Synergistic effects of wild ungulates and management intensification suppress native plants and promote exotics

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A B S T R A C T

In managed forest landscapes, conflicts among wood production, ungulates, native biodiversity, and exotic species are common. As humanity allocates more land as intensively managed plantations, these conflicts may become more severe. For instance, native ungulates have been implicated in the loss of native plant diversity, declines in timber revenues and the spread of exotic species in many forest systems, yet the synergistic effects of management and ungulate herbivory are not well understood.

We hypothesized that herbicide and herbivore-induced suppression of native forage species promotes the release of exotic species in young forest plantations. Further, we expected herbivory and the retention of native forage via less intensive management would have negative consequences for reforestation objectives. To test this hypothesis, we conducted an experiment that manipulated management intensity (via herbicides) and access of two deer species to vegetation (via exclosures) on 28 operational Douglas-fir plantations of the Pacific Northwest, USA. We recorded yearly plant species cover estimates and tested the effects of herbivory and herbicides on native and exotic plants during the first six years of plantation establishment.

Heavier herbicide treatments reduced the cover and diversity of native plants, and increased the cover of exotics over time, particularly that of exotic herbaceous species. Regardless of herbicide intensity, herbivores reduced the cover of native forage species. In a treatment that represents operational standards applied to over 2.5 million ha in the region, the suppression of native species by deer corresponded with an increase in exotic species cover by 23 percent, resulting in equitable abundance of native and exotic plants. As expected, Douglas-fir growth was suppressed when herbivores were present and vegetation was left untreated by herbicides, although the presence of deer promoted both crop-tree growth and the relative abundance of exotics in our most intensive treatment, presumably due to the added suppression of native competitors.

Our findings suggest that wild ungulates amplify management-driven shifts toward exotic species in intensively managed forest plantations. Exotic plant forage status and adaptations to frequent disturbance seem to be key mechanisms for the synergistic effects we observed. Without herbicides, diverse assemblages of native species are buffered from herbivory and exotic species proliferation, with potential tradeoffs for timber production. Our results highlight the role of management intensity in modifying the interactions among exotic plants and native herbivores, contributing to a mechanistic understanding of the role of native biodiversity in regulating exotic species spread. Our data provide further support for growing evidence that synergistic effects of multiple drivers can facilitate exotic plant proliferation.

1. Introduction

As intensive natural resource management becomes prevalent, native species continue to decline while exotic species proliferate, with annually estimated costs of invasions previously exceeding $120 billion in the US alone (Pimentel et al., 2005). Aside from ecological and economic considerations, the loss of native species has implications for ecosystem services provided to humans (e.g., timber production, cultural goods, traditional medicines, foraging and hunting grounds; Chapin et al., 2000, Liebhold et al., 2017, Von Hagen et al., 1996). In intensive agricultural and silvicultural systems, non-crop plants are often controlled mechanically and chemically to promote the yield of crop species. As a result, exotics often invade in the wake of the human-caused disturbances (Hobbs and Huenneke, 1992, Liebhold et al.,

2017). The transition from natives to exotics often simplifies community structure and is hypothesized to alter natural processes, such as herbivore-plant interactions, which may feed back to further increase invasion (Hobbs and Huenneke, 1992, Vavra et al., 2007). Previous studies have shown that diverse communities are more resistant to herbivory and invasion (Kennedy et al., 2002, Stokely et al., 2018), although the variation of traits for both native and exotic species are suggested to be determinant factors (Chapin et al., 2000).

Globally, forestlands are a major source of biodiversity and natural resources, with intensively managed forest plantations providing up to two-thirds of industrial wood products on only 7 percent of global forest land (Brockerhoff et al., 2013, Carle and Holmgren, 2008, Kanninen, 2010). Timber harvesting often results in soil disturbance, in some cases facilitating invasion by exotic plant species (e.g., Sutherland and Nelson, 2010). Timber harvesting can also release a diverse variety of native early-successional plant species that have evolved with disturbances (Halpern and Spies, 1995). As a result, managers often re-plant crop trees at high densities and prescribe vegetation management practices (e.g., herbicides) to control understory vegetation, reduce harvest rotation ages, and increase revenues for timber companies (Wagner et al., 2006). Herbicides are well known to promote crop-tree productivity and vegetation management studies have revealed that they can also promote the relative abundance of exotics (Dinger and Rose, 2009).

Mammalian herbivores are also often viewed as a major cause of exotic species proliferation, because foraging of native vegetation may reduce the competitive advantage of natives, releasing exotics with traits adapted to frequent above-ground disturbance (e.g., enemy release hypothesis, Eschtruth and Battles, 2009, Keane and Crawley, 2002). Wild and domestic ungulates have been attributed to declines in native plant diversity and the spread of exotic-herbaceous species in many regions (Habeck and Schultz, 2015, Fleming et al., 2009, Putman, 1996, Vavra et al., 2007). However, in some cases, grazing by domestic ungulates has been an effective tool for controlling exotics and promoting plant diversity (Davies et al., 2016), depending on factors such as site productivity, plant traits and forage quality (Huston, 2004, Mitchell et al., 2006). Further, management and disturbance history likely contribute to the varied effects of ungulates on exotic proliferation, since foraging is intrinsically tied to the disturbances that alter plant community composition (Fleming et al., 2009, Hobbs and Huenneke, 1992, Pekin et al., 2016, Vavra et al., 2007).

Timber-harvesting operations promote forage production, attracting ungulates and other fauna, resulting in herbivory-mediated changes to early-successional communities (Geary et al., 2017, Stokely et al., 2018) and human-wildlife conflict when browsing negatively affects crop-tree production (Beguin et al., 2016, Stokely and Betts, 2019). Yet, the ways that vegetation management mediates the effect of ungulates on exotic species remains unclear, and to our knowledge, no studies have tested for the interactive effects of herbicides and ungulates on exotic species over multiple years (Habeck and Schultz, 2015). If such interactive effects exist, they are likely to be most relevant in areas where both intensive plantation forests and native ungulates are common. Western Oregon is dominant producer of softwood lumber and plywood in the US and plantation forests account for > 22% of the statewide forestland, providing two thirds of the yearly statewide timber harvest (Donnegan et al., 2008). In parallel, native ungulates, such as black-tailed deer (*Odocoileus hemionus colombianus*) and Roosevelt elk (*Cervus canadensis roosevelti*), are common in the region and rely on young forest plantations to acquire adequate forage for survival and reproduction (ODFW, 2003, ODFW, 2008). Recent attention has focused on the value of native early-successional vegetation as a major source of broadleaf diversity and foraging habitat for a variety of wildlife species (Hagar, 2007, ODFW, 2008, Stokely et al., 2018).

