Evaluating the consistency of understorey vegetation response to forest thinning through synthetic analysis of operational-scale experiments

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Summary

We attempted to extend the inference scope of several detailed songbird habitat restoration studies in western Oregon to the broader region through a reanalysis and synthesis of five large-scale management experiments. This previous work demonstrated the importance of understorey vegetation to songbird habitat. However, individual studies have shown conflicting results regarding how vegetation responds to restoration thinning. Understorey vegetation covers 4–6 years after thinning was strongly related to pre-treatment conditions (indexed by the unthinned control treatment). Baseline models that accounted for the pre-treatment conditions showed that herbaceous cover consistently, but only slightly, increased following thinning. Shrub cover, however, tended to decrease following thinning when the pre-treatment cover was >30 per cent. Each study had limited replication and most had limited geographic and environmental conditions, leading to the inconsistent findings when analysed separately. The reanalysis approach allowed us to test the repeatability of specific finding and demonstrated the applicability of restoration thinning for enhancing habitat in western Oregon.

Introduction

Understorey vegetation in forest stands is important to wildlife habitat and conserving biodiversity. It is generally expected that understorey vegetation will respond to thinning of dense overstoreys due to increased light levels at the forest floor and increased nutrient and water availability through reduced overstorey tree competition (Coates and Burton, 1997; Drever and Lertzman, 2001). The actual responses, however, have varied from strong increases to a neutral or negative response (Alaback, 1982; Bailey *et al.*, 1998), possibly because overstorey competition remains

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high (Fahey and Puettmann, 2008), or due to high disturbance during thinning (Roberts, 2004).

Understorey vegetation, especially shrub cover, strongly modifies songbird responses to thinning treatments for several species (Hagar, 2004; Cushman *et al.*, 2008). Neotropical songbirds appear to partially choose breeding territories based on the fine-scale forest structure, including understorey vegetation (McGarigal and McComb, 1995; Hagar, 2004; Cushman *et al.*, 2008), with the preferred habitat structure dependent on the species functional and life history traits (Hagar, 2004). Understorey shrubs, especially tall deciduous shrubs, are an important component of habitat for many species, particularly ground-nesting and foraging species such as MacGillivray's warbler and song sparrow (Hagar *et al.*, 2004). Our primary concern was with enhancing songbird habitat, but understorey vegetation is also important to small mammals (Martin and McComb, 2002), upland amphibians (McComb *et al.*, 1993a) and invertebrates (Schowalter, 1995). We used results from studies on songbird responses to thinning in western Oregon to guide hypothesis testing in this synthesis (Hayes *et al.*, 2003; Hagar *et al.*, 2004).

Several large-scale operational studies were initiated during the 1990s in young Douglas-fir forests in western Oregon to test density management alternatives for increasing late-successional habitat for plant and animal species (Monserud, 2002; Poage and Anderson, 2007). Structural legacies from past management have profoundly altered forest development in the Douglas-fir region (Tappeiner *et al.*, 1997). Various density management treatments were implemented to reduce overstorey tree density, promote spatial heterogeneity at several scales (McComb *et al.*, 1993b; Cissel *et al.*, 2006) and increase understorey vegetation growth and diversity. Treatments were designed to provide forest structures more similar to those developing under natural disturbance regimes, while still providing for timber production and harvesting. Large-scale management experiments (LSMEs) in young forests are an important part of adaptive management of natural resources on public lands (Walters and Holling, 1990). Despite the advantages of being designed manipulative experiments, each of the LSMEs has relatively low replication and low statistical power to test for treatment differences. The LSMEs treatment units were generally large (20–60 ha), in order to elicit a wildlife response and to compare the economic feasibility of the treatments. The layout, treatment and management costs in these studies are high, thus constraining replication (Monserud, 2002). There is substantial variability within study sites, due to the size of the treatment units; moreover, replications are usually geographically and often floristically distinct. In these respects, the study designs have many similarities to replicated case studies (Yin, 2003) or minimally replicated paired-intervention experiments (Murtaugh, 2000). Even for studies in the same forest type (e.g. young Douglas-fir forests in western Oregon), data collection protocols and the suites of wildlife studied often differed between studies, so synthesis of research findings across studies is rare (Poage and Anderson, 2007). These challenges with operational experiments are not unique to forest management (Walters, 1986). Managers, however, rely on study findings, and so developing effective approaches to research synthesis is a priority.

Our main objective was to evaluate the magnitude and consistency of understorey vegetation response in Douglas-fir forests of western Oregon, USA, and in particular the response of tall deciduous shrub cover which is an important mediator of songbird response to thinning (Hayes and Hagar, 2002). Specifically, we related understorey vegetation response to thinning intensity and examined the consistency of response across sites to help address our wildlife conservation goals. The analysis involved 80 experimental units, including unthinned controls and different intensity thinning treatments. We combined data from all available studies in western Oregon to provide a broad range of conditions sampled and to increase our ability to detect significant trends. A secondary objective was to evaluate synthesis methods appropriate for combining results from different studies.

Methods

Data sources

The five LSMEs used in this study all come from young (35–90 years at initiation) low-elevation Douglas-fir forests of western Oregon (Table 1).

Table 1: Study and treatment characteristics

Study	Sites (no.)	Treatments*	Age† (years)	Site index‡ (m)	Site distance§ (km)	Elevation range‖ (m)	Basal area¶ (m^2 ha^{-1})			% BA removed	
							C	L	M	L	M
DMS initial	7	C, L, M, M#	45–65	37–42	250	285–695	59	44	31, 30#	24	45, 47#
DMS rethin	4	C, M	63–98	32–41	157	225–550	54	NA	32	NA	39
Tillamook	4	C, L, M	33–43	NA	24	305–915	32	24	20	36	26
UAMP	4	C, L, L#, M	36–47	27–40	8	540–920	40	32, 34#	26	22, 15#	36
YSTDS	4	C, L, L#, M	33–43	32–42	34	440–910	49	28, 23#	18	43, 53#	63

NA, not available.

