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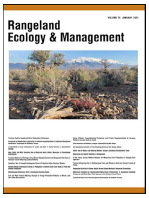

Original Research

Mastication Treatments Increase Perennial Herbaceous Cover Across Soil Types in Southeastern Colorado Piñon-Juniper Woodlands[☆,☆☆]

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ABSTRACT

Tree-removal treatments have been broadly applied across piñon-juniper ecosystems of the western United States to reduce tree cover, stimulate understory plant production, and promote habitat for shrub- and grassland-obligate wildlife species. Mastication treatments have become an increasingly common approach, yet the efficacy of these treatments can vary on the basis of a variety of factors, including soil characteristics, woodland structure, and grazing pressures. Here, we assessed vegetation responses to mastication treatments across three dominant soil types in two-needle piñon (*Pinus edulis* Engelm. [Pinaceae])—one-seed juniper (*Juniperus monosperma* [Engelm.] Sarg.) woodlands in southeast Colorado, United States, a region characterized by monsoonal precipitation, limited presence of introduced plant species, and relatively high grazing intensity by cattle and wildlife. We found that mastication treatments were effective at increasing herbaceous plant cover and species diversity (by 1.2 × and 1.5 ×) and at reducing the amount of exposed soil (60% reduction) 3 yr following treatment. This was mainly due to increases in native perennial grasses. Further, there were limited (and insignificant) increases in cover of annual plants and low abundance of introduced species in treated plots. Understory plant responses to treatment were similar across soils with a range of available water capacities. The increase in understory plant cover and richness paired with the low abundance of introduced species suggests that mastication treatments increase forage production for cattle and wild ungulates. In addition, the lack of soil type differences in treatment response suggests that mastication treatment placement does not need to prioritize soil type and can instead focus on other key areas of importance, such as wildlife habitat connectivity, historic woodland structure, and treatment feasibility.

Introduction

Piñon-juniper ecosystems are a widespread, biodiverse, and culturally significant vegetation type found across western North America (Floyd 2003). This ecosystem provides forage for livestock, wildlife habitat, fuelwood, and pine nuts and thus has been extensively used by humans (Fogg 1966; Gottfried et al. 1995). For more than a century, management of piñon-juniper ecosystems has largely consisted of tree-removal treatments (Redmond et al. 2014a; Hartsell et al. 2020). In recent years, these treatments have been implemented to achieve various goals of reducing fire risk, increasing forage production for livestock, improving habitat for shrub- and grassland-obligate wildlife species, and restoring ecosystem properties after increases in tree density (Greenwood et al. 1999; Redmond et al. 2014a; Bombaci and Pejchar 2016; Hartsell et al. 2020). At the same time, there is considerable concern around recent drought-related tree die-off (Breshears et al. 2005), declines in tree-obligate wildlife species (Boone et al. 2018;

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Boone et al. 2021), and losses of the culturally important piñon and juniper trees (e.g., Koyiyumptewa 1993; Miller and Albert 1993). It is thus critical to understand the efficacy of tree-removal treatments at accomplishing management goals and identify areas on the landscape where treatments are most effective given the need to also preserve woodlands. Mechanical mastication treatments reduce tree cover by grinding trees into mulch and have become an increasingly common method of tree removal, especially across the Colorado Plateau (Redmond et al. 2014a; Jain et al. 2018). Compared with tree removal via prescribed fire, mastication is less restricted to favorable weather, causes less soil erosion and instability, and better preserves belowground microbial communities (Owen et al. 2009; Karban et al. 2022).

Mastication treatments in piñon-juniper woodlands across the western United States have generally been effective at increasing herbaceous plant abundance and diversity, resulting in greater forage production (Ross et al. 2012; Young et al. 2013a; Roundy et al. 2014a; Bybee et al. 2016; Fick et al. 2022). Responses to mastication include increases in perennial grass cover (Havrilla et al. 2017: 11 × more cover; Redmond et al. 2013: 21 × more cover; Roundy et al. 2014a: up to 8 × more cover), which is a management priority in many areas to help resist invasion by introduced species (Blank and Morgan 2012), reduce erosion (Pierson et al. 2007, 2013), and provide forage for wild and domestic ungulates (Holechek 1984). Despite potential benefits, mechanical mastication has some risks. Following treatment, mechanically masticated areas across the southwest have consistently had higher occurrence and cover of introduced species than undisturbed areas (Owen et al. 2009; Coop et al. 2017; Redmond et al. 2014b; Havrilla et al. 2017). There is also the potential for post-treatment soil disturbance, erosion, and reduced infiltration due to increased water runoff and unpredictable plant responses to microsites created by mulch piles (Brockway et al. 2002; Cline et al. 2010; Young et al. 2013b). Mastication of live trees in piñon-juniper systems can also directly disturb bird species dependent on piñon-juniper woodlands (Magee et al. 2019) and can reduce carbon sequestration when decaying plant material releases carbon back to the atmosphere (Battaglia et al. 2009; Dicus et al. 2009).

Resource-rich sites that can support more herbaceous cover may be favorable for mastication to maximize herbaceous plant abundance and forage production. The extent of herbaceous community responses to mastication treatments is expected to vary greatly on the basis of pretreatment herbaceous species composition, soil properties, and woodland structure (Miller et al. 2005; Romme et al. 2009; Stephens et al. 2016). Mastication of the piñon-juniper overstory increases the availability of vital resources, such as soil water, nutrients, and sunlight (Bates 2005; Ramirez et al. 2008; Roundy et al. 2014c). Piñon-juniper woodlands with deep soil profiles may be expected to show greater increases in understory biomass after mastication, as they tend to have higher water-holding capacity and may produce more herbaceous biomass than areas with shallow soils (Romme et al. 2009). On the other hand, shallow soils restrict the rooting zone for piñon and juniper trees such that they compete more with grasses and forbs for water (Jameson 1970; Breshears and Barnes 1999; Miller et al. 2000; Grossiord et al. 2017). Therefore, there may be a greater response of understory vegetation to tree removal on shallow soils due to competitive release. Regardless of soil type, tree canopies significantly reduce solar radiation and precipitation reaching the understory (Breshears et al. 1997) and soil nutrient levels are often higher under tree canopies (Padien and Lajtha 1992; Rau et al. 2009). Therefore, the extent that mastication treatments will increase herbaceous cover also depends on the position under the tree canopy (Ramirez et al. 2008). The unique assemblage of understory species at a site will also influence mastication response, as some understory species are more commonly associated with microhabitats under piñon and juniper canopies, while others are inhibited by canopy cover and tend to occur in open areas (Schott and Pieper 1985; Bates et al. 1998).

