

Reconciling biodiversity with timber production and revenue via an intensive forest management experiment

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Abstract. Understanding how land-management intensification shapes the relationships between biodiversity, yield, and economic benefit is critical for managing natural resources. Yet, manipulative experiments that test how herbicides affect these relationships are scarce, particularly in forest ecosystems where considerable time lags exist between harvest revenue and initial investments. We assessed these relationships by combining 7 yr of biodiversity surveys (>800 taxa) and forecasts of timber yield and economic return from a replicated, large-scale experiment that manipulated herbicide application intensity in operational timber plantations. Herbicides reduced species richness across trophic groups (−18%), but responses by higher-level trophic groups were more variable (0–38% reduction) than plant responses (−40%). Financial discounting, a conventional economic method to standardize past and future cash flows, strongly modified biodiversity–revenue relationships caused by management intensity. Despite a projected 28% timber yield gain with herbicides, biodiversity–revenue trade-offs were muted when opportunity costs were high (i.e., economic discount rates $\geq 7\%$). Although herbicides can drive biodiversity–yield trade-offs, under certain conditions, financial discounting provides opportunities to reconcile biodiversity conservation with revenue.

Key words: biodiversity; economic analysis; forest management; intensive forestry; land expectation value; plantations; timber yield.

INTRODUCTION

Surging human demand for resources poses the critical challenge of reconciling biodiversity conservation with commodity production. Addressing this challenge requires a sound understanding of trade-offs among commodity production, economic viability, and biodiversity (Flynn et al. 2009, Phalan et al. 2011, Tscharntke et al. 2012, FAO 2015). As management of many agricultural and silvicultural systems worldwide has intensified and caused biodiversity declines, yield–biodiversity trade-offs have become focal points to compare the sustainability of different production scenarios (Phalan et al. 2011, Fischer et al. 2017). Indeed, biodiversity

often trades off strongly against food production in intensively managed agricultural systems (Tscharntke et al. 2005, Tilman et al. 2011, Fischer et al. 2017), but economic benefit rather than yield is likely to determine landowners' management decisions. To identify sustainable and realistic production scenarios, we therefore need to understand the effects of intensified management on both yield and financial gains, and under which economic scenarios economic–ecological relationships reflect yield–biodiversity trade-offs.

Pesticides are ubiquitously applied to promote yields in intensive production systems worldwide (4×10^9 kg of active ingredients applied globally per year; Zhang 2018). For example, herbicides are often used in intensively managed tree plantations to reduce competing vegetation, which has the effect of increased tree growth and survival. These plantations often have a rotation cycle of 20–70 yr (i.e., the period from planting to harvest), with herbicides being applied during plantation

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establishment. Intensifying production has been forwarded as a means to meet global timber demand without spreading out harvest impacts into remaining unmanaged intact forest ecosystems (Binkley 1997), which are often in tropical forests (Betts et al. 2017, Moran and Kanemoto 2017). Indeed, intensively managed plantations provide almost half of the global industrial round wood (Payn et al. 2015). Despite their potential value, herbicide applications have been controversial from both human (Rolando et al. 2017) and ecosystem health perspectives (Benbrook 2016).

Management intensification can be a viable economic decision for landowners, but only if revenues outweigh costs. Perennial crops with longer rotation cycles, such as timber or oil palm, face relatively high initial input costs (e.g., plantation establishment and management) while revenues do not accrue until considerably later at harvest. Thus, initial investment in these production systems is associated with substantial opportunity costs with respect to alternative investments. To account for this time lag between initial investment and revenue, future cash flows are typically adjusted using a discount rate representing potential returns on alternative investment opportunities; higher discount rates weight current cash flows more heavily. This conventional financial discounting is a standard economic method to compare economic returns among alternative forest management regimes (Amacher et al. 2009). Although financial discounting has previously been integrated into biodiversity–timber-production simulations (Lichtenstein and Montgomery 2003) to our knowledge, its impact on how biodiversity across species groups trades off against economic gain has not been examined experimentally in forest systems.

Here, we addressed two objectives using long-term, experimental data. First, we evaluated whether the relationship between revenue and biodiversity parallels biodiversity–yield trade-offs. Second, we quantified how the cost of capital and associated discount rates alter this relationship. If intensification causes biodiversity–yield trade-offs, but revenue gains fare poorly against alternative investments, then landowners may choose to use less-intensive management approaches, resulting in “win-win” biodiversity–profitability scenarios. Given that plant diversity often increases diversity at higher trophic levels (Scherber et al. 2010), we expected intensive forest management to increase crop tree growth and reduce biodiversity across species groups leading to more severe timber production–biodiversity trade-offs. Further, we hypothesized that revenue gains from initial investments (herbicide application) will depend on the rate of return expected by landowners (i.e., the discount rate). Under high discount rates, revenue should be strongly affected by high initial herbicide costs. We therefore expected that the increase in discounted herbicide costs would not be compensated for by increases to timber yields afforded by herbicide application. Thus, profitability and biodiversity should become decoupled, and result in “win-win” biodiversity–profitability scenarios.

We addressed these objectives using a broad-scale, manipulative, forest management experiment in the Oregon Coast Range, USA. Within a randomized complete block study design, we experimentally treated 32 entire operational forest plantations (size 12.9 ± 2.4 ha [mean \pm SD]; Betts et al. 2013) with either an untreated control, or three intensities of herbicide application (i.e., light, moderate, or intensive) during early stand development to control competing vegetation (Fig 1A, Appendix S1: Fig. S1). The Moderate treatment, and to a lesser degree the Light treatment, represent common herbicide applications that are implemented on much of the 2.5 million ha of industrial forest lands in the U.S. Pacific Northwest (Stokely et al. 2018), in a region accounting for 28% of the U.S. softwood lumber production (Oregon Forest Resources Institute 2019). We quantified biodiversity during the first seven years after initial clearcutting (Appendix S1: Fig. S2) because this is a period characterized by high biodiversity and provides important habitat for specialized early seral associated species exhibiting strong regional declines (Swanson et al. 2011, Phalan et al. 2019). Our final data set comprised >140,400 observations of 835 species and morphospecies representing widely varying taxonomic levels within eight different species groups (2–316 species).