We hypothesized that the suppression of native species by silvicultural herbicides and herbivory would cause a release in exotic species, and that whether plants are considered forage or non-forage
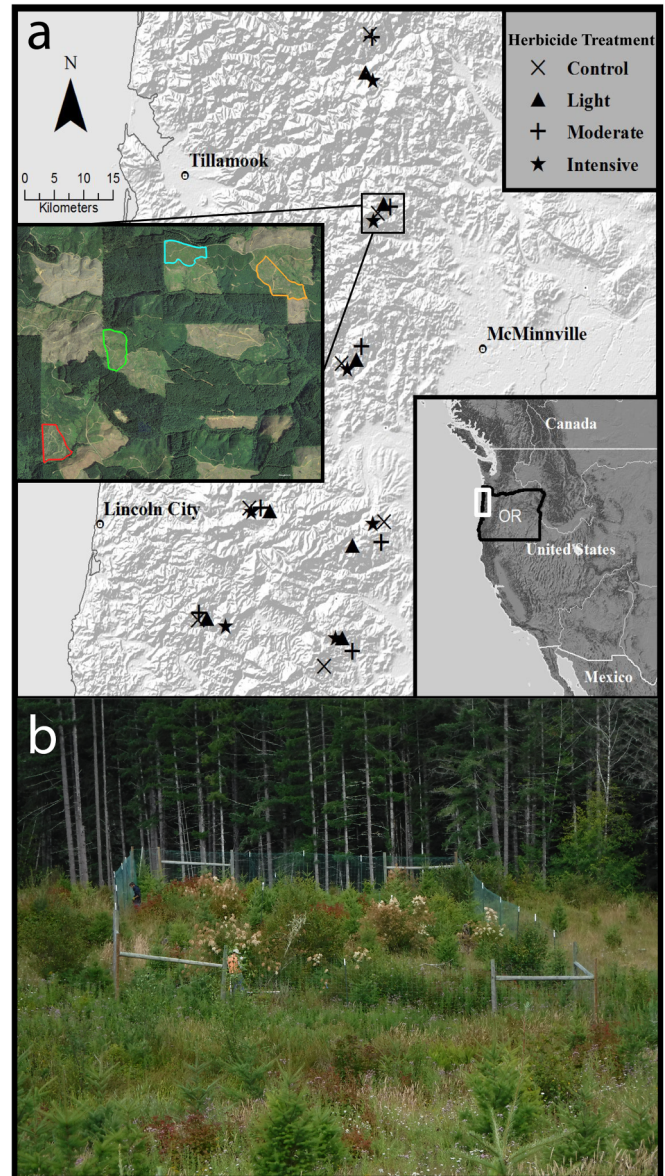

Fig. 1. Study extent (a) of experimental blocks, along a 100 km gradient in the Oregon Coast Range. Each of the seven blocks contained 4 herbicide treatments (untreated Control, Light, Moderate and Intensive), randomly applied at the scale of whole harvest units (ca. 10–19 ha). Within each stand, we randomly assigned a plot for exclosure construction (b) with a randomly located adjacent open plot of the same dimension (225 m^2); for a companion study, ungulate exclosures were paired with bird exclosures (background).

species would be a key mechanism for the release. We expected that the selection of native forage species by herbivores should promote both exotic non-forage species and crop-tree growth. Alternatively, we hypothesized that if exotics assemblages were primarily composed of forage species, then deer and elk would regulate their release. Further, we expected that the retention of native species via less intensive management would have negative consequences for crop-tree growth. To test these hypotheses, we implemented a large-scale experiment that manipulated both the intensity of forest plantation management and access to vegetation by deer and elk (Betts et al., 2013; Stokely and Betts, 2019) and measured plant species responses during the first six years of plantation development.

2. Methods

We conducted the experiment in the northern Oregon Coast Range, USA (Fig. 1). The region is characterized as dissected, low elevation mountains with steep slopes, high net primary productivity and well-drained soils, having a temperate-moist climate (Spies et al., 2007). Precipitation falls primarily as rain from October through June and varies from ~100–400 cm year^{-1}, depending on coastal proximity (Daly, 2019, NRCS, 2018). We selected sites along a 100 km N-S longitudinal gradient within the *Tsuga heterophylla* (western hemlock) climax vegetation zone, which is dominated by second and third-growth stands of *Pseudotsuga menziesii* (Douglas-fir) and scattered composition of *Abies grandis* (grand fir), *Abies procera* (noble fir), *Alnus rubra* (red alder) and *Acer macrophyllum* (big-leaf maple).

Understory plant associations include *Acer circinatum* (vine maple), *Rhododendron macrophyllum* (Pacific rhododendron), *Holodiscus discolor* (oceanspray) *and Polystichum munitum* (sword fern; see Franklin and Dyrness 1988 for plant association descriptions). Many wildlife species are associated with disturbed early-successional plant communities, including numerous birds, rodents, *Ursus americanus* (black bear), black-tailed deer and elk (Hagar, 2007). Estimated densities of black-tailed deer and Roosevelt elk range form 3.7 to 5.3 deer km^{-2} and 1.1 to 3.0 elk km^{-2} across the entire geographical extent (Oregon Department of Fish and Wildlife, unpublished data). Populations of both species are spatially variable and concentrated in areas with high composition of early-successional vegetation, but remain relatively consistent year round, because they do not display inter-annual migrations (ODFW, 2003, ODFW, 2008).

