Forest Ecology and Management xxx (2013) xxx–xxx

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Initial experimental effects of intensive forest management on avian abundance

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ARTICLE INFO

Article history:
Available online xxxx

Keywords:
Biodiversity
Early successional forest
Herbicide
Imperfect detection
Intensive forest management
Plantation forestry

ABSTRACT

Components of biodiversity in intensively managed forest stands may be reduced in comparison to naturally regenerated stands. Use of herbicides to suppress herbaceous and woody plant species that compete with planted seedlings has been implicated in negative impacts. We designed a large-scale experimental study to test the influence of intensive forest management on the abundance of early seral bird species in the Oregon Coast Range, US. Experimental applications consisted of 'Intensive' (i.e., heavy use of herbicides), 'Moderate' and 'Light' treatments, as well as controls with no herbicide application. In relation to the control, abundance of six out of thirteen bird species was significantly reduced in at least one of the three treatments. Leaf-gleaning insectivorous birds were more negatively affected by heavier herbicide treatments in general than bird species with other foraging behavior. Long-term bird population trends, derived from the Breeding Bird Survey, were correlated with the effect of intensive treatment; species more negatively associated with intensive treatments at the stand scale, were more likely to be in decline across the Pacific Northwest, US. Our results also indicate that reducing intensity of herbicide applications has positive effects on early seral bird abundance during the first 2 years of stand growth – particularly those species exhibiting negative population trends. To balance biodiversity conservation and timber production, research examining the tradeoffs between reduced application of herbicide and tree growth is required.

1. Introduction

Structurally and compositionally diverse early seral forest is declining in some locations worldwide (Angelstam, 1998; Najera and Simonetti, 2006; Thomas et al., 2006) and, in many instances, declining below the historic range of variability (Spies and Johnson, 2007). This trend is of conservation concern because early successional stages are generally associated with high species diversity and food web complexity (for review see Swanson et al., 2011). Further, many species seem to be linked to this forest condition for critical parts of their life histories (Hagar, 2007). For example, previous research has linked changes in the availability of early seral habitat with population trends of vertebrate species (Litvaitis, 1993; Hunt, 1998; Betts et al., 2010).

Decline in availability of complex early seral forest has been attributed to two primary factors. First, fire suppression and reductions in timber harvest in many developed countries have reduced the amount of early seral forest being created (Kennedy and Spies, 2005; Kauppi et al., 2006; Spies et al., 2007). Second, stands disturbed by both timber harvest and natural disturbance tend to be managed intensively under an industrial model in order to produce wood fiber as rapidly as possible. Intensive forest management (IFM) in the Pacific Northwest of the United States (Oliver and Larson 1996), as in many parts of the globe (Najera and Simonetti, 2006), temporarily inhibits development of herbaceous plants and early seral broadleaf shrubs, and reduces competition with commercially valuable planted conifers (Adams et al., 2005). Such practices increase wood production, but may simplify the forest ecosystem both spatially and temporally. Though species diversity of intensively managed plantations may be similar to less intensively managed stands during some periods of their development (Ellis and Betts, 2011), it has been argued that such plantation forestry truncates the longevity of pre-canopy closure establishment period (Donato et al., 2012).

Conservation and management programs require more information about bird response to herbicide treatments in the Pacific Northwest, U.S. Available evidence on this topic is generally circumstantial (Lautenschlager and Sullivan, 2004); it is therefore

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http://dx.doi.org/10.1016/j.foreco.2013.06.022

not possible to infer causality from these findings because apparent relationships between IFM and biodiversity could be confounded by other factors. Also, forest practice policies in many areas, including the Pacific Northwest, US, prevents natural regeneration following harvest, requiring landowners to replant quickly and provide a 'free to grow' condition for planted seedlings. Such policies reduce the possible range of early seral composition represented by sampling, which limits inference to stands within a fairly narrow range of IFM that does not include unmanaged controls (Jones et al., 2012). The few manipulative studies that exist tend to examine only one or two treatments in relation to a control (Easton and Martin, 1998) and are poorly replicated (Lautenschlager, 1993). As a result, statistical power may be low, thus weakening inference about any potential management recommendations from a study. Ideally, gradients in management intensity should be reflected in sampling designs, allowing for the detection of potential *degrees* of IFM that might minimize trade-offs between timber production and biodiversity (Iglay et al., 2012).

Here, we report results of a 2-year manipulative experiment designed to address the question of how a gradient in IFM influences biodiversity in early seral stands of the Oregon Coast Range, US. In this paper, we capitalized on a well-replicated randomized block design, conducted with samples at the scale of entire forest stands, to test whether IFM influences the abundance of passerine bird species. Birds are considered to be biodiversity indicators (Schulze et al., 2004; Venier and Pearce, 2004; Gregory et al., 2006) and perform important ecosystem services (Sekercioglu et al., 2004). Many of the bird species examined in the present study have previously shown strong sensitivities to IFM in correlative studies conducted at stand (Morrison and Meslow, 1983; Jones et al., 2011; Ellis et al., 2012) and landscape scales (Betts et al., 2010). These sensitivities are hypothesized to be indirectly caused by declines in broadleaf shrubs. Compared to conifers, the leaves of these hardwood species may support more abundant arthropods, which are important prey food sources for insectivorous birds (Hammond and Miller, 1998; Hagar, 2007; Hagar et al., 2012). Likewise, many Neotropical passerines nest in dense broadleaf shrubs. Therefore, we expected leaf-gleaning, insectivorous and shrub nesting birds to respond more negatively to IFM than species more generalized in their foraging and nesting habits.