In this study, we evaluate herbaceous vegetation responses to mechanical mastication treatments in southeastern Colorado piñon-juniper woodlands across three common soil types, which represent a broad gradient in soil depth and available water capacity (AWC; the amount of plant-available water in the soil). Despite extensive use of mastication treatments throughout piñon-juniper woodlands, there have been no published studies to our knowledge that assess the efficacy of these treatments for accomplishing management objectives in this region with high monsoonal precipitation, low occurrence of invasive plant species, and relatively high grazing pressure by cattle and wildlife. Our study sought to address the question: What are the short-term effects (3 yr post treatment) of mastication on groundcover and understory vegetation across soil types and microsites in southeastern Colorado? Given that our study site is managed for livestock production and wild ungulate habitat, we were also interested in the impact of mastication on understory vegetation palatable to domestic and wild ungulates.

Water is the dominant limiting resource in semiarid piñon juniper systems (Ramirez et al. 2008); therefore, we hypothesized that mastication treatments would result in increased herbaceous vegetation (i.e., forage production) in all soil types, but that the amount of increase would vary by soil type due to differences in AWC and soil depth. We also hypothesized that the largest increase in plant cover would occur in microsites located directly below tree canopies due to increased light and water availability following tree removal, but that interspace microsites would also have increased plant cover due to increased soil water availability.

Methods

Study area

Our study area was located at Chancellor Ranch in southeastern Colorado (37.394378, -103.826432). Chancellor Ranch is a 50,417 acre property owned by the Colorado State Land Board and leased to a private rancher who manages for multiple uses, including livestock production and habitat for wild ungulates like bighorn sheep. The Purgatoire herd of bighorn sheep that resides in this area is one of the largest herds in the state (~475 individuals) (Colorado Parks and Wildlife 2021). During the study period (2018–2021), a herd of approximately 450–500 pairs of cattle were grazed during the summer on all pastures. Our study plots were located within pastures grazed for roughly 30 d by the herd each summer, with the timing of grazing varying by year.

The study area consists primarily of *Juniperus monosperma* (Engelm.) Sarg. (one-seed juniper; hereafter "juniper") savanna in the uplands, with persistent woodlands containing both juniper and *Pinus edulis* Engelm. (Pinaceae) (two-needle piñon; hereafter "piñon") along canyon rims (Amme et al. 2020). A previous study that quantified changes in woodland distribution at Chancellor Ranch found evidence of both woodland expansion and contraction since Euro-American settlement (Amme et al. 2020). Woodland expansion occurred on rocky, shallow soils that are commonly associated with canyon edges, whereas contraction occurred primarily in deeper soils, possibly due to woodcutting over the past century.

Mean annual precipitation is 346 mm, which primarily (85%) falls during the growing season (March through October), with about 36% of mean annual precipitation falling during the monsoon season from July through September (PRISM Climate Group 2021). Mean temperature during the growing season is 16.3°C (PRISM Climate Group 2021). Dominant herbaceous species across all soil types include *Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths (blue grama), *Pleuraphis jamesii* Torr. (James' galleta), and *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama). *Hesperostipa neomexicana* (Thurb. Ex J.M. Coult.) Barkworth. (New Mexico feathergrass) is also a dominant species on shallow and mid soil types (see soil type descriptions later), and *Elymus elymoides* (Raf.) Swezey (squirreltail) is also dominant on mid and deep soil types. Shrubs do not make up a large percentage of cover in this area, but the most prevalent include *Cylindropuntia imbricata* (Haw.) F.M. Knuth (tree cholla), *Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit (winterfat), and species in the genus *Opuntia* (pricklypear) on mid and deep soils and *Gutierrezia sarothrae* (Pursh) Britton & Rusby (broom snakeweed) on shallow soils.

Site Selection and Treatments

To test the effects of mechanical mastication on understory vegetation across a broad gradient of soil depth, we selected five sites in each of three dominant soil types: 1) Almagre-Villedry complex soils, which are deep, loamy soils with high soil AWC of 17.2 cm (referred to as "deep"); 2) Villedry-Travessilla complex, which have intermediate soil depth and an AWC of 11.7 cm ("mid"); and 3) Travessilla sandy loam, which comprises shallow soils with a low AWC of 6.0 cm ("shallow"; see Tables S1 and S2 [available online at 10.1016/j.rama.2023.01.013] for soil complex descriptions). The soil types were determined using soil data from the US Natural Resources Conservation Service Soil Survey Geographic Database (SSURGO), which was updated for the area the yr (2018) we established our study (USDA NRCS 2018). At each of the 15 sites, we established paired treatment and control plots that were 10 × 50 m with a 20-m buffer around each plot. Sites were located from 0.2 to 6.2 km away from each other and had similar elevations (1 567–1 606 m) and relatively flat slopes (1.9–3.7 degrees). Treatments were applied to the plot and buffer area. Treatment plots were masticated in fall of 2018 with a hydro-ax attached with a front-end attachment to a BARKO 930B tractor with wheels, owned by the Colorado State Land Board and operated by the National Wild Turkey Federation. All trees within each treated plot were masticated (cut down and mulched), and mulch was left on site. Shrubs were not targeted for treatment, but if under a tree, they were likely also mulched. Some small juvenile trees may have been missed if they were too small to masticate.

