



## Bird-vegetation associations in thinned and unthinned young Douglas-fir forests 10 years after thinning



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### ABSTRACT

Quantitative associations between animals and vegetation have long been used as a basis for conservation and management, as well as in formulating predictions about the influence of resource management and climate change on populations. A fundamental assumption embedded in the use of such correlations is that they remain relatively consistent over time. However, this assumption of stationarity has been rarely tested – even for forest birds, which are frequently considered to be ‘indicator species’ in management operations. We investigated the temporal dynamics of bird-vegetation relationships in young Douglas-fir (*Pseudotsuga menziesii*) forests over more than a decade following initial anthropogenic disturbance (commercial thinning). We modeled bird occurrence or abundance as a function of vegetation characteristics for eight common bird species for each of six breeding seasons following forest thinning. Generally, vegetation relationships were highly inconsistent in magnitude across years, but remained positive or negative within species. For 3 species, relationships that were initially strong dampened over time. For other species, strength of vegetation association was apparently stochastic. These findings indicate that caution should be used when interpreting weak bird-vegetation relationships found in short-term studies and parameterizing predictive models with data collected over the short term.

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### 1. Introduction

Stable bird-vegetation associations are a key underlying assumption in wildlife management (Wiens, 2002; Ahlering and Faaborg, 2006), species distribution modeling (Wiens, 2002) and models that project species responses to management. Many quantified bird-vegetation relationships derived from 2- or 3-year studies are used to project species response to management up to 150 years into the future (Larson et al., 2004; Wintle et al., 2005). Effectiveness of efforts to manage bird habitat, and reliability of distribution models and projections of population size in the future depends on how well bird-vegetation relationships described from a 2- or 3-year long study represent overall, long-term relationships. Additionally, existing mid- and long-term (7–30 years) studies of bird assemblages and bird-habitat associations (Wiens et al., 1986; Winter et al., 2005; Rotenberry and Wiens, 2009) point to the dynamic nature of bird communities over time even in systems without major disturbance events (e.g., Holmes and Sherry, 2001). The assumption that an ecosystem is in equilibrium is even less likely to be valid in a system recently disturbed by management

activities, such as thinning, because vegetation can change and develop rapidly following disturbance (Davis and Puettmann, 2009).

Management priorities on federal lands in the Pacific Northwest (PNW) have changed from primarily timber production to include the protection of native species and their habitat (Thomas et al., 2006). Several studies were initiated to investigate forest thinning as a technique to restore diversity in young (30–40 year-old) structurally simple Douglas-fir forests that were previously managed for timber production, and to promote development of mature forest characteristics. The response to thinning of vegetation (Davis et al., 2007; Davis and Puettmann, 2009; Wilson et al., 2009), bird community and individual species (Hagar et al., 2004), small vertebrates (Garman et al., 2000; Manning et al., 2012), arthropods (Yi, 2003) and fungi (Pilz et al., 2006) have been investigated for up to ten years after thinning.

Short and longer-term bird responses to forest thinning have been extensively studied (Hansen et al., 1995; Chambers et al., 1999; Hayes et al., 2003; Hagar et al., 2004; Verschuyll et al., 2011). Birds' responses to forest thinning are hypothesized to be mediated by post-thinning changes in vegetation structure and composition and the associated resources (Hagar and Friesen, 2009; Verschuyll et al., 2011). An expansive number of studies relate bird community composition to the structure and composition of the vegetation community (MacArthur and MacArthur, 1961; Orians and Wittenberger, 1991; Cushman and McGarigal, 2004;

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Lee and Rotenberry, 2005). Yet the link between forest birds and vegetation has rarely been tested over the long term. Understanding the causative link between forest management practices and bird response is important per se as young, structurally homogeneous, Douglas-fir forests comprise a large percentage of forests in the PNW (Bolsinger and Waddell, 1993; Kennedy and Spies, 2004), up to 40% of forests in Western Oregon (Kennedy and Spies, 2004).

Our objectives in this study were to test the consistency (is bird species A always associated with vegetation characteristic X) and strength (is the magnitude of the relationship constant over time) of bird-vegetation associations in time. Therefore, we advanced the following hypotheses:

**Proximate Cue Hypothesis:** If birds use vegetation characteristics as proximate habitat quality cues, then bird-vegetation associations are expected to be apparent immediately after forest thinning. In this case, vegetation variables associated with birds and the strength of association are consistent in thinned and unthinned forests, assuming an ideal free distribution (IFD; Fretwell and Lucas, 1969). Under assumptions of IFD, bird density along a habitat gradient should be positively related to habitat quality and consistent over time.

**Decoupling Hypothesis:** Birds may use several proximate cues to gather information about habitat quality (Doligez et al., 2003; Ahlering and Faaborg, 2006; Betts et al., 2008). Vegetation characteristics may serve as ultimate resources for reproductive success (cover, nesting site, or nest material) or be associated with such resources (e.g., by supporting an insect community upon which birds feed). A disturbance event, such as forest thinning, may temporarily dissociate, or “decouple”, the link between proximate cues and ultimate resources (e.g., Knick and Rotenberry, 2000). Therefore, we hypothesized that initially weak or unstable bird-vegetation associations may strengthen and stabilize as time since thinning increases.

**Population Size Hypothesis:** Observed bird-vegetation associations and their strength are likely to be influenced by demographic factors (McPeck et al., 2001), social interactions (e.g., Betts et al., 2008), competition (MacArthur, 1958) and scale of observation (Orians and Wittenberger, 1991). We did not have information on competition and conspecific interactions, but attempted to account for variability in bird-vegetation associations due to varying local population size. Bird-vegetation associations may not be indicative of preference when habitat is saturated, e.g., under ideal despotic or ideal preemptive distribution (Wiens, 1976; Rodenhouse et al., 1997; McPeck et al., 2001). During high-population years high-quality habitats may become fully occupied, and the remainder of individuals may be forced to settle in low-quality habitats. Thus, even low-quality habitats will be occupied and, therefore, observed association with a given vegetation characteristic may weaken. Hence, we hypothesized that bird-vegetation associations would weaken in years of high (estimated) population numbers.

## 2. Methods

### 2.1. Area and treatment description

We used previously collected bird (Hagar et al., 2004; Hagar and Friesen, 2009) and vegetation (Davis et al., 2007; Davis and Puettmann, 2009) data from the Young Stand Thinning and Diversity Study. The YSTDS is a long-term silvicultural experiment located on the west slopes of the Oregon Cascade Mountains in the Willamette National Forest (Davis and Puettmann, 2009; Hagar and Friesen, 2009). The thinning study was implemented as a randomized block experiment, with four replicate blocks. Blocks had

similar overstory composition, management history and size. At the beginning of the study in 1994–1996 the blocks consisted of stands dominated by 40–50-year old Douglas-fir, planted after regeneration harvest (Davis et al., 2007).

Each block received four treatments, randomly assigned to stands within the block. Stand areas ranged from 14 to 38 ha for thinned stands, and up to 53 ha for control stands. The treatments were unthinned Control (CON) with approximately 700 trees per hectare (tph), Heavy Thin (HT) with residual density of 200 tph, Light Thin (LT) with 250–300 tph and Light Thin with Gaps (LG) that included evenly-spaced (approximately every 2 ha) 0.2 ha circular clearcut gaps in a matrix with an average density of 250–300 tph. Stands were thinned from below, with approximately even spacing, preferentially leaving minority tree species to increase diversity. Treatments were implemented from 1995 to 1997 in a staggered manner (Davis and Puettmann, 2009).

### 2.2. Bird data summary

Bird data were collected using standard point count methodology (Ralph et al., 1995). Each surveying station was visited three or four times within a breeding season. Data were collected during breeding seasons of 1998, 1999, 2001, 2006, and 2007. For more details see Hagar et al. (2004). We summarized counts of birds by summing counts for each species across repeated visits to each point count station within a year. Species with distributions that had a large number of zero counts and a small range of non-zero counts ( $\leq 3$  detections per site per year) were collapsed to Bernoulli distribution (0's and 1's only). Distributions with a large range of non-zero counts ( $> 3$  detections per site per year) were attributed to Poisson distribution. We used species occurrence (Bernoulli-distributed counts) or abundance (Poisson-distributed counts) as dependent variable in our models.