2. Methods

2.1. Study area

We established 32 study stands, ranging in size from 12 to 16 ha each, in the Oregon Coast Range, US. Study stands occurred in 8 distinct blocks spanning a 100 km (N–S) portion of the northern Oregon Coast Range (Fig. 1). To reduce within-block variation, all four stands within a block are located within 5 km of each other. Within all block but one (Tillamook), all experimentally treated stands were designed to be >1 km apart to avoid influence from adjacent treatments (see *treatments* below). One study block with treated stands <1 km apart was selected due to the unavailability of alternatives on Oregon Dept. of Forestry land. We note that in this case, adjacency could have the effect of making our results more conservative (individuals from the control stand couldpotentially move to the treated stands reducing effect sizes). The climate of the Oregon Coast Range consists of cool, wet winters and mild, dry summers. All sampled stands are in the western hemlock zone (Franklin and Dyrness, 1988) and range in elevation from 210 to 850 m. Early-seral plantations in this area are dominated by Douglas-fir (*Pseudotsuga menziesii*) saplings, with minor components of grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Dominant shrub/woody species include California hazelnut (*Corylus cornuta* sub-spp. *californica*), oceanspray (*Holodiscus discolor*), vine maple (*Acer circinatum*), big-leaf maple (*Acer macrophyllum*), cascara(*Rhamnus purshiana*), salmonberry (*Rubus spectabilis*) and red alder (*Alnus rubra*). Smaller understory broadleaf species include *Vaccinium* spp., salal (*Gaultheria shallon*), and Oregon grape (*Mahonia nervosa*) which can dominate stands post-harvest. The herbaceous community is comprised of many native and non-native herbaceous plants with swordfern (*Polystichum munitum*) and brackenfern (*Pteridium aquilinum*) often dominating.

2.2. Treatments

We used a randomized complete block design and randomly applied one of four treatments to each of the four stands in each of the eight blocks ($n = 32$). All 32 stands were clearcut in fall 2009 and were planted in spring 2010 with Douglas-fir (*P. menziesii*), the major commercial species in the region. Our objective was to test combined effects of the suite of herbicides and surfactants used in typical operations rather than to examine the effect of a particular chemical. Therefore, we applied a full suite of chemicals to sites with the aim of creating a gradient in management intensity across four treatments (Table 1, Fig. 2). Importantly, within a treatment, the same amount and type of chemicals were applied across all blocks. The 'site preparation' treatment occurred before stands were planted and consisted of 0.10 kg ha^{-1} Escort (DuPont, Willmington, Deleware; active ingredient (ai) 60 percent *metsulfuron methyl*), 7.01 L ha^{-1} Accord (Dow AgroSciences LLC, Indianapolis, Indiana; a.i. 41.5 percent *glyphosate*), 1.75 L ha^{-1} Chopper (BASF Corporation, Florham Park, NJ; a.i. 27.6 percent *imazapyr*), 0.21 kg ha^{-1} Oust (DuPont, Willmington, Deleware; a.i. 75 percent *sulfometuron methyl*), and 1.75 L ha^{-1} MSO (methylated seed oil, as surfactant) applied aerially via helicopter. First year (2011) spring herbaceous release spray consisted of 2.98 kg ha^{-1} Velpar (DuPont, Willmington, Deleware; a.i. 75 percent *hexazinone*), and 2.24 kg ha^{-1} 2,4-D (Dow AgroSciences LLC, Indianapolis, Indiana; a.i. 97.5 percent *2,4-dichlorophenoxy acetic acid*) applied aerially via helicopter or with ground-based backpack sprayers. Second year (2012) spring herbaceous release spray consisted of 0.14 kg ha^{-1} Oust XP (DuPont, Willmington, Deleware; a.i. 75 percent *sulfometuron methyl*), 0.42 kg ha^{-1} Transline (Dow AgroSciences LLC, Indianapolis, Indiana; a.i. 40.9 percent *clopyralid*), and 1.49 kg ha^{-1} Velpar (DuPont, Willmington, Deleware; a.i. 75 percent *hexazinone*) applied aerially via helicopter or with ground-based backpack sprayers. Only two treatments had been applied prior to summer 2011 (Table 1). Thus, Moderate and Intensive stands had not yet been differentiated during the first year of data collection (Table 1).

2.3. Sampling

We used a stratified random approach to select three point count plots in each stand and to maximize the distance between survey locations and stand edge while sampling representative portions of the treatment area. In analysis, we used the average of the three counts within a stand as our response variable (see *Analysis* below). We sampled birds at each of the 96 point count locations in 2011 and 2012. Each point was sampled four times during the breeding season (May 28 – July 3rd). The survey order and observer were varied throughout the season to avoid associated biases. Point count survey guidelines followed Ralph et al. (1995) except that we used a 10-min time interval for sampling. Censuses began at sunrise and were completed by 10 am. Every bird seen or heard was recorded with an associated behavior. First and closest detection distances from the census point were

Please cite this article in press as: Betts, M.G., et al. Initial experimental effects of intensive forest management on avian abundance. Forest Ecol. Manage. (2013), http://dx.doi.org/10.1016/j.foreco.2013.06.022