Approximately 45% of the Coast Range is composed of intensively managed industrial forestlands, including roughly 4% managed state forestry lands (Spies et al., 2007). Forest plantations are harvested on short rotations (i.e., ~40–50 years) using cable and ground-based clear-felling operations, followed by dense plantings of Douglas-fir (i.e., ~1100 trees ha^{-1}) and typically two herbicide application entries (i.e., site-preparation and spring herbaceous treatments, with coppicing maple treatments if necessary).

2.1. Experimental design

We selected seven distinct study blocks for our experiment, each of which contained four clearcut stands (~13 ha in area) that were selected based on the criterion of being 1 to 5 km apart within each block. We attempted to reduce within-block variability in environmental conditions while minimizing the potential for animal movement to confound effects among herbicide treatments. Among the seven distinct study blocks, we randomly assigned stands to one of four herbicide treatments (untreated Control, Light, Moderate and Intensive treatments), applied at whole harvest-unit scales and with the commencement of treatments starting in the fall of 2010. The four herbicide treatments represented a gradient in forest management intensity with varying chemical mixture intensities, specificity and application timing among treatments (Table 1, Appendix A). The Light herbicide treatment represented management practices more common on state forestlands and the Moderate treatment reflected common management on private industrial forestlands (i.e., aerially treated site preparation – pre and post emergent herbicide, and year 1 herbaceous – post emergent herbicide). The untreated Control and Intensive treatment are not currently applied in the region for typical management, but represented extremes in the treatment intensity spectrum. In the early spring of 2011, all stands were planted by reforestation professionals at approximately 1100 trees ha^{-1} with 2-year old, bare-root Douglas-fir seedlings, the major commercial species in the region.

Within each of the experimental stands, we randomly selected a point location from 30-m grid cells using Geographical Information Systems (GIS version 9.3) for the construction of a 15 × 15 m, 2.4-m tall wildlife exclosure (hereafter 'Excluded' plot; Fig. 1b). We then

Table 1

Timeline of experimental treatments for untreated Control (C), Light (L), Moderate (M) and Intensive (I) herbicide treatments. Chemicals and rates of application are listed in Appendix A.

Activity	Season	Year (post-harvest)	Treatment C	L	M	I
Clearcut timber harvest	Fall-Spring	2009 – 2010 (0)	x	x	x	x
Broad spectrum site preparation	Fall	2010 (0)			x	x
Planted at ~ 1100 trees/ha	Spring	2011 (1)	x	x	x	x
Herbaceous spray	Spring	2011 (1)		x	x	x
Exclosure construction	Spring	2011 (1)	x	x	x	x
Herbaceous spray	Spring	2012 (2)				x
Broadleaf spray	Fall	2012 (2)		x		x
A. macrophyllum coppice spray	Fall	2012 (2)			x	
Herbaceous spray	Spring	2013 (3)				x
Broadleaf spray	Fall	2014 (4)				x

randomly selected one adjacent plot of the same dimension from a population of 12 potential plots, located 15 m from each side of the exclosure where deer and elk were allowed access to vegetation (hereafter 'Open' plot). We attempted to locate exclosures a minimum of 50 m from stand edges while avoiding roads, large skid trails, slash piles, burn piles and extreme slopes, all of which precluded exclosure construction. Topographic features limited the size of exclosures, although the fence size and randomization was sufficient to obtain representative plant species samples from the larger stand area. Further, our exclosure sizes were comparable or larger than other exclusion studies that report strong effects of herbivory on plant composition (Bellingham et al., 2016, Smit et al. 2015, Tanentzap et al., 2009). The fence mesh size was large enough (10 × 8 cm) to allow access by the other, smaller herbivorous mammals in the region (i.e., rodents & lagomorphs), while being tall enough to exclude deer and elk.

From 2011 to 2016, we identified vascular plants to the species level and visually measured the ocular cover of each species, during the peak in vegetation production (July–August), from 12, 1 × 1 m quadrats, systematically located throughout each Excluded and Open plot. Regardless of plant architecture and size, we measured species cover to the nearest 1%, counted as 1% if the species canopy occupied the majority of a 10 × 10 cm quadrant within each quadrat; species that occupied < 1% were counted as 0.5%. We calculated the average cover of each species among the quadrats to obtain a plot-level average per species. In each open plot, we also tallied the number of quadrats with evidence of ungulate herbivory for each species among the six years, and attempted to separate out rodent herbivory from the dataset (i.e., small amounts of damage on foliage and characteristic sharp incisor angles on stems). Using the USDA plant database (NRCS, 2017), we assigned each species to 'native' or 'exotic' status, forb, graminoid, fern, shrub, deciduous tree and coniferous tree life forms and forage and non-forage groups (Appendix B). We classified native, exotic and noxious status based on Oregon state records (compiled from Neill and Puettmann, 2013). We used information provided by Cook et al. (2016) and Ulappa (2015) to assign each species to forage groups, based on potential digestible energy and whether the species was accepted as forage by deer and elk in captive animal trials conducted throughout the region.

To test our hypotheses, we calculated species richness of native and exotic species and summed the cover of all species for each of the following groups (allowing cover to exceed 100% due to overlapping canopies): native species, exotic species, native forage, exotic forage, native non-forage and exotic non-forage. We also calculated the relative abundance of exotics as the summed cover of exotic species divided by the cover of all species. We estimated the mean relative abundance of native and exotic life-form groups for each herbicide × herbivory plot to assess the composition of exotic and native species. We then tallied the number of plant samples with and without evidence of herbivory for

Table 2
Common exotic species and life-history characteristics. "Longevity" relates to the average number of growing seasons a particular species can live. "Forage" relates to the potential nutritional quality to deer and elk. "Resprouting potential" relates to the mechanism which a particular species uses to replace lost above-ground stems. "Reproduction" relates to the primary form of reproduction and "Noxious" status is whether each species is determined to be a noxious invasive species by the State of Oregon.