### 2.3. Summary of vegetation characteristics

We used published species accounts (Marshall et al., 2003) to select vegetation characteristics out of the ones available in the YSTDS. We summarized covers of forbs and low shrubs by averaging the sum of absolute covers of species attributed to the respective structural groups (i.e., forbs and low shrubs, tall shrubs) across sixteen (16) 0.1 m<sup>2</sup> subplots within 0.1 ha vegetation sampling plots (Davis and Puettmann, 2009). The sums of absolute vegetation covers in structural groups were used as explanatory variables to predict bird occurrence and abundance. The tall shrub structural group included coniferous and hardwood saplings; the low shrub structural group included bracken and sword ferns (*Pteridium aquilinum*, and *Polystichum munitum*). Each group was summarized by adding intercept lengths of component species along two 14.5-m sub-transects within each vegetation sampling plot (Davis and Puettmann, 2009), and dividing the intercept sum by the total length of the two transects (sum of TS/(14.5 m \* 2) × 100%). Total shrub cover was defined as a sum of low and tall shrub covers. We calculated total tree density (dbh > 8 cm), including all tree species, as well as density of broadleaf and coniferous trees separately. Tree densities were calculated for the plot and then divided by plot area to provide density per hectare. Vegetation data were collected in 1997, 1999, 2001 and 2006.

We estimated crown lengths and tree heights for all trees using relative dominance (based on dbh distributions within the stand) and species-specific regression coefficients from a limited crown length sample (Davis et al., 2007). Average canopy closure and coefficient of variance of canopy closure were calculated from five canopy closure measurements at each plot. Vegetation variables were normalized, i.e., distribution centered on zero and divided by its standard error. Thus, the unit of change for vegetation

characteristic is one standard error of the respective vegetation characteristic distribution, not one percent of its cover.

#### 2.4. Correspondence of bird and vegetation data

Locations of vegetation and bird samples did not coincide spatially in all stands. To make the closest possible correspondence between the two types of data, we identified the nearest vegetation plot for 58 point count stations using GPS coordinates of both plot types. Vegetation data from the plots nearest to point count locations were used as explanatory variables. The distance between point count stations and the closest vegetation plot varied from 3 to 175 m. Sixty-nine percent (69%) of vegetation plots fell within 75 m of point counts, and 93% of vegetation plots were within 100 m of point count plots. Given that territories of most passerines in our study range from 1 to 10 ha (Robbins et al., 2001) we expect that vegetation plots were sufficiently close to bird point count stations to represent at least a part of bird territory. Results of analyses were not different when only data from the nearest (<75 m) plots were used. Therefore, we included all of the bird-vegetation pairs for analyses. In 1998 and 2007 bird data were collected, but not vegetation data. For these years, we used vegetation data from 1999 and 2006 respectively. A total of 58 bird-vegetation plot pairs were used in the study.

#### 2.5. Statistical analyses

We examined relationships to vegetation characteristics for eight bird species that were sufficiently common in our data (that is, we considered abundance data to be robust): Swainson's thrush (*Catharus ustulatus*), MacGillivray's warbler (*Oporornis tolmei*), Oregon junco (*Junco hyemalis*), Pacific wren (*Troglodytes troglodytes*), golden-crowned kinglet (*Regulus satrapa*), Pacific-slope (*Empidonax difficilis*) and Hammond's flycatchers (*Empidonax hammondi*), and hermit warbler (*Dendroica occidentalis*). Additionally, these species are representative of a range of response patterns to thinning treatments: positive (MacGillivray's warbler, Oregon junco, Hammond's flycatcher), negative (hermit warbler, Pacific wren, Pacific-slope flycatcher) or changing direction over time (Swainson's thrush, golden-crowned kinglet) (Hagar and Friesen, 2009; Hagar et al., 2004).

To test the Proximate Cue and the Decoupling Hypotheses we had to determine which vegetation characteristics were important in explaining occurrence or abundance of each species. To avoid missing important variables for each species we tested the performance of several vegetation characteristics per species and used Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) to rank relative performance of models. We used expert opinion and published species accounts (Marshall et al., 2003) to determine vegetation characteristics likely to be associated with each species. We then parameterized univariate and multivariate models with vegetation characteristics as explanatory variables and bird occurrence or abundance as dependent variables. Multivariate vegetation models were considered for forest species associated with understorey vegetation, Swainson's thrush and MacGillivray's warbler. Additionally, multivariate models including vegetation variables and indicator of treatment were used to test for a disturbance effect on bird-vegetation associations. The models were limited to the vegetation characteristics available in the vegetation data of the YSTDS. Some potentially important vegetation characteristics, such as downed wood and snag size or snag density could not be used in this study and, therefore, were not tested.

We were interested in whether the effect of thinning intensity (i.e., treatment type) on birds was mediated by specific vegetation characteristics. If this was the case, we expected that models based

on specific vegetation characteristics would be more parsimonious than treatment-based models, and, therefore, would receive greater support from the data. Thus, for each bird species, we tested performance of at least four vegetation-based models, one treatment-based model, and a null model (Table 1 and Appendix A).

Both Poisson and logistic regressions require that bird observations at each point count station are independent of those at all other stations. The nested design of the original experiment (point count stations are nested within stands, and stands are nested within blocks) violated that assumption. We represented the lack of independence by introducing random effects of stand and block into models. Abundance or occurrence of a species within a year was modeled as a function of fixed effects of either (a) vegetation characteristics, or (b) treatment type, or (c) constant occurrence or abundance and random effects of block and stand (with the exception of MacGillivray's warbler and Pacific-slope flycatcher; models for these species included random effects of block only due to the small range of variation in occurrence records across all point-count stations). We used logistic and Poisson regressions to model occurrence and abundance, respectively. Pearson residuals were examined for each model to ensure that model estimates were not heavily influenced by a few unusual observations.

To examine stability of the effect of vegetation characteristics on bird response we chose one vegetation-based model (most consistently-supported vegetation-based model through the 6 years) per species and compared magnitude of effects of vegetation characteristics on bird occurrence or abundance among years. Before examining parameter estimates, we ensured adequate model fit by graphing residuals against fitted values. No patterns indicating bias were detected. For logistic models, area under receiver-operator curve (AUC) and calibration plots were examined to ensure adequate model fit. Conventionally, AUC values over 0.7 are considered acceptable (Hosmer and Lemeshow, 2000). All of AUC values were above 0.6 and the majority of AUC values were above 0.8.

Confidence intervals are usually used to estimate the uncertainty associated with an estimate as well as evaluate its statistical significance. There is no standard method for computing confidence intervals for fixed effects in generalized mixed effects models due to an uncertain number of degrees of freedom in such models (Nakagawa and Cuthill, 2007). Confidence intervals presented here were calculated using asymptotic theory (assuming normal distribution of estimates) and are considered "approximate" because that assumption is violated. In addition to calculating "approximate", 95% confidence intervals (CI from here on) for estimates of the effect of vegetation characteristics we used the drop-in-deviance test after Zuur et al.'s (2009) example to confirm non-zero effect of vegetation characteristics. Approximate CI and the drop-in-deviance test results were mostly in agreement (Table 2), therefore we refer to CI alone in text, although both are presented in tables. Statistical analyses were carried out in R versions 2.12 and 2.13.1.

#### 2.6. Post hoc hypotheses

##### 2.6.1. Post hoc hypotheses overview

High variability in the magnitude of response of 6 bird species to vegetation characteristics (see Section 3) prompted us to develop post hoc hypotheses addressing potential reasons for the observed variation, in addition to Population Size Hypothesis, which was advanced originally. We explored whether observed fluctuations in effect size were related to population size (Population Size Hypothesis), time since thinning (Disturbance Hypothesis) or change in limiting resources as vegetation characteristics develop (Threshold Response Hypothesis).

The ratio of vegetation effect size to its standard error has been used previously as an indicator of the strength of bird-vegetation

**Table 1**  
Explanation of variable abbreviations and models used in the analysis.

Model type: bird occurrence or abundance is a function of...	Variable and model names	Model meaning
Treatment type	TRTMT	~Con + LG + LT + HT
Constant abundance	Null	~1
Vegetation characteristics	avgCC	~Average canopy cover
	CanCoV	~Canopy coefficient of variance
	CRD	~Crown depth
	CRDV	~Crown depth variance
	cStem	~Conifer density
	cStem_CON	~Conifer density + control treatment
	cStem_CRD	~cStem + CRD + cStem * CRD
	cStem_shr	~cStem + shrub cover
	cStem_shr_int	~cStem + shrub cover + cStem * shrub cover
	cStem_TS	~cStem + tall shrub cover
	forb	~Forb cover
	GAP	~Gap presence within 100 m
	LGcon	~Large conifer density (>20 cm dbh)
	LGcon_TS	~Large conifer density + tall shrub cover
	LS	~Low shrub cover
	LS_stemCount	~Low shrub cover + tree density
	lshr	~Low shrub cover
	minSoil	~Mineral soil cover
	ncon	~Non-coniferous tree density
	shr	~Total (low and tall) shrub cover
	shr_cStem	~Total shrub cover + conifer density
	shr_cStem_CON	~Total shrub cover + conifer density + control

associations (Betts et al., 2010). We assumed that local (observed in the study area only) abundance was an indicator of local population size. We used prevalence, defined as percent of sites where a species was detected across all point count sites, as an estimate of local abundance for Bernoulli-distributed species and total number of detections divided by the number of site visits, for Poisson-distributed species.

