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ARTICLE

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Thinning restores ungulate foraging habitat in historically logged forests

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Abstract

Legacies of land use can persist for decades, thereby impacting populations, communities, and ecosystems long after the original disturbance has concluded. The coastal rainforests of western North America were fundamentally transformed by commercial logging throughout the 20th century, resulting in depauperate second-growth forests that provide limited understory production and foraging habitat for herbivores. The Tongass National Forest in Alaska, USA, is the largest contiguous tract of coastal temperate rainforest in the world, but nearly 200,000 ha of second-growth forest have created a need to restore understory plant communities and foraging habitat for ungulates like Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), a regional indicator of forest health and key subsistence resource for local and Indigenous communities. We leveraged a 16-year adaptive management experiment—the Tongass-Wide Young Growth Studies (TWYGS) program—to test the effects of precommercial thinning on forage availability and use by deer in second-growth forests. We measured plant communities, presence–absence of browse, and slash debris in 14,908 quadrats across 730 plots and found that plant community composition, understory forage biomass, digestible energy, and digestible protein were all significantly higher in thinned plots versus controls. Precommercial thinning also doubled browse probabilities relative to unthinned stands, and plots treated within 35 years of stand initiation experienced the highest gains. Deer selected for both plant quantity and plant quality, as browse was positively associated with both digestible energy and digestible protein. Conversely, slash debris generated by precommercial thinning reduced browse probability by an average of 11.3%, but these effects attenuated as slash decomposed over the course of the study. We found no effects of landscape composition on relative browse probability, indicating that fine-scale resource quality and accessibility were the strongest drivers of habitat use by deer over nearly two decades of sampling. Collectively, our results show that precommercial thinning is a valuable management tool that increases forage and deer habitat use in second-growth coastal rainforests. This study highlights the enduring legacies of forest disturbance and underscores

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the value of adaptive management experiments with long-term monitoring to optimize habitat management for wildlife.

KEYWORDS
adaptive management, Alexander Archipelago, browse, foraging, legacy effects, restoration, silviculture, ungulate

INTRODUCTION

Habitat degradation, fragmentation, and loss are widespread threats to biodiversity, and the legacies of such land-use change can persist for decades to centuries, altering population, community, and ecosystem processes well after the original disturbance has concluded (Bürgi et al., 2017; Foster et al., 2003; Newbold et al., 2015; Song et al., 2018). For example, legacies of logging and forest conversion have fundamentally reshaped the structure and composition of temperate forest communities across portions of the United States, with measurable effects lasting hundreds of years (Alaback, 1982; Foster et al., 1998; Rhemtulla et al., 2009). Consequently, land managers are increasingly tasked with restoring altered landscapes to historical conditions through active manipulation that aims to reestablish viable habitat for flora and fauna alike (Franklin & Johnson, 2012; Jacobs et al., 2015), but the efficacy of such approaches is often uncertain (DeLuca et al., 2010). Adaptive management programs that couple large-scale experiments with sustained monitoring are a promising yet often unrealized approach to understanding the mechanisms regulating restoration success (Månsson et al., 2023; Spies et al., 2019; Westgate et al., 2013), and more experiments are needed to optimize the restoration of forests with legacies of human disturbance (Carey, 2003; Keith et al., 2011; Williams, 2011).

The Pacific coastal temperate rainforest spans nearly 4000 km along the western coast of North America, from California through British Columbia, CAN to Prince William Sound in Alaska, USA (Bidlack et al., 2021; DellaSala et al., 2011). This globally rare ecosystem was historically dominated by structurally complex old-growth forests (>300 years old) with layered canopies and diverse understory plant communities (DellaSala et al., 2011) but widespread logging across the Pacific coast of North America has significantly altered the abundance and distribution of this habitat over the last century (Albert & Schoen, 2013; Halpern & Spies, 1995; Strittholt et al., 2006). Within this ecosystem, the Tongass National Forest and surrounding lands in southeast Alaska remain the largest contiguous coastal temperate rainforest in the world (DellaSala et al., 2011). Across southeast Alaska, however, approximately 300,000 ha of forest were logged during the late 20th century on state, federal, and Tribal lands (Crotteau, McClellan, et al., 2020), with productive old-growth forests harvested at disproportionately high levels (Albert & Schoen, 2013). Large-scale, clearcut logging dominated the region, resulting in homogenous, even-aged stands devoid of the structural and compositional heterogeneity generated by natural disturbances (e.g., windthrow; Harris, 1974, Kramer et al., 2001). Post-clearcut regeneration occurs rapidly in this highly productive ecosystem, ultimately giving rise to dense conifer stands within 20–30 years (Alaback, 1982). Following canopy closure, limited light penetration in these regenerating forests leads to understory communities with significantly lower diversity and biomass production compared to neighboring old-growth forests, and stem exclusion may last for more than a century (Alaback, 1982; Tappeiner & Alaback, 1989; Wallmo & Schoen, 1980). This pattern of secondary succession is typical of Pacific coastal rainforests (Franklin et al., 2002; Halpern & Spies, 1995; Schoonmaker & McKee, 1988), and today, these depauperate second-growth forests remain an enduring legacy of industrial logging across the Pacific coast.

Low diversity second growth forests can have adverse impacts on wildlife, including reduced habitat, forage, and movement (Dellasala et al., 1996; McArthur et al., 1993; Smith & Flaherty, 2023). Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) are the most common ungulate in Alaska's coastal rainforest and are distributed from British Columbia, CAN north to Prince William Sound, Alaska, USA (Larsen & McMillan, 2023; Macdonald & Cook, 1996). Black-tailed deer are a key subsistence food for rural and Tribal communities across the region, providing as much biomass as harvested salmon (*Oncorhynchus* spp.) to more than a third of regional households (Hanley, 1993; Kruse & Muth, 1990). However, black-tailed deer respond strongly to clearcut logging and secondary forest succession (Hanley, 1984; Schoen & Kirchhoff, 1990; Wallmo & Schoen, 1980). Inadequate understory biomass in second growth forests can limit forage intake by deer, while second growth canopies provide little snow interception, resulting in high snow accumulation that further reduces forage availability in winter

(Gilbert et al., 2017; Hanley & McKendrick, 1985; Hanley & Rose, 1987; Kirchhoff & Schoen, 1987). The lack of preferred understory forage (e.g., evergreen forbs) in regenerating forests is particularly problematic for black-tailed deer and has been connected to nutritional limitation and reduced carrying capacities (Hanley & McKendrick, 1985; Hanley & Rogers, 1989), prompting calls for active management of second growth forests to increase deer forage (Cole et al., 2010; Deal, 2007; Hanley, 2005). Black-tailed deer are also the primary prey of the Alexander Archipelago wolf (*Canis lupus ligoni*)—a regional endemic that has been petitioned multiple times for protection under the Endangered Species Act—leading to additional concerns about second growth forest management and the consequences for wildlife across southeast Alaska (Gilbert et al., 2022; Roffler et al., 2018). Consequently, black-tailed deer have been proposed as an indicator of forest health for the region, suggesting that the management of habitat for deer can balance biological, cultural, and economic needs in Pacific temperate rainforest ecosystems (Hanley, 1993, 1996).