* Treatment designations were C, unthinned control; L, light intensity thinning and M, moderate intensity thinning.

† Age of stand at time of treatment.

‡ Site index is the expected height of dominant trees at age 50 years.

§ Site distance is the maximum distance between sites.

‖ Elevation range of study sites.

¶ Average basal area measured 4–6 years post-harvest.

\# The treatment was applied non-uniformly within a treatment unit.

Each study included an unthinned control and different thinning treatments in a complete block design. Treatments were applied consistently within individual studies. Each of the five studies was replicated across a range of environmental and edaphic conditions but was unreplicated within a single location. There were 80 treatment units used in the analysis, with vegetation measurements on 1500 plots. The treatment units were operationally delineated and harvested using a variety of logging methods, depending on terrain and season. The treatment units were generally greater than 10 ha to allow for concurrent wildlife response and economic feasibility studies. Several more LSMEs exist in the Pacific Northwest and British Columbia (Monserud, 2002); however, we focused on western Oregon forests to explicitly tie inferences to parallel songbird studies in the region and to include studies that were reasonably similar. Vegetation data from a single time frame of 4–6 years post-harvest were used in the analysis.

Density management study—initial thinning

The initial thinning component of the Density Management Study (DMS) was installed in unmanaged second-growth forests that originated following extensive clear-cutting and burning in the 1930s and 1940s. The study was designed to evaluate density management alternatives in young stands on the development of late-successional forest structure (Cissel *et al.*, 2006). Seven replications of this study were distributed across the Cascade and Coast Ranges (Table 1) on lands administered by the Bureau of Land Management (BLM) (Cissel *et al.*, 2006). This study had the widest geographic distribution, with large differences in understorey vegetation composition across sites. Treatment units averaged 28 ha, with a range between 14 and 69 ha. The three density management treatments were defined by the target residual density and included light (~300 tph residual) and moderate thinning (~200 tph residual). In addition, there was a variable density treatment with alternating light, moderate and heavy (~100 tph residual) thinning in approximately equal area proportions. Study sites were harvested between 1997 and 2000, depending on location. Thinning in all treatments was proportional across the diameter classes of trees. Additional spatial heterogeneity was provided by including uncut leave islands and artificial gaps of 0.1, 0.2 and 0.4 ha over 10 per cent of the area in the moderate and variable density units. Vegetation monitoring plots were installed 5–6 years post-thinning and were randomly located throughout the treatment areas including within the gaps and leave islands. Each treatment unit contained between 14 and 24 0.1-ha plots to measure overstorey trees. Each plot contained four nested 20 m^2 subplots to monitor vegetation. The per cent cover was estimated visually for all individual species in the subplots during the early to midsummer.

Density management study—rethinning

The rethinning component of the DMS was installed in second-growth forests that had been commercially thinned 17–22 years previous, with the same goal as the DMS initial thinning study (Cissel *et al.*, 2006). These represented the oldest stand ages in our analysis, with stands being 63–98 years old at study initiation. Four replications were installed in the Cascades and Coast Ranges (Table 1) on BLM lands with a geographic range as wide as the initial thinning component. Treatment units averaged 19 ha. The entire study area had been commercially thinned, so the control represented forest development several years post-thinning. Approximately, half the stand was thinned a second time between 1997 and 2000. The marking guidelines were to proportionally thin across size classes to 75–150 tph retention, which removed 39 per cent of the basal area (BA) (Table 1). Between 6 and 13 plots were installed in each treatment unit. Vegetation monitoring was identical to the DMS initial thinning study, with plots installed 5–6 years post-harvest.

Tillamook study

The Tillamook study was established in 35- to 45-year-old Douglas-fir stands in the northern Oregon Coast Range to evaluate thinning alternatives to increase wildlife habitat quality (Suzuki and Hayes, 2003). Stands were regenerated by seeding and planting following extensive burning between 1933 and 1951 following logging but were otherwise unmanaged. Four sites were selected in the area which were relatively homogeneous, dominated by Douglas-fir and had moderate to high site quality. Treatments were applied in a randomized complete block design and included an unthinned control, light and moderate intensity thinning. Treatment units were 26–40 ha each. Logging occurred between autumn 1994 and spring 1995. Thinning preferentially removed the lower crown class trees. Marking guidelines were by residual relative density (RD) of ~4.3 and 3.2 for the light and moderate intensities, respectively. RD is a measure that equates standing biomass relative to a biological maximum that varies somewhat by species and site. The measure integrates average tree size and density, computed as $RD = BA/\sqrt{QMD}$, where BA is the stand basal area ($m^2\ ha^{-1}$) and QMD is the quadratic mean diameter (cm) (Curtis, 1982). The control treatment RD averaged 7.0, while the biological limit for Douglas-fir is ~10 (Curtis and Marshall, 1986). The control stands had 460–650 tph, while residual densities were 240–320 and 180–220 tph for the light and moderate intensity thinning, respectively. Vegetation was measured in the summer, 5 years post-harvest on 25 0.07-ha plots in each treatment unit. Overstorey trees were measured on the 0.07-ha plots. Total shrub and herb cover was visually estimated in two 79 m^2 subplots nested within each plot, with shrubs separated into tall and low forms by height (1.4 m).

