1 **Bird-vegetation Associations in Thinned and Unthinned Young Douglas-fir Forests**

2 **Ten 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.

   Keywords: Bird-vegetation associations; young Douglas-fir forests; forest thinning; disturbance; response variability; long-term experiment.

1. Introduction

   Stable bird-vegetation associations are a key underlying assumption in wildlife management (Wiens, 2002; Ahlering, 2006) , species distribution modeling (Wiens, 2002) and models that project species responses to management. Many quantified bird-vegetation relationships derived from two- or three-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 two- or three-year long study represent overall, long-term relationships. Additionally, existing mid- and long-term (7-30 years)

65   studies of bird assemblages and bird-habitat associations (Wiens *et al.*, 1986; Winter *et*
66   *al.*, 2005; Rotenberry and Wiens, 2009) point to the dynamic nature of bird communities
67   over time even in systems without major disturbance events (e.g., Holmes and Sherry,
68   2001). The assumption that an ecosystem is in equilibrium is even less likely to be valid
69   in a system recently disturbed by management activities, such as thinning, because
70   vegetation can change and develop rapidly following disturbance (Davis and Puettmann,
71   2009).

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

82   Short and longer-term bird responses to forest thinning have been extensively
83   studied (Hansen *et al.*, 1995; Chambers *et al.*, 1999; Hayes *et al.*, 2003; Hagar *et al.*,
84   2004; Verschuyl *et al.*, 2011). Birds' responses to forest thinning are hypothesized to be
85   mediated by post-thinning changes in vegetation structure and composition and the
86   associated resources (Hagar and Friesen, 2009; Verschuyl *et al.*, 2011). An expansive
87   number of studies relate bird community composition to the structure and composition of
88   the vegetation community (MacArthur and MacArthur, 1961; Orians and Wittenberger,
89   1991; Cushman and McGarigal, 2004; Lee and Rotenberry, 2005). Yet the link between
90   forest birds and vegetation has rarely been tested over the long term. Understanding the
91   causative link between forest management practices and bird response is important per se
92   as young, structurally homogenous, Douglas-fir forests comprise a large percentage of
93   forests in the PNW (Bolsinger and Waddell, 1993; Kennedy and Spies, 2004), up to 40%
94   of forests in Western Oregon (Kennedy and Spies, 2004).

95   Our objectives in this study were to test the consistency (is bird species A always

96   associated with vegetation characteristic X) and strength (is the magnitude of the

97   relationship constant over time) of bird-vegetation associations in time. Therefore, we

98   advanced the following hypotheses:

99   Proximate Cue Hypothesis: If birds use vegetation characteristics as proximate

100   habitat quality cues, then bird-vegetation associations are expected to be apparent

101   immediately after forest thinning. In this case, vegetation variables associated with birds

102   and the strength of association are consistent in thinned and unthinned forests, assuming

103   an ideal free distribution (IFD; Fretwell and Lucas, 1969). Under assumptions of IFD,

104   bird density along a habitat gradient should be positively related to habitat quality and

105   consistent over time.

106   Decoupling Hypothesis: Birds may use several proximate cues to gather

107   information about habitat quality (Doligez *et al.*, 2003; Ahlering and Faaborg, 2006;

108   Betts *et al.*, 2008). Vegetation characteristics may serve as ultimate resources for

109   reproductive success (cover, nesting site, or nest material) or be associated with such

110   resources (e.g., by supporting an insect community upon which birds feed). A disturbance

111   event, such as forest thinning, may temporarily dissociate, or "decouple", the link

112   between proximate cues and ultimate resources (e.g., Knick and Rotenberry, 2000).

113   Therefore, we hypothesized that initially weak or unstable bird-vegetation associations

114   may strengthen and stabilize as time since thinning increases.

115   Population Size Hypothesis: Observed bird-vegetation associations and their

116   strength are likely to be influenced by demographic factors (McPeek *et al.*, 2001), social

117   interactions (e.g., Betts *et al.*, 2008), competition (MacArthur 1958) and scale of

118   observation (Orians and Wittenbrger, 1991). We did not have information on competition

119   and conspecific interactions, but attempted to account for variability in bird-vegetation

120   associations due to varying local population size. Bird-vegetation associations may not be

121   indicative of preference when habitat is saturated, e.g., under ideal despotic or ideal

122   preemptive distribution (Wiens, 1976; Rodenhouse *et al.*, 1997; McPeek *et al.*, 2001).

123   During high-population years high-quality habitats may become fully occupied, and the

124   remainder of individuals may be forced to settle in low-quality habitats. Thus, even low-

125   quality habitats will be occupied and, therefore, observed association with a given

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126   vegetation characteristic may weaken.   Hence, we hypothesized that bird-vegetation

127   associations would weaken in years of high (estimated) population numbers.