Precommercial thinning has considerable potential to enhance wildlife habitat in second growth forests (Carey, 2003; Dodson et al., 2012), including the restoration of ungulate forage through increases in understory plant diversity and biomass production (Figure 1A; Doerr & Sandburg, 1986; Hanley, 2005). Prior studies have demonstrated that thinning can provide 2–6× more understory forage biomass compared to unthinned stands, significantly increasing the potential carrying capacity for deer (Cole et al., 2010; Crotteau, Rue-Johns, & Barnard, 2020). Early application of precommercial thinning (e.g., 15–30 years following stand initiation) appears particularly advantageous and may even provide higher quantities of forage than old-growth forests, likely because understory vegetation already present in regenerating stands is amplified by the increased light penetration following thinning (Hanley et al., 2013). Accordingly, nearly half of all second growth stands (~81,000 ha) in the Tongass National Forest have already been thinned (Crotteau, McClellan, et al., 2020). Past research on precommercial thinning, however, has focused almost exclusively on the production of plant biomass as a proxy for deer foraging habitat and has rarely considered resource quality, accessibility, or even the use of such habitat by deer. For instance, while thinning can increase resource quantity (i.e., understory biomass), resource quality may not improve because most plant biomass (e.g., shrubs) has low digestibility and protein content (Hanley et al., 2012; Hanley & McKendrick, 1985). Moreover, precommercial thinning can generate high levels of woody debris (i.e., "slash"; Figure 1B), triggering concerns that thinning creates barriers to deer movement that ultimately limit access to foraging habitat (Farmer et al., 2006; McClellan et al., 2014). Thus, a detailed understanding of how resource quantity, quality, and accessibility interact to drive deer foraging in managed forests is needed to assess the long-term effects of precommercial thinning on deer foraging habitat in second growth forests.

Here, we leverage a 16-year adaptive management experiment—the Tongass-Wide Young Growth Studies (TWYGS) program—to test the effects of precommercial thinning on deer forage and habitat use in second growth forests of southeast Alaska. The TWYGS program is a series of experiments developed in part to assess the efficacy of silvicultural treatments for wildlife habitat improvement in the Tongass National Forest (McClellan, 2008). We use long-term data from the TWYGS experiments to (1) test the effects of precommercial thinning on understory forage availability and (2) test the relative effects of thinning versus environmental conditions on ungulate browsing. Specifically, we quantify differences in forage quantity and quality between thinned and unthinned plots across stand ages, and we use a series of Bayesian binomial mixed-effects models to assess the influence of forage quantity, quality, and accessibility on summer browse probabilities in thinned and unthinned stands across nearly 20 years of forest succession. We hypothesized that precommercial thinning would significantly increase forage availability and browse probability compared to unthinned control stands, and we predicted that younger forests (e.g., 15–25 after stand initiation) would experience the greatest browsing. More proximately, we predicted that plant quality (e.g., digestible energy [DE] and digestible protein [DP]) would be the primary driver of browsing, but we expected this to be mediated by slash cover, which we hypothesize limits browsing. Lastly, we quantified the influences of plant communities and landscape composition on relative browse probabilities at multiple spatial scales to inform the placement of future thinning efforts, and we predicted browse rates would be highest in plots adjacent to preferred deer habitats (e.g., open canopy).

METHODS

Study area

This study was situated in southeast Alaska's Alexander Archipelago and spans the Tongass National Forest (Appendix S1: Figure S1), which includes thousands of islands with mountainous terrain, steep slopes, and glacial fjords. The maritime climate is cool and wet, with 200–600 cm of annual precipitation and seasonal temperatures that range from 0 to 15°C between winter and

FIGURE 1 (A) Tongass-Wide Young Growth Studies (TWYGS) site on Prince of Wales Island, AK contrasting control (unthinned, left) and treatment (pre-commercially thinned, right) plots in a second growth forest recovering from clearcut logging. (B) Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) foraging at a TWYGS site with high quantities of slash debris from precommercial thinning. Photo credit: Sheila Spores, USFS (left), Jeffrey Barnard, USFS (right).

summer, respectively (Crotteau, Rue-Johns, & Barnard, 2020). Forests are dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), with understory biomass largely in the form of shrubs, including blueberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), devil's club (*Oplopanax horridus*), and rusty menziesia (*Menziesia ferruginea*; Hanley et al., 2013). Evergreen forbs provide important forage for deer, especially bunchberry dogwood (*Cornus canadensis*), five-leaved bramble (*Rubus pedatus*), fernleaf goldthread (*Coptis aspleniifolia*), and threeleaf foamflower (*Tiarella trifoliata*; Hanley & McKendrick, 1985), but the abundance of these species varies across sites, seasons, treatments, and forest succession (Crotteau, Rue-Johns, & Barnard, 2020; Hanley & Barnard, 2014). Sitka black-tailed deer are the dominant herbivore across the study area; however, moose (*Alces alces*) and elk (*Cervus elaphus*) have localized populations stemming from both introductions and natural colonization (Colson, 2013; Hundertmark et al., 2006; Kirchhoff & Larsen, 1998).

Experimental design

All data (Manlick, 2025) were collected as part of the TWYGS program, a series of experiments developed by an interagency working group in 2001 to understand the effects of precommercial thinning treatments on wildlife, specifically deer forage and understory biomass (McClellan, 2008). Treatments were designed for practical application by forest managers at operational scales (>4 ha per treatment) and were widely replicated across the Tongass National Forest at more than 50 sites (Appendix S1: Figure S1). We focus on three coordinated experiments designed to test the effects of precommercial thinning on deer forage across stand ages: (1) 15–25 years; (2) 25–35 years; and (3) >35 years following stand initiation (Crotteau, Rue-Johns, & Barnard, 2020). Study locations differed according to stand age and experiment, but all experimental units were thinned between 2002 and 2006 using a randomized block design. Each site was comprised of randomly assigned control and treatment blocks with up to five 0.05-ha (22.4 m × 22.4 m) fixed area plots, each containing a minimum of twelve 1-m^2 quadrats arranged in a cross pattern and fixed at the plot center. Block, plot, and quadrat sample sizes varied slightly between experiments due to variation in secondary treatments. For example, each experiment included unique, age-appropriate prescriptions for tree retention that varied in stem density (i.e., trees per hectare) and secondary treatments such as tree pruning (see Appendix S1: Methods for complete details on experimental design). Previous research has shown that secondary treatments did not lead to significant differences in plant biomass (Nelson et al., 2024); therefore, we pooled all treatment data into thinned or unthinned categorical variables for downstream analyses following Crotteau, Rue-Johns, and Barnard (2020). Sites were surveyed up to three times post-treatment starting in 2007 and ending in 2023. Logistical constraints reduced the number of sites surveyed through time, but all experiments received three measurements that ranged from 4 to 16 years post-treatment.