Uneven-aged management project

The Uneven-Aged Management Project (UAMP) was installed in 36–47 year old stands of Douglas-fir within the H.J. Andrews Experimental Forest, on the Willamette National Forest in the Cascade Range (Anderson, 2007). The study was designed to test alternative partial harvest approaches to conversion of even-aged stands to an uneven-aged condition. However, only the first harvest has occurred, so this study was similar to the others for evaluating vegetation response to thinning. Residual density targets for the initial thinning treatments were based on RD (Curtis, 1982). An unthinned control (average RD 7.6) was included. Initial treatments included light (RD 4.3) and moderate (RD 2.9) intensity thinning. In addition, a spatially variable treatment was included that was a light intensity thinning with numerous small gaps (~0.05 ha each) accounting for 10 per cent of the treatment unit. Stands were harvested in 2000. Thinning was generally from below, removing small diameter, suppressed and intermediate crown class trees.

Light and heavy thinned stands were underplanted throughout with a mix of Douglas-fir, western hemlock, western red cedar and western white pine seedlings (~1070 tph total). In stands thinned with gaps, only the gaps were planted using the same mix of species at higher density (~1690 tph). Vegetation was sampled 5 years post-treatment on 5–13 0.1-ha circular plots within each treatment unit, equalling a sampling intensity of 7–15 per cent of the unit area. Plots were located by systematically placing transects within each treatment unit and then randomly locating plots along transects. Overstorey trees were measured within the 0.1-ha plots. Per cent cover of tall shrubs and tree saplings was measured along two 14.5 m planar transects nested within each plot (Bonham, 1989). Per cent cover of individual species (except tall shrubs) was estimated on 0.1-m^2 subplots at eight evenly spaced points along each transect (Anderson, 2007).

Young stand thinning for diversity study

The Young Stand Thinning for Diversity Study (YSTDS) was installed in 35- to 45-year-old Douglas-fir plantations on the Willamette National Forest in the Cascade Range (Davis *et al.*, 2007). The study was designed to evaluate density management alternatives on the development of late-successional forest structure. The study was established at four sites that represented the range of vegetation typical of the National Forest (Table 1). Thinning treatments included an unthinned control, two light and one moderate intensity thinnings. Treatments were randomly assigned in a complete block design, with a few randomization exceptions due to public perception concerns. The controls averaged 770 tph. Marking guidelines for the light and moderate thinnings targeted 250–300 and 120–135 tph, respectively. Stands were harvested between 1995 and 1997. Thinning preferentially removed the lower crown class trees. In one of the light thinning units at each site, 0.2 ha artificial gaps were created and evenly distributed over the stand, equalling 20 per cent of the stand area in gaps. Stands were harvested between 1994 and 1996. Treatment units averaged 30 ha. An average of 22 vegetation monitoring plots were installed in each treatment unit, equalling a sampling intensity of 7–15 per cent of the unit area. Plots were located by systematically placing transects within each treatment unit and then randomly locating plots along the transects. Overstorey and understorey vegetation measurements followed the same sampling protocol as the UAMP study.

Analytical methods

The analytic methods we employed involved a synthetic reanalysis of the original data. The vegetation data were averaged at the treatment unit level for analysis since inferences were sought at these operational scales (i.e. stand scales). Response variables included the per cent cover for tall shrub, total shrub and herbaceous life forms, as well as total vegetation cover. The per cent cover of each response variable was first averaged across subplots (or planar transects) within a vegetation plot and then across all plots within each treatment unit. Overstorey tree measurements were simply averaged across plots within a treatment unit. Minor variation in how variables were measured could affect inferences and will be addressed later. Likewise, we did not account for sampling error within a treatment unit.

Treatments were grouped into unthinned controls and light or moderate intensity thinnings (Table 1). Although each study design was somewhat different, it was apparent from examination of the pre-harvest condition and the harvest intensities (as a proportion of the basal area removed) that thinning treatments were sufficiently similar for grouping. Retaining an indicator variable for individual studies in the model would also account for such systematic differences in experimental design and tree marking guidelines. The exception to this was that the heterogeneous treatments that included artificial gaps, leave islands or variable density sub-blocks were different across studies. To account for this, an indicator variable was used to denote whether any portion of the treatment was applied non-uniformly (Table 1) and possible interactions with study were assessed.

The linear model used was

$$\begin{aligned} Y_{ijk} &= \mu + S_i + T_j + B_{ik} + H_j + (HS)_{ij} \\ &\quad + \beta_1(\text{Baseline})_{ik} + \beta_2 R_{ijk} + \varepsilon_{ijk}, \end{aligned} \tag{1}$$

where Y_{ijk} was the response variable for study i, treatment j and site k, μ was the overall mean, S_i was a fixed effect class variable for study (experiment), T_j was a fixed effect class variable for treatment, B_{ik} was a random class variable for study site (block), H_j was an indicator variable with $H = 1$ if a treatment was spatially variable and $H = 0$ otherwise, HS_{ij} was an interaction effect between H_j and S_i, Baseline$_{ik}$ was a continuous fixed effect for the unthinned control vegetation cover, which was used in baseline models only, with estimated slope β_1, R_{ijk} was a continuous fixed effect describing the residual overstorey with estimated slope β_2 and ε_{ijk} was residual error $\sim N(0, \sigma^2{}_i)$, with separate estimates for each study.

The mixed linear models were fitted using the Mixed Procedure in SAS (SAS, 2002). Variance components were estimated using maximum likelihood (ML) and tested using a Wald's z test. Fixed effects in the model were tested with an F test, using the Satterthwaite approximation for error degrees of freedom to account for possible heterogeneous error variances. Each model included fixed effects and was fitted with ML to allow valid comparisons with an Akaike information criterion (AIC) (Burnham and Anderson, 1998).