METHODS

Experimental design

We established 32 study plantations (hereafter “stands,” 12–16 ha each) clustered into eight distinct blocks spanning a 100-km (north-south) portion of the northern Coast Range Mountains of western Oregon, USA (Fig. 3; Betts et al. 2013). Stands were clearcut in fall 2009/winter 2010 and were planted in spring 2011 with Douglas-fir (*Pseudotsuga menziesii*), the primary commercial species in the region. The four stands in each block were no further apart than 5 km to reduce within-block variation (Fig. 3).

Within each block, we established stands to represent one of four treatments across a gradient in forest management intensity: (1) control (no herbicide application), (2) light (a lighter operational standard), (3) moderate (a heavier operational standard), and (4) intensive (successive years of herbicide treatment to greatly reduce competing shrubs and most grass species, not applied operationally). Treatments were randomly assigned to stands within each block. Herbicide applications were applied consistently across stands during 2010–2015. Details of the products applied, and the timing are described in Appendix S1 (*Herbicide applications*) and Fig. S1. Chemicals and application rates were held constant across treatments for all blocks in the study because our objective was to test the combined effects of the suite of herbicides and surfactants used in typical

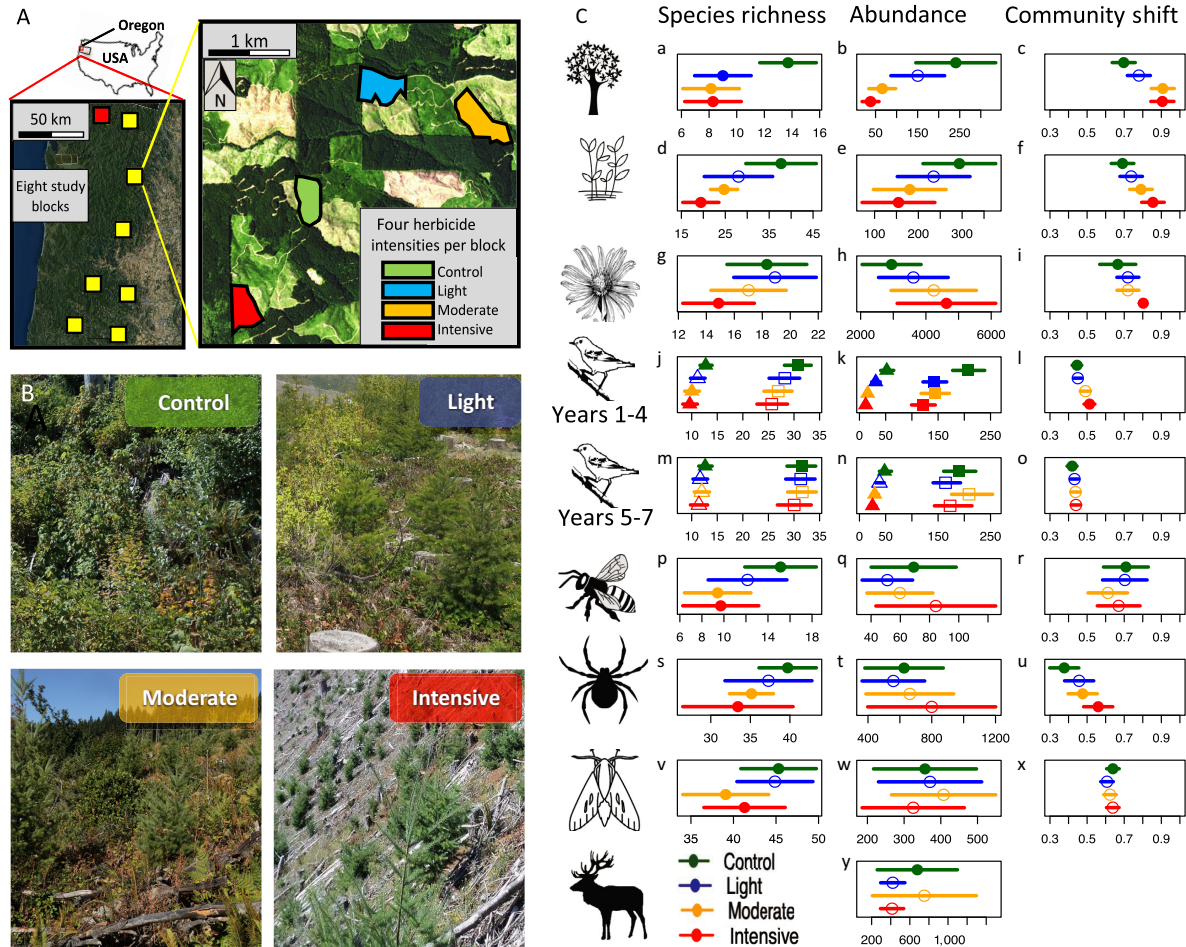


FIG. 1. Herbicides cause biodiversity changes in plantation forests. (A) Spatially blocked study sites (yellow squares, $n = 8$ blocks), where management was experimentally altered, and biodiversity assessed during the first 7 yr after plantation establishment. Each block had four stands treated with differing management intensity. In the red square, only birds, moth and crop tree growth were assessed. (B) Typical experimental units showing differences in vegetation in year 5 of the experiment. (C) Estimated total species richness, total abundance, and community shift across a gradient in herbicide intensity for 835 species. A total of 140,406 individual plant and animal detections were distributed across woody species (a–c), herbs (d–f), animal-pollinated flowers (f–i), birds (j–o), pollinators (p–r), leaf-gleaning arthropods (s–u), macro-moths (v–x), and ungulates (y). Shown are treatment estimates (circles) and their 95% confidence intervals (bars). Solid symbols indicate a significant difference from untreated control sites, for the light, moderate, and intensive treatments. For birds, posterior means for leaf-gleaning species (triangles) and non-gleaning species (squares) are shown, with the corresponding 95% Bayesian credible interval. Community shift is a Bray-Curtis-similarity-based index describing how communities shift compared to untreated stands within the same block (see *Methods*). For the control stands, the community shift indicates how much the community differs from all other control stands across all blocks.

operations rather than to examine the effect of a particular chemical.