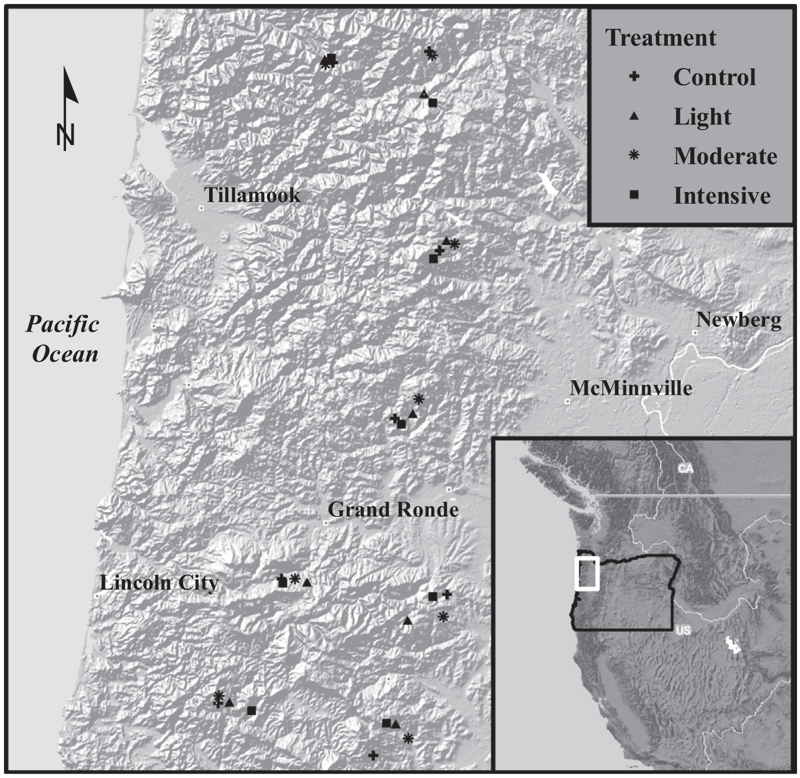

Fig. 1. Geographic location of eight study blocks containing four treatments in Oregon Coast Range, US.

Table 1
Timing of the application of four treatments (control, light, moderate, intensive) from 2010 to 2012 in the Oregon Coast Range, US.

Treatment	Year post-harvest	Control	Light	Moderate	Intensive
Site-preparation (broadleaf vegetation spray)	0			X	X
Planted: Approx. 1100 trees/ha	1	X	X	X	X
Herbaceous spray	1		X	X	X
Herbaceous spray	2				X

estimated with detections beyond a 50 m radius distance band considered "out" of the survey plot.

Ocular estimates of broadleaf shrub and herbaceous cover were taken for all non-coniferous plants by species within 3–3 m radius subplots each centered 20 m from avian census locations. The bearing to the initial subplot was selected at random; remaining plots were located to maintain 120 degrees separation from other plots. Cover estimates for each species, taken within the 3 m radius plots were then summed to achieve total (sometimes overlapping) shrub cover estimates for the three 3 m-radius subplots (Ellis et al. 2012). This method was chosen to help quantify the three-dimensional nature of the woody vegetation. As a result of its use, summed point level cover estimates across species were allowed to exceed 100 percent.

2.4. Analysis

We assume that the replicated counts n_{ij} are obtained from R spatially dispersed plots (i) on each of J sampling visits (j), where the (unobserved) plot population, N_i, is closed during the period of sampling. The N-mixture model (Royle, 2004) describes counts arising from a hierarchical model with two components: a state process where the true plot abundances N_i are assumed to be random variables with distribution $f(N, \lambda)$ and an observation process where counts n_{ij} follow a binomial distribution, conditional on the unobserved N_i and detection probability p_{ij}. A general description of the model with Poisson counts is:

$$N_i \sim \text{Poisson}(\lambda_i)$$

$$n_{ij}|N_i \sim \text{Binomial}(N_i, p_{ij})$$

In the N-mixture model, the plot-specific abundances N_i are considered nuisance parameters and are numerically integrated from the likelihood function to obtain joint estimates of λ and p. One advantage of this framework is that the parameters λ and p can be allowed to vary as a function of covariates, typically via a link function for the mean parameter (e.g., log-link for abundance, logit-link for detection probability). Important assumptions for these models include (1) in-plot population closure during the period of sampling, (2) independence of counts across plots, (3) the assumed distribution of plot-level abundance across the area of interest (e.g., Poisson), and (4) the structural form of parameterizations for mean abundance and detection probability. We did not assess the assumption of within-season closure at the individual point-count scale due to the sparcity of data for most species in our study (Rota et al., 2009). If the closure assumption is violated, this would result in an upward bias in our abundance estimates across all treatments.

For all analyses, we fit N-mixture models using the 'pcount' function in the package 'unmarked' in the software program R (R Development Core Team, 2010). We obtained approximate asymptotic variances of parameter estimates from the inverse Hessian evaluated at the maximum likelihood estimates (Royle, 2004). For all analyses reported here, we used a Poisson distribution for