Data collection

Vegetation, slash, and ungulate browsing data were collected at a series of 1-m^2 quadrats for all experiments. Aerial percent cover (in percentage) was estimated for all vascular plant species per quadrat and then converted to species- and tissue-specific estimates of plant biomass (in grams per square meter) using localized allometric equations (Rue-Johns et al. 2021). Biomass estimates were then used to estimate DE (in kilojoules per square meter) and DP (in grams per square meter) per quadrat following established conversion factors (Hanley et al., 1992, 2012, Parker et al., 1999; see Appendix S1: Methods for complete details). Slash percent cover (in percentage) was measured as the proportion of each quadrat containing residual woody branches and stems from felled trees; however, slash was not uniformly measured across control and treatment quadrats because cover was assumed to be zero in control plots when the experiments were established. To test this assumption, we used 114 slash cover measurements that were present in the data and found that slash cover was significantly lower ($F_{1,\ 12{,}835} = 59.5$, $p < 0.001$) in control ($\bar{x} = 0.17$) than treatment ($\bar{x} = 0.39$) quadrats. We therefore fixed slash cover to zero for all control quadrats, but downstream analyses were performed with and without control data to assess the sensitivity of results to this assumption. Browsing was recorded in each quadrat as the presence or absence of recent ungulate damage to understory plants, defined as visible ungulate clipping in the current growing season. No pretreatment data were collected for any metric.

Statistical analysis

To test the effects of precommercial thinning on forage availability, we first pooled all quadrats and calculated mean understory forage biomass, mean DE, and mean DP at the plot level for each measurement (i.e., approximately 5, 10, and 15 years post-treatment) following Crotteau, Rue-Johns, and Barnard (2020). We then used unpaired two-sample t tests with a Benjamini–Hochberg false discovery rate correction (Benjamini & Hochberg, 1995) to test for differences between thinned and unthinned plots at each measurement interval and each stand age. We assessed significance at $\alpha = 0.05$, 0.01, and 0.001.

We used Bayesian binomial mixed-effects models to assess the impact of precommercial thinning treatments, forage composition, and forage accessibility on the probability that a quadrat was browsed (hereafter, "browse probability"). First, we assessed the fixed effects of treatment, time since treatment, forage quantity and quality (DE, DP), and slash cover on browse probability at the quadrat scale (1-m^2) using presence–absence of browse as the response variable (Table 1). We developed a suite of eight a priori models plus a null model (Appendix S1: Table S1) that incorporated all covariates as well as various interactions between forage quantity, forage quality, slash cover, and time since treatment. All models included a nested random effect (site/block/plot) to account for potential autocorrelation within localized measurements. To assess the potential influence of fixing slash cover to zero in all unmeasured control quadrats, we ran the same suite of models using only data from treated quadrats and removed the categorical "treatment" term (Table 1, Appendix S1: Table S2). Models were implemented in the R package *rstanarm* with default priors (~normal[location = 0, scale = 2.5]) and a logit link to accommodate the binomial structure of the data (Goodrich et al., 2020). We ran four chains with 3000 iterations each and discarded the first 1000 iterations of warmup. All models exhibited convergence ($\hat{R} = 1.0$) and effective posterior sample sizes >1000. We then used a series of posterior predictive checks to ensure model fit and that models approximated mean values from the data (Appendix S1: Figure S2). To compare models, we calculated the expected log predictive density (ELPD) for each model using approximate leave-one-out cross-validation in the R package *loo* (Vehtari et al., 2017, 2024). We used a Pareto K threshold of 0.7 to account for potential outliers, identified top models via highest ELPD, and calculated model weights using pseudo-Bayesian model averaging (Yao et al., 2018).

To understand how landscape composition surrounding precommercial thinning treatments impacts the relative probability of deer browsing, we extracted the random effects for each plot from our top browse model above and used them as the response variable in a second set of models (Appendix S1: Figure S3). Random effects represent the conditional mode for a given factor, here the difference between a given plot and the mean predicted response (i.e., intercept). As a response variable, random effects then provide a plot-level estimate of predicted browse probability relative to the overall study mean, while simultaneously accounting for quadrat-level fixed effects such as treatment, forage, and slash cover. Browse models contained 730 plot-level random effects, and we used random effects from 663 plots for landscape analyses as 67 plots were removed due to lack of spatial data. Random effect values exhibited limited evidence of spatial structure (Appendix S1: Figures S3 and S4) and were modeled directly in all downstream analyses.

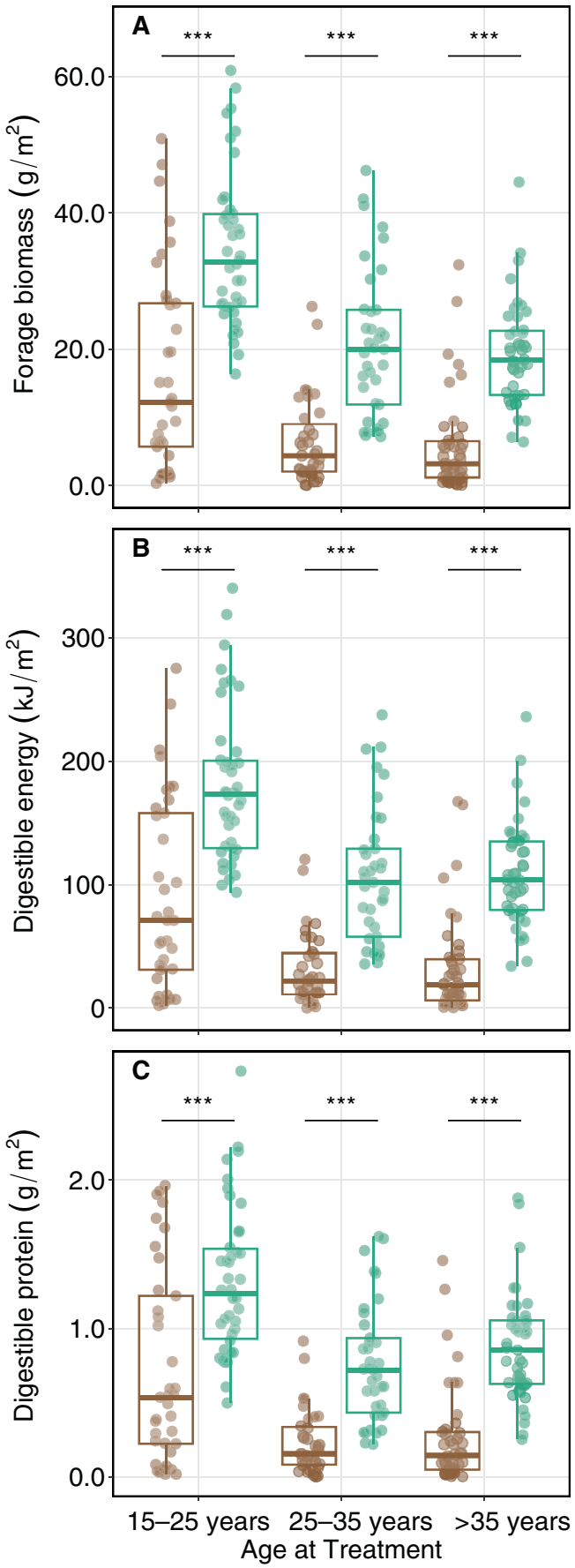
To characterize landscape composition surrounding study plots at multiple scales, we estimated landcover composition in 100, 200, and 1000-ha landscapes surrounding

TABLE 1 Response and predictor variables used in Bayesian binomial mixed-effects models to assess the impact of precommercial thinning on Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in southeast Alaska, USA, including variable descriptions, predicted effects on browse probability, range (mean) of values, and unit of measurement.