Biodiversity surveys

We quantified early-seral biodiversity for eight different species groups from 2011 to 2017, with 2–7 yr of data per group. An overview of the sampling years for all investigated species groups is given in Appendix S1: Fig. S2. To our knowledge, this is the most extensive experimental intensive forest management (IFM) study in terms of management intensity and breadth of species groups considered.

Woody plants and herbs

Within each stand from 2011 to 2016, we measured plant species cover and richness in a randomly located 15×15 m permanent vegetation plot. We used Geographical Information Systems (ArcGIS version 9.3; ESRI, Redlands, California, USA) to randomly select plots, located a minimum distance of 50-m from treatment boundaries while attempting to avoid large slash piles, burn piles, roads, and slopes over 60%. To obtain plot-level species cover estimates, we averaged the ocular cover of each species among 12, 1×1 m quadrats, systematically placed throughout each plot. Plots covered

all inter-cardinal slope aspects and ranged from 6% to 58%. We restricted vegetation measurements to seven of the eight blocks due to the logistics of a companion wildlife exclusion study (Stokely et al. 2018) in which slope steepness precluded construction of bird and ungulate exclosures in one block. Our vegetation data were derived from the unexcluded control plots of the wildlife exclusion study. We considered all non-woody forbs and graminoids as herbs.

Ungulates

To assess the stand use by wild ungulates (black-tailed deer *Odocoileus hemionus colombianus* and Roosevelt elk *Cervus canadensis roosevelti*), we deployed camera traps (Bushnell Trophy Camera, model 119436, Cody Overland Park, Kansas, USA) in the corner of each vegetation plot at 1.5 m from the ground in order to maximize field of view (Stokely and Betts 2019). Camera traps were set to continuously take photos every 7–14 s when triggered by motion and an infrared signature. We estimated detection as the number of photos taken of individuals within 10 m of the camera per day per sampling period (May–October from 2012 to 2015) for each species (details in Stokely et al. 2018, Stokely and Betts 2019). We included the number of active camera days as an offset in the further analysis of ungulate detections, as the total observation time per stand ranged from between 397 to 736 d due to camera malfunction in some cases. Ungulate detection by camera traps was not biased as a function of treatment (Appendix S1: Fig. S3).

Leaf gleaning arthropods

We sampled arthropods in the same permanent plots from which we measured plant communities, and we thus restricted arthropod surveys to seven of the eight blocks (details are given in Harris et al. [2020]). Within each plot, the observer walked three evenly spaced parallel transect lines across the length of the plot, sweeping a net before them at ankle to waist height, and sweeping sufficiently hard to dislodge arthropods without damaging the vegetation. We identified every arthropod to the family level, and following identification, released all arthropods in the plot. Surveys occurred annually in July and once in August from 2012 to 2015. As arthropods could only be determined to family, we used family richness as a proxy for species richness in this group (hereafter, species richness).

Moths

Moths were sampled in 2012 and 2013 using three blacklight traps in each of the 32 stands (details are given in Root et al. [2017]). Traps were placed once per month between May and August in both years. All stands within an entire block were sampled concurrently

for the same nights, totaling 630 complete trap nights and 5,985 h of sampling. We avoided sampling during cold weather (temperature at dusk $<10^{\circ}\text{C}$), under rainy conditions and five nights before and after a full moon, as this decreases moth trapping efficiency substantially (McGeachie 1989, Luis and Marcel 1997). Only complete trap nights were used for further analysis. To account for the uneven number of sampling nights between stands, we used the total number of visits as an offset for moth abundance. For the number of moth species, we used species richness, rarefied to the smallest number of individuals detected per stand (function *rarefy*, package *vegan* (Oksanen et al. 2013)).

Pollinators

We quantified pollinator abundance over four years (2012–2015) using two observation rounds per year (July and August). We made observations on 28 stands, in eight randomly chosen 1×1 m plots per stand ($n = 224$ plots) for a total of 8,960 observation minutes. We allowed pollinators to acclimate to observers during the first minute, and then noted all arthropods and birds that touched the reproductive parts of flowers within the plot during a 5-minute period. Pollinator species richness was quantified in a more intensive effort during three surveys in June, July, and August/early September 2015, respectively. Each round consisted of two visits to each stand on two subsequent days. We determined three locations per stand (pollinator richness plots, $n = 84$ plots), placed in representative portions of stands, maximizing distance among locations while avoiding stand edges. At every pollinator richness plot, an observer determined four 1×2 m subplots, situated 25 m away from the pollinator richness plot, one in each cardinal direction (north, east, south, west, $n = 28 \times 3 \times 4 = 336$ subplots). We observed each subplot for 10 minutes (20,160 minutes in total). Invertebrates touching reproductive plant organs were caught and killed for identification in the lab. In addition, observers walked slowly back to the plot center after the 10-minute period, collecting all pollinators within the 1-m wide transect. For each block and round, two stands were surveyed in the morning and two stands in the afternoon of the first visit. This order was switched for the second visit. Observations only occurred during favorable weather conditions ($<50\%$ cloud cover, no rain, no strong winds).

Flowers

Availability of animal-pollinated flowers (hereafter flowers) was sampled during June–September 2015 paralleling the pollinator species richness observations. Surveys were conducted by walking along the 1×25 m pollinator transects ($n = 28 \times 3 \times 4 = 336$ transects = 8,400 m^2 total). All floral resources within the transects were determined to species, if possible, and the number of open blossoms (or heads [*Asteraceae*]/spires [*Lupinus*

spp.] estimated. Plants of the genus *Crepis*, *Hypochaeris*, and *Hieracium* were not distinguished, and treated as the same morphospecies.