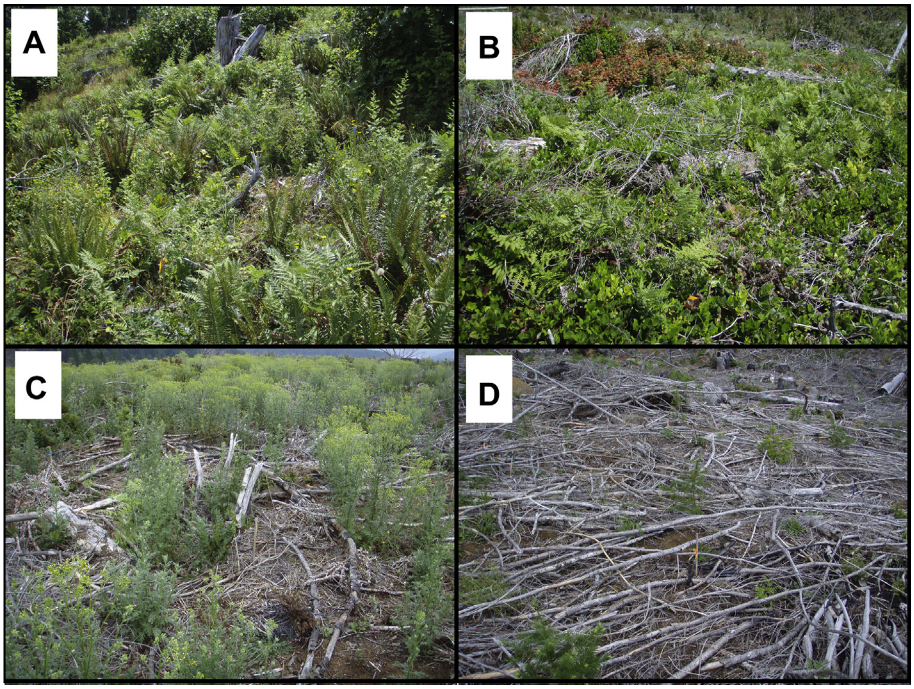

Fig. 2. Representative examples of four intensive forest management treatments applied in this study in the second year of the study ranging from Control (A), Light (B), Moderate (C) and Intensive (D) herbicide application, Oregon Coast Range, US.

the plot-level abundances, N_i. Several approaches are available to obtain estimates of abundance from the fitted model, as described in Royle (2004). We estimate expected abundance from λ directly, using the pooled count from the three 50 m radius plots.

We considered the model based on the experimental design, in which abundance varied by year and treatment. The effect of elevation was not a focus of our study, but prior studies have found associations between avian abundance and elevation (Terborgh, 1977) and we wanted to control for this source of variation; we therefore included it as a predictor of abundance in all models. We modeled detection probability as a function of percent cover of broadleaf plants. This was a more parsimonious way to include an effect of the treatments (which primarily reduce broadleaf cover) on detection than a categorical treatment effect. In addition, we included linear and quadratic terms for Julian date (January 1 = 1, December 31 = 365) because avian detection rates are known to vary seasonally (Kéry et al., 2005). We centered and scaled the continuous covariates. Our specific model was:

$$N_i \sim \text{Poisson}(\lambda_i)$$

$$n_{ij} \sim \text{Binomial}(N_i, \text{p}_{ij})$$

$$\begin{aligned}\text{logit}(p_{ij}) = {} & \alpha_0 + \alpha_1 \cdot \text{Percent Broadleaf Cover} + \alpha_2 \cdot \text{Julian Date} \\ & + \alpha_3 \cdot \text{Julian Date}^2\end{aligned}$$

$$\begin{aligned}\log(\lambda_i) = {} & \beta_0 + \beta_1 \cdot \text{Year}(2012) + \beta_2 \cdot \text{Light} + \beta_3 \cdot \text{Moderate} + \beta_4 \\ & \cdot \text{Intensive} + \beta_5 \cdot \text{Light} \cdot \text{Year}(2012) + \beta_6 \cdot \text{Moderate} \\ & \cdot \text{Year}(2012) + \beta_7 \cdot \text{Intensive} \cdot \text{Year}(2012) + \beta_8 \\ & \cdot \text{Elevation}\end{aligned}$$

For each species by year combination, we present estimates (average and 95% confidence interval) of treatment effect contrasts (Kroll et al., 2012). In our parameterization, the treatment contrast compares abundance of each of the three herbicide treatments to the Control. We back-transformed values so that contrasts can be interpreted as either the average percent increase or decrease in abundance due to a specific treatment as compared to the Control. A treatment contrast of 1 indicates that abundance is equal across treatments. In addition, we included contrasts with Moderate as the base-line, given that Moderate is the closest approximation of operational practice in the Oregon Coast Range (Appendix B). We present estimated abundances for species by treatment combination for 2011 and 2012. Following Nichols et al. (2009), we interpret λ as the average number of individuals whose home ranges overlap the 3 point stations within a harvest stand, rather than the average total number of individuals who occur in the harvest stand.

Using the models above, we estimated the effect size (Control–Moderate) for each species from 2012 data. We summarized these results with box plots of effect sizes grouped by species' life history traits. Regional-scale population trends for the Pacific Northwest were derived from the Breeding Bird Survey (BBS; Sauer et al. 2011). The BBS relies on observations made by volunteers along 40 km roadside samples each representing approximately 1° square of latitude and longitude. BBS Trends estimated were for the Pacific Northwest Rainforest (Oregon, California and Washington only) 1983–2011 using hierarchical models (http://www.mbr-pwrc.usgs.gov/bbs/trend/tf11.html).

3. Results

Cover of non-woody vegetation, including grasses, herbs and ferns, decreased with treatment intensity but increased overall from 2011 to 2012 (Table 2). As expected, Control and Light treatments had higher broadleaf plant cover and species richness than Moderate or Intensive treatments in 2011 and 2012 (Table 2), indicating that herbicide treatments had a strong and consistent effect 2 years post-harvest. Broadleaf cover increased in all treatments between 2011 and 2012. Conifer density was similar across treatments and sampling years (Table 2).

We detected 63 bird species during the study period with 3044 total detections recorded in 768 10-min sampling periods.

Table 2
Mean (±SD) for vegetation and stand-location attributes in relation to herbicide treatments applied in the Oregon Coast Range, US, 2011-2012.