Variable	Description	Prediction	Range (mean)	Units
Response				
Browse	Plants within sampled quadrat exhibit evidence of ungulate browsing	Increases with forage quantity, quality, and accessibility	0,1	Presence, absence
Predictor				
Treatment	Thinned versus unthinned treatments	Precommercial thinning increases browse probability	Thinned, unthinned	...
Stand age	Age of forest stand at treatment	Earlier treatment increases browse probability	15, 25, 35	Years
Digestible energy (DE)	Energy per gram of plant biomass per quadrat available to deer after digestion	High forage quantity and quality (DE) increases browse probability	0.0–1251.95 (109.76)	kJ/m^2
Digestible protein (DP)	Protein fraction of total plant biomass per quadrat available to deer after digestion	High forage quality (DP) increases browse probability	0.0–17.16 (0.83)	g/m^2
Slash cover	Proportion of quadrat covered by "slash" debris from precommercial thinning	High slash cover limits access to forage and decreases browse probability	0.0–1.0 (0.28)	...
Time	Time (at survey) since thinning treatment was conducted	Browse probability increases over time following thinning	4.0–16.0	Years

each plot center based on recategorized National Land Cover Database (NLCD) and canopy cover database data from 2016 (Wickham et al., 2021). Final models tested the influence of low canopy cover (<30%) forest, shrubland, muskeg, and developed (e.g., roads) land, as well as the proportion of second growth forest at each scale (Table 2, Appendix S1: Methods). All predictors were square root transformed prior to analysis, and we modeled plot-level coefficients with associated error as a function of proportional landcover composition independently for each scale using Bayesian linear models in *brms*, where the random effect of each plot was weighted by the standard error of the estimate (Bürkner, 2017; Santos et al., 2024). We used identical priors and conditions as above, and all models exhibited convergence ($\hat{R} = 1.0$) and effective posterior sample sizes >1000. We again modeled all plots and treatment-only plots for comparison, as above. We defined significance for all models as 95% credible intervals (CIs) that did not overlap zero.

Lastly, to assess the impact of thinning on plant communities, we calculated individual species occurrence rates, percent contribution to total biomass, and species rank in terms of total biomass within each plot and used unpaired two-sample *t* tests with a Benjamini–Hochberg false discovery rate correction to test for differences between treatments. We then conducted a redundancy analysis (RDA; Legendre & Andersson, 1999) to evaluate the effects of thinning treatment on plant communities and assessed associations between plant community and plot-level gradients of DE, DP, slash percent cover, and ungulate browse probabilities (represented by random effects, as above). The species plant community matrix was composed of the average species-specific biomass observed across all three measurement years and was standardized using the Hellinger method (Legendre & Gallagher, 2001). Sites were restricted to those that received a full set of measurements ($N = 50$). The highest-ranking 14 species that make up ~90% of total understory biomass were initially used to populate the community matrix, and the number of species was then systematically reduced (lowest rank first) to optimize explanatory power (R^2). Explanatory variables were centered and scaled using a root-mean-square transformation, and the significance of axes and explanatory variables was tested using a permutation analysis of variance. Thinning was assessed as a factor variable, with the unthinned treatment set as the dummy variable. All analyses were conducted in the r package *vegan* (Oksanen et al., 2013).



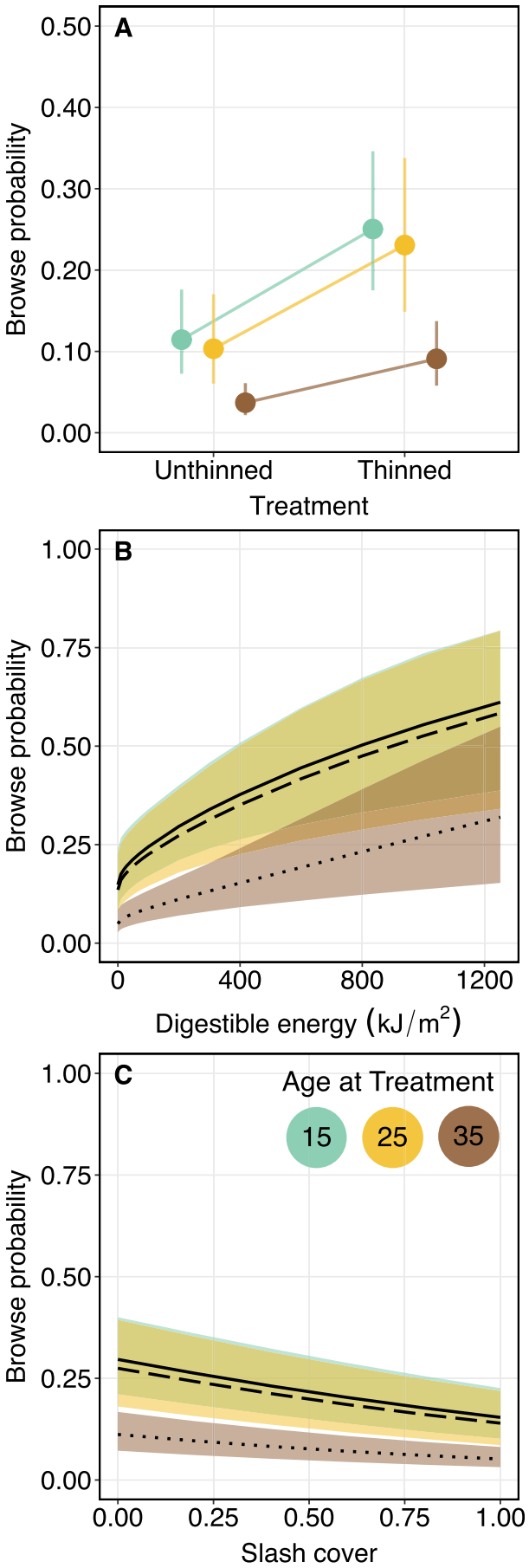
RESULTS

We quantified vegetation, slash, and browse in 4288 control quadrats and 10,620 treatment quadrats from 2007 to 2023. Forage biomass, DE, and DP were all significantly higher in thinned plots than in control plots (all $p < 0.001$; Figure 2) and thinning consistently increased all forage metrics across stand ages and forest succession (Appendix S1: Figure S5). The proportion of quadrats browsed was higher in thinned (24.9%) than control treatments (13.6%). Predictive models that included both treatment and control data were nearly identical to treatment-only models (Appendix S1: Figure S6), we present only the complete data set here.