### 2.6.2. Threshold Hypothesis

Birds likely establish breeding territories along gradients of the most limiting resources (Hilden, 1965). As vegetation develops after thinning, availability of resources may change. If an initially limiting resource reaches levels at which it is no longer limiting, birds are expected to no longer respond to further increases in the resource; i.e., they reach a response “threshold” (Betts et al., 2007). Under this hypothesis, initial positive response to increase in a limiting vegetation characteristic will become zero when it becomes sufficiently abundant. Both understory and overstory vegetation characteristics undergo a rapid development following forest thinning. Tall shrubs are initially damaged but eventually recover after thinning (Davis and Puettmann, 2009; Wilson et al., 2009). ThresholdHypothesis was suggested by a decreasing response of Swainson’s thrush, a known shrub associate (Marshall et al., 2003; Ellis et al., 2012), to tall shrub cover. We used segmented regression, and R 2.13.1 package *segmented* (Muggeo, 2008), to test for presence of thresholds in response of Swainson’s thrush to increases in tall shrub cover. Starting values for threshold

value search were selected based on visual examination of the plot of Swainson’s thrush abundance against tall shrub cover.

### 2.6.3. Disturbance Hypothesis

Forest thinning removed trees and introduced forest floor disturbance associated with harvesting operations. Stands that received Heavy Thin treatment were disturbed more than Control and Light Thin stands (Allen, 1998). Soon after thinning, tree density may be negatively correlated with resources that reflect the intensity of disturbance. This correlation may dissipate with time since thinning as secondary succession occurs and ephemeral resources associated with disturbance diminish. To test this hypothesis we regressed the strength of association between Oregon junco abundance and tree density against time and assessed the strength of response in thinned-only and control-only stands.

### 2.7. Accounting for imperfect detection

Failure to account for imperfect detection has been shown to bias occurrence records and ultimately study conclusions (MacKenzie et al., 2002). We therefore needed to account for both imperfect detection (MacKenzie et al., 2002) and the lack of independence between sampling stations located in the same stand and block. A mixed effects occupancy model (Kéry, 2010) is the ideal method for accounting for both issues simultaneously. However, a small sample size limited the number of parameters we could estimate. Theoretically, with a large number of visits to an occupied point count station within a breeding season, the probability of detecting a species at the point count stations at least once is expected to approach one. We collapsed detection histories across all within-season visits to calculate average ‘naïve’ occurrence rate, i.e., when not accounting for imperfect detection, and compared it to occupancy estimates that accounted for imperfect detection. For three out of four species for which we modeled occurrence, the two estimates of occupancy were within 6% of each other. Occupancy estimates for golden-crowned kinglet differed, on average, by 25% between the two estimation methods (Yegorova unpublished data). Based on these findings, we decided that not accounting for the violation of independence among the sampling points could more critically bias our results than not accounting for imperfect detection.

## 3. Results

### 3.1. Consistency of bird-vegetation associations over time

For 6 bird species, association with specific vegetation characteristics or combinations of vegetation characteristics was inconsistent across years as evidenced by changes in the relative AICc rankings of vegetation-based models. Only two out of eight species, Pacific-slope flycatcher and MacGillvray’s warbler, had a consistent ranking of vegetation models among years (Appendix A).

The treatment-based model (Table 1) was a reliable predictor of bird occurrence or abundance for 4 species: Hammond’s flycatcher (AICc  $w_{\text{TRTMT}^{\text{97-99},07}} > 0.9$ ), Pacific wren (AICc  $w_{\text{TRTMT}^{\text{97-07}}} > 0.9$ ), MacGillvray’s warbler (AICc  $w_{\text{TRTMT}^{\text{98,06,07}}} > 0.5$ ), and Oregon junco (AICc  $w_{\text{TRTMT}^{\text{97-99,06-07}}} > 0.7$ ) (Appendix A).

### 3.2. Magnitudes of bird-vegetation associations

As expected, response to vegetation characteristics varied substantially across the eight species. Within species, the relationship between bird response and vegetation characteristics remained in a consistent direction (i.e., positive or negative) for all species across years. However, consistent with the AICc results, the

**Table 2**

Estimates of vegetation effects on bird species abundance or occurrence. Note, that the confidence intervals are approximate (see Section 2) and Chi square statistic and associated *p*-value are given for the Drop-in-deviance test for the “full” model containing the variable of interest and a “reduced” model, where the term of interest is dropped (e.g. full model (mgwa = shrubs + coniferous\_stems) and reduced model (mgwa = coniferous\_stems)).

Species and vegetation variables	Year	Estimate	~95% CI	Chi <sup>2</sup> (Pr(>Chi <sup>2</sup> ))
A. Effect of shrub cover on odds of occurrence of MacGillivray's Warbler (after accounting for the effect of stem density)	1997	3.35	(0.84, 13.3)	2.86 (0.09)
	1998	2.50	(0.49, 12.8)	1.16 (0.28)
	1999	3.64	(1.06, 12.4)	4.61 (0.03)
	2001	1.14	(0.40, 3.21)	0.05 (0.82)
	2006	1.42	(0.62, 3.27)	0.68 (0.41)
	2007	2.46	(1.04, 5.84)	4.73 (0.03)
B. Effect of stem density on odds of occurrence of MacGillivray's Warbler (after accounting for the effect of shrub cover)	1997	0.09	(0.01, 0.59)	12.9 (<0.01)
	1998	0.01	(0.001, 0.20)	26.1 (<0.01)
	1999	0.13	(0.03, 0.52)	13.5 (<0.01)
	2001	0.06	(0.01, 0.33)	21.0 (<0.01)
	2006	0.13	(0.04, 0.44)	18.1 (<0.01)
	2007	0.13	(0.039, 0.44)	18.2 (<0.01)
C. Effects of large (>20 cm dbh) conifers on mean odds of occurrence of pacific-slope flycatcher	1997	2.79	(1.17, 6.60)	6.29 (0.01)
	1998	1.84	(0.93, 3.64)	1.87 (0.17)
	1999	2.78	(0.92, 8.38)	5.04 (0.02)
	2001	2.04	(1.10, 3.80)	4.92 (0.03)
	2006	2.77	(1.42, 5.38)	8.09 (<0.01)
	2007	2.84	(1.23, 6.59)	6.09 (0.01)
D. Effects of conifer density on mean odds of occurrence of Hammond's flycatcher	1997	0.94	(0.90, 0.99)	15.91 (<0.01)
	1998	0.99	(0.95, 1.03)	8.45 (<0.01)
	1999	0.95	(0.92, 0.98)	18.98 (<0.01)
	2001	0.97	(0.94, 1.002)	7.13 (<0.01)
	2006	0.99	(0.96, 1.018)	1.36 (0.24)
	2007	0.97	(0.94, 0.99)	3.80 (0.05)
E. Effects of tall shrub cover on mean abundance of Swainson's thrush	1997	1.22	(0.94, 1.59)	2.048 (0.15)
	1998	1.24	(1.01, 1.48)	7.501 (0.01)
	1999	1.32	(1.13, 1.55)	9.627 (<0.01)
	2001	1.08	(0.90, 1.29)	0.657 (0.42)
	2006	1.03	(0.85, 1.25)	0.081 (0.78)
	2007	0.97	(0.81, 1.17)	0.079 (0.78)
F. Effects of conifer density on mean abundance of Oregon junco	1997	0.57	(0.41, 0.78)	1.44 (0.23)
	1998	0.58	(0.48, 0.71)	0.04 (0.84)
	1999	0.55	(0.44, 0.70)	0.01 (0.91)
	2001	0.74	(0.59, 0.92)	2.28 (0.13)
	2006	0.74	(0.55, 1.01)	4.96 (0.03)
	2007	0.72	(0.53, 0.99)	2.03 (0.15)
G. Effects of conifer density on mean odds of occurrence of golden-crowned kinglet	1997	1.035	(1.01, 1.05)	9.36 (<0.01)
	1998	1.003	(0.97, 1.03)	0.04 (0.84)
	1999	1.014	(0.99, 1.04)	1.01 (0.32)
	2001	1.006	(0.98, 1.03)	0.15 (0.70)
	2006	1.026	(0.99, 1.05)	2.60 (0.11)
	2007	1.013	(0.99, 1.03)	1.85 (0.17)
H. Effects of conifer density on mean abundance of hermit warbler	1997	0.94	(0.86, 1.04)	1.44 (0.23)
	1998	0.96	(0.64, 1.44)	0.04 (0.84)
	1999	0.99	(0.89, 1.11)	0.01 (0.91)
	2001	0.91	(0.81, 1.03)	2.28 (0.13)
	2006	0.87	(0.78, 0.98)	4.96 (0.03)
	2007	0.93	(0.83, 1.03)	2.03 (0.15)

