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RESEARCH ARTICLE

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Experimental evaluation of herbicide use on biodiversity, ecosystem services and timber production trade-offs in forest plantations

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Abstract

1. The value of non-commodity ecosystem services provided by forests is widely recognized, but intensive forest management practices are increasing, with uncertain consequences for a multitude of these services. Quantitative relationships among biodiversity conservation, timber production and other ecosystem services remain poorly understood, especially during the early-successional period of intensively managed forestlands.
2. We manipulated management intensity in regenerating forest plantations to test the prediction that treatments aimed at maximizing timber production decrease biodiversity conservation and non-timber services. We measured species richness of 3 taxonomic groups and 13 proxies for provisioning, cultural and regulating services within stands randomly assigned to one of the three herbicide application intensities or an untreated control.
3. Herbicides increased allocation of net primary production to crop trees, increasing projected timber volume and revenues at 40- and 60-year harvest ages. Commonly used herbicide prescriptions reduced culturally valued plants by 71%, wild-ungulate forage by 41%, avian richness by 20% and pollinator floral resources by 42%, the latter being associated with 38% fewer pollinator species. However, agriculturally valued bumblebees, pollination of blueberries, avian-mediated arthropod control, wild ungulate observations and regulation services tied to forest productivity appeared unaffected by increasing management intensity and timber production.

4. Species richness and flora-provided services in young forest plantations exhibited strong trade-offs with projected timber production, whereas post-treatment vegetation regeneration and site-level variation likely maintained a range of other services. Although vegetation recovery is important for supporting wildlife and some ecosystem services on industrial forestlands, it is unlikely that any single prescription can optimize both timber and non-timber benefits to society across managed forest landscapes. Instead, producing different services in discrete portions of the landscape may be necessary.
5. *Synthesis and applications*. We tested the effects of intensive forest management via herbicides on ecosystem services and found that biodiversity responses and services from early-successional vegetation trade-off against timber production. A number of services appeared to be compatible with timber production, although no single prescription optimized the full range of services. Stand-level biodiversity conservation and a variety of services could potentially be provided by treatment skips and less-intensive management on productive sites, although it is unlikely that all services can be optimized without landscape-level planning.

KEYWORDS
biodiversity conservation, ecosystem services, forest economics, forest management, herbicides, plantation, timber, trade-offs

1 | INTRODUCTION

In recent decades, environmental policies and management have focused on the importance of ecosystem services—defined as the value of provisioning, regulating, supporting and cultural benefits that humans derive from nature (Costanza et al., 2017). Although economic systems are supported by provisioning services such as food and fibre, other potential benefits that humans derive from biodiversity and ecological processes are less well quantified, especially the degree to which they are influenced by commodity production (Bennett et al., 2009). Indeed, many aspects of biodiversity and natural variability (e.g. competing vegetation, herbivores, disease, natural disturbances) may be perceived as ecosystem disservices in production systems due to concern for adverse effects on the provisioning of goods to society (Ceausu et al., 2019). Intensive land management practices often aim to control natural variability to facilitate a steady production of economically valuable crop species (Wagner et al., 2006).

A growing body of research indicates that biodiversity promotes ecosystem functioning (Cardinale et al., 2012), and consensus is emerging that biodiversity loss reduces the efficiency by which ecosystems produce biomass, store carbon and recycle nutrients (Felipe-Lucia et al., 2020). Because management can directly or indirectly alter biodiversity and ecological processes, some ecosystem services may also decline with intensive land uses that aim to optimize a specific service. Management objectives that focus on producing a narrow range of ecosystem services may therefore trade-off against a variety of other ecosystem services (Felipe-Lucia et al., 2020; Martin-Lopez et al., 2014).

Timber production constitutes an economically quantifiable ecosystem service and, as the global demand for wood products increases, more forestland is predicted to be under high-production intensive forest management (Food & Agriculture Organization of the United Nations, 2018). Forest plantations account for only ~7% of forestland globally yet provide ~33% of legally sourced roundwood volume to global markets (Barua et al., 2014; Brockerhoff et al., 2013). Intensively managed plantations in temperate regions are often characterized by even-aged forest management, via the application of clear-cut harvest operations, vegetation management (e.g. herbicides) and dense monospecific tree plantings. These practices favour the production of high-value timber species by controlling early-successional floristic conditions that would otherwise impede crop-tree growth and development (Wagner et al., 2006).

A wealth of information is available on the management, processes and biodiversity of early-successional forest stages in temperate latitudes, including responses following natural disturbances, timber harvesting and intensive management (Bormann et al., 2015; Donato et al., 2012; Hagar, 2007; Halpern & Franklin, 1990). Although numerous studies have investigated vegetation and taxon-specific responses to herbicide use in silvicultural systems (Lautenschlager & Sullivan, 2002; McComb et al., 2008; Stoleson et al., 2011; Wagner et al., 2006), we still know little about the relationships among ecosystem services provided early in succession under different management scenarios (Kroll et al., 2020). A number of ecosystem services provided in managed forest landscapes have also been examined using correlative data collected at broad spatial scales (Felipe-Lucia et al., 2018; Gamfeldt et al., 2013; Nelson et al., 2009), or assessed in literature reviews and by expert opinion (Brockerhoff et al., 2013; Kremen & Merenlender, 2018; Paul et al., 2020). Experimental approaches that manipulate vegetation in regenerating stands can provide stronger inference on the potential range of ecosystem services provided as a function of management intensity (Turner et al., 2013).

Managed forests in the Pacific Northwest region of North America provide an ideal setting to quantify the effects of intensive management on ecosystem services. The region contains some of the most productive forests in the world (Van Tuyl et al., 2005), with approximately 28% of forest cover being planted timberlands (Oswalt et al., 2019). Specifically, Oregon leads the national softwood lumber and plywood production, contributing 16% and 28% of the US production, respectively (Oregon Forest Resources Institute, 2019).

We established a 6-year experiment in the Oregon Coast Range, USA, that manipulated management intensity via varying degrees of herbicide application, and quantified 16 ecosystem service and biodiversity responses with high economic or societal value in the region (Reid et al., 2005; Table 1). Our objectives were to (a) quantify how management to promote timber growth and revenues influences a range of ecosystem services and (b) test whether these ecosystem services exhibit positive relationships or trade-offs with timber production. We predicted that ecosystem services provided in young forest plantations would be reduced by the direct effects of herbicides on vegetation and subsequent indirect effects on taxa at higher trophic levels. We predicted that such reductions would result in strong trade-offs with timber production but also expected positive relationships for responses related to tree growth and removal of competing vegetation (i.e. standing carbon, litter decomposition; Devine et al., 2011; Flamenco et al., 2019). Finally, we expected that intermediate herbicide intensities may be sufficient to initially control competing vegetation and promote timber production, but low enough in application to retain non-timber services and biodiversity.

2 | MATERIALS AND METHODS

We conducted our experiment along a 100 km longitudinal gradient in the northern Oregon Coast Range, USA (Kroll et al., 2017; Stokely & Betts, 2019; Figure 1). The region is primarily composed of second- and third-growth stands of native Douglas-fir trees *Pseudotsuga menziesii* with approximately 41% managed as private industrial, 25% as federal reserve and matrix lands, 22% as private non-industrial and 12% as state forest lands (Spies et al., 2007). The region is characterized as dissected, low-elevation mountains with steep slopes, high net primary productivity and well-drained soils (Spies et al., 2007), with a 100–400 cm precipitation gradient falling primarily as rain from October through June each year (Daly, 2019).

We established a randomized-complete block experimental design with 28 harvested stands (ranging from 9 to 19 ha in size), clustered into seven distinct study blocks and including an eighth block for timber and avian surveys (N = 32 stands). Each block contained four separate forest stands, primarily composed of merchantable Douglas-fir trees that were harvested using cable and ground-based clear-felling operations in the fall 2009 to winter 2010. For each block, we randomly assigned each stand to one of four treatments: intensive, moderate, light and an untreated control, each receiving the same seasonal timing and chemical application rates among blocks (Table 2, Appendix S1.1; Kroll et al., 2017). The light treatment consisted of aerial applications of spring-herbaceous (2011) and fall woody-broadleaf treatments (2012). The moderate included aerial applications of a broad-spectrum, site preparation spray (2010), aerially applied spring herbaceous spray (2011), and follow-up on-the-ground spot treatments of clump-sprouting maple where present (2012; 3/8 stands). The intensive treatment included an aerial site preparation (2010), repeated aerial spring herbaceous (2011, 2012, 2013) and fall woody-broadleaf treatments (2012, 2014). Moderate treatments reflected the management regime commonly applied on private industrial forestlands, whereas light treatments represented less-intensive management typical of state forestlands. The control and intensive treatment represents extremes in vegetation retention and management, respectively, and are beyond operational norms. Each stand was replanted in spring 2011 at approximately 1,100 trees/ha with native nursery-stock Douglas-fir seedlings, the major commercial species in the region.