Birds

We randomly placed three point-count plots within each stand so as to maximize the distance between survey locations, and distance to edge. At each of 96 point-count locations, we sampled the avian community from 2011 to 2017. Each point was sampled four times during the breeding season (28 May–3 July). To avoid bias caused by time of day or weather, we varied survey order, time of survey, and observers throughout the season. We recorded data in a manner consistent with the point-count survey guidelines described by Ralph et al. (1995) within a 10-minute time interval, resulting in a total of 26,880 minutes of observation. Censuses began at sunrise and were completed by 10:00. Technicians recorded all bird detections and estimated first detection distances from the census point. We excluded detections that occurred >50 m from the census point. For all analyses, we summed detections across three point-count stations within a harvest unit to obtain one response per harvest unit per visit. We made this decision to avoid spatial autocorrelation of point-count stations within harvest units, to help with model convergence by reducing the number of species that are not observed at the analysis level, and because the experimental unit was the harvest unit (individual point-count stations are subsamples).

Using three 3-m radius subplots, we quantified broad-leaf vegetation cover around each point count location on an annual basis. We recorded all woody, non-coniferous plants by species within each subplot, each centered 20 m from avian census locations. The bearing to the initial subplot was selected randomly; remaining plots were separated at 120° intervals from other plots. Total cover for each plant species was based on the sum of measurements (sometimes overlapping) for the three 3-m radius subplots (Ellis and Betts 2011). We chose this method to quantify the three-dimensional nature of the woody vegetation. As a result, summed point-level cover totals across species could exceed 100%. We estimated percent cover and species richness of woody vegetation by treatment and year. We then integrated these vegetation measures into the detection part of the avian statistical models (see *Analyses*).

ANALYSES

Herbicide effects on biodiversity

We first analyzed whether herbicides affected three measures of biodiversity: species richness, abundance, and species identities. We used the total number of species detected per stand over the entire observation period as a measure species richness. Similarly, we pooled the number of individuals sampled per stand over the

entire observation period. Finally, we implemented an ordination-based community shift index (CSI; Kormann et al. 2018) to assess how herbicide treatments affected species abundances jointly in relation to untreated control stands within the same block. In particular, CSI is based on Bray-Curtis similarity and indicates the difference in species abundances between a plantation and its corresponding control plantation, proportional to summed abundances of the two plantations together. For plantation i , CSI is defined as

$$CSI_i = \frac{\sum_{k=1}^p |A_{ik} - C_k|}{\sum_{k=1}^p A_{ik} + C_k}$$

where p is the total number of species occurring on the i th plantation OR the corresponding within-block control site, A_{ik} is the abundance of the k th species on plantation i , and C_k the abundance of the k th species on the control plantation located within the same block as plantation i . CSI is bounded by 0 and 1, with small values indicating a community similar to the untreated control stand within a block, and values close to 1 indicating a strongly altered community. We used linear mixed effect models with block as random intercept to analyze herbicide effects on the three response variables for each individual species except birds (Pinheiro et al. 2014). We chose the best fitting variance structure per model (Gaussian, VarExp, VarPower, varIdent (form = ~1| Treatment)) using corrected Akaike Information Criteria (AIC_c) and residual plots, to account for residual heteroscedasticity. Final models were fitted using restricted maximum likelihood. Models were fitted using R (R Core Team 2018).

To assess avian community patterns, we capitalized on the spatially and temporally replicated sampling and implemented Bayesian models to account for the experimental design and variation of detections probabilities between stands (i.e., multispecies site occupancy and multispecies N -mixture abundance models (Dorazio and Royle 2005, Zipkin et al. 2009, Yamaura et al. 2012). In brief, the occupancy and abundance process models included terms for block, treatment, year, and the treatment \times year interaction. The species-specific detection model (for both occupancy and abundance responses) included terms for year, percent cover of woody vegetation, and quadratic ordinal date (for details, see *Statistical details for bird analysis*; Appendix S1: Table S1). To evaluate specific predictions about avian responses to herbicide treatments, we included a hyper-prior in the model to distinguish leaf-gleaner and non-leaf-gleaner guilds (Kroll et al. 2017). Under the hierarchical community models, we assumed that species-specific effects for a given parameter are drawn from one of two common normal distributions, depending on the foraging guild's association with broadleaf plants. We used the estimated latent occupancy and abundance state variables to compute species richness, total abundance and CSI per stand and associated credibility intervals.

Bayesian models were fit using JAGS (Plummer et al. 2003) called from R version 3.5.1 (R Core Team 2018) using the jags function in package R2jags version 0.05–07 (Su and Yajima 2012), with three Markov chains of length 100,000 with a burn-in period of 20,000 and 1/80 thinning. A detailed description and statistical code are given in the Supporting Information (Data S1 Kormann_Jags_Code.R).

Estimating timber yields and revenue

We calculated the expected yield and economic performance under different rotation ages and across a range in economic scenarios. For this, we first projected the growth of 6,601 trees for 105 yr and used those yield estimates to inform discounted cash flow analysis.

Tree lists

We conducted tree growth projections from a list of planted crop trees (*P. menziesii*) and naturally regenerated conifer and hardwood species, measured from 18 to 20 systematically located plots within each stand. All plots were measured at the end of the growing season in 2015 (i.e., October–December) and consisted of a 5-m radius plot, in which planted-crop trees were tagged and measured. We also established a nested 3-m radius plot in which naturally regenerating conifer and hardwood species were tagged and measured. Measurements included stem diameter at 15 cm from root collars, diameter at breast height (DBH, i.e., 1.37 m) and height to apical leader. To avoid overestimates of hardwood regeneration, stems from coppice-sprouting hardwood clumps were only included if the diameter for each stem was at least 80% the size of the largest stem within each sprouting clump. From the 3-m radius plots, we tallied the number of naturally regenerating conifer seedlings <20 cm in height and assigned all a height of 15 cm. During the growing season of 2015 (i.e., July–September), we ocularly estimated the cover of competing vegetation, grouped by forb, graminoid, fern, and broadleaf shrub and non-commercial broadleaf woody (i.e., excluding *Alnus rubra*, *Acer macrophyllum*, and *Prunus emarginata*) life-form functional groups. Stand-level cover averages for each life-form were summed for use within the projection models.