Overall, browse likelihood at the quadrat level was best explained by the positive effects of treatment (i.e., thinning; $\beta = 0.95$, 95% CI = 0.65–1.27) and DE ($\beta = 0.06$, CI = 0.03–0.10), contrasted by a strong negative effect of slash cover ($\beta = -1.64$, CI = −210 to −1.20; Figure 3). Regardless of the stand age at the time of treatment, thinning led to browse probabilities more than 2× higher than unthinned stands (odds ratio = 2.6, CI = 1.92–3.55); however, the magnitude of these effects differed greatly depending on stand age at treatment (Figure 3A). Median browse probability in thinned stands declined with age at treatment and was 0.25 (0.18–0.35) when treated at 15–25 years, 0.23 (0.15–0.34) at 25–35 years, and 0.09 (0.06–0.14) when treated at an age of >35 years (Figure 3A). Browse probability was consistently low in unthinned stands, with estimates of 0.11 (CI = 0.07–0.18), 0.10 (0.06–0.17), and 0.04 (0.02–0.06) in the 15–25 year, 25–35 year, and >35 year old stands, respectively. Ultimately, our models indicate that browse probability was greatest in thinned stands <35 years old where forage quantity and quality was high (>400 kJ/m^2 DE; Figure 3B). Conversely, slash cover reduced browse probabilities by an average of 11.3% across stand ages, for example dropping from 0.30 (0.21–0.40) to 0.15 (0.10–0.23) in the 15–25 year old stands when comparing 0% and 100% slash cover (Figure 3C).

We found variable effects of DP ($\beta = -0.09$, CI = −0.52 to 0.35) and time since treatment ($\beta = -0.02$, CI = −0.04 – 0.01) on browse probability individually,

FIGURE 2 Box plot comparisons of plant biomass (A), digestible energy (B), and digestible protein (C) between thinned (green) and unthinned (brown) plots across stand ages at treatment. Points denote mean values for each plot, box and whiskers represent the interquartile range (IQR) ± 1.5× IQR, and horizontal lines represent median values. Significant differences between treatments were determined via two-sided *t* tests corrected for multiple comparisons and are noted by asterisks.



but both covariates exhibited meaningful interactions in our top model (Figure 4). First, time since treatment and DP interacted directly ($\beta = 0.05$, CI = 0.03–0.08) such that 97.5th percentile quadrats yielded browse probabilities >0.30 in thinned stands, but only after approximately 8 years post-treatment (Figure 4A). Similar effects were predicted among 97.5th percentile DP control quadrats, where browse probability reached 0.32 (0.20–0.47) after 16 years of forest succession, substantially higher than mean browse probabilities in control blocks (0.11, CI = 0.07–0.18). Second, time since treatment also interacted with slash cover such that the negative effects of slash on browse probability attenuated over time (Figure 4B). For example, complete (i.e., 100%) slash cover within a quadrat reduced browse probabilities by 17% and 15% compared to no slash at 4 and 8 years post-treatment, respectively, but by 16 years post-treatment browse probabilities were constant at 0.35 (0.23–0.48), regardless of slash cover (Figure 4B).

Landscape composition showed no significant effects on relative browse probability across the 100-ha, 200-ha, and 1000-ha scales, as all covariates had 95% CIs that overlapped zero (Table 2). Results did not vary between models using all plot data and treatment-only data (Appendix S1: Figure S7). Across scales, we detected consistent positive effects of shrubland ($\bar{\beta} = 0.11$) and second-growth forest ($\bar{\beta} = 0.03$) on relative browse probability, consistent negative effects of low-canopy cover forest ($\bar{\beta} = -0.29$) and muskeg ($\bar{\beta} = -0.04$), and equivocal effects of low-cover development (Table 2).

Of the fourteen species that make up 90% of total biomass, we found that nearly all increased significantly in response to thinning (Table 3). Individual species biomass was 2–9× greater in thinned stands, and species occurred 1.5–3× more frequently in thinned over unthinned stands. Differential responses to thinning resulted in variation in species rankings, but *Vaccinium* spp., *Menziesia ferruginea*, and *Tsuga heterophylla* were all top contributors regardless of treatment. Redundancy analysis confirmed significant associations between the plant community and thinning treatment, DP, DE, slash, and ungulate browsing (Figure 5). A community of six species optimized explanatory power (*Vaccinium* spp., *Rubus spectabilis*, *Menziesia ferruginea*, *Tsuga heterophylla*, *Athyrium fili-femina*, and *Cornus canadensis*) and revealed that thinned

FIGURE 3 Predicted effects of thinning (A), thinning plus digestible energy (in in kilojoules per square meter; B), and thinning plus proportion of slash cover (C) on browse probability for stands treated at 15–25 (green, solid line), 25–35 (yellow, dashed line), and > 35 years old (brown, dotted line). Error bars and ribbons represent 95% credible intervals for predicted effects.

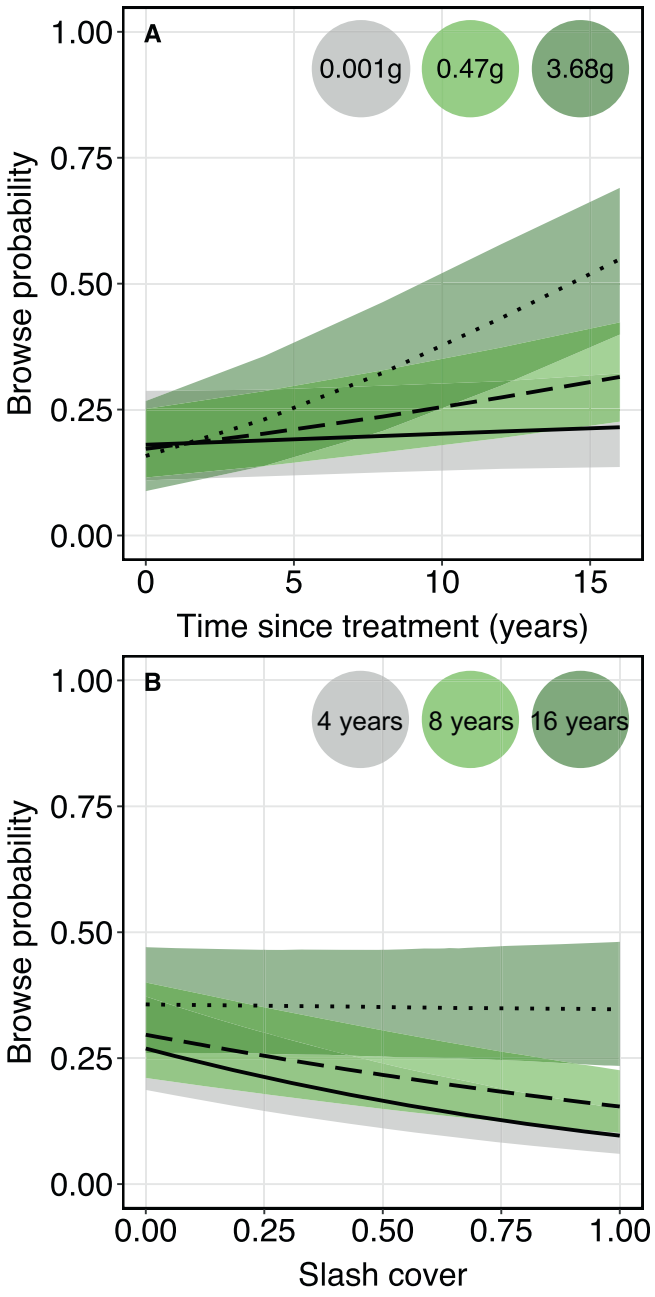


FIGURE 4 Interactive effects of forage quality (digestible protein, grams per square meter), proportion of slash cover, and time since treatment (years) on browse probability in thinned stands. (A) Predicted browse probability under low (0.001 g/m^2; gray, solid line), median (0.47 g/m^2; light green, dashed line), and high (3.68 g/m^2; dark green, dotted line) digestible protein quantities from 4 to 16 years post-treatment. Low, high, and very high forage represent the 2.5, 50, and 97.5 percentiles of digestible protein across quadrats. (B) Predicted browse probability 4 years (gray, solid line), 8 years (light green, dashed line), and 16 years (dark green, dotted line) after treatment across a gradient of proportional slash cover. Ribbons represent 95% credible intervals for predicted effects.