2.1 | Flora sampling

Within a 225-m^2 plot, randomly assigned to each stand, we visually estimated the cover and recorded the presence of inflorescences for each vascular plant species from 12, 1-m^2 quadrats (Stokely & Betts, 2019). We tallied the number of species native to Oregon that were detected within 225-m^2 plots, including an average richness across years and accumulated richness (i.e. average-annual richness and total species observed, respectively; Appendix S1.2). Pollinator floral resource abundance was determined by tallying the number of quadrats with inflorescences present for each species known to be pollinated by animals, and then summing observations across species per plot from 2011 to 2016. To quantify variation in pollination and subsequent berry production (Benjamin & Winfree, 2014), we deployed four sentinel highbush blueberry plants *Vaccinium corymbosum* in containers that were fenced to avoid the confounding effects of ungulate herbivory in spring 2016, using mean wet-weight berry mass as a measure of pollination services (Appendix S1.3; Isaacs & Kirk, 2010).

For culturally valued plants, we used information from Von Hagen et al. (1996) to categorize plants as having value as wild foods, traditional medicines and economically valuable non-timber forest products, and summed cover estimates for this group across 2011–2016 (Appendix S1.2). To estimate forage production for ungulates hunted as big game, we developed allometric biomass-regression equations, developed from clipped plots, to estimate the net forage biomass produced within the 225-m^2 plots from 2011 to 2016, using cover and height covariates (Appendix S1.2).

TABLE 1 Ecosystem service and biodiversity response variables, with relevance for society and ecological functioning, representing provisioning, regulating, cultural and biodiversity categories. Timber, carbon and revenues were projected to 2051 and 2071 from field data collected in 2012 and 2015. We refer to ecosystem services provided by non-timber vegetation as flora-provided services and note that certain services can be included under multiple ecosystem-service categories (e.g. bumblebees as provisioning [agricultural pollination] and regulating services [maintenance of plant diversity])

Response	Proxy	Year	Category	Relevance or function
Flora				
Native plant richness	Native plant conservation	2011–2016	Biodiversity	Conservation organizations, wildlife
Floral resources	Pollen source	2011–2016	Biodiversity/regulating	Conservation organizations, pollinators
Blueberry pollination	Pollination services	2016	Cultural/regulating	Indigenous communities, foragers, wildlife, pollination
Culturally valued plants	Non-timber forest products	2011–2016	Cultural	Indigenous communities, foragers, floral industry
Wild ungulate forage	Wild-ungulate conservation	2011–2016	Cultural/biodiversity	Hunters, conservation and hunting organizations
Fauna				
Wild ungulate observations	Hunting potential	2012–2015	Cultural/biodiversity	Hunters, state conservation funding
Pollinator richness	Pollination potential	2015	Biodiversity/regulating	Plant reproduction and diversity
Bumblebee counts	Crop pollinators	2015	Provisioning/regulating	Local farmers, berry and seed crops
Avian richness	Bird conservation	2011–2016	Biodiversity	Bird watchers, arthropod control, seed dispersal
Avian-herbivore control	Herbivore control	2012–2015	Regulating	Top-down pest regulation
Productivity				
Timber projection	Timber provisioning	2012, 2015	Provisioning	Timber industry, state forests, wood products
Revenue projection	Timber revenues	2012, 2015	Provisioning	Timber industry, economy
Standing carbon projection	Carbon storage	2012, 2015	Regulating	Carbon policies, climate regulation
Soil carbon stocks	Carbon storage	2015	Regulating	Soil health, climate regulation
Soil nitrogen concentration	Soil nutrition	2015	Regulating	Productivity, nutrient cycling
Litter decomposition	Nutrient cycling	2015–2016	Regulating	Decomposition, nutrient cycling

2.2 | Fauna sampling

To quantify the use of plantations by wild ungulates, we deployed motion/infrared activated camera traps (Bushnell Trophy Camera, model 119436; n = 28) within each 225-m^2 plot and recorded the average number of photos taken per day (~May to October) from 2012 to 2015 of individual black-tailed deer *Odocoileus hemionus columbianus* and Roosevelt elk *Cervus canadensis roosevelti* (Appendix S1.4).

To estimate pollinator richness, invertebrate pollinators touching inflorescences within 12, 1 m × 2 m random-stratified plots located in 2015 were caught via nets or an aspirator during a 10-min period, dispatched in ethanol, dried, pinned and identified to species level (Appendix S1.5). We also sampled for agriculturally valued yellow-faced bumblebees (*Bombus vosnesenskii*; Rao & Stephen, 2009) using

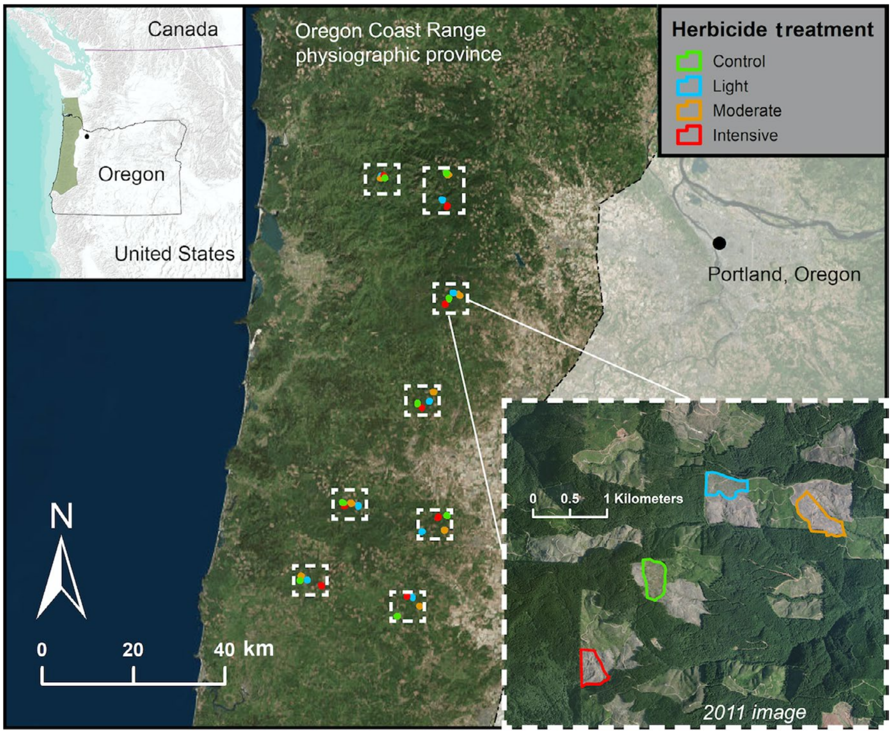

FIGURE 1 Study extent showing the geographical distribution of experimental research blocks, with four treatments within each study block (i.e. three herbicide treatments and an untreated control), distributed along a 100 km north-south gradient in the Coast Range Physiographic Province, Oregon, USA

TABLE 2 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 S1.1. Spot treatment of *Acer macrophyllum* only occurred on 3/8 moderate treatments stands (i.e. where present)

Activity	Season	Year (post-harvest)	Treatment C	L	M	I
Clear-cut timber harvest	Fall–Spring	2009–2010 (0)	x	x	x	x
Site preparation spray	Fall	2010 (0)			x	x
Planted at ~1,100 trees/ha	Spring	2011 (1)	x	x	x	x
Herbaceous spray	Spring	2011 (1)		x	x	x
Herbaceous spray	Spring	2012 (2)				x
Broadleaf spray	Fall	2012 (2)		x		x
Acer macrophyllum spray	Fall	2012 (2)			x	
Herbaceous spray	Spring	2013 (3)				x
Broadleaf spray	Fall	2014 (4)				x

12 blue vane traps per stand; 6 traps were filled with propylene glycol and 6 left dry, each deployed with a stratified-random approach consistent with pollinator richness methods and sampled over three consecutive sampling rounds from May to August 2015. Yellow-faced bumblebees were carefully washed of propylene glycol using hot water, soap and ethanol, then-air dried, pinned for identification and tallied per stand (Appendix S1.6).

To estimate average-annual and accumulated avian richness, we randomly established 3, 50-m radius plots within each stand to conduct point count surveys from 2011 to 2016 (Ralph et al., 1995). Point counts included all birds located within the 50-m radius (including aerial insectivores, but not fly-over individuals) and were sampled between sunrise and 10 a.m. by separate observers for a 10-min period per point count. Each count was conducted four times during the breeding season and aggregated to obtain a stand-level estimate. We estimated avian richness in each stand using N-mixture occupancy modelling approach using the JAGS function in the 'R2JAGS' package (Kroll et al., 2020; Su & Yajima, 2020; Appendix S1.7). We estimated the regulating service of avian-mediated herbivore control as the log-response ratio of herbivorous arthropod abundance within 225-m^2 netted bird exclosures, to arthropod abundance within ungulate exclosures open to birds—collected via sweep nets, restricted area leaf searches and pitfall traps (detailed sampling methods are given in Harris et al., 2020 and Appendix S1.8).