Study sites were considered random effects and a variance component was estimated for this effect (McCulloch and Searle, 2001). Predicted site effects were best linear unbiased predictions, assumed normally distributed about the fixed effects mean. Each study design was somewhat distinct so study (S_i) was considered a fixed effect. The residual error variance was estimated separately for each study. The necessity for separate errors was assessed using AIC, by comparing models with uniform and heterogeneous errors. Pooled residual error models were used where appropriate. A single or several continuous variables R_{ijk} were included that described the residual overstorey structure, including measures of stocking (RD), density (tph) and light interception (CC). Basal area and RD were highly correlated in these young stands (r = 0.96), and RD was chosen based on previous work in the region. The overstorey structure variables were included primarily to determine their influence on the expected heterogeneous residual errors. That is, we know from past studies, that pre-harvest conditions varied and that the treatments were not uniformly applied across all sites within a study. Accounting for such differences might eliminate the need for modelling heterogeneous error structures and thus improve model precision. The assumption of normally and uniformly distributed residuals was assessed using Levene's test and by graphical interpretation.

The baseline covariate was the vegetation cover of the unthinned controls within the same site. We also compared log transformations of the baseline covariates with untransformed models. The response variables were always left untransformed. Models including the baseline variable accounted for pre-treatment differences in vegetation (Vickers and Altman, 2001). The baseline variable was the same vegetation component but for the unthinned control for a site (Baseline$_{ik}$ in equation (1); n = 57 treatment units). In other words, the unthinned control shrub cover served as the baseline variable for models predicting shrub cover in thinned treatments.

Baseline models are common in medical studies, where pre- and post-treatment conditions are known for each subject (Vickers and Altman, 2001). In our case, the response and baseline variables came from the same study site (block). This approach allowed us to account for systematic variability associated with each site that was unrelated to the thinning treatments. While we did not have pre-treatment vegetation surveys for all of these studies, we used the unthinned control as a proxy in these closed canopied forests. This assumed that the unthinned controls adequately approximated the pre-harvest conditions and that the treatment units at a site were similar in this regard. Another approach would be to manually adjust for the control treatment vegetation and perform the analysis on the difference between the thinned and unthinned treatments. Instead, we chose a baseline model because this allowed us to examine responses relative to the control values (linear, asymptotic, etc.). Such patterns are obscured by analysing post- to pre-treatment differences.

A primary goal of this study was to assess the consistency of vegetation responses to thinning treatments. We estimated 90 per cent confidence intervals (CIs) for site means and also 90 per cent prediction intervals for a new replication (Neter *et al.*, 1996). These confidence and prediction intervals are conditioned on the fixed effects in the model and the residual error, which could depend on study design if residual errors were found to be heterogeneous.

Results

Baseline models for predicting vegetation cover

The baseline models were strong predictors of vegetation cover. The control vegetation covariate was significantly related to vegetation cover in thinned treatments for all life forms (Table 2). In addition, AIC was lower for the baseline *vs* the non-baseline models for each vegetation life form, although the difference was slight for tall shrubs and total cover. A log transformation of the baseline covariate for tall shrub cover was necessary to account for an apparent curvilinear trend, while total shrubs and herbs showed linear responses (Figure 1). This transformation resulted in a better model (lower AIC and residual error) than linear or square root transformed alternatives. The fitted lines in Figure 1 represent an average response across studies and were evaluated with the mean RD when this variable was significant. These average responses were used to visually gauge vegetation responses relative to the control cover.

The shape of the treatment response compared with the baseline measurements was quite variable (Figure 1). Moreover, total shrub response was strongly dependent on the baseline values (as indexed by the unthinned controls). Site and treatment units with low shrub cover in the unthinned controls tended to have substantially greater shrub cover 4–6 years post-treatment, while those with greater baseline values showed a consistent negative response (Figure 1a). Treatment-specific parameters only influenced the elevation of these linear relationships ($P = 0.53$ for the interaction effects with β_1). Tall shrubs showed a similar but diminishing effect where baseline values were similar to treatment responses at low baseline values. At greater baseline tall shrub cover, there was a marked decrease in cover in the treatments. Herbs were also the only vegetation component to show a consistent increase over the unthinned baseline (Figure 1c), with a baseline slope not significantly different from 1.0 ($P = 0.36$). Only herbs showed a significant interaction between study and the baseline covariate ($P = 0.001$); however, none of the slopes (β_{1i}) were significantly different from 1.0, so these were pooled in the final model. This result might have been due to relatively low replication for tests involving study effects, and we tried to guard against over-parameterization by pooling across studies. The YSTDS and UAMP studies also had a restricted range of herb cover in the controls which may have resulted in the imprecise slope estimates.

The fitted baseline models had similar residual errors across studies for shrub and tall shrub components, as judged by a lower AIC for models with pooled *vs* unpooled errors (Littell *et al.*, 2006). Although the herb cover model still showed heterogeneous errors, pooling resulted in similar model inferences and responses, therefore all vegetation components were evaluated with pooled errors. Residuals were adequately distributed for each model. Residuals from equation (1) for total shrub and herb cover were uncorrelated ($r = -0.16$, $P = 0.23$), which suggested independent responses by these ecologically distinct life forms.

The large site variance components, σ_b^2, indicated that sites had strongly different average vegetation cover, the causes of which were independent of the treatment effects. There was a similar interpretation for the significant study effects (S_i); however, these related more to experimental site selection, treatment unit size and other operational causes. The baseline models substantially reduced the total model variance $(\sigma_b^2 + \sigma_e^2)$ which are combined when making predictions for new sites since the site effects are not predictable *a priori* (Littell *et al.*, 2006). The increase in precision related to predictions at new sites came primarily from reducing the site variance, σ_b^2, rather than the residual variance (Table 2). An exception to this was a relatively unchanged σ_b^2 for tall shrubs, which was significant in both the unadjusted and baseline models ($P = 0.03$ and 0.01, respectively).