and unthinned stand conditions were statistically different in multivariate space ($p < 0.001$). RDA axis 1 explained 39% of variance and exhibited a positive alignment with browse ($p < 0.001$), DE ($p < 0.001$), DP ($p < 0.001$), and slash cover ($p < 0.001$). RDA axis 2 explained only 3% of the variance and exhibited a negative alignment with slash cover ($p < 0.001$). Thinning treatment was primarily aligned with RDA axis 1, indicating that browse, total DE, total DP, and slash cover were all greater in thinned over unthinned stands (Figure 5).

DISCUSSION

Forest thinning has been proposed as a potential management strategy to restore wildlife habitat and mitigate the legacies of industrial logging that can persist for centuries (Hanley, 2005; Lindenmayer, 2009; Sullivan et al., 2021). Our results clearly illustrate that precommercial thinning increased ungulate forage and habitat use in second growth temperate rainforests, but we also show that the positive effects of thinning depend on the timing of intervention. Consistent with expectations, we found that ungulate browsing was maximized by thinning younger stands, forage quality increased browse probability, and foraging habitat improved over the course of our 16-year experiment. However, we also show that slash residues produced by precommercial thinning have the potential to offset habitat improvements. Collectively, these results demonstrate that precommercial thinning is an effective management tool to increase foraging habitat for ungulates in historically logged forests, but the timing and placement of thinning treatments should be considered in order to maximize the positive effects.

We used long-term vegetation and browsing data from an adaptive management experiment and found that precommercial thinning treatments significantly increased forage availability and the probability of ungulate browsing in all age classes. Early application of thinning had the strongest effects, as thinning stands <35 years since stand initiation led to substantially higher browse probabilities than both unthinned controls and thinned stands >35 years old (Figure 3). Thinning of older stands ultimately yielded minimal gains, and this inflection point was underscored by the fact that browse rates were higher in unthinned plots <35 years old than they were in thinned plots >35 years old. Optimal conditions for precommercial thinning, however, can be fleeting. Of the estimated 180,000 ha of second growth on the Tongass National Forest, over 120,000 ha are already >35 years old, with another 40,000 or more hectares transitioning to this less favorable stand age over the next decade (Kleinhenz, 2020). Our findings indicate that thinning in the remaining ~12,000 ha of second growth forests under 35 years old will provide the greatest benefits to understory recruitment and ungulate foraging habitat.

TABLE 2 Model coefficients (credible interval) for landscape-level predictors of deer browse at 100-ha, 200-ha, and 1000-ha scales.

	Coefficient (credible interval)		
Covariate	**100 ha**	**200 ha**	**1000 ha**
Developed	−0.01 (−1.19, 1.17)	−0.01 (−1.32, 1.27)	0.15 (−1.02, 1.33)
Forest	−0.26 (−0.77, 0.22)	−0.37 (−0.93, 0.18)	−0.22 (−0.94, 0.53)
Muskeg	−0.07 (−0.57, 0.43)	−0.02 (−0.55, 0.52)	−0.04 (−0.71, 0.63)
Shrub	0.15 (−0.28, 0.58)	0.14 (−0.35, 0.64)	0.04 (−0.38, 0.45)
Second growth	0.02 (−0.15, 0.19)	0.02 (−0.16, 0.20)	0.06 (−0.18, 0.29)

Note: Landcover variables were calculated as the proportion of each cover class with low canopy cover (<30%) surrounding plot centers. All covariates were square root transformed.

TABLE 3 Species ranks in terms of their contribution to total biomass and mean (±1 SE) biomass (in grams per square meter) and percent occurrence (in percentage) for the top 14 species that make up approximately 90% of biomass in unthinned and thinned stands.

	Rank (biomass)		Biomass (g/m^2)		Percent occurrence (%)	
Species	**Unthinned**	**Thinned**	**Unthinned**	**Thinned**	**Unthinned**	**Thinned**
Vaccinium spp.	1	1	**2.64 ± 0.38**	**5.78 ± 0.31**	**6.2 ± 0.4**	**9.6 ± 0.3**
Menziesia ferruginea	2	3	**0.86 ± 0.13**	**2.55 ± 0.16**	**15.1 ± 1.9**	**38.9 ± 1.6**
Tsuga heterophylla	3	4	**0.83 ± 0.12**	**1.76 ± 0.11**	**25.8 ± 1.7**	**38.6 ± 1.2**
Lysichiton americanus	4	12	0.61 ± 0.17	0.84 ± 0.12	4.4 ± 0.9	6.3 ± 0.7
Dryopteris expansa	5	7	**0.46 ± 0.06**	**1.20 ± 0.07**	38.0 ± 1.8	40.0 ± 1.1
Picea sitchensis	6	8	**0.40 ± 0.06**	**1.06 ± 0.10**	**9.0 ± 0.9**	**17.6 ± 0.8**
Rubus spectabilis	7	2	**0.39 ± 0.08**	**3.69 ± 0.25**	**10.6 ± 1.1**	**37.5 ± 1.3**
Oplopanax horridus	8	9	**0.37 ± 0.09**	**0.98 ± 0.11**	**3.4 ± 0.7**	**7.1 ± 0.7**
Gymnocarpium dryopteris	9	11	**0.35 ± 0.06**	**0.94 ± 0.06**	**23.0 ± 2.1**	**32.3 ± 1.4**
Cornus canadensis	10	6	**0.34 ± 0.07**	**1.24 ± 0.11**	**14.7 ± 2.1**	**32.9 ± 1.64**
Athyrium fili-femina	11	5	**0.28 ± 0.06**	**1.29 ± 0.10**	**10.2 ± 1.1**	**22.4 ± 1.0**
Thuja plicata	12	13	**0.27 ± 0.09**	**0.54 ± 0.09**	**2.0 ± 0.4**	**3.9 ± 0.4**
Blechnum spicant	13	10	**0.17 ± 0.03**	**0.99 ± 0.10**	**9.8 ± 1.1**	**21.2 ± 1.2**
Rubus pedatus	14	14	**0.13 ± 0.03**	**0.39 ± 0.03**	**13.0 ± 1.9**	**22.4 ± 1.4**

Note: Significant differences between treatments were determined via two-sided t tests corrected for multiple comparisons and are noted in bold.