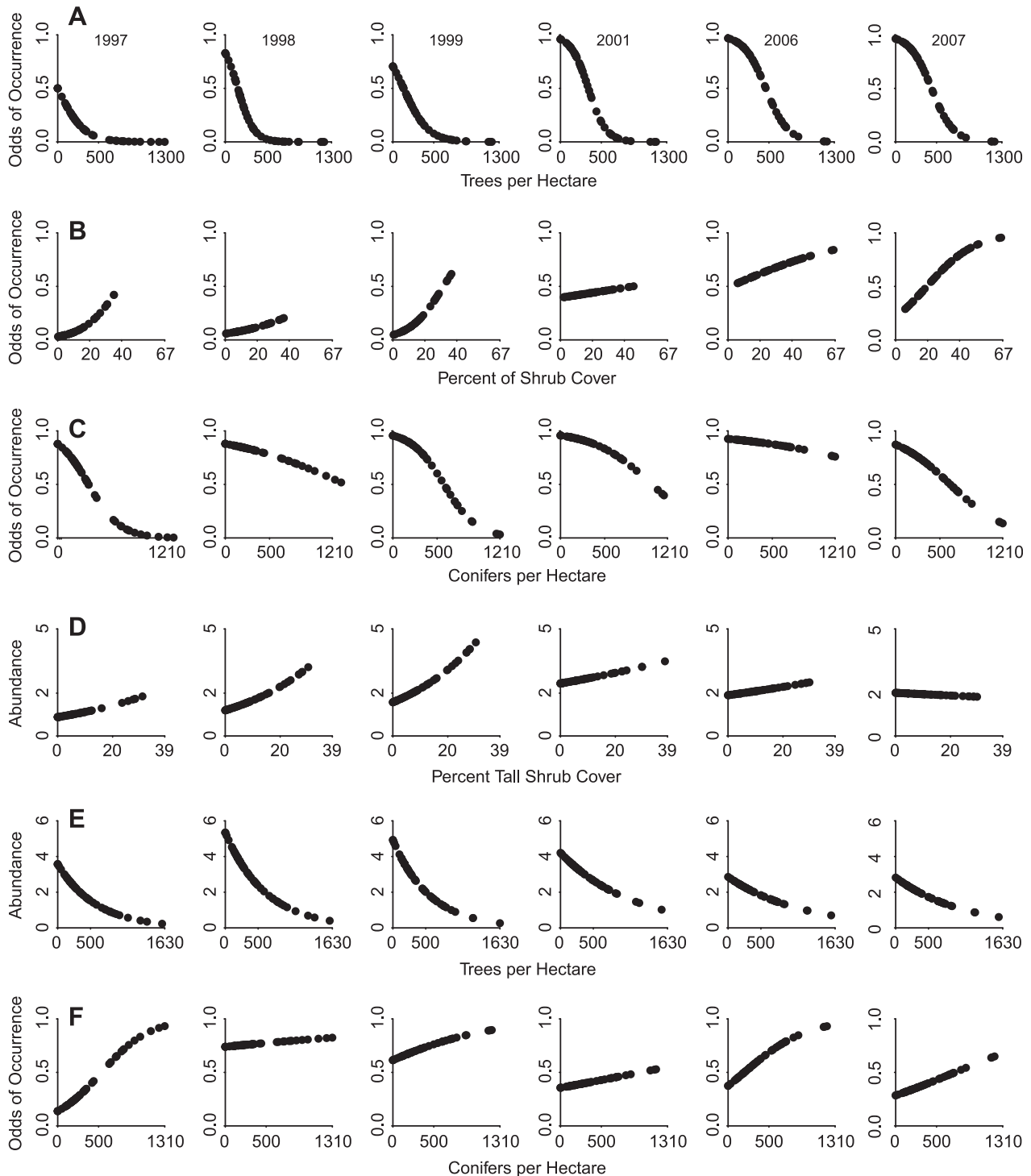
magnitude of bird-vegetation association, expressed by the slope of logistic or Poisson regression curve, varied greatly from year to year (Fig. 1). Statistical significance of response magnitude varied from year to year for most species. In some years CI's for the respective estimates overlapped one, indicating no statistically significant response across years, however in other years we found the response to be statistically significant (Table 2). The degree of annual fluctuation in the magnitude was highly variable across species and years. However, confidence intervals for the estimates overlapped, suggesting that the estimates were not statistically different from each other despite large variation in size (Table 2). For each species, one of three general patterns of variation emerged: (1) A vegetation variable remained an important predictor of bird response across years, but the magnitude of its association with bird response varied among years; (2) the magnitude of bird-vegetation associations gradually declined over time; and (3)

none of the tested vegetation characteristics were associated with bird response.

### 3.2.1. Bird-vegetation associations with non-directional year-to-year variation in magnitude

The occurrence of three species (MacGillivray's warbler, Pacific-slope flycatcher, and Hammond's flycatcher) varied along gradients of vegetation characteristics, but the magnitude of the effect of the vegetation characteristics on occurrence of these species changed across years, without an apparent trend (Fig. 1A–C, graph for Pacific-slope flycatcher not shown).

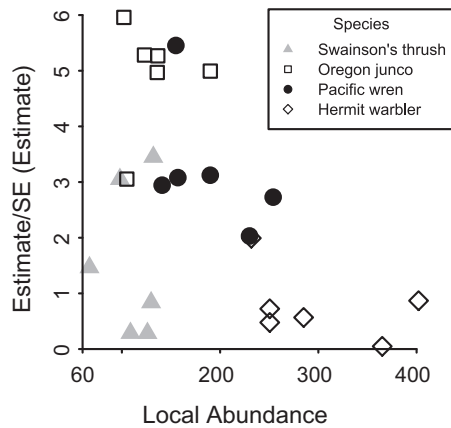
Occurrence of MacGillivray's warbler was negatively associated with tree density and positively associated with shrub cover, after accounting for the effect of tree density. The negative effect of tree density on occurrence varied in magnitude over the 10-year study



**Fig. 1.** Relationships between vegetation gradients and species occurrence or abundance. Note different independent variables on the x-axes. (A) MacGillivray's warbler and tree density (after accounting for the effect of shrubs) and (B) MacGillivray's warbler and shrub cover (after accounting for the effects of tree density); (C) Hammond's flycatcher and conifer density; (D) Swainson's thrush and tall shrub cover; (E) Oregon junco and tree density; (F) golden-crowned kinglet and conifer density.

but CI's never overlapped one (Table 2A). Mean odds of occurrence for MacGillivray's warbler as a function of tree density varied by a factor of ten (10) among years (from 0.01 in 1998 to 0.13 in 2007) (Table 2A, Fig. 1A). The positive effect of the size of the shrub cover on occurrence varied in magnitude among years and was not always statistically different from one (Table 2B, Fig. 1B).

Pacific-slope flycatcher was positively associated with density of large (>20 cm dbh) trees (Table 2C). The magnitude of response varied from 1.84 in 1998 to 2.84 in 2007, by a factor of 1.54. Hammond's flycatcher was negatively associated with conifer density (Table 2D), with mean odds of occurrence approaching one at tree densities near zero (Fig. 2C), suggesting species' preference for



**Fig. 2.** Population Size Hypothesis (Poisson species): relationship between estimated local abundance and strength of vegetation effect (expressed as ratio of effect estimate to its standard error). For species with asterisk (\*) symbols on the graph represent strength of association with the Heavy Thin stands.

small (0.1 ha) forest openings or vicinities of small forest openings. The magnitude of response remained relatively consistent (0.94–0.99) for this species, however it was only statistically significant in the first year after thinning (Table 2D).

### 3.2.2. Bird-vegetation associations with decreasing magnitude of over time

The magnitude of bird-vegetation associations of three species (Swainson's thrush, Oregon junco, and golden-crowned kinglet) decreased over time (Fig. 1D–F).

Abundance of Swainson's thrush was positively associated with tall shrub cover only in the first 3 years post-thinning (Fig. 1D, Table 2E). This apparent decrease over time in the association of Swainson's thrush abundance with tall shrub cover was statistically significant (slope =  $-0.06$ ,  $p = 0.04$ , adjusted  $R^2 = 0.60$ ).

Abundance of Oregon junco was negatively associated with total tree density but the magnitude of the association decreased over time (slope =  $0.25$ ,  $p = 0.049$ , adjusted  $R^2 = 0.58$ ). Note that the slope is positive because the association between Oregon Junco and tree density became less negative (Fig. 1E, Table 2G).