Scientific name	Family	Longevity	Forage	Resprouting	Reproduction	Noxious
Daucus carota	Apiaceae	Biennial	Forage	Taproot	Seed	No
Torilis arvensis	Apiaceae	Annual	Forage	None	Seed	No
Cirsium arvense	Asteraceae	Perennial	Non-forage	Yes	Seed	Yes
Cirsium vulgare	Asteraceae	Biennial	Non-forage	Taproot	Seed	Yes
Crepis capillaris	Asteraceae	Annual/Biennial	Forage	None	Seed	No
Erechtites minima	Asteraceae	Annual/Perennial	Non-forage	None	Seed	No
Hypochaeris radicata	Asteraceae	Perennial	Forage	Taproot	Seed	No
Lactuca serriola	Asteraceae	Perennial	Forage	Taproot	Seed	No
Leucanthemum vulgare	Asteraceae	Perennial	Non-forage	Rhizome	Vegetative	No
Mycelis muralis	Asteraceae	Annual	Forage	None	Seed	No
Senecio sylvaticus	Asteraceae	Annual	Non-forage	None	Seed	No
Cerastium glomeratum	Caryophyllaceae	Annual	Forage	None	Seed	No
Hypericum perforatum	Clusiaceae	Perennial	Forage	Rhizome	Seed	Yes
Vicia hirsuta	Fabaceae	Annual	Forage	Unkown	Seed	No
Vicia sativa	Fabaceae	Annual	Forage	None	Seed	No
Agrostis capillaris	Poaceae	Perennial	Forage	Rhizome	Seed	No
Aira caryophyllea	Poaceae	Annual	Non-forage	None	Seed	No
Holcus lanatus	Poaceae	Perennial	Forage	Yes	Seed	No
Poa pratensis	Poaceae	Perennial	Forage	Rhizome	Vegetative, Seed	No
Vulpia bromoides	Poaceae	Annual	Non-forage	Unkown	Seed	No
Rumex acetosella	Polygonaceae	Perennial	Forage	Rhizome	Vegetative, Seed	Yes
Digitalis purpurea	Scrophulariaceae	Biennial	Non-forage	None	Seed	No

both native and exotic forage species for each stand per year from 2012 to 2015. Additionally, we used information form Neill and Puettmann (2013) to assess other various traits of the common exotic species found in our study (Table 2). Within each plot, we also tagged each planted Douglas fir and measured the bole diameter (10 cm from the root collar) from 2011 to 2015 and calculated the total basal area for each open and excluded plot per stand.

2.2. Statistical analyses

To test our hypotheses, we employed a repeated-measures, complete block, split-plot design. We tested for the additive and interactive effects of herbicides, herbivory and time on native and exotic species richness, cover, forage groups, exotic relative abundance and Douglas-fir basal area. To test whether herbivores reduce native plant cover, thereby releasing exotics, we quantified our response variable as the difference in exotic plant cover between open and excluded plots. We then modeled this variable as a function of the difference in native cover between open and excluded plots, herbicide treatment, year and their interactions.

To account for repeated measures and spatial dependency between nested sampling units (i.e. stands within blocks, plots within stands) we fit block, stand, and plot as random effects and weighted residuals by year and herbicide treatment to meet statistical assumptions. For exotic species responses we found some minor positive temporal auto-correlation at the first time lag (ACF = 0.25), but estimates were consistent with models we fit for each year individually, so we deemed the autocorrelation as non-problematic. All aforementioned tests were fit in the R statistical program (R Core Team, 2018) using mixed-effects models with the *nlme* package (Pinheiro et al. 2018) and we used the *emmeans* package to estimate means and conduct pairwise comparisons with Tukey adjusted confidence intervals (Length et al. 2018). To test whether deer and elk disproportionately browsed native species across treatments, we fit a generalized linear mixed-effects model with a binomial distribution and a logit link, using the *nlme* package (Bates et al. 2015). The model was fit as odds of a forage plant being browsed as a function of the interaction between herbicide treatment and native or exotic status, with block, stand and observation-level random effects.

3. Results

We observed 131 native species, representing a variety of broadleaf shrubs, trees, forbs, ferns and graminoids and 41 exotic species, which were primarily forbs and graminoids (Table 2 and Appendix B). We found evidence for our hypothesis that both herbicides and herbivory cause a release of exotic species when native species are suppressed (Fig. 2 and Table 3), although counter to our hypothesis, released exotics were often forage rather than non-forage plants.

Heavier herbicides (i.e. Moderate and Intensive treatments) had a strong initial negative effect on native plant cover and richness, and despite the recolonization and regrowth of natives over time, they were unable to recover to control levels by the end of the study (Figs. C.1 and C.2 in Appendix C). With the lack of native plant cover in Moderate and Intensive herbicide treatments, exotic species rapidly colonized the stands post herbaceous herbicide treatments (i.e., 2011 for the Moderate and 2013 for the Intensive treatment; Fig. 2 and Table 1). Despite a decline in native species with increasingly intensive herbicide treatments, the odds of native-forage species being browsed was consistent among herbicide treatments (approximately 21 percent of sampled forage species [95% CI = 17.0, 25.7]). However, as exotic species became increasingly prevalent, the odds of herbivory on exotic-forage species increased from 14% in the Control (95% CI = 9.1, 22.6) to 40% in the Moderate (95% CI = 25.9, 59.0) and 42% in the Intensive treatment (95% CI = 27.5, 65.2).