2.3 | Forest productivity and regulating services

The year following planting (2012), we tagged and measured planted seedlings in 18–20, systematically located, 5-m radius plots and re-measured height and bole diameters of planted and naturally regenerating tree species in 2015 (Appendix S1.9). We also measured the cover of competing vegetation within nested 3-m radius plots. We modelled timber production for a 40- and 60-year harvest rotation by combining two regional tree growth models (SMC-ORGANON and CIPSANON; Hann, 2011 and Mainwaring et al., 2016, respectively). We used economically relevant tree lists and competition metrics in conjunction with annualized growth equations developed by the Center for Intensive Planted-forest Silviculture to project tree growth from 5 to 20 years after planting. The equations accounted for the effect of competing vegetation and potential tree mortality and resulting tree lists were transferred to a tree growth model optimized for plantations in the Pacific Northwest (Hann, 2011), projected out to 40 and 60 years, common rotation ages for private industrial and state forestlands, respectively. We include board feet (bf) as the standard measure of timber volume in the United States; a conversion factor of 150–175 bf/m^3 can be used, although variation in tree growth forms across stands (e.g. taper) may lead to conversion error for stands outside of standard operational treatments (i.e. trees within untreated controls).

To assess the expected revenue of the harvested trees, we calculated a common proxy for the willingness to pay for forest land, the land expectation value (LEV), for two commonly applied discount rates (4% and 6%). This measure accounts for costs associated with the stand establishment (e.g. tree stock, herbicide application) and income and costs associated with future harvest (Appendix S1.10).

We modelled live-tree carbon storage at 40- and 60-year harvest rotation ages using growth models described above and assuming a carbon content of 50% while including non-timber arborescent hardwood species (Appendix S1.11; Matthews, 1993; Ung et al., 2008). To measure soil carbon stocks, we collected and pooled four 625 cm^2 organic horizon samples and four 0–30 cm mineral soil cores from each 225-m^2 plot (Appendix S1.12). We also measured nitrogen concentrations in the 0–15 cm mineral soil layer to assess nitrogen leaching potential and effects of herbicide use on soil nutrient status. To estimate decomposition rates, we deployed 3 litter bags filled with Douglas-fir needles between March and early-April 2016 and collected bags at approximately 3, 6 and 12 months, drying the needles at 50°C for 72 hr. We calculated daily decomposition constants based on changes in dry-weight measurements (Appendix S1.12).

2.4 | Statistical analyses

To assess how each ecosystem service varied as a function of herbicide treatments and projected timber yield, we constructed linear mixed and generalized linear mixed-effects models, including 'study block' as a random effect (Tables S1 and S2). We also fit mixed-effects models with a quadratic function to test for threshold relationships between ecosystem services and timber production, but did not find evidence that those models described the data better than non-quadratic models (Table S3). All analyses were performed in the R statistical program (R Core Team, 2019) using the lmer or glmer functions in the 'LME4' package (Bates et al., 2015). We included herbicide treatment and yield as explanatory variables, respectively, and timber yield was scaled to mean = 0 and *SD* = 1 to facilitate model convergence. We used the dispersion_glmer function in the 'BLMECO' package (Korner-Nievergelt et al., 2015) to test for overdispersion in count responses. We modelled count responses using a Poisson distribution and a log link when no overdispersion was evident, and used a negative binomial distribution otherwise. Goodness-of-fit was assessed through visual examination of plotted residuals.

We applied a Bayesian framework to calculate 95% credible intervals (CrI) for all parameter estimates and for model inference (Korner-Nievergelt et al., 2015). We simulated 10,000 random samples from the joint posterior distribution of the model parameters using the sim-function from the 'ARM' package (Gelman et al., 2007). We then used the 2.5% and 97.5% quantiles of those simulations as the lower and upper limit of the 95% CrI, respectively (presented in parentheses in text).

3 | RESULTS

The effects of increasingly intensive management to promote timber production were most evident for the species richness of all taxa sampled, pollinator floral resources, ungulate forage production and culturally valued plants, while we found little evidence for effects of herbicide use on blueberry pollination, avian-herbivore control, ungulate observations and regulating ecosystem services tied to forest productivity (i.e. soil carbon, nitrogen, litter decomposition). Untreated controls contributed the most flora-provided services and biodiversity while projected timber yield and revenues benefitted strongly from management intensification (Figure 2).

3.1 | Direct flora responses

As expected, both accumulated and average-annual species richness of native plants were strongly reduced by increasingly intensive herbicide treatments, resulting in 30.5% (12.3%, 44.9%) fewer species per year in the light treatment compared to control stands, 49.4% (34.8%, 60.6%) fewer with moderate and 56.5% (42.8%, 66.4%) fewer with the intensive treatment (Figure 3a; Tables S1 and S2), resulting in a negative relationship between native plant species richness and projected timber yield (Figure 4a). Similarly, pollinator floral resources were 33.2% (20.7%, 43.6%) lower in the light, 42.1% (31.3%, 51.4%) lower in the moderate and 56.0% (47.9%, 63.2%) lower in the intensive treatments compared to the untreated control, resulting in a trade-off with timber production (Figures 3b and 4b).

The production of pollinator-dependent blueberries did not differ significantly among herbicide treatments (Figure 3c). However, culturally valued plants were negatively correlated with timber projections (Figure 4d) and compared to the control, net cover for these

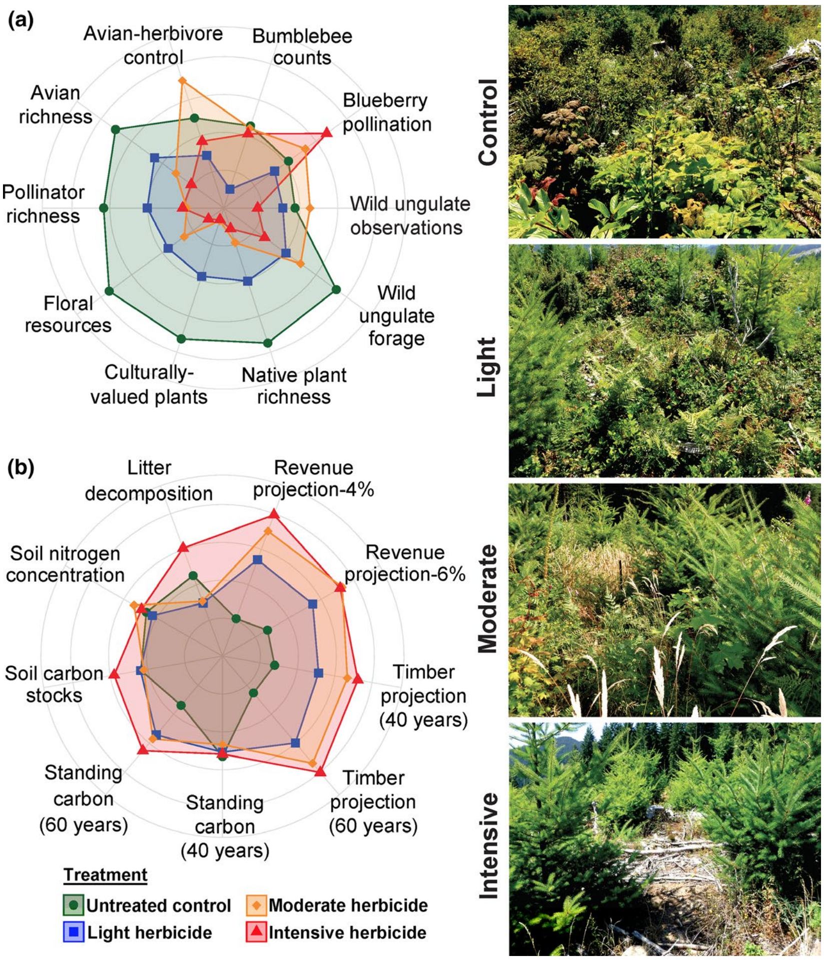

FIGURE 2 Radar diagram illustrating the relativized value of plantations for providing ecosystem services and species richness across three herbicide treatments and an untreated control (left panels); treatment values were relativized by maximum and minimum credibility intervals across treatments from each model, with plot centers representing the lower 2.5% credibility interval. Relative to treated stands, untreated controls promoted species richness and flora-provided services (a). Projected timber volume and expected revenues were optimized with heavier treatment intensities, whereas regulating services were not detectably affected by management (b; Figure 3). Photos taken in 2016 (5-year post-planting) depicting the effects of herbicides on early successional vegetation and crop tree development across treatments (right panels)

plants was reduced by 38.0% (15.1%, 54.4%) for the light treatment and 71.2% (60.1%, 78.9%) and 71.6% (61.7%, 79.0%) for the moderate and intensive treatments, respectively (Figure 3d). Similarly, the production of forage for wild ungulates was reduced by all herbicide treatments, particularly for the intensive treatment (reduction of 64% [39.2%, 90.3%]), resulting in a trade-off with timber production (Figures 3e and 4e).