Occurrence of golden-crowned kinglet varied strongly along the conifer density gradient in the first year of study (1997) with nearly zero odds of occurring near small gaps (0 tph) and nearly certain presence near densest forest patches (Fig. 1F). However, in all subsequent years this species was almost uniformly distributed along the conifer density gradient (Fig. 1F, Table 2G).

### 3.2.3. No detected response to examined vegetation characteristics

We did not detect a response to any of the tested vegetation characteristics for two species, Pacific wren and hermit warbler (Appendix A). However, Pacific wren was strongly associated with treatment type in all six sampling periods:  $\Delta AIC_{\text{treatment}} = 0$ ,  $\Delta AIC_{\text{next\_best\_model}} \geq 3$  for all 6 years (see Appendix A). The effect of treatment, however, was not correlated with tree density: CI's for estimates of the stem density effect overlap zero for all 6 years (Table 2H). While average tree densities varied drastically among treatment types, plot-level tree densities varied widely within each treatment. Thus, there was a tree density overlap at the plot level among treatment types, which explains the seemingly contradictory strong treatment effect but a lack of tree density effect. Pacific wrens were less abundant in treated stands compared to Control stands. Ratio of abundance in Heavy Thin stands compared to Controls in 1997 was 0.6, CI (0.43, 0.98) and decreased in subsequent years.

The abundance of hermit warbler also did not correlate consistently with any of the vegetation characteristics tested nor with any of the treatment types. The null model was always within two units of the minimum AICc score (Appendix A), suggesting that either tested vegetation characteristics were irrelevant to this species or the species was ubiquitous.

### 3.2.4. Technical sources of variation

To ensure that the observed variation in the magnitude of vegetation effects was not a statistical artifact of poorly fitting models we calculated AUC scores for the four logistic models fitted to data of each breeding season and to data collapsed across six breeding seasons. AUC scores remained consistently high for two species, MacGillivray's warbler and Hammond's flycatcher ( $AUC_{97-07} > 0.85$ ,  $AUC_{\text{cumulative}} > 0.85$  for both species). AUC scores fluctuated among years for Pacific-slope flycatcher ( $0.67 < AUC < 0.86$ ,  $AUC_{\text{cumulative}} > 0.73$ ) and golden-crowned kinglet ( $0.57 < AUC < 0.91$ ,  $AUC_{\text{cumulative}} > 0.67$ ). Thus, three out of four models had at least "acceptable" ( $\geq 0.7$ ) discrimination power (Hosmer and Lemeshow, 2000).

Overall, mean abundance or mean odds of occurrence of each of the six species for which we found bird-vegetation associations at least doubled along the examined gradient of vegetation characteristics (Figs. 1A–F). Additionally, the magnitude of vegetation effect was mostly statistically different from one (Table 1). Therefore, we consider observed association between vegetation and bird responses biologically significant.

### 3.3. Post hoc results

The Population Size Hypothesis received only weak support. Strength of bird-vegetation associations was weakly (not statistically significant for any given species) related to estimated local abundance (Tables 3 and 4) and did not relate to time since thinning (data not shown) for either "rare" ( $< 150$  detections/year), or "common" ( $> 150$  detections/year) species when each species was examined individually (except for Oregon junco). When pooled, there was a significant negative relationship between strength of

**Table 3**

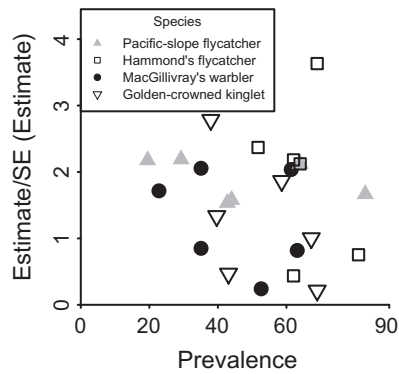
Regression of strength of association between birds and vegetation characteristics on abundance index (Bernoulli species).

Species	Intercept	Slope	$R^2_{\text{adj}}$
Pacific-slope flycatcher	2.83 (0.51), $p < 0.05$	$-0.012$ (0.01), $p = 0.20$	0.081
Golden-crowned kinglet	3.03 (1.57), $p = 0.127$	$-0.03$ (0.02), $p = 0.32$	0.06
MacGillivray's warbler	1.86 (1.05), $p = 0.15$	$-0.012$ (0.02), $p = 0.60$	$-0.16$
Hammond's flycatcher	3.62 (3.60), $p = 0.37$	$-0.03$ (0.05), $p = 0.65$	$-0.18$
Cumulative	2.24 (0.63), $p < 0.05$	$-0.01$ (0.36), $p = 0.36$	$-0.005$

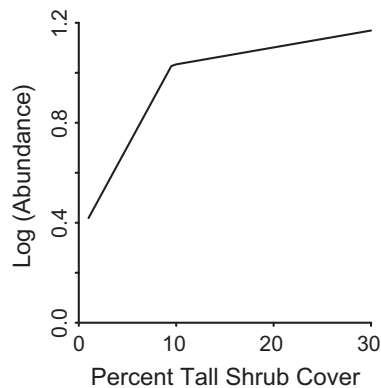
**Table 4**

Regression of strength of association between birds and vegetation characteristics on abundance index (Poisson species).

Species	Intercept	Slope	$R^2_{\text{adj}}$
Pacific wren	4.82 (1.29), $p = 0.02$	$-0.01$ (0.001), $p = 0.26$	0.12
Oregon junco	4.35 (2.05), $p = 0.102$	0.0042 (0.01), $p = 0.79$	$-0.23$
Swainson's thrush	1.98 (3.37), $p = 0.59$	$-0.005$ (0.03), $p = 0.89$	$-0.24$
Hermit warbler	2.00 (1.29), $p = 0.19$	$-0.004$ (0.004), $p = 0.39$	$-0.01$
Cumulative	4.44 (0.79), $p < 0.001$	$-0.01$ (0.004), $p = 0.018$	0.19



**Fig. 3.** Population Size Hypothesis (Bernoulli species): relationship between estimated local bird prevalence and strength of vegetation effect (ratio of the effect estimate to its standard error).



**Fig. 4.** Swainson's thrush: illustration of a threshold response to increasing cover of tall shrubs.

association and local abundance for common species (slope =  $-0.01$ ,  $p < 0.002$ ,  $R_{adj}^2 = 0.19$ ) driven by among-species differences (Fig. 3). No statistically significant association was found for rare species when they were pooled (slope =  $-0.01$ ,  $p = 0.36$ ) (Fig. 3).

The Threshold Hypothesis was supported for Swainson's thrush. The model containing a threshold term received a considerably greater support than the model without one ( $AIC_{no\_threshold} - AIC_{threshold} = 13.4$ ). Segmented regression suggested a threshold at 9% cover of tall shrubs, CI (5.5, 13.9). See Fig. 4 for an illustration. Abundance of Swainson's thrush increased with greater tall shrub cover (factor of 1.07, CI (1.01, 1.14) for every 1% tall shrub increase) up to the threshold value and was flat for additional tall shrub cover increases above the threshold value (factor of 1.01, CI (1.001, 1.14) for every 1% tall shrub increase).

The Disturbance Hypothesis was supported for Oregon junco. As predicted, the abundance of this species did not respond to variation in tree density in Control stands; CI for the effect of tree density in Control stands included zero in all six seasons (CI's not shown). Strength of association (ratio of vegetation effect estimate to its standard error) between Oregon junco abundance and conifer density decreased over time (analysis included data from both treated and control stands): slope =  $-0.25$ ,  $p = 0.049$ ,  $R_{adj}^2 = 0.58$ .

#### 4. Discussion

Few studies have quantified bird-vegetation relationships in the long term and examined their consistency over time. The studies that have done so were primarily focused on shrub-steppe or

grassland systems (Wiens et al., 1986; Wiens, 2002; Winter et al., 2005; Rotenberry and Wiens, 2009). To our knowledge, this is one of the first long-term manipulative studies to document variation in bird-vegetation relationships over time in a forest system.

The assumption of tight bird-habitat relationships is often the basis of wildlife management and conservation (Wiens, 2002; Ahlering and Faaborg, 2006). The variation in strength of association between vegetation variables and bird response we documented over more than ten years has important implications for natural resource management and planning. Short term studies (Hansen et al., 1995; Guenette and Villard, 2005; Betts et al., 2006; Hewson et al., 2011) may capture only a small part of the range of bird responses to vegetation characteristics and thus create an impression of stable relationships between birds and vegetation. However, explicitly including variability in bird-vegetation relationships may be crucial when projecting species responses to management scenarios and evaluating short-term effects of management.