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129   **2. Methods**

130   **2.1 Area and Treatment Description**

131   We used previously collected bird (Hagar et al., 2004, Hagar and Friesen, 2009)

132   and vegetation (Davis *et al.,* 2007, Davis and Puettmann, 2009) data from the Young

133   Stand Thinning and Diversity Study. The YSTDS is a long-term silvicultural experiment

134   located on the west slopes of the Oregon Cascade Mountains in the Willamette National

135   Forest (Davis and Puettmann, 2009; Hagar and Friesen, 2009). The thinning study was

136   implemented as a randomized block experiment, with four replicate blocks. Blocks had

137   similar overstory composition, management history and size. At the beginning of the

138   study in 1994-1996 the blocks consisted of stands dominated by 40- to 50-year old

139   Douglas-fir, planted after regeneration harvest (Davis *et al.*, 2007).

140   Each block received four treatments, randomly assigned to stands within the

141   block. Stand areas ranged from 14 to 38 ha for thinned stands, and up to 53 ha for control

142   stands. The treatments were unthinned Control (CON) with approximately 700 trees per

143   hectare (tph), Heavy Thin (HT) with residual density of 200 tph, Light Thin (LT) with

144   250-300 tph and Light Thin with Gaps (LG) that included evenly-spaced (approximately

145   every 2 ha) 0.2 ha circular clearcut gaps in a matrix with an average density of 250-300

146   tph. Stands were thinned from below, with approximately even spacing, preferentially

147   leaving minority tree species to increase diversity. Treatments were implemented from

148   1995 to 1997 in a staggered manner (Davis and Puettmann, 2009).

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150   **2.2 Bird Data Summary**

151   Bird data were collected using standard point count methodology (Ralph et al.,

152   1995). Each surveying station was visited three or four times within a breeding season.

153   Data were collected during breeding seasons of 1998, 1999, 2001, 2006, and 2007. For

154   more details see Hagar et al. (2004). We summarized counts of birds by summing counts

155   for each species across repeated visits to each point count station within a year. Species

156   with distributions that had a large number of zero counts and a small range of non-zero

157 counts (≤ 3 detections per site per year) were collapsed to Bernoulli distribution (0's and

158 1's only). Distributions with a large range of non-zero counts (>3 detections per site per

159 year) were attributed to Poisson distribution. We used species occurrence (Bernoulli-

160 distributed counts) or abundance (Poisson-distributed counts) as dependent variable in

161 our models.

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163 **2.4 Summary of Vegetation Characteristics**

164 We used published species accounts (Marshall *et al.*, 2003) to select vegetation

165 characteristics out of the ones available in the YSTDS. We summarized covers of forbs

166 and low shrubs by averaging the sum of absolute covers of species attributed to the

167 respective structural groups (i.e., forbs and low shrubs, tall shrubs) across sixteen (16) 0.1

168 m^2 subplots within 0.1 ha vegetation sampling plots (Davis and Puettmann, 2009). The

169 sums of absolute vegetation covers in structural groups were used as explanatory

170 variables to predict bird occurrence and abundance. The tall shrub structural group

171 included coniferous and hardwood saplings; the low shrub structural group included

172 bracken and sword ferns (*Pteridium aquilinum*,and *Polystichum munitum)*. Each group

173 was summarized by adding intercept lengths of component species along two 14.5-m

174 sub-transects within each vegetation sampling plot (Davis and Puettmann, 2009), and

175 dividing the intercept sum by the total length of the two transects (sum of TS/(14.5m*2)

176 *100%). Total shrub cover was defined as a sum of low and tall shrub covers. We

177 calculated total tree density (dbh>8cm), including all tree species, as well as density of

178 broadleaf and coniferous trees separately. Tree densities were calculated for the plot and

179 then divided by plot area to provide density per hectare. Vegetation data were collected

180 in 1997, 1999, 2001 and 2006.

181 We estimated crown lengths and tree heights for all trees using relative

182 dominance (based on dbh distributions within the stand) and species-specific regression

183 coefficients from a limited crown length sample (Davis *et al*., 2007). Average canopy

184 closure and coefficient of variance of canopy closure were calculated from five canopy

185 closure measurements at each plot. Vegetation variables were normalized, i.e.,

186 distribution centered on zero and divided by its standard error. Thus, the unit of change

187   for vegetation characteristic is one standard error of the respective vegetation

188   characteristic distribution, not one percent of its cover.

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190   **2.5 Correspondence of Bird and Vegetation Data**

191   Locations of vegetation and bird samples did not coincide spatially in all stands.

192   To make the closest possible correspondence between the two types of data, we identified

193   the nearest vegetation plot for 58 point count stations using GPS coordinates of both plot

194   types. Vegetation data from the plots nearest to point count locations were used as

195   explanatory variables. The distance between point count stations and the closest

196   vegetation plot varied from 3 to 175 meters. Sixty nine percent (69 %) of vegetation plots

197   fell within 75 meters of point counts, and 93% of vegetation plots were within 100 meters

198   of point count plots. Given that territories of most passerines in our study range from 1 –

199   10 ha (Robbins *et al.*, 2001) we expect that vegetation plots were sufficiently close to

200   bird point count stations to represent at least a part of bird territory. Results of analyses

201   were not different when only data from the nearest (< 75 m) plots were used. Therefore,

202   we included all of the bird-vegetation pairs for analyses. In 1998 and 2007 bird data were

203   collected, but not vegetation data. For these years, we used vegetation data from 1999

204   and 2006 respectively. A total of 58 bird-vegetation plot pairs were used in the study.