Vegetation Sampling

Sampling was conducted between late July and early August 2018 (pretreatment) and 2021 (3 yr post treatment). The yr 2018 and 2019 were below average in precipitation (2018: 311 mm total, 46% during monsoon; 2019: 298 mm total, 34% during monsoon), whereas 2020 was dry but with a strong monsoon (288 mm total, 57% during monsoon), and 2021 was average (305 mm total, 40% during monsoon) (PRISM Climate Group 2022). Growing season temperatures were near average in 2019 and 2021 (16.1°C and 16.8°C, respectively) and slightly higher than average in 2018 and 2020 (17.4°C and 17.2°C, respectively) (PRISM Climate Group 2022). Pretreatment vegetation sampling was conducted to establish baseline assessments of groundcover, plant community composition, and woodland structure in both control and treated plots. At each plot, we established a 50-m transect in the center of the plot that ran south to north. We used the line-point intercept method to characterize ground cover and plant community composition, which was done by dropping a pin flag from chest height at each meter and recording all plants intercepted by the pin and upwards, as well as the ground cover (biological soil crust, bare soil, rock, plant litter, wood, mulch, or plant base). We identified plants to the species level when possible and recorded their status (live or dead). To assess woodland structure, we recorded the diameter at root collar (DRC), canopy area, species, height, and location along the transect of all trees in the 50 × 10 m plot that were $>$ 1 m in height.

Due to relatively low tree cover across the study area (8% mean cover across plots pretreatment [2018]), we conducted targeted sampling of understory vegetation beneath and adjacent to trees (or where trees were previously located in the masticated plots) to assess the effects of treatments three yr after mastication (2021). To do this, we established six 0.25-m^2 quadrats directly beneath and adjacent to three trees (or mulch piles where trees previously existed for masticated plots) in each plot. Trees were selected by sampling the closest tree to the 0-m, 25-m, and 50-m points along the transect. Quadrats were then established at three microsites on the north and south sides of the tree bole: directly beneath tree canopies (referred to as "under"), along the canopy edge ("edge"), and 2 m beyond the edge of the tree canopy ("inter"). In each quadrat we recorded percent cover of all plant species rooted within the quadrat using ocular estimates, with a maximum of 100% cover per species. Percent cover values were summarized by taking the average across all trees ($n = 3$) and cardinal directions (north, south) for each microsite (under, edge, inter) in each plot. These values were then used to estimate plant diversity, richness, and cover by species and functional group in each microsite in treated and untreated plots. All data are provided in the accompanying dataset (Nigro et al. 2023).

Analyses

Pretreatment differences between soil types

We first assessed whether treatment and control plots differed in tree and understory plant cover before mastication (summer 2018). To do this, we performed 2-way analysis of variance (ANOVA) models with treatment (masticated vs. control); soil type (deep, mid, shallow); and their interaction as fixed effects. This was done using the *aov* function in the *stats* package in R (R Core Team 2022). Plots of residuals for all ANOVA models performed were visually examined to confirm that models met ANOVA assumptions of homogeneity of variances and normality of residuals. When significant differences were detected, we used the Tukey's honestly significant difference test to examine pairwise comparisons (*TukeyHSD* function in the *stats* package). Given the lack of differences between pretreatment and control plots in 2018 (see Results), we only used the 3-yr post-treatment data for all subsequent analyses.

Three-year post-treatment effects of mastication on understory plant cover, diversity, and bare soil

We used species cover data from the quadrat sampling to evaluate the impacts of treatment, soil type, and microsite on total cover; species richness; diversity; functional group (annual, perennial grass, perennial forb, and shrub) cover; and introduced species cover. Species richness (N_0) was calculated as the sum of species occurrence across each type of microsite (interspace, canopy edge, under canopy) within each treatment replicate. Species diversity was calculated using the Shannon-Wiener Index ($- \Sigma[(p_i \times ln(p_i)]$), where p_i is the proportional cover of each species in each type of microsite within a treatment replicate. The Shannon-Wiener Index is indicative of both species number and evenness in a given community, with larger values reflecting greater diversity. To assess differences in plant richness, diversity, and cover in each functional group across treatment and soil types, we fit ANOVA models. We first performed fixed-effect 3-way ANOVAs with treatment type (two levels), soil type (three levels), and microsite type (three levels) as the predictor variables to assess whether microsite type interacts with treatment or soil type to influence plant responses.

We found no interacting effects with microsite and soil type or microsite and treatment across all models ($P > 0.63$) and subsequently performed simpler ANOVAs with fixed effects of treatment type and soil type, an interaction of treatment and soil types, and the fixed effect of microsite type to account for pseudoreplication at the treatment level (multiple samples of each microsite within a treatment).

We used line-point intercept data to assess the effects of mastication treatments and soil type on the relative proportion of bare soil across plots. We calculated the proportion of bare soil points relative to other ground cover categories along each transect and used ANOVA models with treatment, soil type, and the interaction between the two as predictor variables. Findings of significant main effects for all ANOVAs were further explored with pairwise comparisons of soil and microsite types, where applicable, using post-hoc Tukey's HSD tests.

We assigned species palatability scores to aid in interpretation of the results. Plant palatability scores were assigned as "high," "medium," or "low" on the basis of palatability data from the US Department of Agriculture (USDA) Plant List of Accepted Nomenclature, Taxonomy, and Symbols (PLANTS) and USDA Fire Effects Information System (FEIS) databases, expert knowledge, and other sources (Howard 1992, 1997, 2006; USDA Forest Service 1937; USDA NRCS 2022; Zlatnik 1999). Palatability data were available for 40 of the 54 species identified to species level in 2021 (Table S3 [available online at 10.1016/j.rama.2023.01.013]).

Three-year post-treatment effects of mastication on understory plant community composition

To assess the post-treatment effects of mastication treatments on plant community composition across soil types, we analyzed species cover data from the quadrat sampling with a distance-based redundancy analysis (dbRDA), based on a principal coordinates analysis. This is a constrained ordination approach that is based on linear models of species responses to certain environmental variables and allows for the use of any distance measure (McCune et al. 2002). We used a Bray-Curtis dissimilarity index, calculated from square-root transformed relative species cover data. Cover data were relativized by dividing the cover of each species in each microsite (under, edge, inter) at each plot by the sum of all species cover for that microsite and plot. We then examined differences in species cover on the basis of treatment type, soil conditions, and microsite. The dbRDA was run using the package *vegan* (Oksanen et al. 2022) in R. We used a nonparametric permutational multivariate analysis of variance (PERMANOVA) to test the significance of treatment, soil type, and microsite on species composition. In addition, to determine which species were most indicative of different soils (deep, mid, shallow); microsites (under, edge, inter); and treatments (control vs. masticated), we performed an indicator species analysis with the package *indicspecies* (De Caceres and Legendre 2009) in R and overlaid the positions of the best indicator species on our dbRDA biplot.