3.2 | Indirect fauna responses

Despite a negative effect of herbicide treatments on net forage production, we did not detect any differences in observations of wild ungulates, or a significant relationship between ungulate observations and timber production. On the other hand, species richness of pollinators was 37.7% (15.4%, 54.2%) and 35.8% (13.1%, 53.4%) lower with moderate and intensive herbicide treatments, respectively, resulting in a negative relationship with timber yield (Figures 3g and 4g). Although pollinator species richness was not affected by the light treatment, only the light treatment reduced the abundance of agriculturally valuable yellow-faced bumblebees (63.4% [3.95%, 86.3%] reduction; Figure 3h).

Control stands contained an average of 32 bird species per year and average-annual avian richness was reduced by 19.8% (3.64%, 32.8%) in the moderate and 24.9% (9.44%, 37.6%) in the intensive treatment (Figure 3i). We found a negative relationship between average-yearly avian species richness and timber yield (Figure 4i), although we did not find evidence that herbicide treatments affected accumulated avian species richness across years or that a trade-off with projected timber yield was evident (Tables S1 and S2). We found evidence that birds controlled the abundance of herbivorous arthropods (Figure 3j), although the strength of avian-mediated arthropod control was not affected by herbicide treatments, nor did it vary with projected timber yield.

3.3 | Forest productivity

The majority of our experimental stands, including control and light treatments, ranged from 55 to 75 thousand board feet for 40-year projected harvest rotation ages, with much variation in stand-level species richness and ecosystem service values within that range. With moderate and intensive herbicide treatments, timber yield projections for a 40-year rotation age were 19.3% (3.28%, 35.2%) and 22.1% (6.36%, 38.1%) greater than stands not treated with herbicides, respectively (corresponding to an increase of 10.6 × 10^3 bf/ha with moderate [1.8, 19.3] and 12.1 × 10^3 bf/ha with intensive [3.5, 20.9], respectively; Figure 3k). Similarly, projected revenues

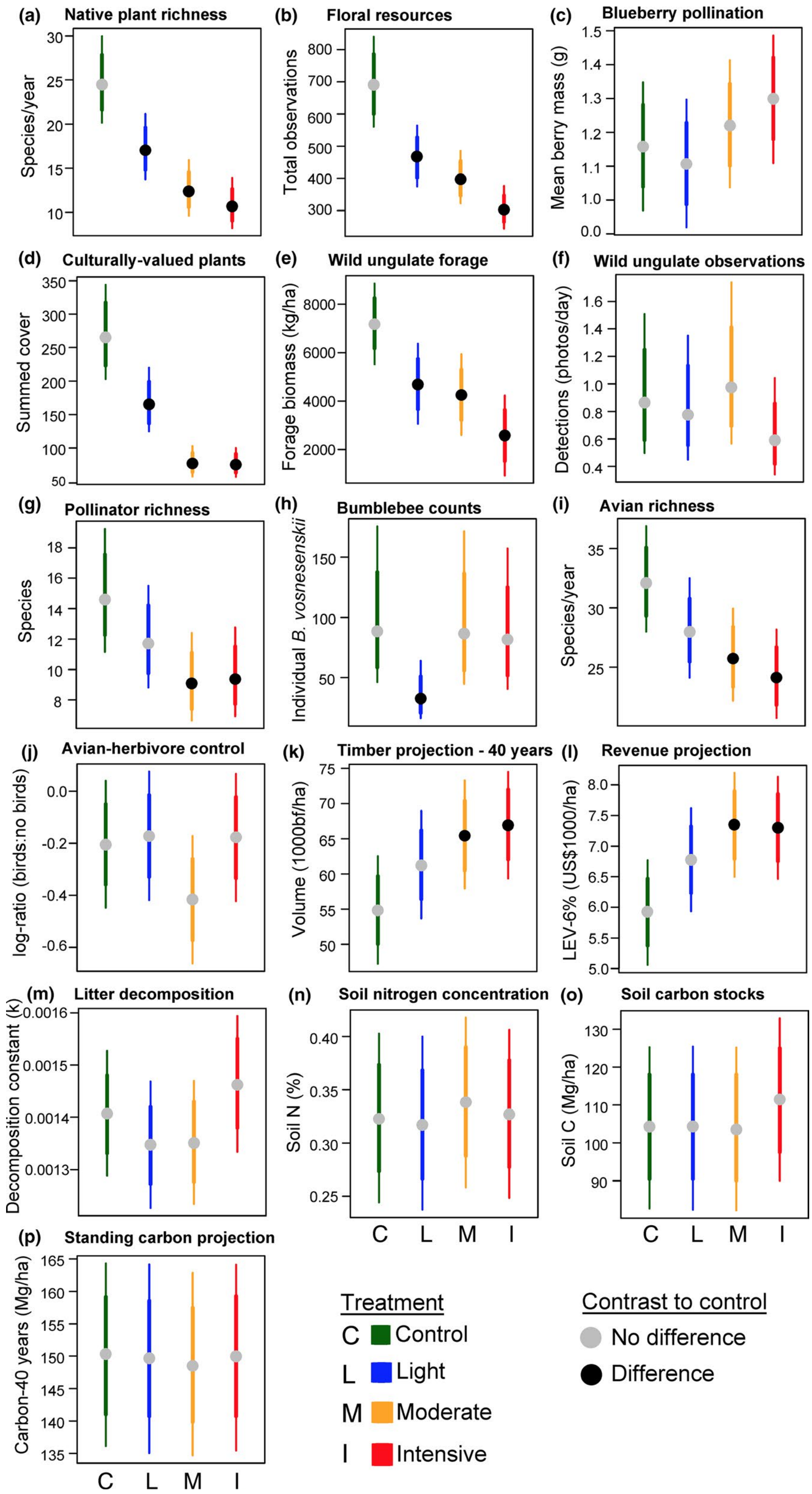

FIGURE 3 Herbicide effects on ecosystem services. Filled circles represent means, thick bars are predicted 80% credibility intervals and thin bars are 95% credibility intervals. Black points represent evidence for a difference between each herbicide treatment contrasted to the control (i.e. credibility interval contrasts do not overlap zero). Credibility intervals are colour coded for each herbicide treatment. Moderate and intensive herbicide treatments promoted timber production and expected revenues. With increasingly intensive herbicide treatments, declines were evident for native plant species richness (a), pollinator floral resources (b), culturallyvalued plants (d), wild ungulate forage (e), pollinator species richness (g) and average-annual avian species richness (i)

were approximately 24.1% (6.60%, 40.7%) greater for moderate and 23.3% (6.58%, 40.2%) greater for intensive treatments, relative to the control at a 6% discount rate. Only at a 60-year harvest rotation age and a lower discount rate (i.e. 4%), did the light herbicide treatment increase timber production and projected revenues above the untreated control (19.0% [3.76%, 34.4%] yield gain and 21.1% [7.46%, 34.8%] revenue gain; Table S1).

We did not detect effects of management intensification on regulating services related to forest productivity, and relationships between timber production versus litter decomposition, soil nitrogen concentrations and soil carbon stocks were all neutral (Figures 3m–o and 4k–m). As expected, we found a strong positive relationship between projected live-tree carbon storage and timber production (Figure 4n). For both 40- and 60-year stand projections, we did not detect any treatment effects as carbon storage was highly variable across stands (Figure 3p).

Hierarchical clustering of a correlation matrix for all services showed strong grouping of responses, revealing trade-offs, positive and neutral relationships among ecosystem service and biodiversity responses (Figure 5). The correlation matrix was consistent with our timber yield trade-off analyses, also showing a negative relationship between timber revenues and culturally valued plants, wild-ungulate forage, native plant species richness, pollinator floral resources, pollinator species richness and avian species richness. Positive relationships were also evident among species richness and flora-provided ecosystem service responses, whereas neutral relationships were evident between regulating services and all other responses.

4 | DISCUSSION

Our findings indicate that intensive management to promote timber production and revenues reduces species richness and associated ecosystem services and these reductions were primarily tied to the direct effects of herbicide in controlling competing vegetation. Herbicide-mediated reductions and trade-offs against projected timber yield were primarily evident for culturally valued plants, wild-ungulate forage, pollinator floral resources, and species richness of native plants, pollinators and birds. Regulating and fauna-provided services were maintained across treatments while flora-provided services and species richness of all sampled taxa also tended to be positively associated with each other, consistent with Nelson et al. (2009).