205

206   **2.6 Statistical Analyses**

207   We examined relationships to vegetation characteristics for eight bird species that

208   were sufficiently common in our data (that is, we considered abundance data to be

209   robust): Swainson's thrush (*Catharus ustulatus*), MacGillivray's warbler (*Oporornis*

210   *tolmei*), Oregon junco (*Junco hyemalis*), Pacific wren (*Troglodytes troglodytes*), golden-

211   crowned kinglet (*Regulus satrapa*), Pacific-slope (*Empidonax difficilis*) and Hammond's

212   flycatchers (*Empidonax hammondii*), and hermit warbler (*Dendroica occidentalis*).

213   Additionally, these species are representative of a range of response patterns to thinning

214   treatments: positive (MacGillivray's warbler, Oregon junco, Hammond's flycatcher),

215   negative (hermit warbler, Pacific wren, Pacific-slope flycatcher) or changing direction

216   over time (Swainson's thrush, golden-crowned kinglet) (Hagar and Friesen, 2009; Hagar

217   *et al.*, 2004).

218   To test the Proximate Cue and the Decoupling Hypotheses we had to determine

219   which vegetation characteristics were important in explaining occurrence or abundance of

220   each species. To avoid missing important variables for each species we tested the

221   performance of several vegetation characteristics per species and used Akaike

222   Information Criterion corrected for small sample size (AICc) (Burnham and Anderson,

223   2002) to rank relative performance of models. We used expert opinion and published

224   species accounts (Marshall *et al.*, 2003) to determine vegetation characteristics likely to

225   be associated with each species. We then parameterized univariate and multivariate

226   models with vegetation characteristics as explanatory variables and bird occurrence or

227   abundance as dependent variables. Multivariate vegetation models were considered for

228   forest species associated with understory vegetation, Swainson's thrush and

229   MacGillvray's warbler. Additionally, multivariate models including vegetation variables

230   and indicator of treatment were used to test for a disturbance effect on bird-vegetation

231   associations. The models were limited to the vegetation characteristics available in the

232   vegetation data of the YSTDS. Some potentially important vegetation characteristics,

233   such as downed wood and snag size or snag density could not be used in this study and,

234   therefore, were not tested.

235   We were interested in whether the effect of thinning intensity (i.e., treatment type)

236   on birds was mediated by specific vegetation characteristics. If this was the case, we

237   expected that models based on specific vegetation characteristics would be more

238   parsimonious than treatment-based models, and, therefore, would receive greater support

239   from the data. Thus, for each bird species, we tested performance of at least four

240   vegetation-based models, one treatment-based model, and a null model (Table 1 and

241   Appendix A).

242   Both Poisson and logistic regressions require that bird observations at each point

243   count station are independent of those at all other stations. The nested design of the

244   original experiment (point count stations are nested within stands, and stands are nested

245   within   blocks) violated that assumption. We represented the lack of independence by

246   introducing random effects of stand and block into models. Abundance or occurrence of a

247   species within a year was modeled as a function of fixed effects of either a) vegetation

248   characteristics, or b) treatment type, or c) constant occurrence or abundance and random

249   effects of block and stand (with the exception of MacGillvray's warbler and Pacific-slope

250   flycatcher; models for these species included random effects of block only due to the

251   small range of variation in occurrence records across all point-count stations). We used

252   logistic and Poisson regressions to model occurrence and abundance, respectively.

253   Pearson residuals were examined for each model to ensure that model estimates were not

254   heavily influenced by a few unusual observations.

255   To examine stability of the effect of vegetation characteristics on bird response

256   we chose one vegetation-based model (most consistently-supported vegetation-based

257   model through the six years) per species and compared magnitude of effects of vegetation

258   characteristics on bird occurrence or abundance among years. Before examining

259   parameter estimates, we ensured adequate model fit by graphing residuals against fitted

260   values. No patterns indicating bias were detected. For logistic models, area under

261   receiver-operator curve (AUC) and calibration plots were examined to ensure adequate

262   model fit. Conventionally, AUC values over 0.7 are considered acceptable (Hosmer and

263   Lemeshow, 2000). All of AUC values were above 0.6 and the majority of AUC values

264   were above 0.8.

265   Confidence intervals are usually used to estimate the uncertainty associated with

266   an estimate as well as evaluate its statistical significance. There is no standard method for

267   computing confidence intervals for fixed effects in generalized mixed effects models due

268   to an uncertain number of degrees of freedom in such models (Nakagawa and Cuthill,

269   2007). Confidence intervals presented here were calculated using asymptotic theory

270   (assuming normal distribution of estimates) and are considered "approximate" because

271   that assumption is violated. In addition to calculating "approximate", 95% confidence

272   intervals (CI from here on) for estimates of the effect of vegetation characteristics we

273   used the drop-in-deviance test after Zuur et al.'s (2009) example to confirm non-zero

274   effect of vegetation characteristics. Approximate CI and the drop-in-deviance test results

275   were mostly in agreement (Table 2), therefore we refer to CI alone in text, although both

276   are presented in tables. Statistical analyses were carried out in R versions 2.12 and 2.13.1.

277

278   **2.7 *Post-hoc* Hypotheses**

279   High variability in the magnitude of response of 6 bird species to vegetation

280   characteristics (see Results) prompted us to develop post-hoc hypotheses addressing

281   potential reasons for the observed variation, in addition to Population Size Hypothesis,

282   which was advanced originally. We explored whether observed fluctuations in effect size

283   were related to population size (Population Size Hypothesis), time since thinning

284   (Disturbance Hypothesis) or change in limiting resources as vegetation characteristics

285   develop (Threshold Response Hypothesis).