Results

Pretreatment differences between soil types

We found no differences in tree cover between treatments in 2018 (ANOVA, $F = 0.03$, $P = 0.87$), but there were differences in tree cover across the soil types (ANOVA, $F = 4.08$, $P = 0.03$), with the deep (high soil AWC) soil type having significantly lower tree cover (5.5% mean tree cover ± 1.41 standard error) than the mid (med soil AWC) soil type (10.2% tree cover ± 0.71 standard error; $P = 0.02$), and the shallow soil type (low soil AWC) having intermediate tree cover (8.4% ± 1.12 standard error). There was no evidence for an interaction between treatment and soil type on tree cover in 2018 (ANOVA, $F = 0.42$, $P = 0.66$). There were no differences in total plant cover between treatments (ANOVA, $F = 0.40$, $P = 0.54$) or soil types (ANOVA, $F = 2.6$, $P = 0.10$) before treatment and no differences in the percent cover of perennial forbs (treatment: ANOVA, $F = 3.27$, $P = 0.15$; soil: $F = 4.06$, $P = 0.11$). Percent cover of perennial grasses did not differ among treatments in 2018 (ANOVA, $F = 0.18$, $P = 0.67$) and percent cover of perennial shrubs didn't differ among soil types (ANOVA, $F = 0.30$, $P = 0.74$). There were significant differences between soil types in the percent cover of perennial grasses before treatment (ANOVA, $F = 3.4$, $P = 0.05$), but we accounted for soil type in our post-treatment models, so this did not affect the results. We also found a difference in perennial shrub cover between treatments before treatment (ANOVA, $F = 5.7$, $P = 0.03$) where perennial shrubs were initially higher in areas that were treated. However, perennial shrubs decreased in cover in treated areas post treatment, which indicates that this initial composition does not affect our interpretation of the results. We also found no significant differences in the proportion of bare ground cover among treated and control plots before mastication treatments in 2018 (ANOVA, $F = 0.02$, $P = 0.88$) or among soil types (ANOVA, $F = 0.65$, $P = 0.53$).

Three-yr post-treatment effects of mastication on understory plant cover, diversity, and bare soil

Across all plots in 2021, we detected 77 morphospecies, 54 of which were identified to the species level (see Table S1). Most morphospecies not identified to the species level ($n = 23$) made up few of the total observations (< 2 points out of 1 500 on LPI and < 1/20th of all cover). The only exception was *Opuntia* sp., which made up ~one-fifth of all cover and hit 5 of the 1 500 points across all line-point intercepts. However, since the *Opuntia* genus is relatively homogenous, we were still able to include it in functional group analyses. Total understory plant cover was 1.2 × (~23%) higher on average in treated (masticated) plots compared with untreated (control) plots in 2021, three yr post treatment ($F = 5.57$, $P = 0.021$), but did not differ significantly across soil types ($F = 0.70$, $P = 0.502$; Fig. 1A). Additionally, the interaction of treatment and soil type was not a significant predictor of mean plant cover ($F = 0.24$, $P = 0.79$). Mean plant cover differed among microsite positions ($F = 17.71$, $P < 0.001$; Fig. 1B), with interspace and canopy edge microsites having > 1.6 × (~65%) greater plant cover than under canopy microsites ($P < 0.001$). Interspace and canopy edge microsites were not different from one another ($P = 0.20$).

Understory plant species richness was significantly different between treated and untreated plots on average, with higher richness (1.7 mean richness difference) in treated plots ($F = 5.51$, $P = 0.02$; Fig. 1A). Mean differences in species richness across soil types were significant ($F = 10.26$, $P < 0.001$), and post-hoc pairwise comparisons indicated that shallow soils had significantly greater species richness (> 3.3 mean richness difference) than the other soil types ($P = 0.002$; Fig. 1A). ANOVA revealed significant differences in mean species richness across microsite positions ($F = 6.37$, $P = 0.003$), with post-hoc comparisons showing that under canopy, microsites had significantly fewer understory plant species on average than canopy edge and interspace positions (≥ −2.6 mean richness difference, $P = 0.014$), which did not differ from each other ($P = 0.918$; Fig. 1B). There was no effect of the treatment by soil type interaction on mean species richness ($F = 0.17$, $P = 0.847$).

Species diversity (Shannon-Wiener Index) was significantly greater in treated plots than untreated plots (0.28 greater mean diversity in treated plots, ANOVA, $F = 15.89$, $P < 0.001$) and significantly different between soil types ($F = 7.96$, $P = 0.001$), with shallow soils having greater diversity ($P \geq 0.24$) than mid and