Treatment	Percent broadleaf cover (%)		Broadleaf species richness (# of species)		Non-woody vegetation cover (%)		Conifer density (stems/ha)		Elevation (m)	Slope (%)
	2011	2012	2011	2012	2011	2012	2011	2012		
Control	27.9 (13.4)	51.2 (17.1)	7.3 (1.1)	6.3 (1.9)	37.6 (16.6)	55.4 (15.4)	1022 (377)	1077 (739)	496 (182)	17.4 (6.4)
Light	32.2 (11.0)	57.2 (17.5)	6.7 (2.6)	5.5 (1.5)	14.6 (9.4)	34.5 (21.4)	786 (311)	790 (389)	484 (180)	20.7 (6.7)
Moderate	4.5 (3.3)	7.6 (7.5)	2.3 (0.9)	2.4 (1.2)	3.5 (3.1)	27.4 (18.8)	928 (263)	763 (228)	485 (158)	16.3 (7.6)
Intensive	3.0 (3.6)	11.0 (8.9)	2.0 (1.5)	1.9 (1.1)	3.0 (2.1)	10.3 (6.7)	900 (153)	881 (244)	528 (151)	16.2 (9.6)

Table 3
Individual detections by treatment and year for species making up greater than 1 percent of total detections, Oregon Coast Range, US, 2011–2012. Species considered previously as being strongly associated with early seral broadleaf forest are designated with a*.

Species	Control		Light		Moderate		Intensive		Total
	2011	2012	2011	2012	2011	2012	2011	2012	
American goldfinch (*Spinus tristis*)	13	37	4	17	1	13	4	28	117
Dark-eyed junco (*Junco hyemalis*)	44	88	60	84	58	80	57	86	557
House wren (*Troglodytes aedon*)	71	126	49	100	28	104	36	82	596
Orange-crowned warbler * (*Vermivora celata*)	0	13	3	12	1	2	2	1	34
Rufous hummingbird * (*Selasphorus rufus*)	10	14	4	20	2	9	1	2	62
Song sparrow * (*Melospiza melodia*)	15	26	13	11	3	8	2	4	82
Spotted towhee (*Pipilo maculates*)	2	16	3	17	9	10	0	4	61
Swainson's thrush * (*Catharus ustulatus*)	0	21	1	8	0	4	0	3	37
Townsend's solitaire (*Myadestes townsendi*)	4	5	2	6	4	5	5	3	34
Violet-green swallow (*Tachycineta thalassina*)	5	22	4	22	16	40	6	39	154
Western bluebird (*Sialia mexicana*)	3	12	4	6	8	19	10	26	88
White-crowned sparrow * (*Zonotrichia leucophrys*)	50	90	16	76	21	51	16	57	377
Wilson's warbler * (*Wilsonia pusilla*)	11	23	7	18	4	3	2	3	71

Nine-hundred sixty-eight detections of 51 species were recorded in 2011 and 2076 detections from 49 species in 2012. House wren (*Troglodytes aedon*), dark-eyed junco (*Junco hyemalis*) and white-crowned sparrow (*Zonotrichia leucophyrys*) made up 50 percent of total detections from both years. We estimated abundance for individual species with greater than 1% (30) of the total detections in 2011 and 2012 combined (Table 3).

Thirteen species were abundant enough to be analyzed individually and made up 75 percent of total detections (Table 3). Four of those species had 15 or fewer detections in 2011 (orange-crowned warbler (*Vermivora celata*), spotted towhee (*Pipilo maculates*), Swainson's thrush (*Catharus ustulatus*) and Townsend's solitaire (*Myadestes townsendi*)), and so we analyzed 2012 detections only for those species. Six of the 13 most abundant species are considered to be early seral broadleaf forest associates (rufous hummingbird, orange-crowned warbler, song sparrow (*Melospiza melodia*), Swainson's thrush, white-crowned sparrow, Wilson's warbler (*Wilsonia pusilla*) (Ellis et al. 2012), whereas the remaining 7 species are more generalized in their distributions (Table 3).

Mid-season species-specific detection probabilities ranged from 0.04 to 0.60 for an individual point count visit. Twelve of 13 species had detection probabilities below 0.35. Species-specific abundance estimates increased for most species between 2011 and 2012 as species colonized the stands post-disturbance (Appendix A). Confidence intervals of abundance estimates were broad for many species, especially those with low numbers of detections.

Treatment contrasts with the Control were statistically significant for at least one treatment × year interaction for four species that have previously been identified as being strongly associated with early seral broadleaf forest (rufous hummingbird, Swainson's thrush, white-crowned sparrow, and Wilson's warbler). Wilson's warbler and rufous hummingbird were the most sensitive species to the Intensive treatment, with abundance estimates – for both years – 5–20% of those in Control (Fig. 3a). Two species that are more generalized in their distributions (American goldfinch [*Spinus tristis*] and house wren) (Figs. 3 and 4; Appendix C) also showed sensitivity to intensive forest management treatments but the magnitude and direction of these effects differed; contrasts with the Control for American goldfinch were more variable, indicating lower abundance estimates for Light and Moderate treatments but not for the Intensive treatment (Fig. 3b). House wren treatment contrasts indicated lower abundance estimates for Moderate and Intensive treatments but not the Light treatment (Fig. 3b).

We did not detect significant differences between treatments and the Control for 6 species (dark-eyed junco, orange-crowned warbler, song sparrow, spotted towhee, Townsend's solitaire, and western bluebird (*Sialia mexicana*)) (Fig. 3a and b). Due to the relatively low number of detections for three of these species (spotted towhee, song sparrow and orange-crowned warbler) parameter estimates were imprecise, so we are not able to reject the possibility of a biologically meaningful effect of herbicide treatments. However, the remaining four species generally showed equal or greater abundances in treated stands. Violet-green swallow (*Tachycineta thalassina*) showed a significant positive response to the moderate treatment in the first year of the study.