286   The ratio of vegetation effect size to its standard error has been used previously as

287   an indicator of the strength of bird-vegetation associations (Betts *et al.*, 2010). We

288   assumed that local (observed in the study area only) abundance was an indicator of local

289   population size. We used prevalence, defined as percent of sites where a species was

290   detected across all point count sites, as an estimate of local abundance for Bernoulli-

291   distributed species and total number of detections divided by the number of site visits, for

292   Poisson-distributed species.

293   *Threshold Hypothesis:* Birds likely establish breeding territories along gradients

294   of the most limiting resources (Hilden, 1965). As vegetation develops after thinning,

295   availability of resources may change. If an initially limiting resource reaches levels at

296   which it is no longer limiting, birds are expected to no longer respond to further increases

297   in the resource; i.e., they reach a response "threshold" (Betts et al., 2007). Under this

298   hypothesis, initial positive response to increase in a limiting vegetation characteristic will

299   become zero when it becomes sufficiently abundant. Both understory and overstory

300   vegetation characteristics undergo a rapid development following forest thinning. Tall

301   shrubs are initially damaged but eventually recover after thinning (Davis and Puettmann,

302   2009; Wilson *et al.*, 2009). Threshold hypothesis was suggested by a decreasing response

303   of Swainson's thrush, a known shrub associate (Marshall *et al*., 2003; Ellis *et al*., 2012),

304   to tall shrub cover. We used segmented regression, and R 2.13.1 package *segmented*

305   (Muggeo, 2008), to test for presence of thresholds in response of Swainson's thrush to

306   increases in tall shrub cover. Starting values for threshold value search were selected

307   based on visual examination of the plot of Swainson's thrush abundance against tall

308   shrub cover.

309   *Disturbance Hypothesis:* Forest thinning removed trees and introduced forest

310   floor disturbance associated with harvesting operations. Stands that received Heavy Thin

311   treatment were disturbed more than Control and Light Thin stands (Allen, 1998). Soon

312   after thinning, tree density may be negatively correlated with resources that reflect the

313   intensity of disturbance. This correlation may dissipate with time since thinning as

314   secondary succession occurs and ephemeral resources associated with disturbance

315   diminish. To test this hypothesis we regressed the strength of association between Oregon

316   junco abundance and tree density against time and assessed the strength of response in

317   thinned-only and control-only stands.

318

319   **2.8 Accounting for Imperfect Detection**

320   Failure to account for imperfect detection has been shown to bias occurrence

321   records and ultimately study conclusions (MacKenzie *et al.*, 2002). We therefore needed

322   to account for both imperfect detection (MacKenzie *et al.*, 2002) and the lack of

323   independence between sampling stations located in the same stand and block. A mixed

324   effects occupancy model (Kéry, 2010) is the ideal method for accounting for both issues

325   simultaneously. However, a small sample size limited the number of parameters we could

326   estimate. Theoretically, with a large number of visits to an occupied point count station

327   within a breeding season, the probability of detecting a species at the point count stations

328   at least once is expected to approach one. We collapsed detection histories across all

329   within-season visits to calculate average 'naïve' occurrence rate, i.e., when not

330   accounting for imperfect detection, and compared it to occupancy estimates that

331   accounted for imperfect detection. For three out of four species for which we modeled

332   occurrence, the two estimates of occupancy were within 6% of each other. Occupancy

333   estimates for golden-crowned kinglet differed, on average, by 25% between the two

334   estimation methods (Yegorova unpublished data). Based on these findings, we decided

335   that not accounting for the violation of independence among the sampling points could

336   more critically bias our results than not accounting for imperfect detection.

337

338   **3. Results**

339   **3.1 Consistency of Bird-Vegetation Associations over Time**

340   For 6 bird species, association with specific vegetation characteristics or

341   combinations of vegetation characteristics was inconsistent across years as evidenced by

342   changes in the relative AICc rankings of vegetation-based models. Only two out of eight

343   species, Pacific-slope flycatcher and MacGillvray's warbler, had a consistent ranking of

344   vegetation models among years (Appendix A).

345   The treatment-based model (Table 1) was a reliable predictor of bird occurrence

346   or abundance for 4 species: Hammond's flycatcher (AICc $wt_{trtmt'97-'99,'07}>0.9$), Pacific

347   wren (AICc $wt_{trtmt'97-'07}>0.9$), MacGillivray's warbler (AICc $wt_{trtmt'98,'06,'07}>0.5$), and

348   Oregon junco (AICc $wt_{trtmt'97-'99,'06-'07}>0.7$)(Appendix A).

349

350   **3.2 Magnitudes of Bird-Vegetation Associations**

351   As expected, response to vegetation characteristics varied substantially across the

352   eight species. Within species, the relationship between bird response and vegetation

353   characteristics remained in a consistent direction (i.e., positive or negative) for all species

354   across years. However, consistent with the AICc results, the magnitude of bird-vegetation

355   association, expressed by the slope of logistic or Poisson regression curve, varied greatly

356   from year to year (Figure 1). Statistical significance of response magnitude varied from

357   year to year for most species. In some years CI's for the respective estimates overlapped

358   one, indicating no statistically significant response across years, however in other years

359   we found the response to be statistically significant (Table 2). The degree of annual

360   fluctuation in the magnitude was highly variable across species and years. However,

361   confidence intervals for the estimates overlapped, suggesting that the estimates were not

362   statistically different from each other despite large variation in size (Table 2). For each

363   species, one of three general patterns of variation emerged: 1) A vegetation variable

364   remained an important predictor of bird response across years, but the magnitude of its

365   association with bird response varied among years; 2) The magnitude of bird-vegetation

366   associations gradually declined over time; and 3) None of the tested vegetation

367   characteristics were associated with bird response.