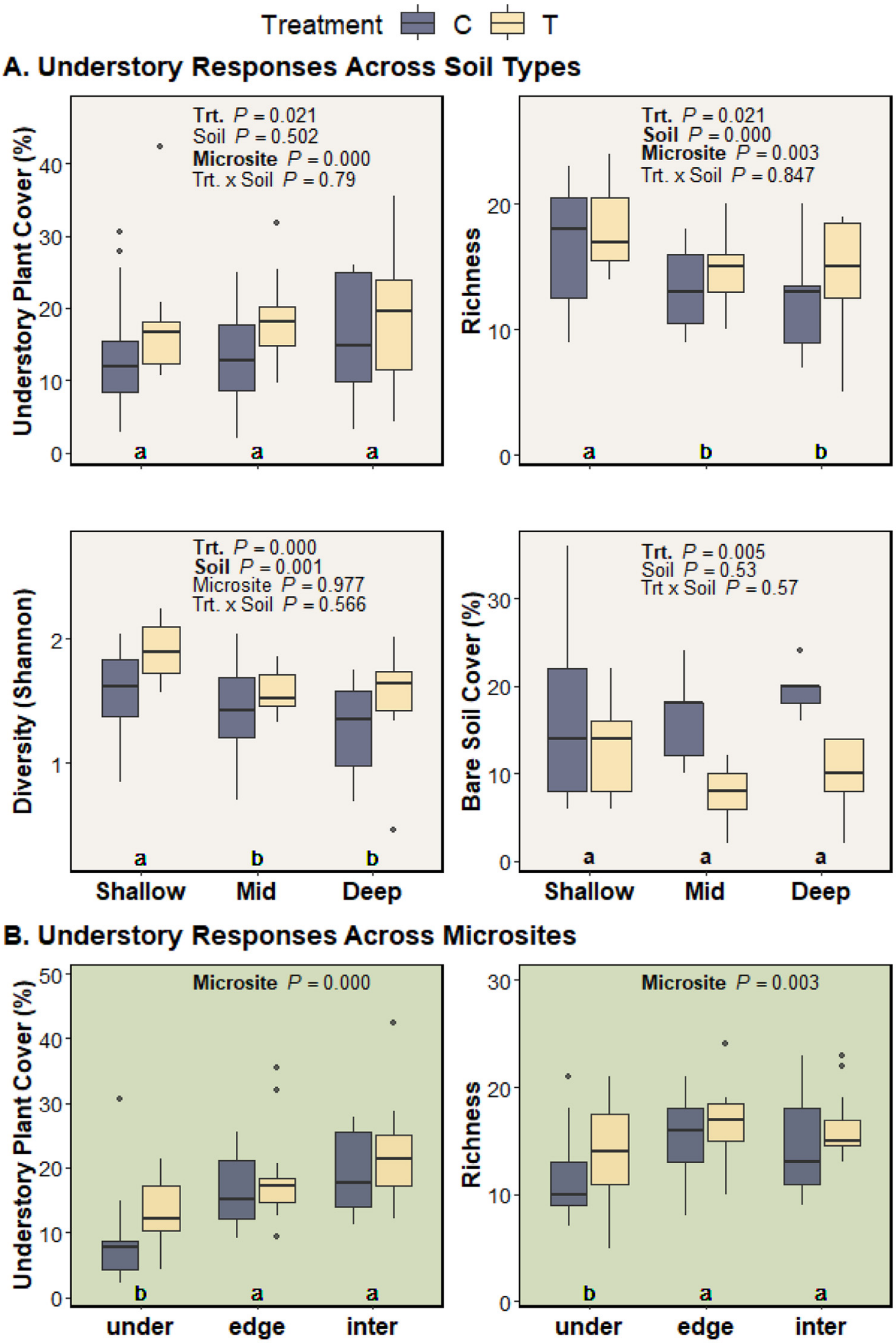

Figure 1. **A,** Effects of mastication treatments on total understory plant cover, plant richness, plant diversity (Shannon-Wiener Index) and bare soil cover across three soil types (shallow = shallow depth with low soil AWC, mid = mid depth and mid soil AWC, deep = deep depth and high soil AWC). Significant differences between soil types are indicated by differing letters below the boxplots. There were significant treatment effects across all response variables, but no interactions between soil and treatment. *P* values for each predictor variable in the analysis of variance (ANOVA) are shown, with significant variables bolded. **B,** When effects of microsite were significant (see ANOVA results in A), we show effects of microsite position (under = beneath canopy of a tree [control plots] or in a mulch pile [treated plots]; edge = at the canopy edge of a tree or mulch pile; inter = within the canopy interspaces) on total understory plant cover and plant richness. There was no significant treatment by microsite interaction; therefore, this term was not included in the final models.

deep soils ($P \leq 0.015$; Fig. 1A). In contrast, mean species diversity was highly variable across microsite positions and no significant differences were detected (ANOVA, mean differences ≤ 0.01, $F = 0.02$, $P = 0.977$). Additionally, the interaction of treatment and soil type was not significant for mean species diversity ($F = 0.57$, $P = 0.566$). Bare soil averaged 17.7% in control plots and 10.1% in treated plots 3 yr post treatment (2021). Mastication treatment areas had significantly less bare soil ($F = 9.6$, $P = 0.005$), but bare soil cover did not significantly differ by soil type ($F = 0.64$, $P = 0.53$). While there was no significant interaction between treatment and

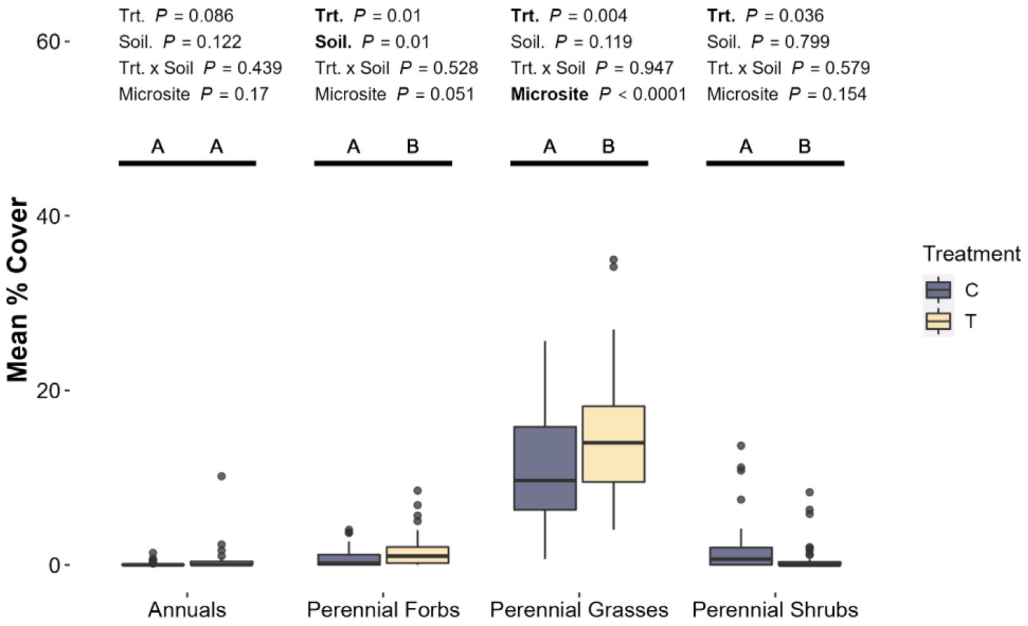

Figure 2. Analysis of variance (ANOVA) comparisons within functional groups showed that mean percent cover was significantly different between treatment and control plots for perennial forbs, perennial grasses and perennial shrubs, but not for annual plants. Significant differences are denoted by letters, where treatment types with differing letters are significantly different from each other. ANOVA results for each functional group are reported at the top of the figure, with significant effects bolded.