When modeled as a group, the 6 early seral associated species had lower abundance estimates in Light, Moderate and Intensive treatments than in Control stands (Fig. 4, Appendix C). We reduced life history traits to coarse categories due to the limited number of species in our study. Shrub-nesting birds and foliage gleaning insectivores responded more strongly to the moderate treatment in general than ground nesting species, cavity nesters, and aerial insectivores (Fig. 5a and b).

Finally, the species with the largest negative effect sizes in our study (primarily early-seral associates, especially shrub nesting, leaf gleaning insectivores) are also ones with the greater estimated long-term population declines (Sauer et al., 2011; Fig. 6).

4. Discussion

Abundance of six of thirteen bird species that are common in early-seral forests of the Pacific Northwest was significantly

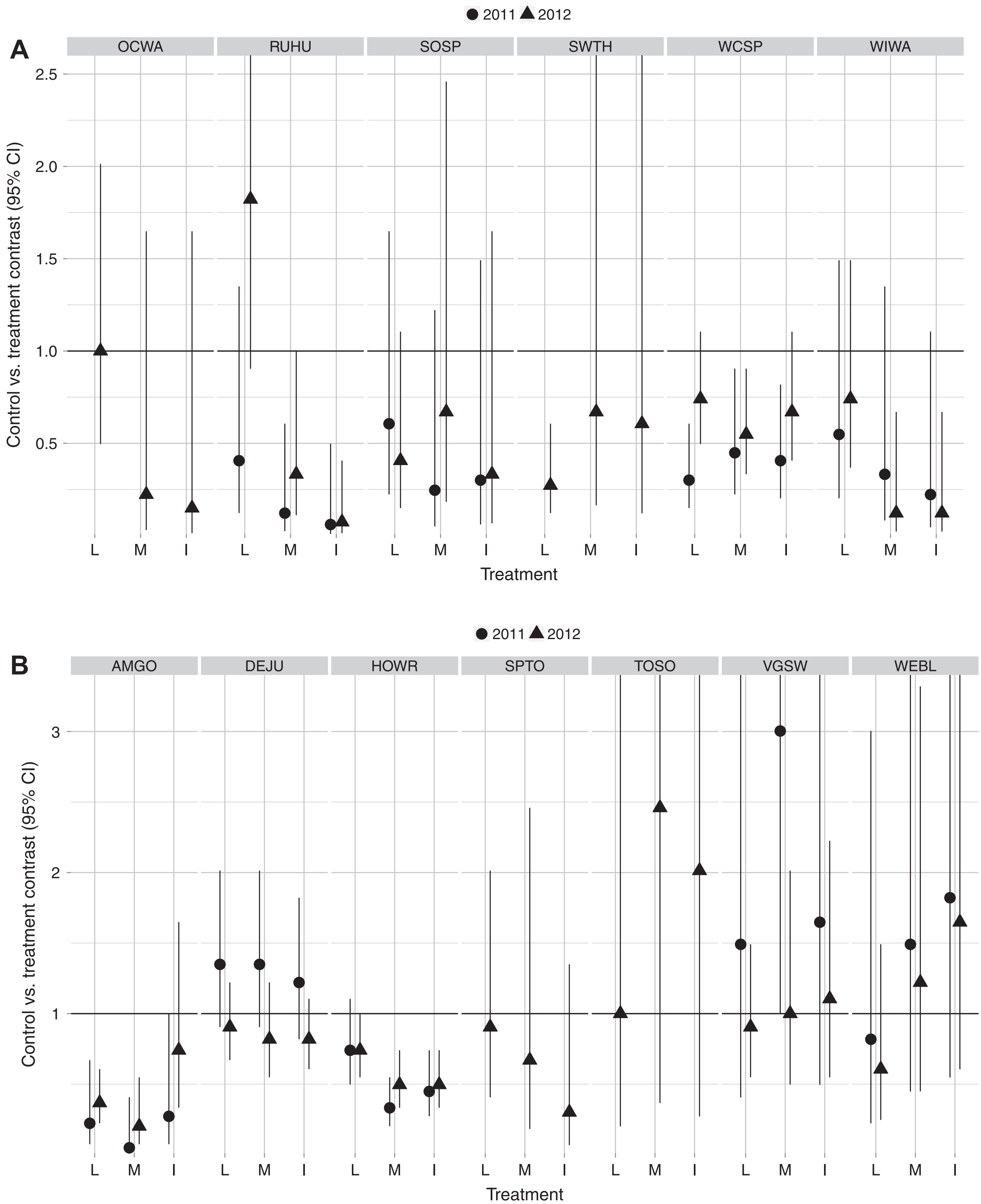

Fig. 3. Back-transformed model estimates (95% confidence interval) for three intensive forest management treatments in relation to untreated controls, Oregon Coast Range, US, 2011–2012, for (A) six common species expected, based on previous research, to be associated strongly with early seral hardwood forest (orange-crowned warbler [OCWA], rufous hummingbird [RUHU], song sparrow [SOSP], Swainson's thrush [SWTH], white-crowned sparrow [WCSP] and Wilson's warbler [WIWA] and (B) seven of the other most common species detected in our study (American goldfinch [AMGO], dark-eyed (Oregon) junco [DEJU], house wren [HOWR], spotted towhee [SPTO], violet-green swallow [VGSW], western bluebird [WEBL] and Townsend's solitare [TOSO]). Treatments comprise Light (L), Moderate (M) and Intensive (I).