368

369   *3.2.1 Bird-vegetation associations with non-directional year-to-year variation in*
370   *magnitude*

371   The occurrence of three species (MacGillivray's warbler, Pacific-slope flycatcher,
372   and Hammond's flycatcher) varied along gradients of vegetation characteristics, but the
373   magnitude of the effect of the vegetation characteristics on occurrence of these species
374   changed across years, without an apparent trend (Figure 1.A-C, graph for Pacific-slope
375   flycatcher not shown).
376   Occurrence of MacGillivray's warbler was negatively associated with tree density
377   and positively associated with shrub cover, after accounting for the effect of tree density.
378   The negative effect of tree density on occurrence varied in magnitude over the 10-year
379   study but CI's never overlapped one (Table 2.A). Mean odds of occurrence for
380   MacGillivray's warbler as a function of tree density varied by a factor of ten (10) among
381   years (from 0.01 in1998 to 0.13 in 2007) (Table 2.A, Figure 1.A). The positive effect of
382   the size of the shrub cover on occurrence varied in magnitude among years and was not
383   always statistically different from one (Table 2.B, Figure 1.B).
384   Pacific-slope flycatcher was positively associated with density of large (>20cm
385   dbh) trees (Table 2.C). The magnitude of response varied from 1.84 in 1998 to 2.84 in
386   2007, by a factor of 1.54. Hammond's flycatcher was negatively associated with conifer
387   density (Table 2.D), with mean odds of occurrence approaching one at tree densities near
388   zero (Figure 2.C), suggesting species' preference for small (0.1 ha) forest openings or
389   vicinities of small forest openings. The magnitude of response remained relatively
390   consistent (0.94 to 0.99) for this species, however it was only statistically significant in
391   the first year after thinning (Table 2.D).
392
393   *3.2.2 Bird-vegetation associations with decreasing magnitude of over time*

394   The magnitude of bird-vegetation associations of three species (Swainson's
395   thrush, Oregon junco, and golden-crowned kinglet) decreased over time (Figures. 1.D-F).
396   Abundance of Swainson's thrush was positively associated with tall shrub cover only in
397   the first three years post-thinning (Figure 1.D, Table 2.E). This apparent decrease over

398   time in the association of Swainson's thrush abundance with tall shrub cover was

399   statistically significant (slope = - 0.06, p=0.04, adjusted R^2= 0.60).

400   Abundance of Oregon junco was negatively associated with total tree density but

401   the magnitude of the association decreased over time (slope=0.25, p=0.049, adjusted

402   R^2=0.58). Note that the slope is positive because the association between Oregon Junco

403   and tree density became less negative (Figure. 1.E, Table 2.G).

404   Occurrence of golden-crowned kinglet varied strongly along the conifer density

405   gradient in the first year of study (1997) with nearly zero odds of occurring near small

406   gaps (0 tph) and nearly certain presence near densest forest patches (Figure 1.F).

407   However, in all subsequent years this species was almost uniformly distributed along the

408   conifer density gradient (Figure 1.F, Table 2.G).

409

410   *3.2.3 No detected response to examined vegetation characteristics*

411   We did not detect a response to any of the tested vegetation characteristics for two

412   species, Pacific wren and hermit warbler (Appendix A). However, Pacific wren was

413   strongly associated with treatment type in all six sampling periods: $\Delta AICc_{treatment}$= 0,

414     $\Delta AICc_{-next\_best\_model} \geq 3$ for all six years (see Appendix A). The effect of treatment,

415   however, was not correlated with tree density: CI's for estimates of the stem density

416   effect overlap zero for all six years (Table 2.H). While average tree densities varied

417   drastically among treatment types, plot-level tree densities varied widely within each

418   treatment. Thus, there was a tree density overlap at the plot level among treatment types,

419   which explains the seemingly contradictory strong treatment effect but a lack of tree

420   density effect. Pacific wrens were less abundant in treated stands compared to Control

421   stands. Ratio of abundance in Heavy Thin stands compared to Controls in 1997 was 0.6,

422   CI (0.43, 0.98) and decreased in subsequent years.

423   The abundance of hermit warbler also did not correlate consistently with any of

424   the vegetation characteristics tested nor with any of the treatment types. The null model

425   was always within two units of the minimum AICc score (Appendix A), suggesting that

426   either tested vegetation characteristics were irrelevant to this species or the species was

427   ubiquitous.