Regardless of herbicide treatment, deer and elk suppressed native plant regeneration throughout the last half of the study (Fig. 2a), causing native cover to be 12.4 percent lower in open compared to excluded plots in 2014 (95% CI = 3.5, 21.3), 13.9 percent lower in 2015 (95% CI = 4.0, 23.6) and 20.6 percent lower by 2016 (95% CI = 5.8, 35.4). The herbivore-mediated suppression of native plants was most evident in the Moderate treatment, with 24.5 percent lower cover with herbivore access than exclusion in 2014 (95% CI = 7.8, 41.2), 37.2 percent in 2015 (95% CI = 11.3, 41.1) and 33.6 percent in 2016, although confidence intervals slightly overlapped with zero in this last year of the study (95% CI = −1.7, 68.9). Although deer and elk controlled exotic plant growth in the Moderate treatment in 2013, during the last year of the study, exotic plant cover was 23.4 percent greater in open plots than exotic cover within exclosures (95%
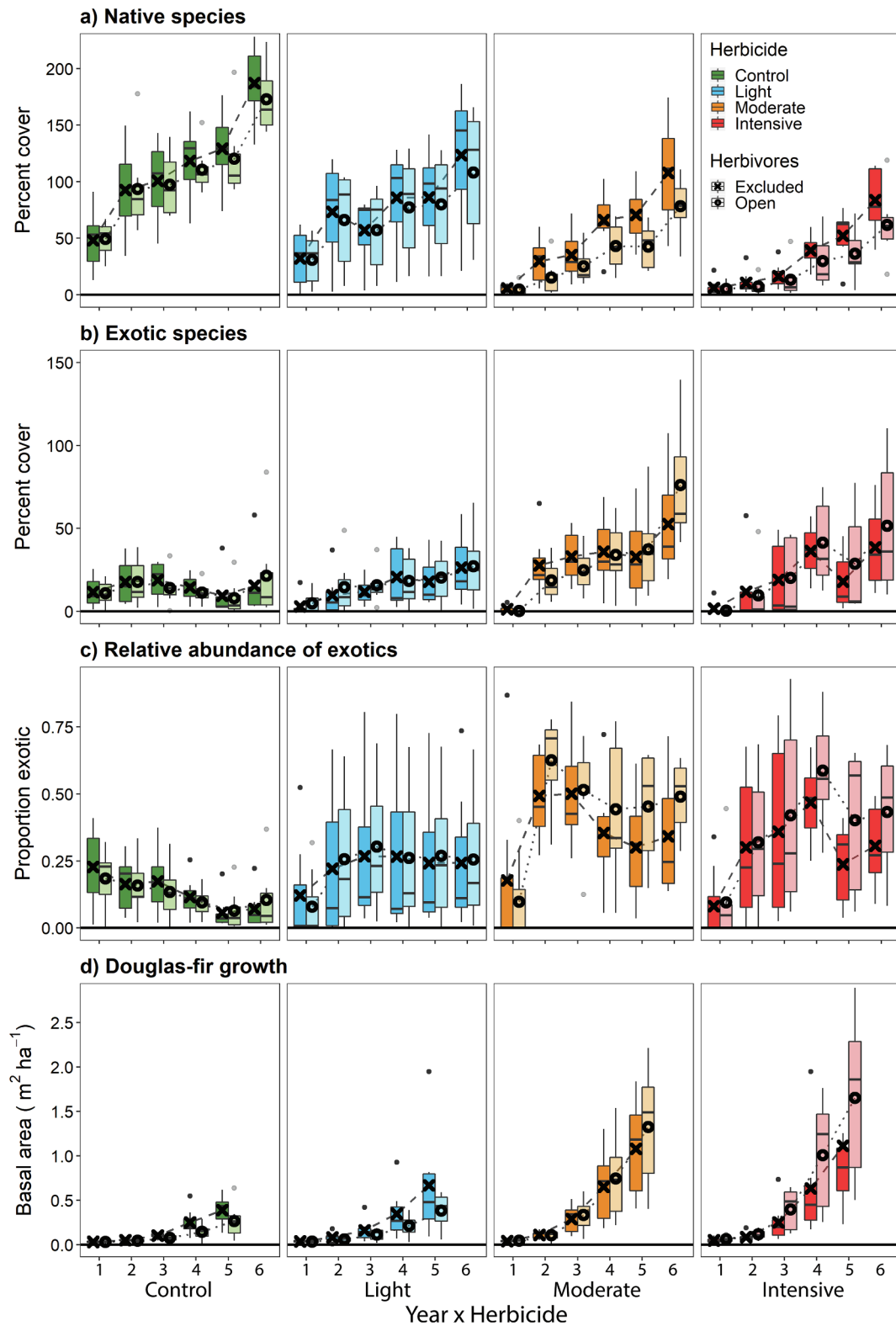
Fig. 2. Boxplots of response variables with herbicide treatment and deer and elk access. The symbols × and o are means, enclosed bars are medians, boxes are interquartile ranges, whiskers are 1.5*interquartile range and dots are outlying data points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

CI = 0.7, 46.2; Figs. 2b and 4a).

Despite greater odds of herbivory on exotic forage species with heavier treatments, herbivore access promoted the relative abundance of exotics in 2015 and 2016 for both Moderate and Intensive treatments, resulting in equitable cover between native and exotic species

(Figs. 2c and 4c). We found evidence that the herbivore-mediated reduction in natives interacted with herbicide treatment to release exotics ($F_{3,96} = 3.38$, $P = 0.02$) and this effect depended on time since harvest (Table 3). Despite an herbivore-mediated reduction of natives corresponding with a reduction of exotics early in the study, we found that

Table 3

F tests from mixed-effects models. For all models, with the exception of exotic release, we fit models with the additive and interactive effects of herbicide , herbivory, and year, including a 3-way interaction and random effects of block, stand and plot. Repeated measures were conducted from 2011 to 2016 for most models although Douglas-fir basal area only included 2011–2015. For the exotic release model, herbivory is the difference in native cover between open and excluded plots and only block and stand were included as random effects.