reduced in at least one of the herbicide treatments in relation to the Control. The Moderate and Intensive treatments reduced the cover of broadleaf shrubs, which generally contain greater abundances of lepidopteron larvae than coniferous and graminoid vegetation (Hammond and Miller, 1998). If greater amounts of hardwood cover result in more prey, the result could be increased foraging efficiency and reduced territory size, potentially explaining the greater bird abundance we observed in the Control and Light treatments (the food value theory of territoriality; Stenger, 1958). Also, increased foliage volume in Control stands may accommodate a greater number and diversity of nesting sites than hardwood-impoverished stands (Morrison and Meslow,1983). This interpretation is supported by the results that shrub nesters and insectivorous birds tended to be more negatively influenced by

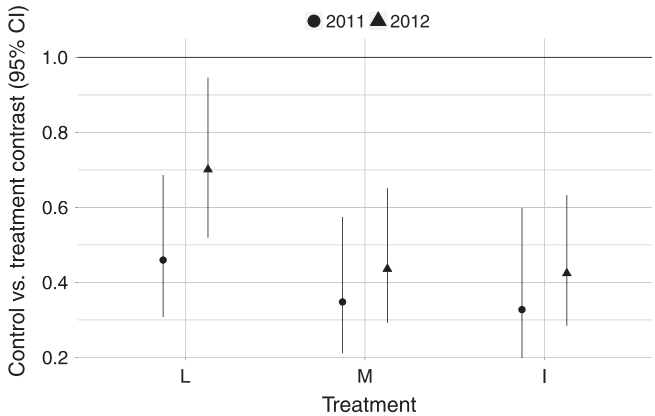

Fig. 4. Back-transformed model estimates (95% confidence interval) for three intensive forest management treatments in relation to untreated controls for species expected to be associated with early seral hardwood forest (orange-crowned warbler, rufous hummingbird, song sparrow, Swainson's thrush, white-crowned sparrow and Wilson's warbler), Oregon Coast Range, US, 2011–2012. Treatments comprise Light (L), Moderate (M) and Intensive (I).

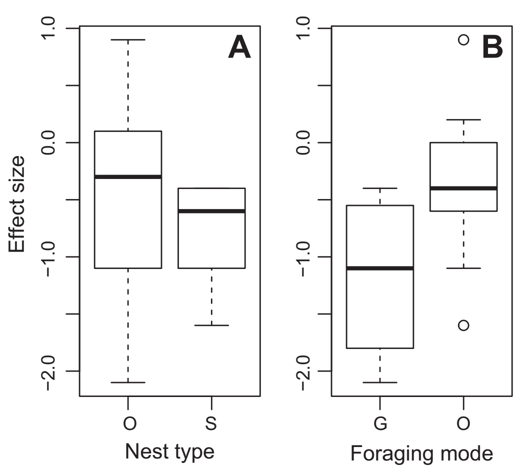

Fig. 5. Boxplots of the association between two life-history traits on modeled effect size (log scale) of the Moderate intensity forest management treatments, Oregon Coast Range, US, 2011–2012. (A) Nest type: shrub (S) vs. other types (ground, cavity; O), (B) foraging mode: leaf gleaner (G) vs. other modes (ground foraging, aerial insectivore; O).

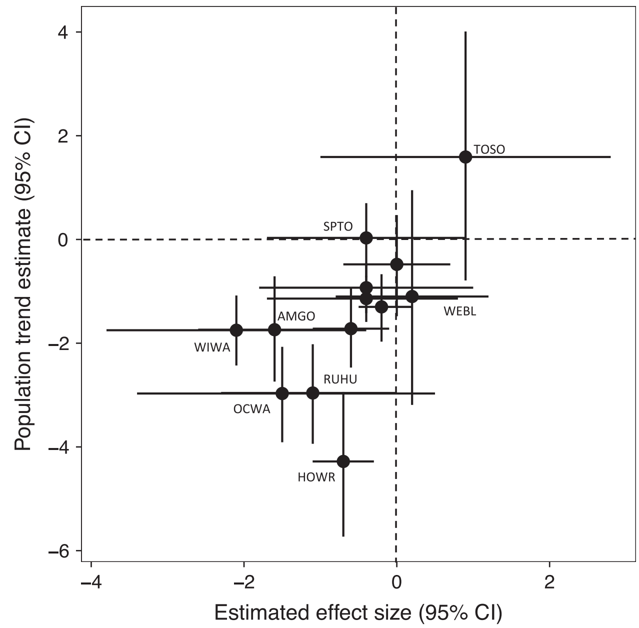

Fig. 6. Correlation between modeled effect size (log scale) of the Moderate intensity treatment (see text for details) and the 30-year population trend for 13 species of forest birds in the Pacific Northwest estimated from the BBS monitoring program. Species most strongly influenced by intensive forest management showed the greatest population declines. Species most and least influenced by intensive treatments are labeled according to species codes in Fig. 3.

our heavier treatments. One of the few previous manipulative studies to examine herbicide effects on bird abundance found increased abundance of conifer shrub nesters in treated stands (Easton and Martin, 1998). Our results do not support this finding, but this is likely due to differences in the ages of treated stands (Easton and Martin 1998: 11–22 years, current study: 1–2 years). Conifers in the current study are not sufficiently large in most cases to support a nest.

The association between species' life history traits and magnitude of species' response to the Moderate and Intensive treatments supports the hypothesis that IFM effects are mediated through availability of food and nest sites. The fact that all species examined did not show consistent declines in relation to herbicide treatments suggests that the reduced abundances we observed for some species were not a direct function of herbicide toxicity. This finding is supported by experimental toxicological studies on the primary herbicides used in our study (Tatum 2004; McComb et al. 2008). Regardless, our life-history results are correlative, so more research is required to assess whether there are cumulative direct effects of herbicides on bird demography.