Growth models and yield

We combined two growth models to project development of the 5-yr-old tree lists for 100 yr, thereby using the most appropriate equations to account for both the competing vegetation in the young plantations and hardwood growth in older stands. We projected tree lists from age 5 to 20 with Center for Intensive Planted-forest Silviculture (CIPS) annualized growth equations (Mainwaring et al. n.d., 2016). These are a set of equations for diameter and height growth, and mortality of Douglas-

fir and western hemlock plantations, and account for the negative effect of competing vegetation cover. Trees of the 20-yr-old projected tree lists were then further grown with SMC-ORGANON, a regional growth model constructed from plantation data in the Pacific Northwest (Hann 2011).

Because the CIPS equations cannot estimate growth of species other than Douglas-fir and western hemlock, we used a different approach to model growth for other tree species present on the plots. Although there were few other conifers sampled, grand fir (*Abies grandis*) and noble fir (*Abies procera*) were grown as western hemlock (*Tsuga heterophylla*). No regional equations were available for bitter cherry (*P. emarginata*), so they were grown as bigleaf maple (*A. macrophyllum*). Red alder (*A. rubra*) diameter growth was accomplished with annualized ORGANON equations (Hann 2011), with the red alder site index assumed to be 50% of the Douglas-fir site index. Bigleaf maple diameter growth was based on a linear interpolation of the ORGANON 5-yr diameter growth equation (Hann and Hanus 2002) for bigleaf maple. Estimated heights of alder and maple were based on ORGANON height:diameter equations (alder [Hann 2011], maple [Wang and Hann 1988]), and ORGANON equations were also used to estimate crown base (alder [Hann 2011], maple [Ritchie and Hann 1987]) and mortality (alder [Hann 2011], maple [Hann and Hanus 2002]). Assignment of diameter to hardwood stems surpassing 1.37 m was based on an equation constructed from data collected from this study. Douglas-fir 50-yr site index (Bruce 1981) used within both models was based on landowner estimates. Western hemlock site index was based on a published conversion equation from the Douglas-fir site index (Nigh 1995).

We determined expected yield (board feet per hectare) from model projections and expected yield gains for each herbicide treatment at three different rotation ages that are typical for the region (40, 50, and 60 yr). We express units in board feet because this is the most common unit for measuring timber volume in the United States, and is not readily converted into cubic meters (1 board foot \cong 0.0024 m³). We fitted a linear mixed effects models in R for each rotation age (Pinheiro et al. 2014), with the expected yield per stand as the response, herbicide treatment as explanatory factor, and block as a random intercept. We chose the best-fitting variance structure per model (Gaussian, VarExp, VarPower, varIdent(form= \sim 1|Treatment)) using small-sample size corrected Akaike Information Criteria (AIC_c) and residual plots, to account for residual heteroscedasticity. We fit final models using restricted maximum likelihood.

Economic value

To compare the economic performance of the different herbicide treatments under a broad spectrum of realistic investment decisions (discount rates ranging from 4% to 10%), we performed a series of cash-flow analyses

(plantation costs, herbicide costs, harvest costs, harvest income) and transformed those into land expectation values (LEV, also called soil expectation value; Faustmann 1849). LEV is a standard discounted cash-flow technique used to compare plantation management strategies with periodic harvest (Amacher et al. 2009). LEV is widely used in forestry and facilitates comparisons of alternative management scenarios, including different intensities of competing vegetation control and different rotation ages (Amacher et al. 2009, Hanewinkel et al. 2013, Spiesman et al. 2016, Yousefpour and Hanewinkel 2016, Petucco and Andrés-Domenech 2018). In particular, LEV calculates the value of a forest plantation under perpetual production, harvested at the rotation age that maximizes revenue for that particular stand. LEV is thus a proxy for the willingness to pay for forest land. Unlike net present value, LEV values are not based on a single timber rotation and can be used to compare financial yields on forest lands subject to different rotation ages. We calculated land expectation values using estimated costs of planting (US\$650/ha), logging (US\$180 per thousand board feet), and hauling (US\$80 per thousand board feet), were based on communications with local professional foresters. Herbicide costs were based on the current costs applying the specific products used (site prep, US\$200/ha; release 1, US\$175/ha; release 2, US\$150/ha). Economic tabulations also included an annual 2% inflation rate and an annual 0.5% timber price increase. All calculations were performed for nominal discount rates of 4%, 5%, 6%, 7%, 8%, 9%, and 10%, representing the spectrum of applied interest rates in the region based on communications with local timber companies.

We then assessed whether herbicides caused differences in expected LEV. Using the maximum LEV across rotation ages for each stand and for each discount rate (e.g., using the rotation age that maximized the LEV for the discount rate under consideration), we compared the expected LEV for each herbicide treatment under a 4%, 7%, and 10% nominal discount rate. We used the same statistical procedure as for the yield analysis, but with LEV as a response variable.

Classification of the relationship between yield, LEV and species richness

To assess whether trade-offs or synergies existed between species richness and yield and LEV, we fit individual linear mixed effect models for each organism group with species richness as the response and yield (rotation age 40 yr), or LEV, as the explanatory variable, respectively. Block was treated as random intercept and variance functions chosen to account for residual heteroscedasticity. For birds, we used the summed stand-level posterior means for gleaner and non-gleaners as the species richness per period. We scaled species richness per taxon and LEVs for each discount rate to [0,1] to allow comparisons between different species groups

and discount rates. We considered the relationship species richness and yield/LEV to be a synergy if the regression coefficient ($\hat{\beta}$) was significantly larger than 0, a trade-off if it was significantly smaller than 0, and to be a neutral relationship if $\hat{\beta}$ was not significantly different from 0.

Finally, we performed a suite of tests to evaluate the robustness of the yield–species-richness, and LEV–species-richness relationships, respectively (for details, see Appendix S4: Fig. S4). As the number of observation years differed between groups, we first investigated whether longer observation periods associated with an increased probability of showing a significant species-richness–yield effect, using a simple logistic regression with significance of the relation (yes/no) as the response, and the duration of the observation period in years as the explanatory variables. Second, we used a Kendall's rank correlation test to assess whether the effect size of the species richness–yield relation (e.g., the relative species loss with increased yield) increased with the number of years that a group had been observed. However, the likelihood of finding a statistically significant trade-off between timber yield and species richness did not increase with the duration of the observation length (logistic regression, $z = 1.39$, $P = 0.17$, Appendix S1: Fig. S3a). Also, the duration of the observation period was not significantly related to the slope of the species-richness–yield relationships (Kendall's rank correlation, $z = -1.14$, $P = 0.25$, Appendix S1: Fig. S3b).