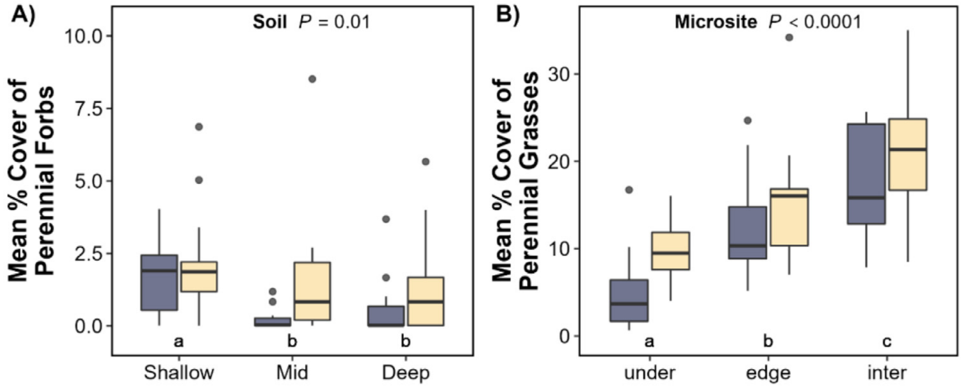

Figure 3. Cover only differed by soil type for **A,** perennial forbs and only differed by microsite for **B,** perennial grasses. Significant differences are denoted by letters, where groups with differing letters are significantly different from each other.

soil type ($F=0.56$, $P=0.58$), the deep soils tended to have a greater reduction in bare soil in treated areas relative to shallow soils (Fig. 1A).

Perennial grass and forb cover were significantly higher in treated (masticated) compared with untreated (control) plots ($F = 8.98$, $P=0.004$; $F = 6.93$, $P=0.01$, respectively). Shrub cover was significantly lower in treated plots ($F = 4.54$, $P=0.04$; Fig. 2). There was no difference in annual plant cover between treated and untreated plots ($F = 3.02$, $P=0.09$). Differences in percent cover across soil types were only significant for perennial forbs ($F = 4.84$, $P=0.01$), with the shallow soil type having greater forb cover (Fig. 3). There were no significant interactions between treatment and soil type among any of the plant functional groups ($P > 0.4$), suggesting that treatment effects were similar regardless of soil type. ANOVA also revealed a significant difference in cover across sampled microsite positions for perennial grasses ($F = 33.08$, $P \leq 0.0001$), with higher cover in interspaces compared with edge (1.35 × higher, $P=0.003$) and under microsites (2.6 × higher, $P \leq 0.0001$; see Fig. 3). There were no significant differences in cover among microsites for the other functional groups.

Cover of introduced species was not different between treatments ($F = 2.98$, $P=0.09$), soil types ($F = 1.72$, $P=0.19$), or microsite positions ($F = 1.72$, $P=0.19$), nor were any of the interactions significant ($P > 0.15$). Although the difference was not significant, introduced plant cover in treated plots was slightly higher than control plots: 0.38% (± 0.15 standard error) cover of introduced species in treatments compared with 0.03% (± 0.01 standard error) in control plots. By contrast, native species cover was 17.61% (± 0.87 standard error) in treatments and 13.84% (± 0.86 standard error) in controls. Only three species of introduced plants were confirmed present in this study: *Salsola tragus* L. (prickly Russian thistle), *Chenopodium album* L. (lambsquarters), and *Tragopogon dubius* Scop. (yellow salsify). *S. tragus* was by far the most frequently observed, appearing in 39 of the 42 quadrats containing introduced species.

Three-yr post-treatment effects of mastication on understory plant community composition

Constrained axes (CAPs) in the dbRDA captured 15.20% of the variance, while unconstrained axes accounted for 84.80% of the