Our results come with the important caveat that we estimated bird abundance only; it is well known that abundance is not necessarily an indicator of reproductive success or survival (Van Horne, 1983). Several previous manipulative forest management studies have found males returning to remain in altered habitats during the first year post-disturbance, while females dispersed to new, potentially higher-quality habitat (Woodcock et al., 1997). Both Mackinnon and Freedman (1993) as well as Easton and Martin (1998) showed temporal lags in response to herbicide treatments; effects did not emerge for at least 1 year. We expect that because our study was initiated immediately post-harvest our abundance estimates reflect colonization by a new avian community (the previous mature stand is unlikely to have supported most of the early seral species reported in this study). Thus, the potential for such temporal lags is mostly eliminated. Further, recent results indicate that density may be correlated with per capita productivity in managed stands and follows an ideal free distribution (Haché et al., 2013). In other words, depressed densities in treated stands may reduce per hectare productivity (i.e., fewer birds producing young), but not necessarily lower individual-level reproduction. Though we have just initiated demographic studies in our experiment, results from a retrospective study in the same region suggest that per capita productivity does not vary across a gradient in management intensity (Ellis et al., 2012; Rivers et al., 2012). Nevertheless, critical future work on our study plots will test the relationship between density and productivity in intensively managed stands.

Donato et al. (2012) argued that plantation forestry severely truncates the longevity of pre-canopy closure establishment period. Negative responses by some species to our most intense treatments, in the very early stages of succession, indicates that truncation can occur at the 'front end' of stand regeneration as well. How long does this truncation continue, particularly in Light and Moderate stands, which approximate operational standards in the Oregon Coast Range? For instance, in eastern Canada, Mackinnon and Freedman (1993) found that bird abundance for all species was similar in stands that had been sprayed with herbicide to that of the unsprayed control after 4 years. However, in a retrospective study conducted in the Oregon Coast Range, Ellis et al. (2012) found that counts of orange-crowned warbler, Wilson's warbler and Swainson's thrush were reduced in stands with lower levels of broadleaf cover, even 5–9 years after initial herbicide treatment.

The longevity and degree of this early stage truncation is likely to depend upon intensity of the initial treatment as well as factors such as previous site management, legacy species, seed beds and local seed sources. Our results indicate that the Light treatment, which differs from the control by only one herbicide application (Table 1), has apparent benefits for a number of species (house wren, rufous hummingbird, Wilson's warbler, orange-crowned warbler) during the first 2 years of stand growth. This result has been proposed as an untested hypothesis in previous studies (Morrison and Meslow, 1983; Santillo et al., 1989), but has only now received empirical support.

The dichotomy, for some species, between the Control and Light vs. the Moderate and Intensive treatments is consistent with our previous work suggesting thresholds in bird abundance at $\sim$10% hardwood cover (Ellis and Betts, 2011). Both the Moderate and Intensive treatments fell below this threshold in the initial 2 years of our study, whereas both the Control and Light treatments contained >30% hardwood cover, even just 1 year after clearcutting and initial treatments.

Our finding that species with the largest negative effect sizes also are the ones with estimated long-term population declines may provide insight into demography of these species at the regional scale. This relationship does not necessarily implicate IFM in these declines, but provides insight into the habitat requirements for these species. Other stressors, particularly forest succession and reduced harvesting on Federal lands, may be contributing factors (Betts et al., 2010). During the first 2 years of stand growth, reducing herbicide treatment intensity may disproportionately benefit those species declining at the greatest rates. For several species, even our Moderate treatment had higher abundance than the Intensive treatment (though not significantly so). The Moderate treatment, more closely approximates the industrial standard on large private landholdings in the Pacific Northwest, US.

What remains to be quantified are the trade-offs between reductions in intensity of herbicide application and growth of merchantable trees (Wagner et al., 2004). Such trade-offs should be considered not only within stands, but at landscape and regional scales. Some components of biodiversity are expected to be reduced in those portions of the forest landscape that are managed primarily for timber production rather than biodiversity conservation (Noble and Dirzo, 1997). Importantly, such tradeoffs come with the important benefit of producing more timber on a reduced area (Maguire et al., 2009), thus reducing pressure on less intensively managed and protected areas. Together, these practices follow the key tenets of the TRIAD approach to conserving biodiversity in managed landscapes (Seymour and Hunter, 1992; Hartmann et al., 2010). However, our current study, as well as previous correlative results (Betts et al. 2010; Ellis and Betts 2011; Ellis et al. 2012), suggest that such trade-offs between biodiversity and timber production may not be as large as previously anticipated. Through the first 2 years of stand growth, the 'Light' treatment was indistinguishable from the control for a number of declining early seral associates. To balance biodiversity conservation and timber production, research examining the tradeoffs between reduced application rates of herbicide and tree growth is urgently required.

Acknowledgments

We thank our many field assistants for diligent work. We thank anonymous reviewers for constructive comments on this manuscript. Access to study sites as well as cooperation in implementing the experimental treatments was granted by Weyerhaeuser, Hancock Timber Resource Group, the Oregon Department of Forestry and Plum Creek Timber. Research funding was provided by grants from the United States Department of Agriculture, Agriculture Food and Research Initiative grant (AFRI-2009-04457), the National Council for Air and Stream Improvement, the Nobel Fund and the Oregon State University College of Forestry Fish and Wildlife Habitat in Managed Forests Research Program to M.G. Betts.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.06.022.

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