Treatment and study effects

Differences between the light and moderate thinning treatments were slight in the baseline models (Figure 1). The light and moderate treatments were significantly different for shrub and herb cover ($P = 0.020$ and 0.046, respectively) but not for tall shrubs ($P = 0.75$). Shrub cover was an

Table 2: Unadjusted and baseline-adjusted model parameters and comparative fit statistics for equation (1)

	Vegetation life form			
Model terms	Total	Shrubs	Tall shrubs	Herbs
	Unadjusted model			
Variances				
σ_b^2	270.2	173.7	27.0	333.2
σ_e^2	104.9	69.1	36.4	54.9
Intercept				
μ	109.88	61.69	22.48	37.20
Study				
DMS initial	5.76*	−25.57	−6.19*	23.95
DMS rethin	48.33	−9.22*	−6.02*	54.04
Tillamook	−12.23*	−22.80	−12.15	13.04*
UAMP	−35.39	−36.97	−7.46	−2.53*
YSTDS	0	0	0	0
Treatment				
Light	3.46*	−5.89	−0.55*	6.28
Moderate	0	0	0	0
Heterogeneity				
H	ns	5.31	ns	ns
RD				
β_2	−7.64	ns	ns	−4.78
	Baseline model			
Variances				
σ_b^2	209.6	98.8	19.0	63.7
σ_e^2	105.3	67.9	36.0	55.3
Intercept				
μ	73.13	30.04	−1.92	23.36
Baseline				
β_1	0.417	0.445	6.503†	0.894
Study				
DMS initial	18.78*	−6.81*	2.69*	15.22
DMS rethin	41.28	−3.28*	−1.24*	27.97
Tillamook	−0.94*	−4.19*	−3.26*	−0.19*
UAMP	−15.01*	−16.67	−1.55*	1.08*
YSTDS	0	0	0	0
Treatment				
Light	3.39*	−5.89	−0.55*	6.78
Moderate	0	0	0	0
Heterogeneity				
H	ns	5.30	ns	ns
RD				
β_2	−7.59	ns	ns	−5.14
ΔAIC‡	−2.7	−9.2	−3.2	−29.8

The baseline models included vegetation cover in the unthinned control as a baseline covariate. The unadjusted models omitted the baseline covariate but were otherwise identical. Only thinned treatments were used in the model comparisons (n = 57 treatment units). Site variance components were significant for each life form. ns denotes that the variable was non-significant ($P > 0.1$) and dropped from the model.

* Effect was non-significant ($P > 0.1$).

† The baseline covariate was transformed as the $\log_e$ of tall shrub cover.

‡ Change in AIC between the unadjusted and baseline models (more negative values indicates better fit with the baseline models).

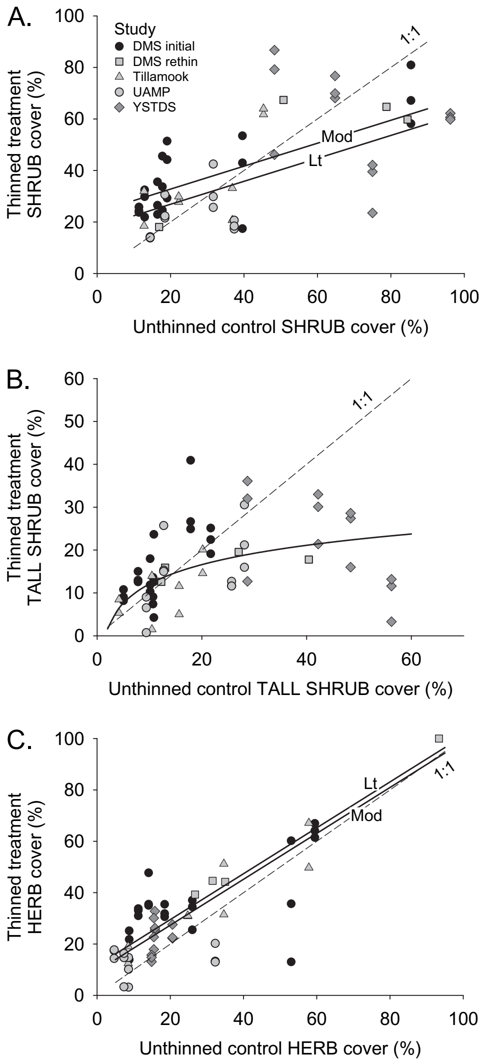

Figure 1. Baseline models showing vegetation responses to thinning as a function of the unthinned control cover [equation (1)]. The fitted responses (solid lines) were averaged over study effects. Light (Lt) and moderate (Mod) intensity thinning treatments were shown separately when significantly different. The baseline covariate for tall shrub cover was transformed as the $\log_e$ of the control cover, resulting in the non-linear form shown. The dashed line represents a 1:1 relationship where the thinned and control values are equal. Responses shown were for non-heterogeneous treatments. Herb responses were computed using the mean RD for each treatment (5.32 and 4.42 for the light and moderate treatments, respectively).

estimated 5.9 percentage points lower in the light thinning treatment compared with the moderate thin (Figure 1). This pattern was reversed with herb cover, with the moderate treatment an estimated 6.8 points higher than the light thin (Figure 1; $P = 0.046$). The study effects (S_i) accounted for systematic differences between studies that would have been common to both thinning treatments.

Individual study effects were included in the linear model as fixed effects. We understood that studies were unique in many factors beyond simply geographic location, and we included the study effect to adjust for these differences. In meta-analyses, such unique studies can represent problems with non-uniform effect sizes or require standardization of the effects (Osenberg *et al.*, 1999). We were able to account for study differences by using a baseline model to account for different pre-treatment values across the different sites. It is important to note that analysing treatment responses (i.e. Y = treatment minus control values) would not have lead to similar inferences since trends across the control values would not have been apparent. The study effect was non-significant for shrub and tall shrub responses in the baseline model but was significant for herbs ($P = 0.01$) where the two DMS studies had 15 and 28 percentage points higher herb cover than the other three studies which were similar (Table 2). The study effect was retained in all of the baseline models to account for these slight differences in comparing predictions across studies.