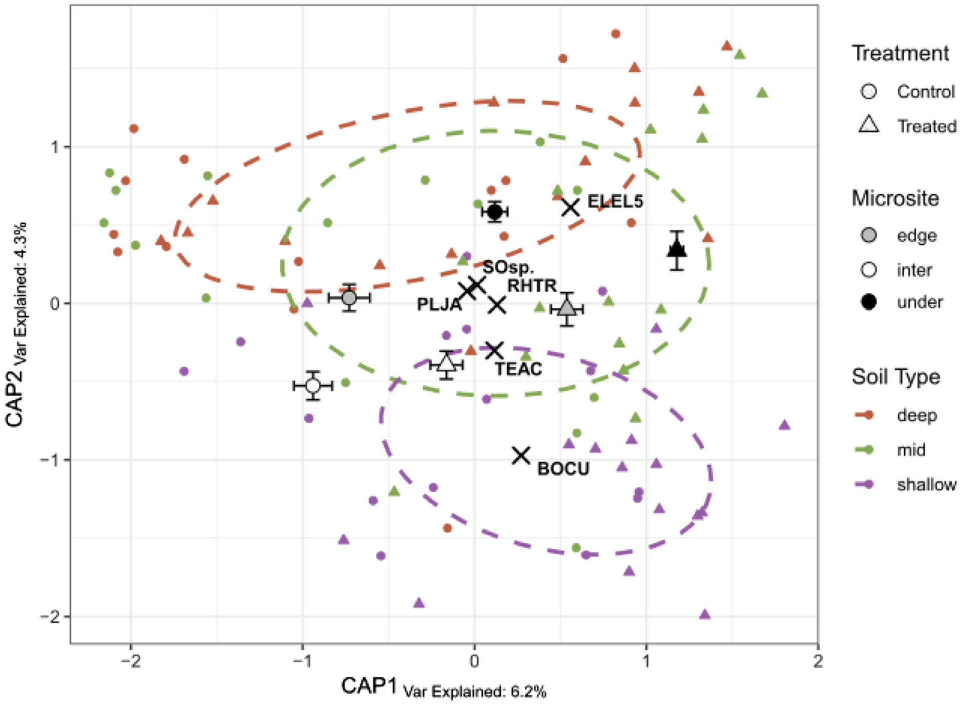

Figure 4. Biplot of the first two constrained axes (CAP1 and CAP2) from the dbRDA. Points represent species composition of each position within each plot, color coded by soil type and shape coded by treatment. Dotted ellipses show 50% confidence ellipses around points in each soil type. Black and gray symbols indicate the average score and standard error on CAP1 and CAP2 for each treatment by position combination (T = treated, C = control). The symbol "×" marks the average score on CAP1 and CAP2 for the six species identified in the Indicator Species Analysis.

Table 1
Indicator species analysis results. Each unique combination of treatment, soil, and position was treated as a group, for which indicator species were identified. Specificity is a measure of relative abundance, whereas fidelity is a measure of relative frequency. The indicator value is calculated as the square root of specificity x fidelity. *P* values indicate the statistical significance of the relationship between a species and group, via a permutation test.

Treatment	Soil	Position	Indicator species	Specificity	Fidelity	Indicator value	*P* value
Treated	Deep	Under	ELEL5 *Elymus elymoides* (Raf.) Swezy	0.2198	1	0.469	0.02
Treated	Mid	Inter	PLJA *Pleuraphis jamesii* (Torr.) Benth.	0.1206	1	0.347	0.025
Treated	Shallow	Under	BOCU *Bouteloua curtipendula* (Michx.) Torr.	0.2084	1	0.457	0.005
Control	Shallow	Under	RHTR *Rhus trilobata* Nutt.	0.5600	0.6	0.58	0.015
			TEAC *Tetraneuris acaulis* (Pursh) Greene	0.3754	0.8	0.55	0.02
Control	Mid	Under	SO sp. *Solanum* sp.	0.7034	0.6	0.65	0.025

variance. Of the constrained axes, the first two axes (CAP1 and CAP2) explained 10.54% of the variance, with CAP1 explaining 6.2% and CAP2 explaining 4.3%. Differences in understory species composition between soil type and microsite are reflected in differences on CAP2, while CAP1 separates composition by treatment (Fig. 4). All fixed effects (treatment, soil type, and microsite) were statistically significant in our PERMANOVA model ($P < 0.001$ for all), indicating that treatment, soil type, and microsite influence understory species composition.

Six indicator species were identified in the indicator species analysis (Table 1). Indicator species were more likely to be identified under trees in control and treated plots post mastication, with *Bouteloua curtipendula* having perfect fidelity (always found) in treated shallow soils under where trees used to exist and *Elymus elymoides* having perfect fidelity in treated deep soils under where trees used to exist. *Pleuraphis jamesii* also had perfect fidelity in treated mid soils in the interspace (see Table 1). However, these three species had very low specificity scores, indicating that although they were always present in each of the aforementioned areas, they were also present in several other areas. *Solanum* sp. (nightshade family) had the highest indicator value because it had relatively high fidelity and specificity values, meaning that in addition to being present in most untreated mid soils under the canopy, it was also not present in most other locations.

Discussion

Mastication treatments are an increasingly common management strategy to increase understory plant cover, improve forage production, and expand habitat for ungulates and grassland-obligate species in many piñon-juniper ecosystems (Redmond et al. 2014a). We found that mastication treatments were effective at increasing understory plant cover and diversity across three common soil types in southeast Colorado, particularly for perennial graminoids. Mastication treatments were similarly effective at increasing native understory plant cover regardless of soil type. This was counter to our initial hypothesis, as we expected to see differences among soil types in understory plant cover following tree removal (Breshears and Barnes 1999). This suggests that soil type does not need to be a major factor in treatment placement in this region.

Mastication effects on plant cover and composition

Mastication treatments were effective at increasing herbaceous plant richness, diversity, and cover, which is consistent with other studies in the region (Owen et al. 2009; Stephens et al. 2016; Havrilla et al. 2017). These changes were largely due to increases in native perennial graminoids, with three native grasses—*E. elymoides, P. jamesii,* and *B. curtipendula*—being most strongly associated with mastication treatments in deep, mid, and shallow soil types, respectively. All three of these species are moderately to highly palatable (USDA NRCS 2022) and provide important forage for livestock and wildlife species, especially *P. jamesii,* which provides suitable forage while actively growing (Simonin 2000), and *B. curtipendula,* which provides forage in both winter and summer (Chadwick 2003). Although we did not directly measure biomass production, we can interpret increases in cover as increases in forage production because the species and functional group composition in control plots was similar to that in treated plots, and where it did differ, other functional types were replaced in favor of perennial grasses (Fig. S1, available online at 10.1016/j.rama.2023.01.013). It is also notable that these highly palatable species were indicators of microsites in masticated areas that were previously under tree canopies, whereas the indicator species for the under microsite in control areas were *R. trilobata, T. acaulis,* and *Solanum* sp., all of which are forbs and/or shrubs that provide little forage for cattle (though *R. trilobata* provides browse and fruit for several wildlife species; Anderson 2004). It is important to note that despite grazing by livestock throughout the study, livestock-preferred species contributed the most to increases in understory cover, suggesting that overgrazing is not occurring. However, further study on the effects of livestock grazing after mastication in this area is needed to understand whether grazing reduces seed production and plant productivity, as it has elsewhere (e.g., Bates 2005; Daryanto and Eldridge 2010). There were relatively few increases in annual forbs and annual grasses following mastication treatments, unlike other studies that have reported large influxes in annuals after mastication (Ross et al. 2012; Redmond et al. 2014b; Havrilla et al. 2017). This may be due to high perennial grass cover in this region relative to others resulting in a greater seed and bud bank of perennial grasses (Allen and Nowak 2008; Ott et al. 2019), or it may be attributed to the 2 below-average precipitation yr that followed the mastication treatment.