428

429   *3.3 Technical Sources of Variation*

430   To ensure that the observed variation in the magnitude of vegetation effects was

431   not a statistical artifact of poorly fitting models we calculated AUC scores for the four

432   logistic models fitted to data of each breeding season and to data collapsed across six

433   breeding seasons. AUC scores remained consistently high for two species, MacGillvray's

434   warbler and Hammond's flycatcher ($AUC_{'97\text{-}'07} > 0.85$, $AUC_{cumulative} > 0.85$ for both

435   species). AUC scores fluctuated among years for Pacific-slope flycatcher

436   ($0.67 < AUC < 0.86$, $AUC_{cumulative} > 0.73$) and golden-crowned kinglet ($0.57 < AUC < 0.91$,

437     $AUC_{cumulative} > 0.67$). Thus, three out of four models had at least "acceptable" (≥ 0.7)

438   discrimination power (Hosmer and Lemeshow, 2000).

439   Overall, mean abundance or mean odds of occurrence of each of the six species

440   for which we found bird-vegetation associations at least doubled along the examined

441   gradient of vegetation characteristics (Figures 1.A-F). Additionally, the magnitude of

442   vegetation effect was mostly statistically different from one (Table 1). Therefore, we

443   consider observed association between vegetation and bird responses biologically

444   significant.

445

446   **3.4 *Post-hoc* Results**

447   The Population Size hypothesis received only weak support. Strength of bird-

448   vegetation associations was weakly (not statistically significant for any given species)

449   related to estimated local abundance (Tables 3 and 4) and did not relate to time since

450   thinning (data not shown) for either "rare" (<150 detections/year), or "common" (>150

451   detections/year) species when each species was examined individually (except for

452   Oregon junco). When pooled, there was a significant negative relationship between

453   strength of association and local abundance for common species (slope= -0.01, p<

454   0.002, $R^2_{adj} = 0.19$) driven by among-species differences (Figure 3). No statistically

455   significant association was found for rare species when they were pooled (slope =-0.01,

456   p=0.36) (Figure 3).

457   The Threshold hypothesis was supported for Swainson's thrush. The model

458   containing a threshold term received a considerably greater support than the model

459   without one ($AIC_{no\_threshold}$ - $AIC_{threshold}$ =13.4). Segmented regression suggested a

460 threshold at 9% cover of tall shrubs, CI (5.5, 13.9). See Figure 4 for an illustration.

461 Abundance of Swainson's thrush increased with greater tall shrub cover (factor of 1.07,

462 CI (1.01, 1.14) for every 1% tall shrub increase) up to the threshold value and was flat for

463 additional tall shrub cover increases above the threshold value (factor of 1.01, CI (1.001,

464 1.14) for every 1% tall shrub increase).

465   The disturbance hypothesis was supported for Oregon junco. As predicted, the

466 abundance of this species did not respond to variation in tree density in Control stands;

467 CI for the effect of tree density in Control stands included zero in all six seasons (CI's not

468 shown). Strength of association (ratio of vegetation effect estimate to its standard error)

469 between Oregon junco abundance and conifer density decreased over time (analysis

470 included data from both treated and control stands): slope = -0.25, p=0.049, R^2_{adj}= 0.58.

471

472 **4. Discussion**

473   Few studies have quantified bird-vegetation relationships in the long term and

474 examined their consistency over time. The studies that have done so were primarily

475 focused on shrub-steppe or grassland systems (Wiens *et al.*, 1986; Wiens, 2002; Winter *et*

476 *al.*, 2005; Rotenberry and Wiens, 2009). To our knowledge, this is one of the first long-

477 term manipulative studies to document variation in bird-vegetation relationships over

478 time in a forest system.

479   The assumption of tight bird-habitat relationships is often the basis of wildlife

480 management and conservation (Wiens, 2002; Ahlering and Faaborg, 2006). The variation

481 in strength of association between vegetation variables and bird response we documented

482 over more than ten years has important implications for natural resource management and

483 planning. Short term studies (Hansen *et al.*, 1995; Guenette and Villard, 2005; Betts *et*

484 *al.*, 2006; Hewson *et al.*, 2011) may capture only a small part of the range of bird

485 responses to vegetation characteristics and thus create an impression of stable

486 relationships between birds and vegetation. However, explicitly including variability in

487 bird-vegetation relationships may be crucial when projecting species responses to

488 management scenarios and evaluating short-term effects of management.

489   Despite variation in the magnitude of estimates, the direction of relationships

490 between vegetation variables and bird responses remained consistent over time for six out

491   of eight species in this study. We caution against the dangers of interpreting weak (not

492   statistically different from zero) bird-vegetation relationships in a short-term study. Our

493   results show that birds that do not have a strong response to vegetation characteristics one

494   year may respond strongly (statistically and biologically significantly) to vegetation

495   characteristics in the following year or the year before. (e.g., MagGillvray's warbler's

496   response to shrub cover). Absence of response in the short-term, therefore, is not

497   necessarily representative of the bird-vegetation associations over the longer-term, and

498   should be interpreted conservatively.

499   We suggest that the lack of detected response of hermit warbler and Pacific wren

500   to any of examined vegetation characteristics may be due to either ubiquitous presence of

501   these species in forested environments or lack of information on pertinent vegetation

502   characteristics. Pacific wrens are known to nest in downed wood and forage in dead

503   foliage near forest floor (Hejl *et al.*, 2002). Quantitative information on these

504   characteristics could not be considered for this study. This is one possible reason why we

505   did not find a strong effect of a specific vegetation characteristic on Pacific wren's

506   abundance.