In addition, we also tested whether species richness–timber yield relationships qualitatively differed between the full data sets and data sets rarefied to single years, for three species groups for which we had long-term data (arthropods, woody plants, herbs). We did so by statistically comparing the slopes of the species richness – yield relation for the entire observation period versus the rarefied annual richness (for details, see Appendix S4: Fig. S4). However, the richness–yield slopes did not significantly differ between the entire data sets vs. the rarefied species richness for any of the three species groups, providing additional evidence that the duration of the observation period did not substantially affect the species-richness–yield relationships (Appendix S1: Table S2).

Finally, we also assessed whether species richness related to yield (40 yr rotation age) and LEV in a nonlinear fashion by fitting mixed effect models with the same specifications as described above for each organism group, but by adding a second-order polynomial of yield and LEV at 4%, 7%, and 10% discount rate as explanatory variables, respectively. If the second-order polynomial was statistically significant, we interpreted this as evidence for a non-linear relationship between species richness and yield or LEV, respectively. However, the second-order polynomial was not significant in any of the models, thus providing no support for nonlinear relations (Appendix S1: Fig. S5, Table S3).

RESULTS

Biodiversity responses to intensive forest management

Averaged across groups and accumulated over the entire observation period, an estimated 11%, 18%, and 22% fewer taxa were present on light, moderate, and intensive stands, respectively, compared to untreated controls (Fig. 1C first column). Moderate and Intensive treatments showed significant species reductions across species groups (Fig. 1C, all $P < 0.05$). As expected, woody plants showed strong reductions in the moderate (−40.6%) and Intensive treatments (−39.6%) and herbaceous species (forbs, ferns, graminoids) were reduced most strongly (Moderate, −34.5%; intensive, −48.5%). Despite these substantial effects for plants, higher-level species groups showed some resilience to treatments via lower-magnitude effects (moderate, −14.6%; intensive, −16.6%; Fig. 1C, first column). Nevertheless, species richness of two higher-level groups responded negatively to herbicide treatments during the initial years of the study (pollinators [moderate, −37.7%; intensive, −35.8%] and leaf-gleaning birds [moderate, −21.2%; intensive, −24.4%]). Effects on overall abundance across years varied by species groups (Fig. 1C, second column); leaf-gleaning birds (Fig. 1C, J, and M) were the only higher-level group that exhibited significantly lower abundance with herbicides. These results indicate that declines in abundance of species sensitive to herbicides are compensated by increases in more resilient species, as groups that persisted on herbicide-treated stands responded neutrally or even positively to intensification. Indeed, our ordination-based community shift index showed significant community-level turnover in abundances in herbicide treatments compared to untreated controls. However, this relationship was found only for groups under moderate and intensive treatments, and only weakly, if at all, within the light treatment (Fig. 1C, third column). Many species common to the control treatments achieved similar abundances under the light herbicide treatment.

Biodiversity–timber trade-offs

Without herbicides, projected mean timber volume reached 54,840 board feet per hectare, 74,687 board feet per hectare, and 94,640 board feet per hectare (Fig. 2) for three typical rotation ages in the region (40 yr, 50 yr, and 60 yr, respectively). Herbicide treatments increased yield significantly by 11.5–30.4% (Fig. 2, $P < 0.01$), although the light treatment was not significantly greater than controls at a 40-yr rotation age (+11.6%, $P = 0.148$). Also, proportional yield gains increased with longer rotation cycles (Fig. 2). Variation in yield decreased with herbicide intensity (Fig. 2A–C), and increased with longer rotation periods.

Our models revealed consistent trade-offs between species richness and timber growth (Fig. 3B).

Importantly, we found little evidence that the duration of sampling in our species data sets affected the likelihood that we would detect statistically significant relationships between timber yield and biodiversity, or alter the effect size of this relationship (Appendix S1: Fig. S4, Table S2). Across the observed gain gradient of 137% in timber production, plant species richness dropped by 42.1% (averaged lower and upper 95% CI = 24.5%, 56.3% respectively), and for higher trophic level species groups dropped by 25% [13.5%, 31.9%], with three out of five higher-level groups showing significant reductions (Fig. 3B).

Land expectation value–biodiversity trade-offs

Significant species–richness–LEV trade-offs occurred for discount rates up to 7% but trade-offs disappeared or even switched to synergies at higher discount rates (Fig. 3C). Synergies resulted when increased future revenue from discounted timber yield gains afforded by herbicide use, are swamped by the high costs of plantation establishment. Herbicide use therefore actually decreases LEV below that of untreated plantations. Species–richness–financial–value functions are congruent with biodiversity–yield functions only under a subset of economic scenarios (discount rates $\leq 7\%$) but not for discount rates typical for riskier investment portfolios. Thus, our study indicates that while substantial biodiversity–yield trade-offs exist in intensive timber production, managers applying high discount rates have the potential to contribute to both biodiversity conservation and economic objectives by reducing initial management intensity. This suggests a novel strategy for harmonizing biodiversity conservation and revenue. Importantly, biotic and abiotic risks frequently cause yield losses (e.g., extreme weather events, wildfires), so this future uncertainty ultimately raises the applied discount rate (Amacher et al. 2009).