Our study suggests that increased presence of introduced species following mastication treatments may not be a major management risk in southeast Colorado relative to other regions. There was a limited abundance of introduced plants across our treatments (mean introduced plant cover was 0.4% in treated areas), unlike other studies that have found substantial influxes of introduced annual forbs and annual grasses following mastication (Redmond et al. 2014b; Havrilla et al. 2017). This could be due to the abundance of existing perennial grasses and/or seed in the seedbank (Allen and Nowak 2008) and also the limited presence of introduced seed sources across treatment areas (Owen et al. 2015). Tree-removal treatments in areas of low pretreatment tree cover (as in this study) are also less likely to be invaded because they do not result in as much of a resource availability pulse (Roundy et al. 2014b). Only three introduced species were present across our sampling area—*T. dubius, S. tragus,* and *C. album*—all of which are annual forbs and only one of which *(S. tragus)* is projected to become more invasive in our study area (McMahon et al. 2021). Another study in northern Arizona also found low introduced species cover 3 yr post mastication when pretreatment cover was low (Rubin and Roybal 2018). As a result, we suggest that managers survey for introduced plants before implementing treatments so that introduced species can be treated beforehand or areas with introduced plants can be avoided. Notably, our study only assessed vegetation response 3 yr post treatment, most of which received below-average precipitation. Thus, the abundance of introduced plants may increase over time, as seen in other studies following mastication and cutting treatments (Bates et al. 2005; Havrilla et al. 2017).

Mastication treatments were similarly effective at increasing native understory plant cover across soil types, despite our hypothesis that they would differ. The lack of difference between soils in understory cover and response to treatment may reflect the unique adaptations of the plant communities on these different soil types or may be an indication that variations in AWC and depth to bedrock of these particular soils are not large enough to affect plant water use partitioning. Even in the deep soils, depth to bedrock is estimated at 97 cm (USDA NRCS 2018), which is still relatively shallow considering that *B. gracilis* and *E. elymoides,* two of the dominant perennial grasses at the site, can have roots extend as deep as 100 cm (Simonin 2000; Anderson 2003). Therefore, it is likely that competition between trees and understory plants was similar across soil types, leading to similar competitive release after tree removal. Alternatively, the differing species composition between soil types (see Fig. 4) may have resulted in similar percent cover changes, even if changes in abundance of individual plants differed (e.g., a small change in abundance of a species with a large canopy will show a similar cover increase to a large change in abundance of a species with a small canopy). Tree cover was also relatively sparse across all soil types (8% ± 0.13 SE) representative of a piñon-juniper savanna (Romme et al. 2009; Amme et al. 2020), so competition between trees and herbaceous plants may not have played a big role in this study.

Understory plant richness, cover, and functional group cover did not respond differently to treatment between different microsites, which is surprising given that microsites under tree canopies likely had more nutrients and experienced much greater increases in light and moisture after treatment than interspace microsites. However, although not statistically significant, understory plant cover did increase the most in microsites under the canopy and could continue increasing in cover with more time. Across all plots, understory plant cover and richness were lower under tree canopies (or mulch piles of masticated trees), mostly due to less perennial grass cover. This is likely due to unfavorable conditions for perennial grass establishment and growth in the shady conditions under intact canopy and the physical barrier of deep mulch piles (Schott and Pieper 1985; Young et al. 2013b; Fornwalt et al. 2017). Discrepancies between microsites in soil nutrients (e.g., Padien and Lajtha 1992; Rau et al. 2009) may also have played a role in dictating plant establishment, though this was not tested. Perennial forb cover was higher in undercanopy microsites across treated and control plots, and five of the six indicator species identified were indicators of under microsites, exemplifying that these microsite positions were especially unique in understory species composition. Despite the lack of treatment by microsite interactions in functional group cover and richness, the dbRDA indicates that understory species composition was distinct between microsite positions and significantly changed after treatment (see Fig. 4). Therefore, although plant cover similarly increased across all soil types and microsites, compositional changes are occurring and may become more apparent in future years.

Conclusion

Numerous studies, including ours, depict an increase in herbaceous cover and richness associated with piñon-juniper thinning (Redmond et al. 2013; Fick et al. 2022). These results align with the management objectives of mastication in this area, which include increasing forage for cattle and wild ungulates. In addition, increased herbaceous species richness and cover increases biodiversity and may promote resistance to invasion (Urza et al. 2019). Our finding that herbaceous cover and richness increased regardless of soil type also provides managers with insight into treatment prioritization. While increased forage for cattle and wild ungulates may be one management priority in piñon-juniper ecosystems, others include managing for woodland-obligate bird species (Magee et al. 2019), soil stability (Owen et al. 2009), carbon sequestration, air pollutant removal (Dicus et al. 2009; Fernandez et al. 2013), and culturally important resources like pine nuts (Miller and Albert 1993), all of which would require leaving trees on the landscape. In addition, wild ungulates and livestock benefit from a mosaic of openings interspersed with wooded areas, as tree cover provides protection for wild ungulates and thermal cover for wildlife and livestock alike (Gottfried et al. 1995).

A balanced approach to management is needed to achieve these various goals. Our study found that mastication was effective at increasing forage production across all soil types, which should give managers more flexibility in grazing management strategies and choosing areas for treatment. For example, treatments can avoid old-growth piñon-juniper woodlands and critical habitat for declining woodland-obligate wildlife species (Bombaci and Pejchar 2016) while increasing forage production in less critical areas. Treatments may also be prioritized in areas where nonwoodland habitat is valued more highly (such as for livestock grazing or habitat connectivity for grass- and shrub-obligate wildlife species) or with poor future woodland climatic suitability (Redmond et al., in review). As managers determine where and why thinning is desired, we encourage a thorough investigation of the multiple consequences and management objectives. Short- and continued long-term monitoring of thinning projects is important to better understand impacts and to ensure that primary objectives of mastication treatments are achieved.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2023.01.013.

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