Our experiment occurred at the scale of entire forest stands, limiting our sample size and likely our ability to detect threshold relationships between timber production and other ecosystem services. However, it is important to note that several of our stands were located on highly productive sites where both timber production and ecosystem services occurred at high levels, including untreated control and light treatment stands. Therefore, thresholds may exist that could serve as 'efficiency frontiers' which optimize the production of both timber and non-timber services, although intrinsic site-level productivity and vegetation composition likely mediate such relationships (Grass et al., 2020; Polasky et al., 2008). Conventional management practices are generally tailored to site-level vegetation characteristics (Lautenschlager & Sullivan, 2002) and are potentially more effective at controlling vegetation than our light and moderate treatments, which were randomly assigned and used standardized herbicide mixtures and application rates. We therefore predict that trade-offs may be more pronounced in non-experimental conditions but also expect that post-treatment vegetation recovery is a key mechanism for supporting wildlife and ecosystem services in forest plantations.

In this study, variation in early successional vegetation influenced herbicide efficacy and post-herbicide vegetation recovery, which likely ameliorated strong effects of the treatments for some wildlife and ecosystem services during stand establishment. For instance, Root et al. (2016) found that declines in moth diversity with herbicide use were moderated by the gradual regeneration and heterogeneity of vegetation within stands, and Ellis and Betts (2011) found that a threshold of 10% woody-broadleaf retention was sufficient to greatly increase the abundance and diversity of broadleaf-associated songbirds. Despite initial reductions in forage production and native vegetation, the post-herbicide retention (i.e. skips in herbicide treatment) and recovery of vegetation likely attracted broadleaf-associated wildlife (Hagar, 2007), such as wild ungulates and songbirds.

Avian-mediated control of herbivorous arthropods was not affected by herbicide treatments, potentially because insectivorous songbird densities were sufficient to control herbivores, regardless of management (Boesing et al., 2017; Harris et al., 2020). Harris et al. (2020) also showed that avian-mediated arthropod control translated to reduced foliar damage to Douglas-fir, but not improved growth, likely because arthropod pests are not a major limiting factor for Douglas-fir growth in western Oregon (Schowalter et al., 1991).

The post-herbicide proliferation of herbaceous plants (often non-native) reported in Stokely et al. (2020) likely supported the floral resources needed by yellow-faced bumblebees in moderate and intensive stands (Krimmer et al., 2019). However, the reduction of native plant species and floral resources appeared to have led to a reduction in pollinator species richness, which did not necessarily result in reductions to the ecological function of pollination for blueberries (Isaacs & Kirk, 2010). This is potentially due to the persistence of abundant and functionally important pollinators such as yellow-faced bumblebees that are common in regenerating Douglas-fir stands (Rivers & Betts, 2021).

The lack of a treatment effect on regulating services tied to forest productivity may have been due to variable environmental and edaphic conditions that outweighed any detectible herbicide effect. Also, vegetation differences that affect energy and water budgets may have not been sufficient to alter decomposition rates among treatments (Edmonds, 1979; Fogel & Cromack, 1977). The lack of differences in soil nitrogen may have also been due to equivalent nitrogen uptake by crop trees or increased leaching losses (Devine et al., 2011). Although we found a positive relationship between timber production

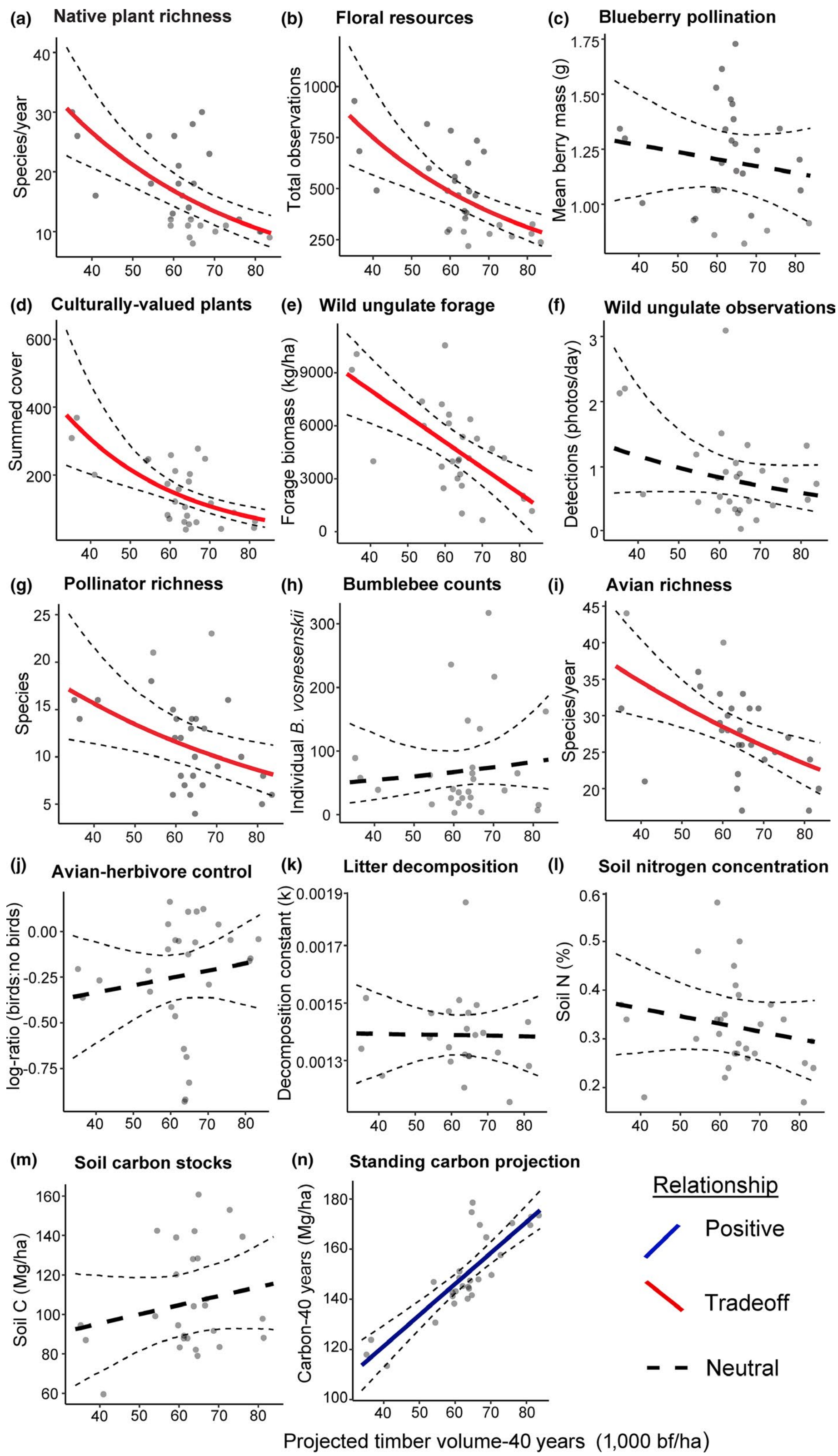

FIGURE 4 Relationship between timber volume (1,000 board ft) projected at 40 years and species richness and ecosystem services. Dotted lines indicate no evidence of a relationship between projected timber volume and response variables, whereas red lines indicate a trade-off and blue lines indicate a positive relationship with projected timber volume. Small dashed lines are 95% credibility intervals and grey dots are raw data points. We found evidence for trade-offs for native plant species richness (a), pollinator floral resources (b), culturally valued plants (d), wild ungulate forage (e), pollinator species richness (g) and avian species richness (i). The only positive relationship we found was for standing carbon projection (n)