507   Observed variation in association between vegetation characteristics and the six

508   bird species for which we detected a response raised the question of underlying causes.

509   We ruled out three potential methodological causes: inappropriate vegetation variables,

510   poor model fit and poor data quality. We believe vegetation variables were ecologically

511   significant to birds because 1) they were consistent with published natural history

512   accounts, and 2) our vegetation-based models performed better than null models

513   (Appendix A). We ruled out poor data quality as a cause of variation because bird and

514   vegetation data were collected consistently, according to standardized protocols, by

515   trained observers. Below we discuss possible ecological causes of variation in the

516   strength of bird-vegetation relationships.

517

518   **4.1 Local Abundance Effects on Bird-Vegetation Associations**

519   We found that strength of bird-vegetation associations within a species was only

520   weakly related to local abundance of that species, providing little support for ideal free

521   (IFD), ideal preemptive (IPD) and ideal despotic distribution scenarios (IDD). For rare

522 species (Bernoulli-distributed), perhaps, local abundances were not large enough to
523 saturate available habitat. When habitat is unsaturated we could expect to observe a
524 pattern consistent with IFD, high odds of occurrence at high-quality sites and low odds at
525 poor-quality sites (Fretwell and Lucas, 1969). However, at low abundance local
526 stochastic processes (predation, local-scale disturbance etc.) as well as demographic
527 stochasticity, inherent to a population, have a greater effect on the overall population size
528 fluctuation than in a medium or large population (Shaffer, 1981).
529   For each common (Poisson-distributed) species, the strength of vegetation effect
530 decreased slightly, but not significantly, with species abundance. Within the common
531 species group, more abundant species had weaker associations with vegetation
532 characteristics than the less abundant species (Figure 2). This negative relationship
533 between response size and local abundance suggests a decreasing affinity for specific
534 vegetation features as bird abundance increases. The weak relationship between bird-
535 vegetation associations and local abundance *within* species suggests that 1) abundance
536 fluctuations are too small to produce a negative effect on the strength of bird-vegetation
537 associations, or 2) available habitat was saturated even at the lowest population size and
538 that bird-vegetation associations within species were at their lowest value and could not
539 erode any further.
540

541 **4.2 Vegetation Threshold Hypothesis**

542   Variation in strength of association between vegetation and Swainson's thrush
543 abundance was consistent with the Threshold Hypothesis. Thresholds in population
544 processes in relation to amount of habitat at landscape scales are predicted by theoretical
545 studies (e.g., Andren, 1999; Fahrig, 2002; McPherson and Jetz, 2007). Recent studies
546 document thresholds in bird occurrence and abundance in relation to vegetation
547 characteristics in PNW forest birds (Betts *et al.*, 2010; Ellis and Betts, 2011). Swainson's
548 thrush has been found to be strongly associated with hardwood vegetation (Ellis *et al.*,
549 2012, Marshall *et al.*, 2003) at stand scales. Thus, a positive association of Swainson's
550 thrush with tall shrubs, a structural group that includes mainly broadleaf tall shrubs and
551 young hardwoods, supports previous findings. However, we cannot rule out that this

552 insectivorous species was not responding to changes in arthropod community or another

553 resource affected by thinning as we did not measure arthropod density in this study.

554

555 **4.3 Thinning-associated Disturbance Effects**

556   We did not find support for the Decoupling Hypothesis. Bird-vegetation

557 relationships were present in the first year of available data for six of the eight species

558 and relationships did not strengthen with time since thinning, contrary to predictions of

559 the Decoupling Hypothesis. However, most stands were thinned in 1995 and 1996 (for

560 details see Beggs, 2004) but sampled for birds in 1997 for the first time, making detection

561 of decoupling between vegetation characteristics and proximate cues potentially difficult.

562   Two species showed evidence of responding to disturbance-related resources, but

563 not in the expected direction. Oregon junco's response was consistent with the species

564 tracking ephemeral, disturbance-related, resources. Golden-crowned kinglets avoided

565 vicinities of low-density forest areas immediately after forest thinning, but returned to

566 approximately homogeneous use of the forest, including areas of low tree density, after

567 the first year. The forest dwelling species examined in this study appear to respond

568 rapidly to vegetation changes or vegetation-associated resources, compared to shrub-

569 steppe birds where time-lags were found in response to habitat alteration (Wiens, 1986;

570 Knick and Rotenberry, 2000).

571

572 **4.4 Treatment Type as Habitat Descriptor**

573   Previous studies documented responses of individual species to thinning in young

574 Douglas-fir stands (Hayes *et al.*, 2003; Hagar *et al.*, 2004), and hypothesized that

575 treatment effects on bird abundances were mediated by vegetation developments after

576 thinning (Verschuyl *et al.*, 2011). We also found evidence of bird responses to vegetation

577 characteristics that were influenced by thinning. However, our results show that, thinning

578 intensity was a more reliable predictor of bird response than vegetation characteristics.

579   Treatment type is a more complex variable than individual vegetation

580 characteristics because it integrates vertical and horizontal vegetation structure at a larger

581 spatial scale than vegetation plots. The spatial scale of treatments (> 15 ha) approximates

582 multiple territories of the species we examined, and may be more relevant to patch-level

583 habitat-selection (sensu Johnson, 1980) than plot-scale vegetation characteristics. These

584 reasons may account for the superior AICc performance of treatment models compared to

585 models with individual vegetation characteristics.