DISCUSSION

We document trade-offs between timber production and biodiversity that have implications for biodiversity conservation as global demands for timber increase (Phalan et al. 2016, Fischer et al. 2017, Betts et al. 2021). Unsurprisingly, our results suggest that although many biodiversity elements occurred on more intensively managed lands, unsprayed controls, in general, supported a greater diversity and abundance of early successional forest species. However, to generate the same wood volume, substantially more land area is required for this gain in early seral biodiversity. For example, only 1.53 ± 0.12 ha (estimate \pm SE) of plantation is necessary to provide 100,000 board feet of timber under a 40-yr rotation with moderate herbicide but 1.83 ± 0.13 ha would be required without herbicides (a 20% increase in land area). Thus, more intensive management may also contribute to regional conservation gains as increased

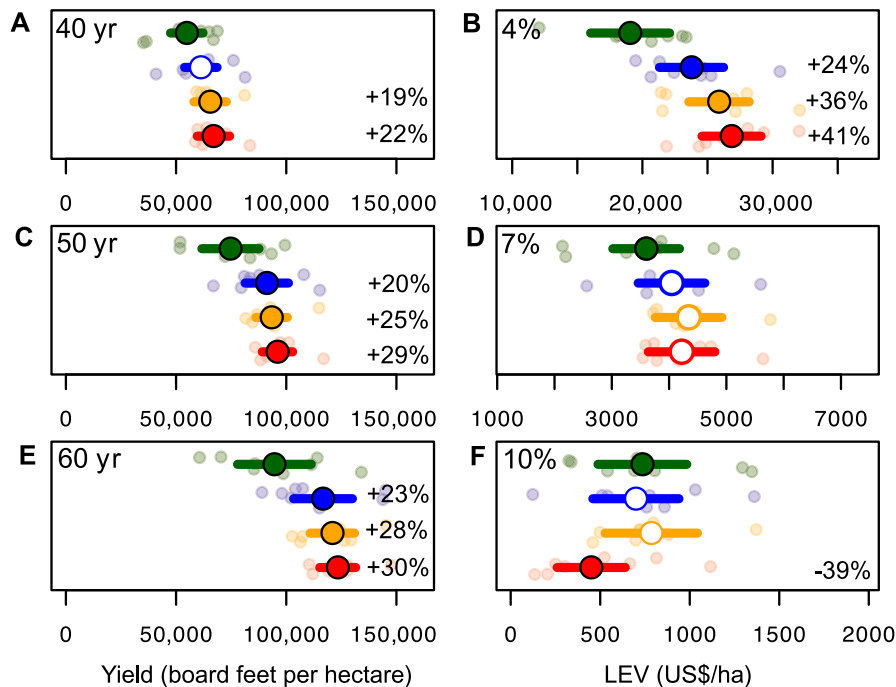


FIG. 2. Herbicide-driven yield gain increases with longer rotation ages, but herbicide-driven profitability gains dampen or even reverse with increasing financial discount rate. The first column shows estimated mean timber yield (board feet per hectare, circles [1 board foot = 0.0024 m²]) and 95% confidence intervals (bars) for plantations harvested at age (A) 40, (C) 50, and (E) 60 yr under each herbicide regime, based on linear mixed effect models. The second column shows the maximum land expectation values (LEV) for 4% (B), 7% (D), and 10% (F) discount rates. Solid circles indicate a significant difference from untreated control sites, for the light, moderate, and intensive treatments. Numbers on the right side of the panels show the mean proportional change compared to the control for significant comparisons.

yields could help secure retention of forest reserves (Phalan et al. 2016). This assumes that increased timber production on intensively managed stands is linked to policies requiring increased reserves, a scenario that could be realized across local, regional, or global scales. Future decisions to minimize trade-offs between biodiversity and production should consider not only the biodiversity gains of less intensive forestry but also the implications for additional land area needed to produce an equivalent amount of timber. An assessment of the landscape-scale implications of forest management intensification versus extensive (low or no herbicide) approaches is beyond the scope of this study. However, future work should weigh gains to early seral biodiversity afforded by reduced herbicide use, versus the potential declines in the amount of late-seral forest resulting from the necessary expansion of less intensive management treatments to achieve similar timber supply. Given that, in the Pacific Northwest, late-seral species are declining at even greater rates than early seral species (Phalan et al. 2019), such landscape-level optimization studies will be of great importance for informing forest policy.

We expected negative effects of herbicide to propagate across species groups throughout the food web (sensu Scherber et al. 2010), especially given that experimental

herbicide application reduced plant richness and abundance by up to two times and four times, respectively, in relation to control sites. However, we found mixed support for this expectation (e.g., birds, moths, and cervids). Further, birds (for which we had longer-term data) increased to levels approximating the control treatment during the 7-yr study (Fig. 1C, M, and N). We speculate that the presence of early successional forest in surrounding landscapes may have subsidized rapid recovery of intensively managed stands with propagules (Leibold et al. 2004). Also, early successional species may be less specialized and more resilient than previously thought. For instance, our related work found that herbicide treatments had small negative effects on moths despite previously reported dependencies on specific food plants (Root et al. 2017).

Importantly, eight years following clearcutting, canopy closure of plantation species had not been reached on our experimental stands. Thus, our estimates for herbicide-driven reductions to early-successional biodiversity are likely to be conservative, given that herbicides accelerate canopy closure of plantation species and thereby likely shorten the species-rich pre-canopy closure period (Kennedy and Spies 2005, Harris and Betts 2021). Further, it is important to note that our measures of biodiversity were focused on species richness and