| Response	Herbivory $F_{1,24}$	P	Herbicide $F_{3,18}$	P	Year $F_{5,240}$	P	Herbivory × Herbicide $F_{3,24}$	P	Herbivory × Year $F_{5,240}$	P	Herbicide × Year $F_{15,240}$	P	3-Way Interaction $F_{15,240}$	P
Native cover (%)	7.41	0.01	25.22	< 0.0001	161.76	< 0.0001	1.30	0.30	3.10	0.01	7.54	< 0.0001	0.36	0.99
Exotic cover (%)	0.14	0.71	4.51	0.02	34.25	< 0.0001	2.30	0.10	1.51	0.19	6.93	< 0.0001	0.69	0.79
Native richness (N)	0.02	0.88	21.24	< 0.0001	172.92	< 0.0001	0.50	0.69	0.46	0.80	6.79	< 0.0001	0.22	1.00
Exotic richness (N)	0.68	0.42	6.87	< 0.01	48.97	< 0.0001	0.31	0.82	0.48	0.79	6.55	< 0.0001	0.55	0.91
Exotic relative abundance	5.73	0.02	4.97	0.01	5.74	0.0001	2.71	0.07	1.04	0.40	8.16	< 0.0001	0.61	0.87
Native forage cover (%)	10.61	< 0.01	24.19	< 0.0001	80.45	< 0.0001	0.22	0.88	2.61	0.03	3.56	< 0.0001	0.19	1.00
Exotic forage cover (%)	0.30	0.59	2.46	0.10	31.21	< 0.0001	0.41	0.75	1.89	0.10	5.86	< 0.0001	1.13	0.33
Native non-forage cover (%)	0.42	0.53	5.75	0.01	82.24	< 0.0001	1.41	0.27	0.72	0.61	3.33	< 0.0001	0.54	0.92
Exotic non-forage cover (%)	0.01	0.94	0.76	0.53	9.88	< 0.0001	0.52	0.67	0.19	0.97	7.43	< 0.0001	0.40	0.98
	$F_{1,24}$	P	$F_{3,18}$	P	$F_{4,192}$	P	$F_{3,24}$	P	$F_{4,192}$	P	$F_{12,192}$	P	$F_{12,192}$	P
Douglas-fir basal area (m² ha⁻¹)	0.30	0.59	10.58	< 0.001	602.73	< 0.0001	4.83	0.01	0.47	0.76	3.86	< 0.0001	0.82	0.63
	$F_{1,96}$	P	$F_{3,18}$	P	$F_{5,96}$	P	$F_{3,96}$	P	$F_{5,96}$	P	$F_{15,96}$	P	$F_{15,96}$	P
Exotic cover (excluded-open)	15.39	0.00	2.94	0.06	3.66	< 0.01	3.38	0.02	4.54	< 0.001	2.19	0.01	1.62	0.08
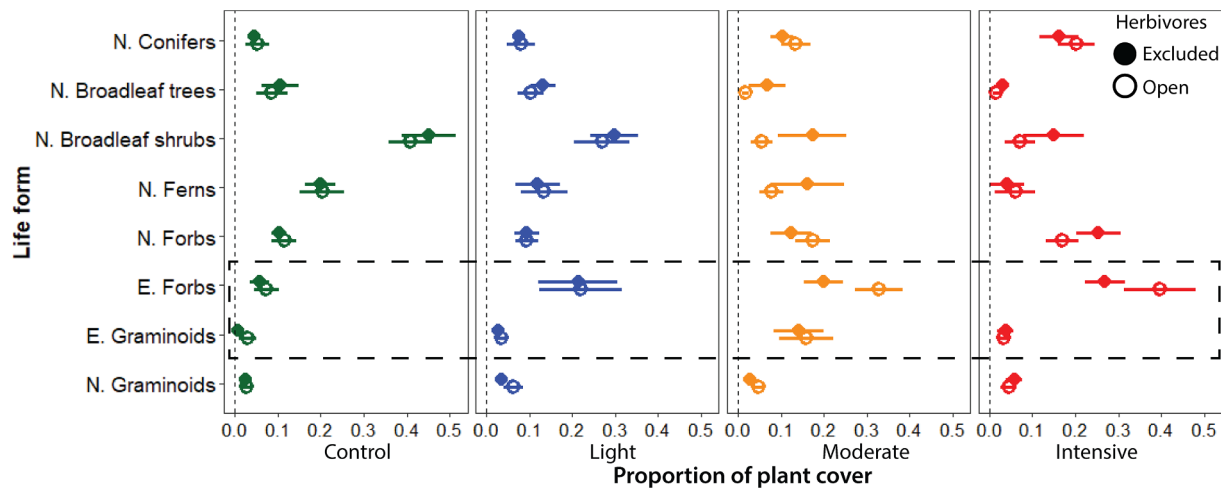
Fig. 3. Relative abundance of native (N.) and exotic (E.) life forms among herbicide treatments in open plots with deer and elk access (open dots) and in exclosures without deer and elk (closed dots). Dots are mean relative abundances and bars are standard errors; exotic species are enclosed by the hashed box. Native broadleaf shrubs dominated Control plots, which also consisted of a variety of broadleaf trees, ferns and forbs. The relative abundance of native broadleaves and ferns decreased with increasingly intensive herbicide treatments, especially in plots open to deer and elk. Exotic forbs increased in abundance with increasingly intensive herbicide treatments and dominated plots where deer and elk had suppressed native life forms.

the continued suppression of natives by deer and elk resulted in the release of exotics during the last two years for the Moderate treatment and three years for Intensive treatment (Fig. 4d).

Native broadleaf shrubs and trees seemed to be most sensitive to the heavier treatments and herbivory, with evidence that fern cover was also greater in exclosures for the Moderate treatment and native forb cover was greater within exclosures in the Intensive treatment. Exotic forbs and graminoids were primarily mat forming and seed dispersed species with high re-sprouting potential (Fig. 3 and Table 2). Four of the exotic species we observed are listed as noxious in the region, and some with strong herbivory-defense mechanisms (e.g., *Cirsium* spp; NRCS, 2017). However, counter to our hypothesis, the exotics that were released by herbivores in the Moderate treatment tended to be forage, rather than non-forage species (Fig. 4b). With deer and elk access in the Moderate treatment, exotic forage species increased in abundance by 10.5 percent in 2015 (95% CI = 1.7, 19.3) and 24.6 percent in 2016 (95% CI = 0.7, 46.2), despite a greater selection of herbaceous forage by deer and elk in that treatment.

As expected, herbicides increased Douglas-fir basal area growth through time (Fig. 2d and 4e), but this effect was altered by the presence of deer and elk ($F_{3,24}$ = 4.83, P = 0.01). In the Control, basal area was 0.56 times lower with herbivore presence than in exclosures (95% CI = 0.3, 0.9), and 1.67 times greater with herbivore presence than in exclosures in the Intensive treatment (95% CI = 1.0, 2.8).