We accounted for differences in the residual overstorey within a treatment unit, but these were all non-significant with the exception of RD on herb and total vegetation cover ($P = 0.006$ and $P = 0.006$, respectively). Part of the study effects on herbs was offset by higher than average RDs in the DMS studies since herb cover was negatively related to RD (Table 2). The DMS studies still had an overall higher herb response to thinning than the others. The possible reasons for this were unclear but indicated a study design effect that was independent of either the pre-treatment vegetation or the residual overstorey characteristics. The DMS studies had the widest geographic distribution of all the LSMEs (Table 1), so site factors or a unique floristic composition were not likely factors.

Accounting for heterogeneous treatments was significant only for total shrub cover ($P = 0.053$), resulting in a moderately higher cover by 5.3

percentage points over non-heterogeneous treatments (Table 2). Although we expect that artificial gaps will have higher vegetation cover, the gaps were a small proportion of the treatment units (10–20 per cent of treatment area) and were partly offset by unthinned leave islands (Table 1). Smaller gaps (<0.4 ha) tend to have vegetation composition and cover similar to the thinned matrix except in a small portion at the centre (Fahey and Puettmann, 2007), further reducing their influence. The interaction between study and the heterogeneity indicator variable $(HS)_{ij}$ was non-significant for all vegetation life forms and was dropped from the models.

Patterns of variability

One of the primary questions in this study was to estimate how consistently vegetation responds to thinning. Given how effective the baseline model explained vegetation cover, we computed CIs for each study based on the unthinned control averages (Figure 2). Ninety per cent CIs for the shrub mean cover varied by ~20 percentage points, depending on study and the unthinned means. CIs for the other life forms were similarly wide. We presented CIs in this manner because we were interested in predicting actual cover values rather than treatment responses. Thinning tended to homogenize total shrub and tall shrub cover across studies and sites, increasing in stands with initially sparse cover and decreasing in stands with relatively greater cover. Herb cover was less predictable, but thinning generally increased herb cover for each study. Ninety per cent prediction intervals for new thinning units were considerably more variable (results not shown) and were approximately twice as wide for shrub and herb cover, indicating the difficulty in predicting vegetation response to thinning at a new site, even when baseline (i.e. pre-treatment) conditions are taken into account. Prediction intervals for tall shrubs were ~50 per cent wider than the CIs.

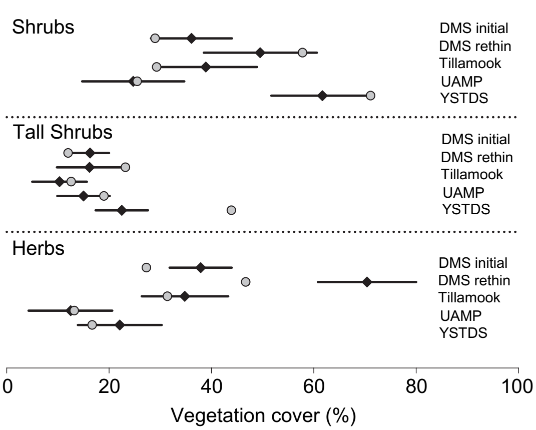

Figure 2. Mean vegetation cover (♦) 4–6 years following moderate intensity thinning and 90 per cent CIs for the means shown as heavy lines for each study. The means and CIs were estimated using the average baseline (i.e. unthinned control) value for each study (shown as •).

Discussion

Baseline models for predicting vegetation response

Vegetation cover appeared strongly dependent on site-specific pre-treatment values; however, the response patterns to thinning varied by life form (Figure 1). The response patterns we found have been suggested elsewhere in general terms (Deal, 2001; Davis *et al.*, 2007). However, we were able to show consistent trends across studies and present quantitative predictions through the reanalysis approach. Young Douglas-fir forests often have a nearly closed canopy and sparse understorey vegetation due to strong competition for light and other resources. Once forests reach 40–60 years old, however, understorey vegetation in unmanaged stands becomes highly variable both within and between individual stands (Spies, 1991; Bailey *et al.*, 1998) with the inevitable natural gaps and hardwood patches adding moderate relief to the understorey. It was not surprising then that thinning response was partly dependent on the pre-treatment (control) conditions. However, the strong linear relationship between shrubs and herbs to the unthinned baseline values was not expected.

We can partly explain the patterns of vegetation response (Figure 1) by the level of competition exerted by the overstorey. Uniformly, dense overstoreys will tend to have sparse understorey of clonal shrubs (Tappeiner *et al.*, 1991), shade-tolerant ferns and clonal herbs

(Bailey *et al.*, 1998). The amount and type of vegetation in unmanaged stands will also partly depend on water and nutrient status of the site (Pabst and Spies, 1998; Sheridan and Spies, 2005). However, it was unclear how the total or component vegetation covers would respond to thinning. Several retrospective studies of commercial thinning have qualitatively suggested that tall shrub cover decreases due to harvesting damage (Lindh and Muir, 2004). Another possible scenario was that vegetation would respond solely to the thinning treatments. That is, we would find a uniform cover for shrubs, herbs and total cover depending on thinning intensity, irrespective of the pre-treatment values. Under this scenario, vegetation cover would be proportional to available site resources, as indexed by the overstorey BA or RD, and the slopes of the relationships with the control covers would be non-significant (i.e. equal to zero). Although there was considerable residual error in estimating the baseline slopes, these were significant for all vegetation components, including total cover. It was apparent that the study sites (i.e. blocks) exerted a lasting influence on vegetation cover and hence response to the treatments.

