure and tree densities associated with beaver activity can be well predicted with distance from waterbodies, which are easily mappable landscape features. We have additionally offered evidence that beaver forage preferences are strongly influenced by differences in the size distributions of available stems across species, and perhaps only secondarily by differences in digestible energy content. Furthermore, we demonstrate the ability to predict the probability of harvest for individual size classes and species of trees with high accuracy based on distance from these waterbodies. This information can be used to inform forest management practices such as the management of riparian buffers and wildlife habitat enhancement as beaver populations, and the impacts associated with them, continue to proliferate throughout northeastern North America.

CRediT authorship contribution statement

Michael J. Mahoney: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization. **John C. Stella:** Conceptualization, Methodology, Validation, Formal analysis, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118331.

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