Despite variation in the magnitude of estimates, the direction of relationships between vegetation variables and bird responses remained consistent over time for six out of eight species in this study. We caution against the dangers of interpreting weak (not statistically different from zero) bird-vegetation relationships in a short-term study. Our results show that birds that do not have a strong response to vegetation characteristics one year may respond strongly (statistically and biologically significantly) to vegetation characteristics in the following year or the year before. (e.g., MacGillivray's warbler's response to shrub cover). Absence of response in the short-term, therefore, is not necessarily representative of the bird-vegetation associations over the longer-term, and should be interpreted conservatively.

We suggest that the lack of detected response of hermit warbler and Pacific wren to any of examined vegetation characteristics may be due to either ubiquitous presence of these species in forested environments or lack of information on pertinent vegetation characteristics. Pacific wrens are known to nest in downed wood and forage in dead foliage near forest floor (Hejl et al., 2002). Quantitative information on these characteristics could not be considered for this study. This is one possible reason why we did not find a strong effect of a specific vegetation characteristic on Pacific wren's abundance.

Observed variation in association between vegetation characteristics and the six bird species for which we detected a response raised the question of underlying causes. We ruled out three potential methodological causes: inappropriate vegetation variables, poor model fit and poor data quality. We believe vegetation variables were ecologically significant to birds because (1) they were consistent with published natural history accounts and (2) our vegetation-based models performed better than null models (Appendix A). We ruled out poor data quality as a cause of variation because bird and vegetation data were collected consistently, according to standardized protocols, by trained observers. Below we discuss possible ecological causes of variation in the strength of bird-vegetation relationships.

##### 4.1. Local abundance effects on bird-vegetation associations

We found that strength of bird-vegetation associations within a species was only weakly related to local abundance of that species, providing little support for ideal free (IFD), ideal preemptive (IPD) and ideal despotic distribution scenarios (IDD). For rare species (Bernoulli-distributed), perhaps, local abundances were not large enough to saturate available habitat. When habitat is unsaturated we could expect to observe a pattern consistent with IFD, high odds of occurrence at high-quality sites and low odds at



poor-quality sites (Fretwell and Lucas, 1969). However, at low abundance local stochastic processes (predation, local-scale disturbance, etc.) as well as demographic stochasticity, inherent to a population, have a greater effect on the overall population size fluctuation than in a medium or large population (Shaffer, 1981).

For each common (Poisson-distributed) species, the strength of vegetation effect decreased slightly, but not significantly, with species abundance. Within the common species group, more abundant species had weaker associations with vegetation characteristics than the less abundant species (Fig. 2). This negative relationship between response size and local abundance suggests a decreasing affinity for specific vegetation features as bird abundance increases. The weak relationship between bird-vegetation associations and local abundance *within* species suggests that (1) abundance fluctuations are too small to produce a negative effect on the strength of bird-vegetation associations or (2) available habitat was saturated even at the lowest population size and that bird-vegetation associations within species were at their lowest value and could not erode any further.

#### 4.2. Vegetation Threshold Hypothesis

Variation in strength of association between vegetation and Swainson's thrush abundance was consistent with the Threshold Hypothesis. Thresholds in population processes in relation to amount of habitat at landscape scales are predicted by theoretical studies (e.g., Andren, 1999; Fahrig, 2002; McPherson and Jetz, 2007). Recent studies document thresholds in bird occurrence and abundance in relation to vegetation characteristics in PNW forest birds (Betts et al., 2010; Ellis and Betts, 2011). Swainson's thrush has been found to be strongly associated with hardwood vegetation (Ellis et al., 2012; Marshall et al., 2003) at stand scales. Thus, a positive association of Swainson's thrush with tall shrubs, a structural group that includes mainly broadleaf tall shrubs and young hardwoods, supports previous findings. However, we cannot rule out that this insectivorous species was not responding to changes in arthropod community or another resource affected by thinning as we did not measure arthropod density in this study.

#### 4.3. Thinning-associated disturbance effects

We did not find support for the Decoupling Hypothesis. Bird-vegetation relationships were present in the first year of available data for six of the eight species and relationships did not strengthen with time since thinning, contrary to predictions of the Decoupling Hypothesis. However, most stands were thinned in 1995 and 1996 (for details see Beggs, 2004) but sampled for birds in 1997 for the first time, making detection of decoupling between vegetation characteristics and proximate cues potentially difficult.

Two species showed evidence of responding to disturbance-related resources, but not in the expected direction. Oregon junco's response was consistent with the species tracking ephemeral, disturbance-related, resources. Golden-crowned kinglets avoided vicinities of low-density forest areas immediately after forest thinning, but returned to approximately homogeneous use of the forest, including areas of low tree density, after the first year. The forest dwelling species examined in this study appear to respond rapidly to vegetation changes or vegetation-associated resources, compared to shrub-steppe birds where time-lags were found in response to habitat alteration (Wiens et al., 1986; Knick and Rotenberry, 2000).

#### 4.4. Treatment type as habitat descriptor

Previous studies documented responses of individual species to thinning in young Douglas-fir stands (Hayes et al., 2003; Hagar

et al., 2004), and hypothesized that treatment effects on bird abundances were mediated by vegetation developments after thinning (Verschuyl et al., 2011). We also found evidence of bird responses to vegetation characteristics that were influenced by thinning. However, our results show that, thinning intensity was a more reliable predictor of bird response than vegetation characteristics.

Treatment type is a more complex variable than individual vegetation characteristics because it integrates vertical and horizontal vegetation structure at a larger spatial scale than vegetation plots. The spatial scale of treatments (>15 ha) approximates multiple territories of the species we examined, and may be more relevant to patch-level habitat-selection (*sensu* Johnson, 1980) than plot-scale vegetation characteristics. These reasons may account for the superior AICc performance of treatment models compared to models with individual vegetation characteristics.

It is possible that univariate and bivariate vegetation-based models were too simple to adequately represent multi-dimensional habitat quality for the species we examined. However, simple vegetation descriptors have been used successfully in the past to explain bird abundance. Hansen et al. (1995) found statistically significant habitat functions for bird species abundance using tree density measurements by dbh classes. They found that most of their bird species, including the eight species in the present study, responded to total density of trees  $\geq 10$  cm dbh. However, tree density may represent more associated information about habitat in forest stands without recent disturbances, and less in recently thinned forests where understory and overstory vegetation are rapidly developing and relationships between tree density and other vegetation characteristics are changing. Thus, the dynamic relationships between vegetation characteristics and birds in recently thinned forests may explain the relatively poor performance of univariate vegetation models compared to the treatment-based model in our study. The ranges of stand-level tree densities and successional stages in YSTDS were narrow compared to those examined in Hansen et al. (1995), reiterating the importance of context (spatial and successional in this case) for interpreting and applying study results.

#### 4.5. Issues of spatial scale

Dependence of result on observation scale is a classic idea in ecology (Wiens, 1989). The relatively high degree of variability of small-scale bird-vegetation associations in comparison to stable associations with treatment type may be an example of this principle. Both vegetation characteristics and bird responses were measured at small spatial scales. Small-scale sampling revealed the variation in local vegetation characteristics (tree density, shrub cover, etc.) as well as birds' response to small-scale variation in vegetation characteristics that could not be detected at stand scales.

Habitat selection by birds is a multi-scale process (e.g., Johnson, 1980; Orians and Wittenberger, 1991). Both local vegetation characteristics and landscape-level composition have been found important in explaining forest bird community composition in the PNW (Cushman and McGarigal, 2004). We did not account for effects of landscape composition on the local-level species response, implicitly assuming that landscape composition was similar for all examined stands. The forest stands examined in this study were located in the relatively homogeneous matrix of unthinned, young Douglas-forest stands when the study was established. Over the study period, the proportion of thinned stands increased dramatically across the surrounding landscapes (Klaus Puettmann, personal communication), which may have contributed to the amplifying or dampening trends we observed in bird-vegetation associations in some species.

## 5. Conclusions and management implications

Our results should be interpreted as a cautionary note. Temporal variability in bird associations means that important bird-vegetation correlations may be missed in short-term studies. Therefore, inferences and projections made with short-term information should be made cautiously. Efforts to model future distributions or population viability (e.g., Larson et al., 2004) would be most reliable if information about inter-annual variation in the magnitude of bird response to vegetation characteristics is incorporated. Unfortunately, such long-term data are only rarely available for such projection models (e.g., Bird et al., 2012; Gasner et al., 2010). Our study highlights the additional uncertainty of interpreting projections based on short-term studies.