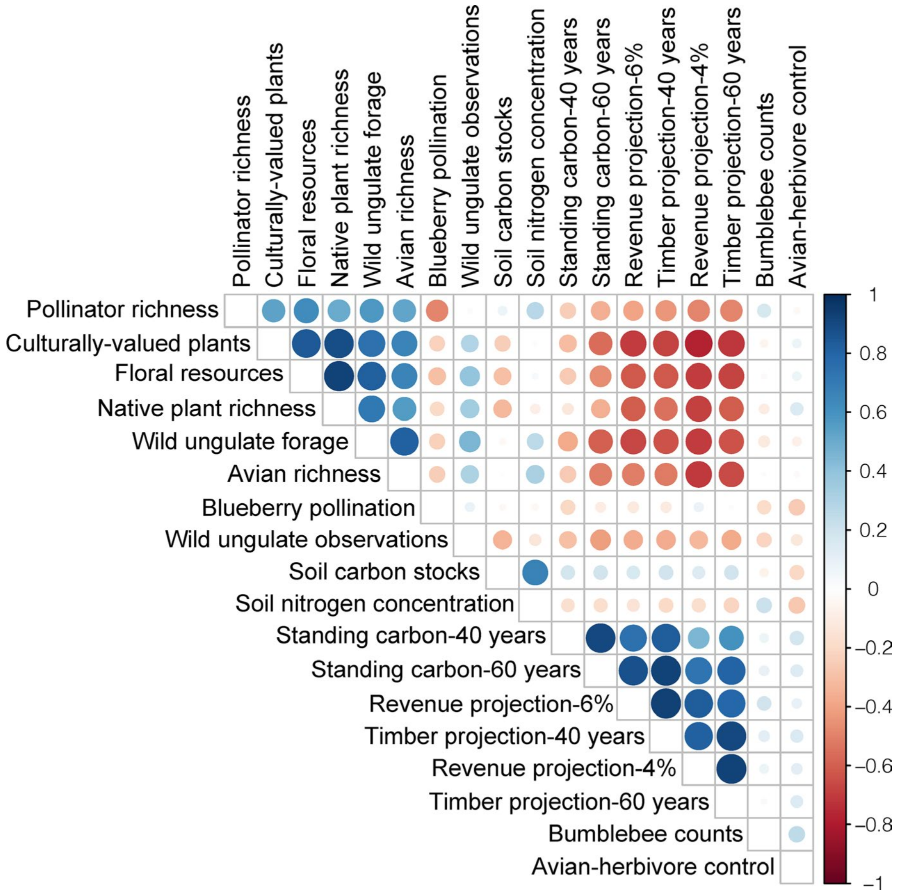

FIGURE 5 Matrix of pairwise correlation coefficients among ecosystem services, organized using hierarchical clustering (Wei and Simko, 2017). Positive relationships (larger-blue dots) were most apparent between species richness responses and flora-provided ecosystem services and between timber production and expected revenues. Trade-offs (large-red dots) were more apparent between timber production/revenues and species richness/flora-provided ecosystem services

and standing carbon stocks, the similarity in projected carbon storage between herbicide treatments and controls likely reflected the inclusion of carbon from non-timber hardwood trees within untreated stands (Figure 3p). Longer-term studies are needed to determine whether intensive vegetation management affects both nutrient cycling and carbon storage at harvest rotation ages (>40 years) and over successive rotations (Powers et al., 2005).

Herbicide use generally accelerates time to canopy closure in Douglas-fir plantations, which truncates the early-successional broadleaf period (Flamenco et al., 2019). The stand-scale truncation of the early successional stage may have consequences for biodiversity later in the rotation (i.e. as early as 12–15 years post-harvest; Harris & Betts, 2021), which we were unable to measure in our study. Thus, our findings may not capture the complete effects of herbicide treatments on early-successional biodiversity and associated ecosystem services, warranting additional research throughout stand succession. Furthermore, the value of planted forests for providing other ecosystem services we had not measured (e.g. water quality/quantity) is likely to be pertinent at spatial and temporal scales not addressed in this study (Segura et al., 2020).

4.1 | Management implications

Despite the high value of timber production in the region, societal values for non-timber services and biodiversity have greatly influenced forest management decisions across private and public forest ownerships (Nelson et al., 2009; Spies et al., 2007; Winkel, 2014). The primary objective of many private-industrial forest managers is to produce revenue via timber production, although societal values for hunting, recreation, regulating services and non-timber forest products are increasingly recognized (Oswalt et al., 2019).

Our findings suggest that although trade-offs existed among some ecosystem services, many of the services we measured can also be maintained in young forest plantations and are compatible with at least some degree of wood production. Our moderate treatment reflected management commonly applied across >2.5 million ha of production forests in the region. This prescription mainly reduced the value of young plantations for flora-provided services and species richness, but was highly effective in promoting timber production and revenues. Our light treatments reflected less intensive management more common on state of Oregon forestlands, where harvests occur over longer rotations (~60 years) and are managed for multiple services other than timber production. Consistent with our predictions and common management of state forests, the light treatment was sufficient to promote timber growth while retaining floral and faunal diversity, but only in the case of 60-year harvest rotation ages. In comparison to the heavier two treatments, the light treatment did not include a site-preparation treatment and mainly benefitted the conservation of culturally valued plants and species richness of songbirds and pollinators, although this apparently came at the cost of yellow-faced bumblebee counts.

Although untreated control stands provided the greatest value for early-successional biodiversity conservation overall, state reforestation laws require that landowners manage vegetation enough to release crop trees from competition, with apparent costs to flora-provided services and native biodiversity. Finally, our intensive treatment did not have much added benefit for timber growth or revenue beyond the moderate treatment and tended to result in the greatest reductions to biodiversity and ecosystem services. It is important to note that the intensive treatment, due to the high cost of repeatedly applying herbicides, is not an economically viable option for most landowners (Kormann et al., 2021).

Overall, we hypothesize that the best stand-level practice to reduce trade-offs among ecosystem services, biodiversity and timber is to adjust herbicide prescriptions so that they retain patches of native vegetation (e.g. spot treatments, non-sprayed strips or patches) but still suppress enough competing vegetation to facilitate tree growth. In many regions, mechanical treatments are commonly used and more likely to retain non-crop tree vegetation than broadcast herbicide treatments (Wagner et al., 2006), although associated costs and feasibility of such treatments in rugged terrain often restrict their large-scale application in the Pacific Northwest.

Despite herbicide-induced reductions in plant diversity in harvested stands, as these stands recover from initial herbicide treatments, they appear to serve as important foraging habitat for ungulates, songbirds and some pollinators within managed forested landscapes. Promoting critical habitat elements for these species (e.g. retention of native broadleaf and herbaceous vegetation) offers potential spillover of fauna-provided services to adjacent forests and agricultural areas (Boesing et al., 2017; Krimmer et al., 2019).

Given the variation in forest ownerships and associated management objectives throughout the region, no single management approach is likely to optimize timber production while conserving a full suite of species and ecosystem services at the stand scale. This finding serves as justification for examining landscape and regional zoning approaches for promoting long-term biodiversity conservation and the maintenance of multiple ecosystem services into the future (e.g. TRIAD; Betts et al., 2021; Polasky et al., 2008; Seymour & Hunter, 1999). We encourage future management and research efforts to quantify and then weigh potential trade-offs among economic values, biodiversity conservation and a range of non-commodity ecosystem services.

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AUTHORS' CONTRIBUTIONS

T.D.S. was responsible for methodology, vegetation, timber and ungulate data collection, and led the writing of the manuscript; U.G.K. was responsible for pollination data collection, statistical design and analysis; M.G.B., J.V. and A.J.K. were responsible for initial study conceptualization, experimental design and avian data collection methods; D.W.F. was responsible for soils data; S.H.H. contributed to the refinement of arthropod data; both D.M.1 and D.M.2 developed timber and revenue projection models; J.A.H., J.W.R. and S.F. were responsible for subject matter editing; all authors contributed critically to the drafting of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Oregon State University Scholar Archives (https://doi.org/10.7267/js956p55h; Stokely et al., 2021) and the Dryad Digital Repository (https://doi.org/10.5061/dryad.bzkh1898j; Stokely et al., 2021).

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REFERENCES

Barua, S. K., Lehtonen, P., & Pahkasalo, T. (2014). Plantation vision: Potentials, challenges and policy options for global industrial forest plantation development. *International Forestry Review*, *16*, 117–127. https://doi.org/10.1505/146554814811724801

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Benjamin, F. E., & Winfree, R. (2014). Lack of pollinators limits fruit production in commercial blueberry (*Vaccinium corymbosum*). *Environmental Entomology*, *43*, 1574–1583. http://doi.org/10.1603/EN13314

Bennett, E. M., Peterson, G. D., & Gordon, L. J. (2009). Understanding relationships among multiple ecosystem services. *Ecology Letters*, *12*, 1394–1404. https://doi.org/10.1111/j.1461-0248.2009.01387.x

Betts, M. G., Phalan, B. T., Wolf, C., Baker, S. C., Messier, C., Puettmann, K. J., Green, R., Harris, S. H., Edwards, D. P., Lindenmayer, D. B., & Balmford, A. (2021). Producing wood at least cost to biodiversity: Integrating Triad and sharing-sparing approaches to inform forest landscape management. *Biological Reviews*, 1–17. https://doi.org/10.1111/brv.12703

Boesing, A. L., Nichols, E., & Metzger, J. P. (2017). Effects of landscape structure on avian-mediated insect pest control services: A review. *Landscape Ecology*, *32*, 931–944. https://doi.org/10.1007/s10980-017-0503-1