586   It is possible that univariate and bivariate vegetation-based models were too

587 simple to adequately represent multi-dimensional habitat quality for the species we

588 examined. However, simple vegetation descriptors have been used successfully in the

589 past to explain bird abundance. Hansen *et al.* (1995) found statistically significant habitat

590 functions for bird species abundance using tree density measurements by dbh classes.

591 They found that most of their bird species, including the eight species in the present

592 study, responded to total density of trees ≥10cm dbh. However, tree density may

593 represent more associated information about habitat in forest stands without recent

594 disturbances, and less in recently thinned forests where understory and overstory

595 vegetation are rapidly developing and relationships between tree density and other

596 vegetation characteristics are changing. Thus, the dynamic relationships between

597 vegetation characteristics and birds in recently thinned forests may explain the relatively

598 poor performance of univariate vegetation models compared to the treatment-based

599 model in our study. The ranges of stand-level tree densities and successional stages in

600 YSTDS were narrow compared to those examined in Hansen *et al*. (1995), reiterating the

601 importance of context (spatial and successional in this case) for interpreting and applying

602 study results.

603

604 **4.5 Issues of Spatial Scale**

605   Dependence of result on observation scale is a classic idea in ecology (Wiens,

606 1989). The relatively high degree of variability of small-scale bird-vegetation

607 associations in comparison to stable associations with treatment type may be an example

608 of this principle. Both vegetation characteristics and bird responses were measured at

609 small spatial scales. Small-scale sampling revealed the variation in local vegetation

610 characteristics (tree density, shrub cover etc.) as well as birds' response to small-scale

611 variation in vegetation characteristics that could not be detected at stand scales.

612   Habitat selection by birds is a multi-scale process (e.g., Johnson, 1980; Orians and

613 Wittenberger, 1991). Both local vegetation characteristics and landscape-level

614 composition have been found important in explaining forest bird community composition

615 in the PNW (Cushman and McGarigal, 2004). We did not account for effects of

616 landscape composition on the local-level species response, implicitly assuming that

617 landscape composition was similar for all examined stands. The forest stands examined

618 in this study were located in the relatively homogeneous matrix of unthinned, young

619 Douglas-forest stands when the study was established. Over the study period, the

620 proportion of thinned stands increased dramatically across the surrounding landscapes

621 (Klaus Puettmann – personal communication), which may have contributed to the

622 amplifying or dampening trends we observed in bird-vegetation associations in some

623 species.

624

625

626 **5. Conclusions and Management implications**

627 Our results should be interpreted as a cautionary note. Temporal variability in bird

628 associations means that important bird-vegetation correlations may be missed in short-

629 term studies. Therefore, inferences and projections made with short-term information

630 should be made cautiously. Efforts to model future distributions or population viability

631 (e.g., Larson et al. 2004) would be most reliable if information about inter-annual

632 variation in the magnitude of bird response to vegetation characteristics is incorporated.

633 Unfortunately, such long-term data are only rarely available for such projection models

634 (e.g., Bird et al. 2012, Gasner et al. 2012). Our study highlights the additional uncertainty

635 of interpreting projections based on short-term studies.

636 As federal forest managers in the PNW are promoting biodiversity and native

637 species habitat in forests previously managed for timber production , detailed information

638 about mechanisms of species response to management is necessary. Our study shows that

639 in the predominantly forested landscape of the west-slope of the Cascade Mountains in

640 Oregon, bird species quickly respond to changes in vegetation characteristics associated

641 with forest thinning. The temporal consistency of qualitative bird responses to thinning,

642 together with biologically significant response of birds to gradients in vegetation

643 characteristics indicates that vegetation characteristics examined here could be used as

644 general guidelines for species-specific habitat management in young Douglas-fir forests

645   in the PNW. For example, our study suggests that maintaining patches of forest with tall

646   shrub cover ≥9% may maximize local abundance of the Swainson's thrush. However, the

647   magnitude of bird response should be assessed for several years after management

648   implementation to account for the variability observed in this study.

649   The success of treatment type in predicting bird response suggests that the spatial

650   scale of thinning treatment and its vegetation 'gestalt' are ecologically relevant to

651   breeding forest birds. Assuming bird abundance reflects habitat quality, which is not

652   always the case (Van Horne, 1983), forest thinning at spatial scales of 10's of hectares

653   may be an effective technique for creating habitat for some of the species associated with

654   well-developed understory vegetation, such as MacGillivray's warbler, or aerial

655   insectivores associated with small forest gaps, such as Hammond's flycatcher.

656   Overall, our results suggest, that long-term monitoring of management effects is

657   crucial despite the associated practical and financial difficulties. Our study highlights an

658   important reason for long-term monitoring of the effects of management efforts. Given

659   the variability in associations between birds and vegetation that we documented, an

660   accumulation of evidence from several long-term studies is needed to establish which

661   vegetation characteristics are most important to each species, and to identify thresholds in

662   levels of vegetation variables to which birds respond. Further quantification of

663   uncertainty in bird-vegetation relationships may allow managers and conservation

664   planners to better assess trade-offs among management effects on multiple resources, and

665   therefore make better management and conservation decisions.

666

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676

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