Similar to sites exerting an unexpected influence on vegetation cover, the five studies were also quite variable in their responses. Treatment units were considered independent replicates in the reanalysis, and so responses were assumed to be independent of the study design. This assumption was adequately met for tall and total shrub cover. On the other hand, it was disconcerting that the pre-treatment (control) vegetation varied systematically between studies (Figure 2). In particular, the YSTDS and the DMS rethinning studies had higher total vegetation covers in the controls than the other studies. Studies were even more variable comparing vegetation life forms, with threefold to fivefold differences between study means. This suggests that study design still has a strong influence on treatment responses since response was so closely tied to pre-treatment conditions. Unfortunately, study design encompasses numerous uncontrolled factors, including harvesting equipment used, treatment unit size, marking guidelines, region (Cascades or Coast Range), floristic composition and soils. These uncontrolled factors can confound treatment responses, restricting their inference scope to similar conditions and possibly making the different studies incomparable.

The results and significance tests rely on the studies being comparable, so this poses a critical question. Certainly, when studies were analysed separately, they were not comparable due to the different and usually narrow ranges of pre-treatment vegetation cover (Figure 2). This might also explain the many inconsistent results in the literature regarding vegetation response to thinning (Wilson and Puettmann, 2007). The strong dependence on pre-treatment vegetation only became apparent when the data were reanalysed together. Our results suggested that accounting for pre-treatment vegetation with a baseline model adequately accounted for study differences and that the studies were comparable for the vegetation life forms studied. This might not be true with other analyses or datasets from these same studies, such as wildlife responses or more general metrics such as diversity or species richness.

Vegetation cover appeared to be strongly site dependent, with only a slight to moderate response even to relatively intense thinning. However, there are still benefits to songbird habitat from thinning, which include higher understorey productivity, insect abundance and berry production (Hayes and Hagar, 2002). Several songbird species also respond to the open conditions following thinning, such as Hammond's flycatchers, red-breasted sapsuckers and western tanagers (Hagar *et al.*, 2004). Our results do not negate these benefits but rather they point out the need to protect tall shrubs from mechanical damage where possible. Unmanaged stands with sparse tall shrub cover were not likely to develop substantial cover in the short (4–6 years) term. Much of the remaining variability in vegetation response might be attributable to different species composition across sites. Understanding the ecological reasons for such wide pre-treatment vegetation differences among sites will clearly be important.

Synthesis approaches for operational-scale studies

Our reanalysis proved to be a useful technique for synthesizing research findings across LSMEs and suggested several implications for Neotropical songbird conservation. We were able to extend the scope of inference from detailed but geographically limited songbird studies in several ways. First, we showed that managers should consider pre-treatment conditions when selecting sites for restoration thinning, particularly when the goal is to enhance habitat for wildlife that respond to understorey vegetation. Second, we showed a slight increase in shrub cover when pre-treatment values were <30 per cent, demonstrating opportunities for enhancing this habitat through thinning. Third, herb and shrub cover was not mutually exclusive, at least at the moderate to low shrub covers found in these studies. Although the herb layer is not directly tied to songbird habitat, it is an important browse for other wildlife (Hayes and Hagar, 2002). These relationships are important to understanding possible trade-offs between habitat elements important to different species. Finally, we demonstrated that the different thinning intensities had a similar (or slightly different) impact on vegetation cover. This allows for greater latitude in achieving other habitat or timber management goals since moderate intensity thinning was not required to achieve increased vegetation cover.

The LSMEs can help guide management as they directly test several assumptions inherent to restoration thinnings in young Douglas-fir forests. LSMEs, however, require a huge investment in personnel and funds (Monserud, 2002). The reanalysis approach taken in this study was critical for identifying consistent trends in vegetation response to thinning, which underscores the need for more synthesis across studies where possible. For our objectives, no single study captured all the variability in pre-treatment values or thinning responses, and consistent trends did not emerge until the 80 replicated treatment units from theses studies were analysed together.

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Conflict of Interest Statement

None declared.

References

Alaback, P.B. 1982 Dynamics of understory biomass in sitka spruce-western hemlock forests of southeast Alaska. *Ecology*. **63**, 1932–1948.

Anderson, P.D. 2007 Understory vegetation responses to initial thinning of Douglas-fir plantations undergoing conversion to uneven-age management. In *Integrated Restoration of Forested Ecosystems to Achieve Multi-resource Benefits: Proceedings of the 2007 National Silviculture Workshop. PNW-GTR-733*. U.S. Department of Agriculture, Pacific Northwest Research Station, Portland, OR, pp. 77–90.

Bailey, J.D., Mayrsohn, C., Doescher, P.S., St Pierre, E. and Tappeiner, J.C. 1998 Understory vegetation in old and young Douglas-fir forests of western Oregon. *For. Ecol. Manage.* **112**, 289–302.

Bonham, C.D. 1989 *Measurements for Terrestrial Vegetation*. John Wiley and Sons, New York, 338 pp.

Burnham, K.P. and Anderson, D.R. 1998 *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.

Cissel, J.H., Anderson, P.D., Olson, D., Puettmann, K.J., Berryman, S. and Chan, S. *et al.* 2006 BLM Density Management and Riparian Buffer Study: Establishment Report and Study Plan. In *U.S. Geological Survey, Scientific Investigations Report 2006–5087*. Reston, VA 144 pp.

Coates, K.D. and Burton, P.J. 1997 A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For. Ecol. Manage.* **99**, 337–354.

Curtis, R.O. 1982 A simple index for density in Douglas-fir. *For. Sci.* **28**, 92–94.

Curtis, R.O. and Marshall, D.D. 1986 Growth-growing stock relationships and recent results from the levels-of-growing-stock studies. In *Douglas-fir: Stand Management for the Future. Proceedings of a Symposium*. C.D. Oliver, D.D. Johnson and J.A. Johnson (eds). College of Forest Resources, University of Washington, Seattle, WA, Contribution no. 55, pp. 281–289.

Cushman, S.A., McKelvey, K.S., Flather, C.H. and McGarigal, K. 2008 Do forest community types provide a sufficient basis to evaluate biological diversity? *Front. Ecol. Environ.* **6**, 13–17.