As federal forest managers in the PNW are promoting biodiversity and native species habitat in forests previously managed for timber production, detailed information about mechanisms of species response to management is necessary. Our study shows that in the predominantly forested landscape of the west-slope of the Cascade Mountains in Oregon, bird species quickly respond to changes in vegetation characteristics associated with forest thinning. The temporal consistency of qualitative bird responses to thinning, together with biologically significant response of birds to gradients in vegetation characteristics indicates that vegetation characteristics examined here could be used as general guidelines for species-specific habitat management in young Douglas-fir forests in the PNW. For example, our study suggests that maintaining patches of forest with tall shrub cover  $\geq 9\%$  may maximize local abundance of Swainson's thrush. However, the magnitude of bird response should be assessed for several years after management implementation to account for the variability observed in this study.

The success of treatment type in predicting bird response suggests that the spatial scale of thinning treatment and its vegetation 'gestalt' are ecologically relevant to breeding forest birds. Assuming bird abundance reflects habitat quality, which is not always the case (Van Horne, 1983), forest thinning at spatial scales of 10's of hectares may be an effective technique for creating habitat for some of the species associated with well-developed understory vegetation, such as MacGillivray's warbler, or aerial insectivores associated with small forest gaps, such as Hammond's flycatcher.

Overall, our results suggest, that long-term monitoring of management effects is crucial despite the associated practical and financial difficulties. Our study highlights an important reason for long-term monitoring of the effects of management efforts. Given the variability in associations between birds and vegetation that we documented, an accumulation of evidence from several long-term studies is needed to establish which vegetation characteristics are most important to each species, and to identify thresholds in levels of vegetation variables to which birds respond. Further quantification of uncertainty in bird-vegetation relationships may allow managers and conservation planners to better assess trade-offs among management effects on multiple resources, and therefore make better management and conservation decisions.

## Acknowledgements

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## Appendix A. AICc tables

Year	Model name	$\Delta AICc$	wt
<i>Oregon junco</i>			
1997	trtmt	0.000	0.943
1997	stemCount	5.866	0.050
1997	null	11.508	0.003
1997	minSoil	12.944	0.001
1997	forb	13.057	0.001
1997	LS	13.090	0.001
1998	stemCount	0.000	0.761
1998	trtmt	2.404	0.229
1998	minSoil	9.834	0.006
1998	null	11.913	0.002
1998	LS	12.063	0.002
1998	forb	13.058	0.001
1999	trtmt	0.000	0.991
1999	stemCount	9.338	0.009
1999	null	19.589	0.000
1999	minSoil	21.505	0.000
1999	forb	21.570	0.000
1999	LS	21.596	0.000
2001	trtmt	0.000	0.986
2001	minSoil	10.508	0.005
2001	stemCount	10.622	0.005
2001	null	12.824	0.002
2001	forb	13.341	0.001
2001	LS	14.057	0.001
2006	stemCount	0.000	0.324
2006	trtmt	0.155	0.300
2006	null	1.337	0.166
2006	minSoil	2.633	0.087
2006	forb	3.260	0.063
2006	LS	3.376	0.060
2007	trtmt	0.000	1.000
2007	stemCount	24.917	0.000
2007	minSoil	25.924	0.000
2007	null	25.915	0.000
2007	LS	27.202	0.000
2007	forb	27.580	0.000
<i>Golden-crowned kinglet</i>			
1997	cStem_TS	0.000	0.388
1997	cStem	0.630	0.283
1997	LGcon	2.763	0.098
1997	cStem_CRD	3.060	0.084
1997	LGcon_TS	3.414	0.070
1997	AvgCC	4.026	0.052
1997	trtmt	7.330	0.010
1997	null	7.607	0.009
1997	TS	9.802	0.003
1997	CRD	9.969	0.003
1998	null	0.000	0.248
1998	CRD	0.464	0.197
1998	AvgCC	1.246	0.133
1998	LGcon	2.208	0.082
1998	TS	2.275	0.079
1998	cStem	2.326	0.077
1998	trtmt	2.471	0.072

## Appendix A (continued)

Year	Model name	$\Delta AICc$	wt
1998	cStem_CRD	2.921	0.058
1998	LGcon_TS	4.330	0.028
1998	cStem_TS	4.547	0.026
1999	LGcon	0.000	0.188
1999	LGcon_TS	0.294	0.162
1999	null	0.488	0.147
1999	AvgCC	0.489	0.147
1999	CRD	1.150	0.106
1999	cStem	1.863	0.074
1999	TS	2.301	0.059
1999	cStem_CRD	2.557	0.052
1999	cStem_TS	2.964	0.043
1999	trtmt	4.407	0.021
2001	null	0.000	0.237
2001	CRD	0.157	0.219
2001	trtmt	1.867	0.093
2001	AvgCC	1.953	0.089
2001	TS	2.058	0.085
2001	LGcon	2.168	0.080
2001	cStem	2.233	0.078
2001	cStem_CRD	2.517	0.067
2001	LGcon_TS	4.439	0.026
2001	cStem_TS	4.472	0.025
2006	LGcon	0.000	0.284
2006	trtmt	1.008	0.172
2006	cStem	1.812	0.115
2006	null	2.024	0.103
2006	LGcon_TS	2.095	0.100
2006	cStem_CRD	2.680	0.074
2006	CRD	3.321	0.054
2006	cStem_TS	4.154	0.036
2006	AvgCC	4.395	0.032
2006	TS	4.408	0.031
2007	null	0.000	0.209
2007	cStem	0.537	0.160
2007	LGcon	0.696	0.148
2007	trtmt	1.090	0.121
2007	CRD	2.197	0.070
2007	AvgCC	2.226	0.069
2007	TS	2.376	0.064
2007	cStem_TS	2.573	0.058
2007	LGcon_TS	2.717	0.054
2007	cStem_CRD	2.963	0.048
<i>Hammond's flycatcher</i>			
1997	TRTMT	0.000	0.983
1997	cStem	8.793	0.012
1997	avgCC	12.970	0.002
1997	null	13.558	0.001
1997	CRD	14.387	0.001
1997	CanCov	15.021	0.001
1997	LC	15.781	0.000
1997	CRDV	15.920	0.000
1998	TRTMT	0.000	0.994
1998	avgCC	12.306	0.002
1998	CanCov	12.385	0.002
1998	null	14.129	0.001
1998	LC	15.762	0.000

## Appendix A (continued)

Year	Model name	$\Delta AICc$	wt
1998	cStem	16.270	0.000
1998	CRD	16.322	0.000
1998	CRDV	16.437	0.000
1999	TRTMT	0.000	0.999
1999	CanCov	14.046	0.001
1999	cStem	16.487	0.000
1999	CRD	28.350	0.000
1999	avgCC	28.940	0.000
1999	LC	32.871	0.000
1999	null	33.169	0.000
1999	CRDV	34.497	0.000
2001	TRTMT	0.000	0.293
2001	cStem	0.878	0.189
2001	avgCC	1.950	0.110
2001	CRDV	1.961	0.110
2001	null	1.691	0.126
2001	CRD	2.406	0.088
2001	LC	3.712	0.046
2001	CanCov	4.070	0.038
2006	CanCov	0.000	0.854
2006	null	5.748	0.048
2006	CRD	7.493	0.020
2006	LC	7.612	0.019
2006	cStem	7.627	0.019
2006	avgCC	7.726	0.018
2006	CRDV	8.110	0.015
2006	TRTMT	9.465	0.008
2007	TRTMT	0.000	0.924
2007	CanCov	6.715	0.032
2007	cStem	8.000	0.017
2007	avgCC	9.281	0.009
2007	null	9.416	0.008
2007	CRD	11.205	0.003
2007	CRDV	11.272	0.003
2007	LC	11.799	0.003
<i>Hermit warbler</i>			
1997	avgCC	0.000	0.287
1997	null	0.048	0.280
1997	stem	0.992	0.175
1997	LGcon	1.637	0.127
1997	cancov	1.735	0.121
1997	trt	6.633	0.010
1998	null	0.000	0.333
1998	LGcon	0.669	0.238
1998	stem	1.317	0.172
1998	avgCC	1.883	0.130
1998	cancov	2.196	0.111
1998	trt	6.002	0.017
1999	null	0.000	0.395
1999	LGcon	1.930	0.151
1999	avgCC	2.110	0.138
1999	trt	3.326	0.075
1999	cancov	2.363	0.121
1999	stem	2.378	0.120
2001	stem	0.100	0.278
2001	null	0.000	0.293

(continued on next page)