Bormann, B. T., Darbyshire, R. L., Homann, P. S., Morrissette, B. A., & Little, S. N. (2015). Managing early succession for biodiversity and long-term productivity of conifer forests in southwestern Oregon. *Forest Ecology and Management*, *340*, 114–125. https://doi.org/10.1016/j.foreco.2014.12.016

Brockerhoff, E. G., Jactel, H., Parrotta, J. A., & Ferraz, S. F. B. (2013). Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. *Forest Ecology and Management*, *301*, 43–50. https://doi.org/10.1016/j.foreco.2012.09.018

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59–67. https://doi.org/10.1038/nature11148

Ceausu, S., Graves, R. A., Killion, A. K., Svenning, J. C., & Carter, N. H. (2019). Governing trade-offs in ecosystem services and disservices to achieve human-wildlife coexistence. *Conservation Biology*, *33*, 543–553. https://doi.org/10.1111/cobi.13241

Costanza, R., de Groot, R., Braat, L., Kubiszewski, I., Fioramonti, L., Sutton, P., Farber, S., & Grasso, M. (2017). Twenty years of ecosystem services: How far have we come and how far do we still need to go? *Ecosystem Services*, *28*, 1–16. https://doi.org/10.1016/j.ecoser.2017.09.008

Daly, C. (2019). *PRISM Climate Group, Northwest Alliance for Computational Science*. Oregon State University. https://prism.oregonstate.edu/

Devine, W. D., Harrington, T. B., Terry, T. A., Harrison, R. B., Slesak, R. A., Peter, D. H., Harrington, C. A., Shilling, C. J., & Schoenholtz, S. H. (2011). Five-year vegetation control effects on aboveground biomass and nitrogen content and allocation in Douglas-fir plantations on three contrasting sites. *Forest Ecology and Management*, *262*, 2187–2198. https://doi.org/10.1016/j.foreco.2011.08.010

Donato, D. C., Campbell, J. L., & Franklin, J. F. (2012). Multiple successional pathways and precocity in forest development: Can some forests be born complex? *Journal of Vegetation Science*, *23*, 576–584. https://doi.org/10.1111/j.1654-1103.2011.01362.x

Edmonds, R. L. (1979). Decomposition and nutrient release in douglas-fir needle litter in relation to stand development. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, *9*, 132–140. https://doi.org/10.1139/x79-025

Ellis, T. M., & Betts, M. G. (2011). Bird abundance and diversity across a hardwood gradient within early seral plantation forest. *Forest Ecology and Management*, *261*, 1372–1381. https://doi.org/10.1016/j.foreco.2011.01.018

Felipe-Lucia, M. R., Soliveres, S., Penone, C., Fischer, M., Ammer, C., Boch, S., Boeddinghaus, R. S., Bonkowski, M., Buscot, F., Fiore-Donno, A. M., Frank, K., Goldmann, K., Gossner, M. M., Hölzel, N., Jochum, M., Kandeler, E., Klaus, V. H., Kleinebecker, T., Leimer, S., … Allan, E. (2020). Land-use intensity alters networks between biodiversity, ecosystem functions, and services. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 28140–28149. https://doi.org/10.1073/pnas.2016210117

Felipe-Lucia, M. R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., Prati, D., Ammer, C., Schall, P., Gossner, M. M., Bauhus, J., Buscot, F., Blaser, S., Blüthgen, N., de Frutos, A., Ehbrecht, M., Frank, K., Goldmann, K., Hänsel, F., … Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature Communications*, *9*, 1–10. https://doi.org/10.1038/s41467-018-07082-4

Flamenco, H. N., Gonzalez-Benecke, C. A., & Wightman, M. G. (2019). Long-term effects of vegetation management on biomass stock of four coniferous species in the Pacific Northwest United States. *Forest Ecology and Management*, *432*, 276–285. https://doi.org/10.1016/j.foreco.2018.09.033

Fogel, R., & Cromack, K. (1977). Effect of habitat and substrate quality on douglas-fir litter decomposition in western oregon. *Canadian Journal of Botany-Revue Canadienne De Botanique*, *55*, 1632–1640. https://doi.org/10.1139/b77-190

Food and Agriculture Organization (FAO) of the United Nations. (2018). *The state of the world's forests: Forest pathways to sustainable development*. United Nations. http://www.fao.org/3/ca0188en/ca0188en.pdf. ISBN: 978-92-5-130561-4

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Froberg, M., Stendahl, J., Philipson, C. D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J., & Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, *4*, 1–8. https://doi.org/10.1038/ncomms2328

Gelman, A., Su, Y. S., Yajima, M., Hill, J., Grazia Pittau, M., Kerman, J., Zheng, T., & Dorie, V. (2007). *arm: Data analysis using regression and multilevel/hierarchical models*. R package version 1.11-1. https://cran.r-project.org/web/packages/arm/index.html

Grass, I., Kubitza, C., Krishna, V. V., Corre, M. D., Mußhoff, O., Pütz, P., Drescher, J., Rembold, K., Ariyanti, E. S., Barnes, A. D., Brinkmann, N., Brose, U., Brümmer, B., Buchori, D., Daniel, R., Darras, K. F. A., Faust, H., Fehrmann, L., Hein, J., … Wollni, M. (2020). Trade-offs between multifunctionality and profit in tropical smallholder landscapes. *Nature Communications*, *11*, 1–12. https://doi.org/10.1038/s41467-020-15013-5

Hagar, J. C. (2007). Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review. *Forest Ecology and Management*, *246*, 108–122. https://doi.org/10.1016/j.foreco.2007.03.054

Halpern, C. B., & Franklin, J. F. (1990). Physiognomic development of pseudotsuga forests in relation to initial structure and disturbance intensity. *Journal of Vegetation Science*, *1*, 475–482. https://doi.org/10.2307/3235781

Hann, D. W. (2011). *ORGANON user's manual, edition 9.1*. College of Forestry, Oregon State University.

Harris, S. H., & Betts, M. G. (2021). Bird abundance is highly dynamic across succession in early seral tree plantations. *Forest Ecology and Management*, *483*, 1–12. https://doi.org/10.1016/j.foreco.2020.118902

Harris, S. H., Kormann, U. G., Stokely, T. D., Verschuyl, J., Kroll, A. J., & Betts, M. G. (2020). Do birds help trees grow? An experimental study of the effects of land-use intensification on avian trophic cascades. *Ecology*, *101*, 1–12. https://doi.org/10.1002/ecy.3018

Isaacs, R., & Kirk, A. K. (2010). Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *Journal of Applied Ecology*, *47*, 841–849. https://doi.org/10.1111/j.1365-2664.2010.01823.x

Kormann, U. G., Stokely, T. D., Verschuyl, J., Rivers, J., Kroll, A. J., Harris, S., Maguire, D., Mainwaring, D., & Betts, M. (2021). Reconciling biodiversity with timber production and revenue via an intensive forest management experiment. *Ecological Applications*, in press.

Korner-Nievergelt, F., Roth, T., von Felten, S., Guelat, J., Almasi, B., & Korner-Nievergelt, P. K. (2015). *Bayesian data analysis in ecology using linear models with R, BUGS, and Stan* (1st ed.). Academic Press.

Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*, *362*, 1–9. https://doi.org/10.1126/science.aau6020

Krimmer, E., Martin, E. A., Krauss, J., Holzschuh, A., & Steffan-Dewenter, I. (2019). Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. *Agriculture Ecosystems & Environment*, *284*, 1–8. https://doi.org/10.1016/j.agee.2019.106590

Kroll, A.J., Giovanini, J., Verschuyl, J., & Betts, M.G. (2017). Assembly dynamics of a forest bird community depend on disturbance intensity and foraging guild. *Journal of Applied Ecology*, *54*, 784–793. https://doi.org/10.1111/1365-2664.12773

Kroll, A. J., Johnston, J. D., Stokely, T. D., & Meigs, G. W. (2020). From the ground up: Managing young forests for a range of ecosystem outcomes. *Forest Ecology and Management*, *464*, 1–11. https://doi.org/10.1016/j.foreco.2020.118055

Kroll, A. J., Springford, A., & Verschuyl, J. (2020). Conservation and production responses vary by disturbance intensity in a long-term forest management experiment. *Ecological Applications*, *30*, 1–12. https://doi.org/10.1002/eap.2148

Lautenschlager, R. A., & Sullivan, T. P. (2002). Effects of herbicide treatments on biotic components in regenerating northern forests. *Forestry Chronicle*, *78*, 695–731. https://doi.org/10.5558/tfc78695-5

Mainwaring, D. B., Maguire, D. A., Rose, R., Dinger, E., Harrington, T., Turnblom, E., & Hann, D. (2016). Final annualized diameter growth, height growth, and mortality equations for douglas-fir in CIPSANON V1. In D. A. Maguire & D. B. Mainwaring (Eds.), *CIPS 2015 annual report* (pp. 12–16). Center for Intensive Planted-forest Silviculture, College of Forestry, Oregon State University.