4. Discussion

Together, our results provide experimental evidence that the compounding effects of herbicides and herbivory on native species release exotic plants in young forest plantations, which in turn promotes Douglas-fir growth. Increasingly intensive herbicide treatments, aimed at promoting crop-tree regeneration efforts, reduced the abundance and richness of native plant species (i.e., broadleaves and ferns) and facilitated the colonization and proliferation of exotics (i.e., forbs and graminoids). Wild ungulate herbivores reinforced the effect of herbicides by further suppressing the development of native plants,
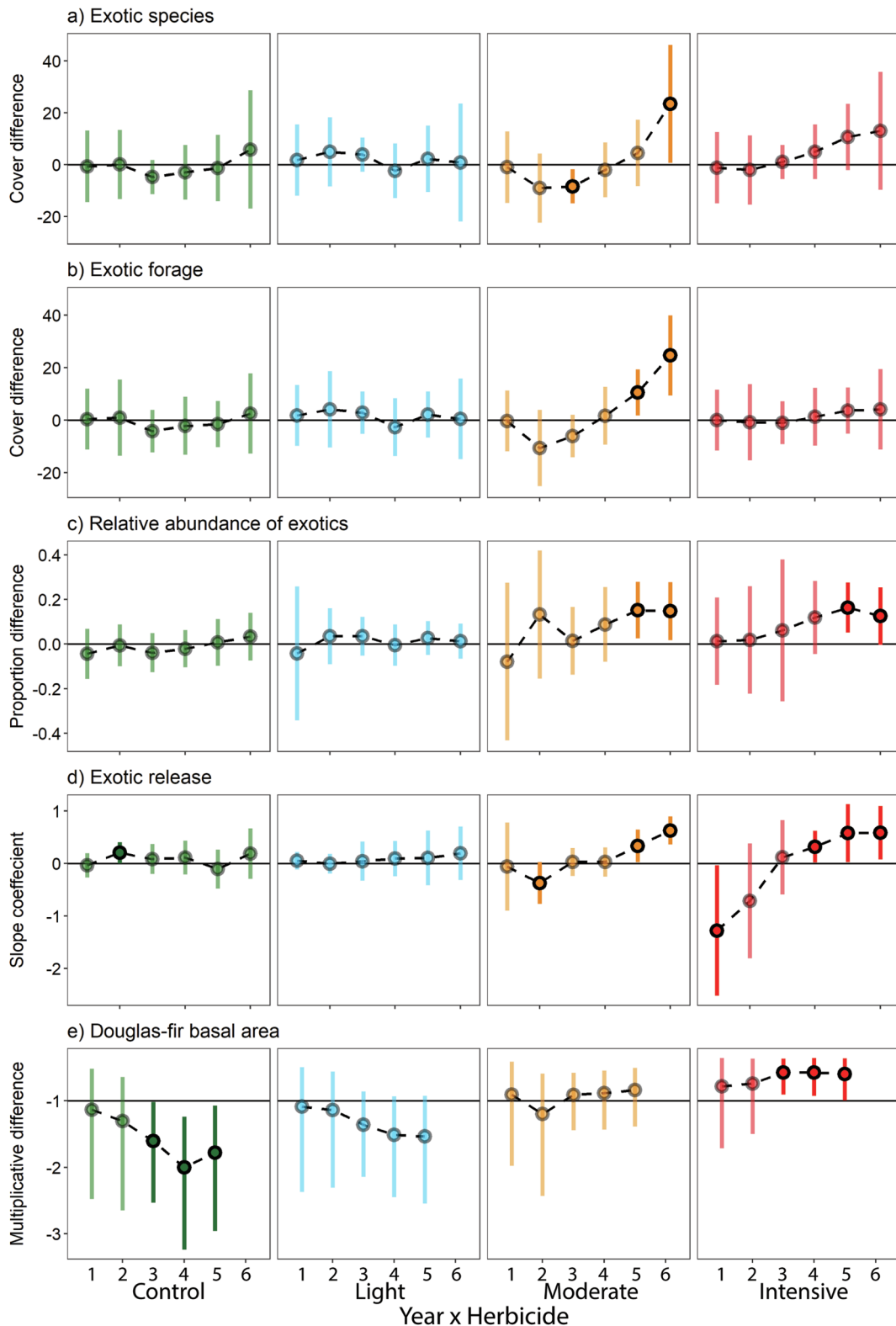
Fig. 4. Effect of herbivory on response variables through time. Dots are the mean effect (median-multiplicative effect for back-transformed crop-tree volume and basal area estimates) and bars are 95% confidence intervals. Values below the line indicate a negative effect and values above the line indicate a positive effect of herbivory. Dark-contrast dots and bars indicate evidence of an effect of herbivory for a given treatment and year.

synergistically amplifying the release of exotics. In the Moderate herbicide treatment, released exotics were primarily herbaceous forage species, which contradicts our hypothesis that released exotics would be non-forage species. Further, as exotic forage species increased in abundance, the selection of those herbaceous forage species by deer and

elk also increased, likely filtering community assembly to favor herbivory-tolerant species (e.g., *Hypochaeris radicata* [hairy cat's ear], *Holcus lanatus* [velvet grass], *Poa pratensis* [Kentucky bluegrass]). However, planted Douglas-fir (a species with relatively low forage quality in the region) also benefitted from herbicides and herbivory via

the removal of other native competitors – especially in the Intensive treatment (Stokely and Betts, 2019). Despite evidence for an effect of herbivory on natives among all experimental units, the unsprayed Control and Light treatments were relatively resistant to strong effects of herbivory and invasion. In turn, the abundance of competing vegetation in Control and Light treatments came at the expense of planted Douglas-fir growth, with evidence that the crop trees were also more sensitive to herbivore access in the Controls.

Many studies investigating the effects of management and disturbance on invasion do not account for the effects of herbivory (Vavra et al. 2007, Wisdom et al. 2006), and many studies that have tied invasion to herbivores generally ignore land management intensity (e.g., Averill et al. 2018). The initial timber harvest in our study was the primary disturbance that released native understory species, immediately promoting plant diversity and forage production (Cook et al. 2016, Halpern and Spies 1995, Liebhold et al. 2017). The management gradient, which was implemented to promote Douglas-fir growth by reducing competition from other plants, reflected an increasing intensity and frequency of disturbance. As expected, the cover and richness of native broadleaf species were substantially reduced with increasingly intensive treatments. This, in turn, promoted crop-tree growth and facilitated invasion in cases where open germination sites were created.