Previous assessments of the TWYGS experiments at five (Hanley et al., 2013) and ten years (Crotteau, Rue-Johns, & Barnard, 2020) post-treatment also reported that understory biomass and nutritional carrying capacities for deer were higher in thinned plots than control plots, but the actual use of restored forage by ungulates was uncertain. Likewise, numerous studies have hypothesized that thinning increases forage and therefore habitat use by ungulates across the western United States (Cole et al., 2010; Cook et al., 2016; Hull et al., 2020), but our results demonstrate that active forest management can more than double browse probability over the no-action alternative. Questions about the long-term efficacy of thinning have ultimately limited its application, as studies have found that secondary canopy closure can limit the positive effects of thinning to 7 years post-treatment (Cole et al., 2010). However, our results indicate that the positive effects of thinning are long-lasting, as forage biomass, forage quality, and browse probability were consistently higher in thinned stands throughout the duration of our 16-year study. Importantly, the positive effects of thinning observed here focused exclusively on summer forage and browsing while winter forage is more likely to limit deer populations, especially in thinned stands when snow depth is high (Hanley et al., 2013; Hanley & McKendrick, 1985). Nevertheless, summer forage intake is critical to maintaining body condition and increasing overwinter survival (Lopez et al., 2025; Parker et al., 1999), particularly in fawns where malnutrition is responsible for up to 30% of mortalities (Farmer et al., 2006; Gilbert

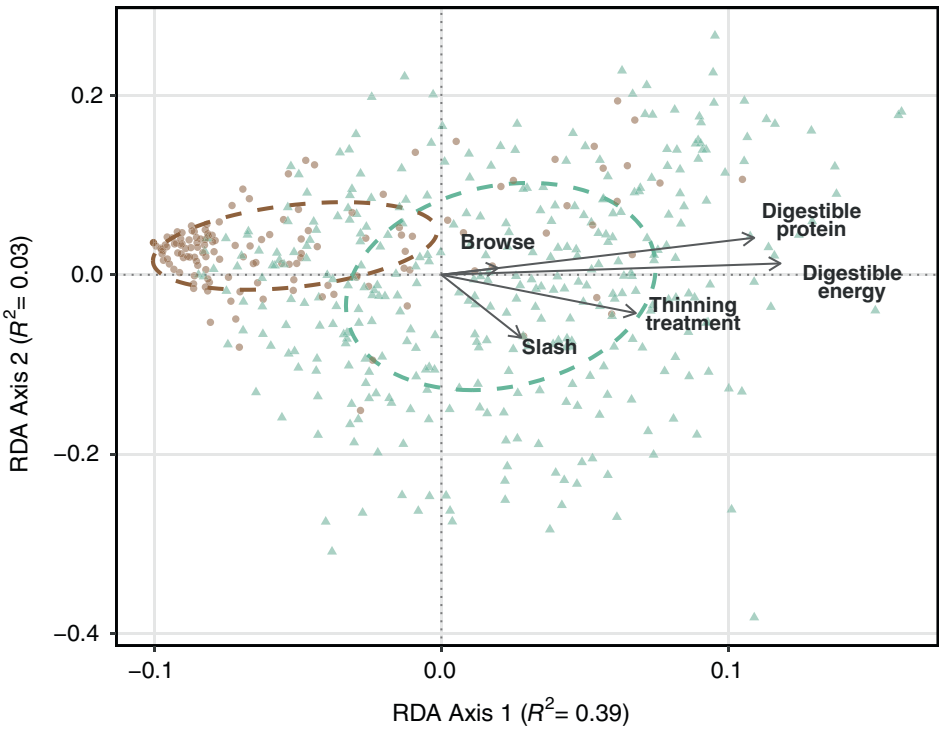


FIGURE 5 Biplot depicting the first two axes of a redundancy analysis (RDA) regressing species biomass on treatment and across gradients of browse, slash cover (%), total digestible energy, and total digestible protein ($R^2 = 0.42$). Ellipses represent 1 SD of the mean loading for thinned and unthinned treatments, and vectors show the direction and strength of the forage, slash, and browse gradients.

et al., 2020). Collectively, our findings indicate that early application of precommercial thinning is the most effective treatment to restore ungulate foraging habitat in summer and that the utility of thinning as a restoration strategy for ungulate foraging habitat diminishes as second growth stands age.

Thinning of second growth forests is generally hypothesized to benefit herbivores by reducing canopy cover, increasing light penetration, and stimulating the development of understory plant communities that more closely resemble old-growth conditions (Lindh & Muir, 2004; Sullivan et al., 2013; Verschuyl et al., 2011). Early application of thinning is hypothesized to be especially beneficial because younger stands with more open canopies can quickly generate understory biomass following treatment, and these predictions have largely proven true across multiple ecosystems (Ares et al., 2010; Hull et al., 2020; Lindgren et al., 2006; Thomas et al., 1999). Our results align with this hypothesis, as stands <25 years at treatment generated the highest forage biomass (~30 g/m^2; Figure 2A). High plant biomass, however, does not necessarily translate to foraging and habitat use by herbivores (Hobbs & Hanley, 1990). For example, thinned plots >35 years old produced nearly identical amounts of forage biomass as plots 25–35 years old (Figure 2A), but browse rates were 2.5× higher in younger stands. This disagreement reflects the complexity of resource selection by ungulates and is likely the consequence of two primary factors: nutritional constraints and forage accessibility.

First, forage selection by ungulates is a nutritional balancing act that involves complex interactions between forage quantity, quality, and digestive efficiencies, among other factors (Hanley, 1997; Parker et al., 2009). Black-tailed deer, like many ungulates, are energetically limited by forage availability and DE (Lopez et al., 2025, Parker et al., 1999). We found that DE was significantly higher in thinned stands and was a primary driver of browse probability, indicating that forage quality and availability drive fine-scale browse selection and habitat use. This selection for DE is consistent across many large ungulates, including elk (Rowland et al., 2018), mule deer (*Odocoileus hemionus*; Tollefson et al., 2010), and caribou (*Rangifer tarandus*; Denryter et al., 2022). The availability and intake of DE often regulate body fat, reproduction, and survival, and our results join a growing body of literature that suggests active management for early seral conditions can benefit ungulates through forage production and sustained DE availability (Cook et al., 2016, Hull et al., 2020). We also observed positive effects of DP on browsing and habitat use through time, a finding consistent with past work showing protein intake is highest in the

summer (Parker et al., 1999), likely to optimize growth and lactation (Hanley & Rogers, 1989; Sadleir, 1980; Wallmo et al., 1977). Redundancy analysis also indicated that deer browse was associated with high DP, and that high protein plants like lady fern and blueberry, as well as preferred evergreen forbs like bunchberry dogwood and five-leaved bramble, all increased with thinning. These findings are encouraging because evergreen forbs are notoriously difficult to manage for in second growth forests (Hanley et al., 2014; Tappeiner & Alaback, 1989), and our results join others suggesting that precommercial thinning can provide high-quality understory forage that increases habitat use by ungulates (Cook et al., 2016; Hanley, 2005).