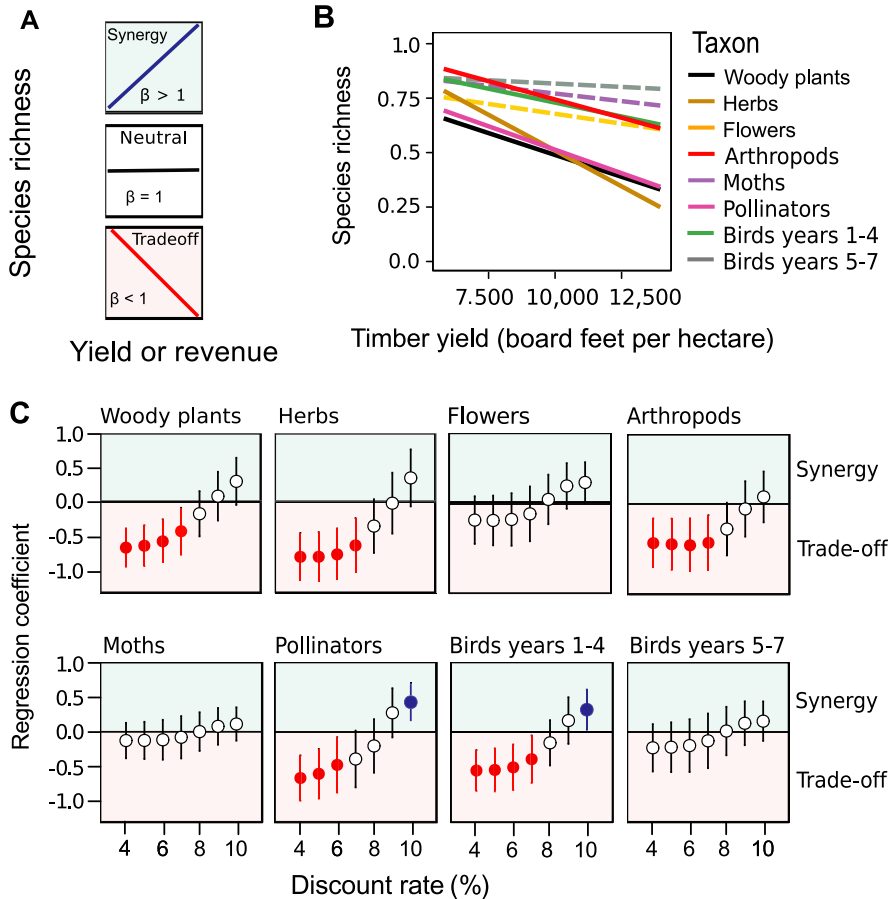


FIG. 3. Trade-offs between species richness and timber revenues dampen or disappear at high discount rate. (A) Conceptual diagram showing examples of functions relating timber yield or revenues (x -axis) and biodiversity (y -axis). Functions can be classified into synergies (blue line; slope > 0), neutralities (black line, slope $= 0$), or trade-offs (red line; slope < 0). (B) The relationship between total timber yield at age 40 yr and species richness for eight species groups. Lines show predicted values based on linear models fitted with restricted maximum likelihood. Dashed lines $P > 0.05$; solid lines $P \leq 0.05$. (C) Effect of the nominal discount rate on the slope (β ; circles) of linear regressions between soil expectation values (LEV, a common indicator of economic performance), and species richness of eight organism groups. Thus, β s > 0 indicate synergies between LEV and species richness (blue dots), β s < 0 trade-offs (red), and a β not significantly different from 0, a neutral relationship (white). Dots show estimated slopes (solid dots $P < 0.05$, open dots $P \geq 0.05$), bars the 95% confidence interval. The black horizontal line shows a slope of 0 (neutral relationship).

abundance rather than on the fitness consequences of herbicide treatments. It is possible that in anthropogenically disturbed systems, density can be a misleading indicator of fitness (Van Horne 1983). However, in companion studies, we did not detect effects of herbicide treatments on nest success or survival of two early seral songbird species (Rivers et al. 2019, 2020).

Our results indicate that herbicide use might not be justifiable under high discount rates, particularly for landowners who place significant value on biodiversity (Giampaoli and Bliss 2011). In our scenarios, vegetation control does not uniformly improve LEV at high discount rates. However, herbicides may still be appealing under a variety of land management approaches. First, policy incentives may inadvertently encourage herbicide application. For example, the Oregon Forest Practices

Act allows regeneration harvest only if crop trees on adjacent stands are adequate in number, dominate the site, and are “free to grow” (typically at least 1.3 m tall; Oregon Department of Forestry 2019). Accelerating early crop tree growth with herbicides therefore guarantees more rapid harvesting opportunities on adjacent stands, a particularly relevant outcome to large landowners. Second, applying herbicides may increase the predictability of forest management outcomes as broad-scale application of herbicides may decrease the risk of “failed” plantations that yield little or no future volume or require replanting at additional cost. Indeed, vegetation management has the capacity to reduce variation in timber yield, particularly in systems where unwanted hardwoods or shrubs have the capacity to out-compete crop trees (Knowe et al. 1992, Nilsson and

Allen 2003, Wagner et al. 2005). Our moderate and intensive treatments significantly reduced variation in timber yield relative to control treatments (Fig. 2).

On the other hand, there may be some unmeasured long-term financial and timber production costs to forest management intensification. For instance, low diversity, structurally simple forests may be more vulnerable to insect pests (Bergeron et al. 1995, Everaars et al. 2011), or fire (Zald and Dunn 2018). These risks are likely to increase in the face of a warming climate (Bentz et al. 2010, Littell et al. 2010), with potential consequences for the economic evaluations of future forest management scenarios. Long-term, landscape-scale studies will be necessary to quantify such potential costs to the current intensive forest management regime in the Pacific Northwest.

Overall, our results show that intensive forest management via herbicide application tends to result in biodiversity–timber-production trade-offs for many species groups although trade-offs were weaker than expected. Also, we found evidence that trade-offs weakened as stand development progressed (e.g., trade-offs were apparent for birds in years 1–4 but not in years 5–7). In contrast, revenue–biodiversity trade-offs dissipated at high economic discount rates. Discounting future harvests for long-term perennial crops may provide opportunities and incentive to reconcile biodiversity conservation with revenue, not only in forest systems, but also in other production systems with long production cycles such as oil palm or viticulture. This result may be particularly relevant in developing regions and emerging markets, where both economic discount rates and the human pressure on biodiversity are particularly high (e.g., Chile, Brazil, Indonesia). Given that most land-use decisions concerning management intensity are driven by the choice of individual landowners, our results offer promise for scenarios where biodiversity is maintained without compromising revenue. We suggest an examination of forest policies that might create unintended incentives to spray that may be economically unjustifiable or ecologically undesirable. We recommend that future research on biodiversity–yield include assessment of trade-offs that are quantified in economic terms and resource production units (Phalan et al. 2011, Batáry et al. 2017, Granath et al. 2018), particularly for commodities requiring a long time lag between initial investment and harvest.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2441/full>

OPEN RESEARCH

Statistical code for bird abundance and occupancy is given in Data S1. Additional data and code (Kormann et al. 2021) for the analysis are available on Zenodo at <http://doi.org/10.5281/zenodo.5018478>