## Appendix A (continued)

Year	Model name	$\Delta$ AICc	wt
2001	cancov	1.236	0.158
2001	avgCC	1.914	0.112
2001	LGcon	2.084	0.103
2001	trt	3.330	0.055
2006	stem	0.000	0.525
2006	LGcon	1.924	0.201
2006	null	2.572	0.145
2006	avgCC	4.444	0.057
2006	cancov	4.809	0.047
2006	trt	6.062	0.025
2007	avgCC	0.000	0.383
2007	LGcon	0.931	0.241
2007	stem	2.194	0.128
2007	null	1.837	0.153
2007	trt	4.180	0.047
2007	cancov	4.168	0.048
<i>MacGillvray's warbler</i>			
1997	shr_cStem	0.00	0.44
1997	shr_cStem_CON	0.61	0.32
1997	cStem	2.39	0.13
1997	trtmt	3.76	0.07
1997	cStem_CON	5.37	0.03
1997	null	10.16	0.00
1997	lshr	12.11	0.00
1997	shr	12.42	0.00
1998	trtmt	0.00	0.41
1998	cStem	0.69	0.29
1998	cStem_CON	2.56	0.11
1998	shr_cStem	2.40	0.12
1998	cStem_shr_CON	3.99	0.06
1998	lshr	19.95	0.00
1998	shr	20.59	0.00
1998	null	20.34	0.00
1999	trtmt	0.00	0.94
1999	shr_cStem_CON	6.24	0.04
1999	shr_cStem	9.11	0.01
1999	cStem_CON	10.52	0.00
1999	cStem	11.32	0.00
1999	lshr	19.80	0.00
1999	shr	20.19	0.00
1999	null	24.28	0.00
2001	trtmt	0.00	0.79
2001	cStem	3.45	0.14
2001	shr_cStem	5.80	0.04
2001	cStem_CON	7.45	0.02
2001	shr_cStem_CON	9.16	0.01
2001	lshr	23.08	0.00
2001	shr	24.43	0.00
2001	null	25.50	0.00
2006	trtmt	0.00	1.00
2006	cStem	14.00	0.00
2006	cStem_CON	14.72	0.00
2006	shr_cStem	15.72	0.00
2006	shr_cStem_CON	17.26	0.00
2006	lshr	31.40	0.00
2006	shr	31.44	0.00
2006	null	38.73	0.00

## Appendix A (continued)

Year	Model name	$\Delta$ AICc	wt
2007	trtmt	0.00	1.00
2007	cStem_CON	14.61	0.00
2007	shr_cStem_CON	14.69	0.00
2007	shr_cStem	21.80	0.00
2007	cStem	24.13	0.00
2007	lshr	35.32	0.00
2007	shr	37.59	0.00
2007	null	51.58	0.00
<i>Pacific-slope flycatcher</i>			
1997	LGcon	0.00	0.48
1997	stemCount	1.48	0.23
1997	trtmt	3.75	0.07
1997	stemCount_CON	3.94	0.07
1997	null	3.89	0.07
1997	avgCC	4.43	0.05
1997	CRD	6.09	0.02
1998	stemCount_CON	0.00	0.30
1998	trtmt	1.04	0.18
1998	LGcon	1.40	0.15
1998	null	1.55	0.14
1998	stemCount	2.34	0.09
1998	avgCC	2.46	0.09
1998	CRD	3.89	0.04
1999	LGcon	0.00	0.34
1999	avgCC	0.13	0.32
1999	stemCount	1.33	0.18
1999	null	2.64	0.09
1999	stemCount_CON	5.65	0.02
1999	trtmt	5.94	0.02
1999	CRD	5.04	0.03
2001	LGcon	0.00	0.28
2001	stemCount	0.06	0.27
2001	trtmt	0.66	0.20
2001	stemCount_CON	1.98	0.10
2001	null	2.52	0.08
2001	CRD	3.68	0.04
2001	avgCC	4.03	0.04
2006	LGcon	0.00	0.54
2006	trtmt	2.50	0.15
2006	stemCount_CON	2.67	0.14
2006	stemCount	3.49	0.09
2006	avgCC	5.98	0.03
2006	null	5.69	0.03
2006	CRD	7.10	0.02
2007	trtmt	0.00	0.70
2007	LGcon	2.93	0.16
2007	stemCount_CON	4.93	0.06
2007	stemCount	6.65	0.03
2007	null	6.62	0.03
2007	avgCC	7.65	0.02
2007	CRD	7.75	0.01
<i>Pacific wren</i>			
1997	trtmt	0.00	0.78
1997	null	4.33	0.09
1997	stemCount	6.39	0.03
1997	CC	6.62	0.03

## Appendix A (continued)

Year	Model name	$\Delta AICc$	wt
1997	LS	6.69	0.03
1997	SHR	6.73	0.03
1997	LS_stemCount	8.86	0.01
1997	stemCount_CON	11.40	0.00
1998	trtmt	0.00	0.75
1998	null	4.34	0.09
1998	stemCount	6.00	0.04
1998	LS	6.32	0.03
1998	CC	6.42	0.03
1998	SHR	6.53	0.03
1998	stemCount_CON	6.62	0.03
1998	LS_stemCount	8.13	0.01
1999	trtmt	0.00	0.58
1999	null	2.95	0.13
1999	stemCount_CON	5.41	0.04
1999	CC	4.33	0.07
1999	SHR	4.60	0.06
1999	LS	4.79	0.05
1999	stemCount	4.98	0.05
1999	LS_stemCount	6.99	0.02
2001	trtmt	0.00	0.74
2001	null	4.90	0.06
2001	stemCount	5.71	0.04
2001	LS_stemCount	6.28	0.03
2001	CC	5.92	0.04
2001	SHR	5.95	0.04
2001	LS	6.18	0.03
2001	stemCount_CON	7.77	0.02
2006	trtmt	0.00	0.74
2006	CC	4.70	0.07
2006	stemCount	4.74	0.07
2006	null	5.53	0.05
2006	stemCount_CON	7.46	0.02
2006	LS_stemCount	7.23	0.02
2006	SHR	7.51	0.02
2006	LS	7.57	0.02
2007	trtmt	0.00	1.00
2007	stemCount_CON	18.63	0.00
2007	null	18.63	0.00
2007	CC	19.70	0.00
2007	stemCount	20.69	0.00
2007	SHR	20.74	0.00
2007	LS	20.76	0.00
2007	LS_stemCount	22.69	0.00
<i>Swainson's thrush</i>			
1997	cStem	0.00	0.21
1997	null	0.34	0.18
1997	TS	0.69	0.15
1997	TS_CON	1.62	0.09
1997	cStem_CON	2.19	0.07
1997	trtmt	2.31	0.07
1997	cStem_shr	2.40	0.06
1997	LS	2.69	0.05
1997	SHR	2.73	0.05
1997	ncon	2.73	0.05
1997	cStem_shr_int	4.98	0.02
1998	TS	0.00	0.40

## Appendix A (continued)

Year	Model name	$\Delta AICc$	wt
1998	cStem	0.92	0.25
1998	TS_CON	3.13	0.08
1998	cStem_shr	3.28	0.08
1998	cStem_shr_int	4.39	0.04
1998	cStem_CON	4.70	0.04
1998	trtmt	5.57	0.02
1998	null	5.10	0.03
1998	LS	5.86	0.02
1998	SHR	6.99	0.01
1998	ncon	7.47	0.01
1999	TS	0.00	0.84
1999	TS_CON	4.65	0.52
1999	null	7.23	0.02
1999	cStem	8.64	0.01
1999	SHR	8.65	0.01
1999	cStem_shr	9.58	0.00
1999	trtmt	10.39	0.00
1999	LS	9.49	0.00
1999	ncon	9.52	0.00
1999	cStem_shr_int	12.05	0.00
1999	cStem_CON	13.01	0.00
2001	null	0.00	0.21
2001	SHR	0.79	0.14
2001	ncon	0.81	0.14
2001	LS	1.21	0.11
2001	trtmt	1.24	0.11
2001	TS	1.74	0.09
2001	cStem	1.88	0.08
2001	cStem_shr	2.07	0.07
2001	cStem_shr_int	3.45	0.04
2001	cStem_CON	6.27	0.01
2001	TS_CON	6.28	0.01
2006	null	0.00	0.27
2006	trtmt	0.46	0.21
2006	ncon	1.89	0.11
2006	cStem	2.10	0.09
2006	SHR	2.22	0.09
2006	LS	2.26	0.09
2006	TS	2.32	0.08
2006	cStem_shr	4.55	0.03
2006	cStem_shr_int	5.29	0.02
2006	cStem_CON	6.72	0.01
2006	TS_CON	7.12	0.01
2007	trtmt	0.00	0.62
2007	null	3.04	0.14
2007	cStem	5.34	0.04
2007	TS	5.36	0.04
2007	ncon	5.44	0.04
2007	SHR	5.44	0.04
2007	LS	5.44	0.04
2007	cStem_CON	7.85	0.01
2007	cStem_shr	7.78	0.01
2007	cStem_shr_int	9.58	0.01
2007	TS_CON	9.78	0.00

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