The altered state of the low-diversity, invaded communities likely amplified the effect of herbivores over time, promoting herbaceous forage species that are adapted to frequent above-ground tissue loss (Grime 1988). Overall, our results seem to support a general trend, wherein the chronic effects of herbivory decrease the production of woody-broadleaf vegetation and promote herbaceous- and exotic-forage species (Geary et al., 2017, Pekin et al. 2014, Rooney 2009, Royo and Carson 2006). Our findings also support the hypothesis that herbivore-mediated release of exotic-herbaceous plants are dependent on the effects of management on native plants (Vavra et al. 2007). Without herbicide treatments (i.e., our untreated Control), the diversity and density of broadleaf vegetation prevented exotic invasion and limited the strong effects of herbivory on community composition.

Numerous mechanisms may be responsible for invasion in the face of herbivory (Kalisz et al. 2014, Vavra et al. 2007). Trampling by ungulates can also damage vegetation and expose soil, allowing the introduction and germination of seeds, and in many cases, animal dispersed propagules (Habeck and Schultz 2015, Vavra et al. 2007). In our study, herbicides initially removed native vegetation and created open germination sites, allowing wind and animal dispersed seeds to invade. The suppression of native species by herbivores promoted a release in exotic forage in our Moderate treatment when forage was allowed to rebound after 2011. The positive effect of herbivory on exotic-herbaceous forage is consistent with other studies, in which persistent herbivore pressure and trampling can promote a foraging-lawn condition when forage species are resilient to above-ground tissue losses (Best and Arcese 2009, McNaughton 1984).

The timing of forage production likely contributed to the synergistic effects that we observed in our study (Geary et al. 2017). Exotic-herbaceous species are primarily available as forage during the early spring through early summer when water is not limiting and vegetation production may exceed forage consumption. The recolonizing native-broadleaf species, however, are generally the most important forage resource during the summer and fall, coinciding with a critical period of forage acquisition and senescence of herbaceous forage (Geary et al. 2017, Cook et al. 2016). Therefore, natives were likely unable to compensate because vegetative production in treated stands approximated consumption by herbivory.

4.1. Conservation and management implications

Conservation efforts have gone to great lengths to control biological invasions, and despite the associated economic costs of conservation

efforts, native biodiversity continues to decline globally (Chapin et al. 2000, Liebhold et al. 2017). The ecological and societal value of native species conservation and the control of exotics has been contentious among scientists and managers, due to uncertainty regarding the ecological functions and societal value of native versus exotic species (Simberloff 2012). Traditionally, numerous indigenous tribes managed landscapes for many of the native broadleaf shrub species in our study, due to their cultural value as food, medicine, shelter and in providing forage for game species such as deer and elk (Von Hagen et al. 1996). In contrast, in many silvicultural systems, native broadleaf species are negatively valued as "weeds" (Dinger and Rose 2009), which suggests a tradeoff exists between economic and cultural values in managed forest landscapes. Our study highlights the value of native species conservation in forest plantations for curtailing exotic species proliferation, while providing potential cultural resources and forage for valued game species. Our results also reveal potential tradeoffs between timber production, foraging habitat and native plant species conservation.

In many regions, particularly the US Pacific Northwest, the conservation of early-successional plant communities is gaining more attention (Swanson et al. 2011) and increasingly, timber harvests are being used on federal lands to emulate natural disturbances, while promoting timber revenues and early-successional biodiversity (Bureau of Land Management, 2016, Franklin and Johnson 2012, Phalan et al. 2019). Well-established native plant assemblages may be relatively resilient to herbivory and exotics following harvest, although reforestation requirements may be at odds with herbivory in this case (Bureau of Land Management, 2016). A body of research also indicates that industrial forests have value for the conservation of early-successional biodiversity (Demarais et al. 2017). However, the combined effects of herbivory and herbicides during the first 6 years of stand establishment had suppressed the native broadleaf component in our Moderate herbicide treatment – which most closely reflects treatments applied to over 2.5 million ha in the PNW (Campbell et al. 2010, Donnegan et al. 2008).

As evident with our most Intensive treatment, the combined effects of herbivory and herbicide may benefit reforestation efforts, resulting in rapid canopy closure and increased timber production but also truncating succession and driving a local decline in native biodiversity. As with other regions, successive timber harvests and intensive management may increase the prevalence of exotic species in the PNW (Liebhold et al. 2017), with implications for forest regeneration and herbivore-exotic plant feedbacks. If land management objectives include both conservation and timber production, less intensive management practices may be needed to promote native species while providing forage and limiting herbivore-mediated proliferation of exotics. Less intensive management may come at the cost of reforestation efforts to promote an even-aged cohort of native trees, resulting in reduced timber production when crop trees are more susceptible to competition and herbivory. However, managing for native foraging habitats at landscape scales may increase nutritional carrying capacity, benefitting deer and elk populations but also increasing their potential for negative effects on native vegetation and crop trees.

We conclude that managers should recognize the ways that land use alters the effects of herbivory when considering options for mitigating herbivore impacts on native plant species. Our study provides clear evidence that the effects of herbivory depend on land management intensification and *vice versa*. In cases where high amounts of natives are conserved, the capacity of herbivores to promote exotics may be substantially reduced or eliminated. When herbicides reduce the abundance and richness of native species, exotics tend to invade. As herbivores rely on early-successional vegetation for forage, they also alter the interactions among native and exotic plants, suppressing natives and facilitating an increase in exotics under common management practices. Further, the effects of increasingly intensive management and exotic proliferation may have consequences for the habitat of other wildlife species (Schmidt and Whelan 1999) and altered ecological

processes such as fire behavior (Brooks et al. 2004), nutrient cycling (Ehrenfeld 2003) and succession. Our findings reveal the need for management and research to account for the interactions among management practices, herbivores and native plants when considering the role of exotic species proliferation in managed landscapes.

Declaration of Competing Interest

Acknowledgements

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.7267/2n49t7709.

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