High-quality forage created by thinning treatments must also be accessible to ungulate consumers, but slash debris generated during precommercial thinning can create substantial obstacles (Figure 1B; McClellan et al., 2014). For example, slash heights >0.5 m can reduce habitat use by 50% or more in mule deer (Lyon & Jensen, 1980), and slash can increase the energetic costs of movement by an order of magnitude (Hanley et al., 1989; Parker et al., 1984). Slash likely limited access to forage in our study as well, as slash cover consistently reduced browse probabilities. It is also possible that reduced mobility due to slash increased predation risk, thereby limiting foraging in thinned stands (Farmer et al., 2006; Gregovich et al., 2024). These negative effects of slash were most pronounced in stands >35 years old, likely because older stands contain larger trees (up to 50 cm in diameter) that generate deeper and more persistent slash obstacles when thinned. However, slash begins to settle and deteriorate after approximately ten years (McClellan et al., 2014), and our results corroborate these findings. The negative effects of slash on foraging weakened 10–15 years post-treatment, to the point that slash cover had no effect on browse rates in the final year of measurement for all stand ages.

The negative effects of slash ultimately create a management challenge, because it means the principal byproduct of precommercial thinning has the potential to offset habitat and forage improvements generated through restoration treatments. This is especially true for older stands, and additional research is needed to optimize restoration of these forests. Directed silvicultural treatments such as commercial thinning, gap harvesting, and tree girdling have all been suggested as potential strategies for restoring forage and ungulate habitat in late-stage second-growth forests (Bauhus et al., 2009; Harris & Barnard, 2017), and commercial thinning has already proved successful in generating understory forage in this system (Crotteau et al., 2022; Zaborske et al., 2002). Alternatively, slash burning and removal have been identified as potential tools to improve ungulate browse (Bergquist & Örlander, 1998; Long et al., 2008), but given the financial and logistical cost of implementing these approaches in this wet and remote environment, our results suggest it may be as beneficial to simply treat larger areas. For example, at the average slash cover (36%) for a stand <35 years old, slash removal is predicted to improve browse probability by approximately 12% in the first 4 years. Thinning an adjacent stand, however, could double the treated area and is predicted to increase browse by 11%. These findings show that while slash does inhibit ungulate browsing, thinning nonetheless improves foraging habitat relative to the no-action alternatives, and we encourage the continued assessment of restoration strategies to promote wildlife habitat in aging second-growth forests.

We tested the effect of land cover composition on relative browse probabilities and found no significant effects of adjacent habitat on site use. This finding suggests that the placement of precommercial thinning treatments did not significantly impact the efficacy of restoration actions for ungulates and that thinning is likely to improve habitat use by deer when applied to similar landscapes. This result is likely because thinning often targets highly productive stands where one would expect to generate adequate deer forage. Further, our experimental sites were chosen based on operational considerations and were not stratified across a gradient of landscape contexts, resulting in a homogenous matrix of habitats across plots. For example, average forest cover within landscapes was 78% across all scales, with open habitats like muskeg and shrub representing less than 5% of land cover combined. Recent studies suggest that black-tailed deer often select for such habitats (Gilbert et al., 2017; Shanley et al., 2021), and we predicted that nearby open cover would serve as a "source" for deer, thereby increasing browse rates in adjacent precommercial thinning sites. We also expected large proportions of second growth forest to reduce browse probabilities due to lower deer densities, yet neither prediction proved true at any spatial scale. Rather, our analyses suggest that forage quality drives habitat use, and our redundancy analysis revealed that thinning fundamentally restructures plant communities to favor ungulate forage and browsing at fine scales. We encourage future research on forest restoration and ungulate foraging to more directly consider the spatiotemporal distributions of plant forage communities, as this would facilitate spatially explicit assessments of nutritional landscapes that can be used to inform forest and wildlife management (McCarley et al., 2020; Merems et al., 2020; Rowland et al., 2018).

We analyzed the effects of precommercial thinning on ungulate browsing, but thinning likely impacts numerous other species dependent on early and late seral forest conditions. For example, increasing forage and

deer populations through precommercial thinning treatments has been recommended as a strategy to maintain persistent populations of endemic Alexander Archipelago wolves in southeast Alaska (Wolf Technical Committee., 2017). Likewise, thinning has been shown to support diverse and abundant small mammal communities that rely on coarse woody debris (e.g., slash) and understory vegetation (Smith & Nichols, 2004; Sullivan et al., 2013, 2021). This in turn could benefit species of concern like martens (*Martes* spp.) and the Northern goshawk (*Accipiter gentilis*) whose population dynamics are linked to small mammal prey (Flynn & Schumacher, 2009; Hanley et al., 2005; Lewis et al., 2006). Thinning is also frequently used in dry forests to reduce fire and fuels, a practice that has proven beneficial to numerous terrestrial wildlife taxa (Stephens et al., 2012; Verschuyl et al., 2011). Increases in understory biomass and diversity associated with thinned forests may also provide secondary benefits in the form of subsistence foods and medicinal plants that are essential to rural and indigenous communities in Alaska (Ballew et al., 2006; Chamberlain et al., 2025; Thornton, 1999). For example, shrubs like blueberries and salmonberries dominated thinned stands and are harvested by up to 90% of households in southeast Alaska, while medicinal plants like devil's club that are traditionally used by Alaska Natives also benefit from precommercial thinning (Hanley et al., 2005). Given the importance of understory shrubs as deer forage combined with the rapid, climate-induced changes in berry production across the region (Hupp et al., 2015; Mucioki, 2024), precommercial thinning may also help sustain cultural heritage and food security in rural Alaska.

Adaptive management has long been touted as a tool to optimize natural resource management and ecosystem restoration (Walters & Hilborn, 1978; Walters & Holling, 1990), but the successful implementation of adaptive management programs has proven surprisingly elusive (Bormann et al., 2007; Månsson et al., 2023; Westgate et al., 2013). Sullivan et al. (2013) argue that optimizing adaptive management for wildlife habitat requires three factors: (1) experiments at the scale of management, (2) decades of intensive monitoring, and (3) extreme variation in treatments. The experiment outlined herein successfully meets these conditions—the TWYGS program was a series of experimental treatments stratified across islands and stand ages and coupled with long-term monitoring to assess the impacts of forest management on black-tailed deer. In total, over 50 sites encompassing more than 700 plots and nearly 2000 ha were intensively monitored for nearly 20 years, with multiple context-specific treatments tailored to stand ages and silvicultural techniques. Most importantly, the TWYGS program was coproduced by an interagency team of scientists and managers who purposefully designed an experiment with practical treatments that could be employed at scale by the Tongass National Forest (McClellan, 2008). The TWYGS program thus provides a successful blueprint for adaptive management to restore wildlife habitat in second growth forests. Our results reaffirm the need for long-term data in adaptive management experiments (Lyons et al., 2008; Williams, 2011) as we detected notable changes in browse rates as a function of time (Figure 4) that were not detected in previous studies (Cole et al., 2010; Kellam, 2023). Just as precommercial thinning is intended to reverse the legacy effects of historical logging, our findings demonstrate that long-term monitoring is needed to understand the legacies of restoration treatments as well.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Manlick, 2025) are available in Figshare at https://doi.org/10.6084/m9.figshare.27297300.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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