Davis, L.R., Puettmann, K.J. and Tucker, G.F. 2007 Overstory response to alternative thinning treatments in young Douglas-fir forests of western Oregon. *Northwest Sci.* **81**, 1–14.

Deal, R.L. 2001 The effects of partial cutting on forest plant communities of western hemlock – Sitka spruce stands in southeast Alaska. *Can. J. For. Res.* **31**, 2067–2079.

Drever, C.R. and Lertzman, K.P. 2001 Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. *Can. J. For. Res.* **31**, 2124–2133.

Fahey, R.T. and Puettmann, K.J. 2007 Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *J. Ecol.* **95**, 1098–1109.

Fahey, R.T. and Puettmann, K.J. 2008 Patterns in spatial extent of gap influence on understory plant communities. *For. Ecol. Manage.* **255**, 2801–2810.

Hagar, J.C. 2004 *Functional relationships among songbirds, arthropods, and understory vegetation in Douglas-fir forests, western Oregon.* Unpublished dissertation, Department of Forest Science, Oregon State University, Corvallis, OR.

Hagar, J.C., Howlin, S. and Ganio, L. 2004 Short-term response of songbirds to experimental thinning of young Douglas-fir forests in the Oregon Cascades. *For. Ecol. Manage.* **199**, 333–347.

Hayes, J.P. and Hagar, J.C. 2002 Ecology and management of wildlife and their habitats in the Oregon Coast Range. In *Forest and Stream Management*. S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner *et al.* (eds). Oregon State University Press, Corvallis, OR, pp. 99–134.

Hayes, J.P., Weikel, J. and Huso, M. 2003 Response of birds to thinning young Douglas-fir forests. *Ecol. Appl.* **13**, 1222–1232.

Lindh, B.C. and Muir, P.S. 2004 Understory vegetation in young Douglas-fir forests: does thinning help restore old-growth composition? *For. Ecol. Manage.* **192**, 285–296.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. and Schabenberger, O. 2006 *SAS for Mixed Models*. 2nd edn. SAS Institute Inc., Cary, NC.

Martin, K.J. and McComb, W.C. 2002 Small mammal habitat associations at patch and landscape scales in Oregon. *For. Sci.* **48**, 255–264.

McComb, W.C., McGarigal, K. and Anthony, R.G. 1993a Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, western Oregon. *Northwest Sci.* **67**, 7–15.

McComb, W.C., Spies, T.A. and Emmingham, W.H. 1993b Douglas-fir forests: managing for timber and mature-forest habitat. *J. For.* **91**, 31–42.

McCulloch, C.E. and Searle, S.R. 2001 *Generalized, Linear and Mixed Models*. Wiley, New York.

McGarigal, K. and McComb, W.C. 1995 Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecol. Monogr.* **65**, 235–260.

Monserud, R.A. 2002 Large-scale management experiments in the moist maritime forests of the Pacific Northwest. *Landsc. Urban Plan.* **59**, 159–180.

Murtaugh, P.A. 2000 Paired intervention analysis in ecology. *J Agric. Biol. Environ. Stat.* **5**, 280–292.

Neter, J., Kutner, M.H., Nachtsheim, C.J. and Wasserman, W. 1996 *Applied Linear Regression Models*. Irwin, Chicago, IL.

Osenberg, C.W., Sarnelle, O., Cooper, S.D. and Holt, R.D. 1999 Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology*. **80**, 1105–1117.

Pabst, R.J. and Spies, T.A. 1998 Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. *Can. J. Bot.* **76**, 298–315.

Poage, N.J. and Anderson, P.D. 2007 *Large-scale Silviculture Experiments of Western Oregon and Washington. Gen. Tech. Rep. PNW-GTR-713*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 44 pp.

Roberts, M.R. 2004 Response of the herbaceous layer to natural disturbance in North American forests. *Can. J. Bot.* **82**, 1273–1283.

SAS 2002 *SAS User's Guide. Version 9*. SAS Institute, Inc., Cary, NC.

Schowalter, T.D. 1995 Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *For. Ecol. Manage.* **78**, 115–125.

Sheridan, C.D. and Spies, T.A. 2005 Vegetation – environment relationships in zero-order basins in coastal Oregon. *Can. J. For. Res.* **35**, 340–355.

Spies, T.A. 1991 Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. In L.F. Ruggiero, K.B. Aubry, A.B. Carey and M.H. Huff (eds). In *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. USDA Forest Service Pacific Northwest Research Station, Portland, OR, pp. 111–121.

Suzuki, N. and Hayes, J.P. 2003 Effects of thinning on small mammals in Oregon coastal forests. *J. Wildlife Manage.* **67**, 352–371.

Tappeiner, J.C., Zasada, J., Ryan, P. and Newton, M. 1991 Salmonberry clonal and population structure: the basis for a persistent cover. *Ecology.* **72**, 609–618.

Tappeiner, J.C., Huffman, D., Marshall, D., Spies, T.A. and Bailey, J.D. 1997 Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. *Can. J. For. Res.* **27**, 638–648.

Vickers, A.J. and Altman, D.G. 2001 Analysing controlled trials with baseline and follow up measurements. *Br. Med. J.* **323**, 1123–1124.

Walters, C.J. 1986 *Adaptive Management of Renewable Resources*. MacMillan, New York, NY, 374 pp.

Walters, C.J. and Holling, C.S. 1990 Large-scale management experiments and learning by doing. *Ecology.* **71**, 2060–2068.

Wilson, D.S. and Puettmann, K.J. 2007 Density management and biodiversity in young Douglas-fir forests: challenges of managing across scales. *For. Ecol. Manage.* **246**, 123–134.

Yin, R.K. 2003 *Case Study Research: Design and Methods*. Sage Publications, Thousand Oaks, CA.

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