Martin-Lopez, B., Gomez-Baggethun, E., Garcia-Llorente, M., & Montes, C. (2014). Trade-offs across value-domains in ecosystem services assessment. *Ecological Indicators*, *37*, 220–228. https://doi.org/10.1016/j.ecolind.2013.03.003

Matthews, G. (1993). *The carbon content of trees*. Forestry Commission Technical Paper No. 4. Forestry Commission, Edinburgh, Scotland. https://www.forestresearch.gov.uk/documents/6904/FCTP004.pdf

McComb, B. C., Curtis, L., Chambers, C. L., Newton, M., & Bentson, K. (2008). Acute toxic hazard evaluations of glyphosate herbicide on terrestrial vertebrates of the Oregon coast range. *Environmental Science and Pollution Research*, *15*, 266–272. https://doi.org/10.1065/espr2007.07.437

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D. R., Chan, K. M. A., Daily, G. C., Goldstein, J., Kareiva, P. M., Lonsdorf, E., Naidoo, R., Ricketts, T. H., & Shaw, M. R. (2009). Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment*, *7*, 4–11. https://doi.org/10.1890/080023

Oregon Forest Resources Institute. (2019). *Oregon forest facts: 2019–2020 edition*. https://oregonforests.org/pub/oregon-forest-facts-2019-20-edition

Oswalt, S. J., Smith, W. B., Miles, P. D., & Pugh, S. A. (2019). *Forest Resources of the United States, 2017*. General Technical Report WO-97. Washington, DC, USA. WO-GTR-97:1-223. https://doi.org/10.2737/WO-GTR-97

Paul, C., Hanley, N., Meyer, S. T., Furst, C., Weisser, W. W., & Knoke, T. (2020). On the functional relationship between biodiversity and economic value. *Science Advances*, *6*, 1–17. https://doi.org/10.1126/sciadv.aax7712

Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., & Tobalske, C. (2008). Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biological Conservation*, *141*, 1505–1524. https://doi.org/10.1016/j.biocon.2008.03.022

Powers, R. F., Scott, D. A., Sanchez, F. G., Voldseth, R. A., Page-Dumroese, D., Elioff, J. D., & Stone, D. M. (2005). The North American long-term soil productivity experiment: Findings from the first decade of research. *Forest Ecology and Management*, *220*, 31–50. https://doi.org/10.1016/j.foreco.2005.08.003

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Ralph, C. J., Droege, S., & Sauer, J. S. (1995). *Monitoring bird populations by point counts*. General Technical Report, U.S. Department of Agriculture, Forest Service, Albany, CA, USA, 191p. https://www.fs.fed.us/psw/publications/documents/psw_gtr149/

Rao, S., & Stephen, W. P. (2009). Bumble bee pollinators in red clover seed production. *Crop Science*, *49*, 2207–2214. https://doi.org/10.2135/cropsci2009.01.0003

Reid, W. V., Mooney, H. A., Cropper, A., Capistrano, D., Carpenter, S. R., Chopra, K., Dasgupta, P., Dietz, T., Duraiappah, A. K., Hassan, R., Kasperson, R., Leemans, R., May, R. M., McMichael, A. J., Pingali, P., Samper, C., Scholes, R., Watson, R. T., Zakri, A. H., … Zurek, M. B. (2005). *Ecosystems and human well-being – Synthesis: A report of the millennium ecosystem assessment*. Island Press. https://pdf.wri.org/ecosystems_human_wellbeing.pdf

Rivers, J. W., & Betts, M. G. (2021). Post-harvest bee diversity is high but declines rapidly with stand age in regenerating Douglas-fir forest. *Forest Science*, *67*, 275–285. https://doi.org/10.1093/forsci/fxab002

Root, H. T., Verschuyl, J., Stokely, T. D., Hammond, P., Scherr, M. A., & Betts, M. G. (2016). Plant diversity enhances moth diversity in an intensive forest management experiment. *Ecological Applications*, *27*, 134–142. https://doi.org/10.1002/eap.1426

Schowalter, T. D., Sabin, T. E., Stafford, S. G., & Sexton, J. M. (1991). Phytophage effects on primary production, nutrient turnover, and litter decomposition of young douglas-fir in western Oregon. *Forest Ecology and Management*, *42*, 229–243. https://doi.org/10.1016/0378-1127(91)90027-S

Segura, C., Bladon, K. D., Hatten, J. A., Jones, J. A., Hale, V. C., & Ice, G. G. (2020). Long-term effects of forest harvesting on summer low flow deficits in the Coast Range of Oregon. *Journal of Hydrology*, *585*, 1–12. https://doi.org/10.1016/j.jhydrol.2020.124749

Seymour, R. S., & Hunter, M. L. (1999). Principles of ecological forestry. In M.L. Hunter (Ed.), *Maintaining biodiversity in forest ecosystems* (pp. 22–61).Cambridge University Press. https://doi.org/10.1017/CBO9780511613029.004

Spies, T. A., McComb, B. C., Kennedy, R. S. H., McGrath, M. T., Olsen, K., & Pabst, R. J. (2007). Potential effects of forest policies on terrestrial biodiversity in a multi-ownership province. *Ecological Applications*, *17*, 48–65. https://doi.org/10.1890/1051-0761(2007)017[0048:PEOFPO]2.0.CO;2

Stokely, T. D., & Betts, M. G. (2019). Deer-mediated ecosystem service versus disservice depends on forest management intensity. *Journal of Applied Ecology*, *57*, 31–42. https://doi.org/10.1111/1365-2664.13532

Stokely, T. D., Kormann, U. G., & Betts, M. G. (2020). Synergistic effects of wild ungulates and management intensification suppress native plants and promote exotics. *Forest Ecology and Management*, *460*, 1–10. https://doi.org/10.1016/j.foreco.2019.117772

Stokely, T. D. (2021). Data from: Experimental evaluation of herbicide use on biodiversity, ecosystem services and timber production tradeoffs in forest plantations. (Version 1) [Dataset]. *Oregon State University Scholar Archives*, https://ir.library.oregonstate.edu/concern/datasets/js956p55h

Stokely, T. D., Kormann, U. G., Verschuyl, J., Kroll, A. J., Frey, D. W., Harris, S. H., Mainwaring, D., Maguire, D., Hatten, J. A., Rivers, J. W., Fitzgerald, S., & Betts, M. G. (2021). Data from: Experimental evaluation of herbicide use on biodiversity, ecosystem services, and timber production tradeoffs in forest plantations. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.bzkh1898j

Stoleson, S. H., Ristau, T. E., deCalesta, D. S., & Horsley, S. B. (2011). Ten-year response of bird communities to an operational herbicide-shelterwood treatment in a northern hardwood forest. *Forest Ecology* *and Management*, *262*, 1205–1214. https://doi.org/10.1016/j.foreco.2011.06.017

Su, Y. S., & Yajima, M. (2020). *R package 'R2jags': A package for running jags from R*. https://cran.r-project.org/web/packages/R2jags/index.html

Turner, M. G., Donato, D. C., & Romme, W. H. (2013). Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: Priorities for future research. *Landscape Ecology*, *28*, 1081–1097. https://doi.org/10.1007/s10980-012-9741-4

Ung, C. H., Bernier, P., & Guo, X. J. (2008). Canadian national biomass equations: New parameter estimates that include British Columbia data. *Canadian Journal of Forest Research*, *38*, 1123–1132. https://doi.org/10.1139/X07-224

Van Tuyl, S., Law, B. E., Turner, D. P., & Gitelman, A. I. (2005). Variability in net primary production and carbon storage in biomass across Oregon forests – An assessment integrating data from forest inventories, intensive sites, and remote sensing. *Forest Ecology and Management*, *209*, 273–291. https://doi.org/10.1016/j.foreco.2005.02.002

Von Hagen, B., Weigand, J. F., McLain, R., Fight, R., & Christensen, H. H. (1996). *Conservation and development of nontimber forest products in the Pacific Northwest; an annotated bibliography*. General Technical Report. Portland, OR, USA. PNW-GTR-375:1-246. https://doi.org/10.2737/PNW-GTR-375

Wagner, R. G., Little, K. M., Richardson, B., & McNabb, K. (2006). The role of vegetation management for enhancing productivity of the world's forests. *Forestry*, *79*, 57–79. https://doi.org/10.1093/forestry/cpi057

Wei, T., & Simko, V. (2017). *R package 'corrplot': Visualization of a correlation matrix (version 0.84)*. https://github.com/taiyun/corrplot

Winkel, G. (2014). When the pendulum doesn't find its center: Environmental narratives, strategies, and forest policy change in the US Pacific Northwest. *Global Environmental Change-Human and Policy Dimensions*, *27*, 84–95. https://doi.org/10.1016/j.gloenvcha.2014.04.009

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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