

AN ABSTRACT OF THE THESIS OF

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Title: Bird-Vegetation Relationships Across Ten Years After Thinning in Young Thinned and Unthinned Douglas-fir Forests.

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Bird-vegetation associations are a base for bird conservation and management, as well as for predictions of the effects of resource management and climate change on wildlife populations. A recent shift in forest management priorities from timber production to native species' habitat conservation on federal lands has emphasized the need to understand the mechanisms underlying the effects of vegetation management on wildlife. The assumption of strong bird-vegetation relationships is rarely tested for forest birds, especially at large temporal extents, which are more likely to reveal instabilities in bird-vegetation relationships than short-term studies. This study aimed to quantify bird-vegetation relationships and investigate their strength in young thinned and unthinned Douglas-fir forest stands over ten to years post thinning. Additionally, this study investigated whether disturbance associated with forest thinning decoupled bird-vegetation relationships in the thinned and unthinned stands. I used abundance or occurrence data for eight bird species collected at 58 point count surveys, conducted during six breeding seasons over ten years following forest thinning. I obtained detailed local-scale vegetation characteristics associated with bird sampling points and modeled bird occurrence or abundance as a function of vegetation characteristics. Vegetation characteristics explaining individual species occurrence or abundance varied among species and among years for any given species. Six out of eight species showed responses to examined vegetation characteristics. For three out

of six species, the effects of vegetation characteristics on bird occurrence or abundance remained consistently positive or negative over time. For the other three species the absolute effect of vegetation decreased over time to that of not statistically different from zero. The estimates of vegetation effects on bird response varied in size among years, though they were not statistically different among years. Magnitude of vegetation effect on bird occurrence or abundance did not increase with time, nor was it related to species prevalence or abundance. I found evidence of a response threshold for one species, Swainson's thrush. I suggest that changing abundance of resources, associated with thinning disturbance, demographic stochasticity associated with small population sizes, as well as large-scale demographic processes and possibly life history traits of examined species, mediate the strength of local-level bird-vegetation associations. Variability of vegetation effects on bird occurrence or abundance over time suggests a greater uncertainty of results of vegetation-related wildlife management efforts than has previously been suggested by short-term studies. Therefore, incorporation of the uncertainty of bird-vegetation relationships into predictive models and continued long-term monitoring of species response to management may be crucial for future successful and effective management decisions.

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Bird-Vegetation Relationships Across Ten Years After Thinning in Young Thinned
and Unthinned Douglas-fir Forests

by
Svetlana Yegorova

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes the release of my thesis to any reader upon request.

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Bird-vegetation relationships in young thinned and unthinned Douglas-fir forests over ten years after thinning.

CHAPTER 1 – INTRODUCTION

Historical Context

Timber extraction and forest management in the Pacific Northwest (PNW) in the 20th century lead to a dramatic decline of old growth and structurally complex mature forests (Bolsinger and Waddell, 1993; Kennedy and Spies, 2004). After harvesting these stands were replaced by intensively managed young Douglas-fir forests. With the passing of the Northwest Forest Plan in 1994, management priorities on federal lands shifted from timber production to managing forests for attributes of mature and old growth forest and habitat provision for native species (Thomas *et al.*, 2006). Forests that were managed with timber production as primary purpose often lacked structural and compositional characteristics of unmanaged forests of the same age, such as large living trees, large standing and fallen dead trees, diverse woody and herbaceous species composition, vertical and horizontal structural heterogeneity (Franklin *et al.*, 1981; Spies and Franklin, 1991; Swanson *et al.*, 2010). All of these characteristics are considered important for native wildlife species (Carey, 2003). Present-day young forests typically lack those structural characteristics and these forests may not be on a trajectory to create those characteristics in the near future. Although some current day PNW old growth forests (west Cascades forests in southern Washington) may have regenerated at high tree density following stand-replacing disturbances (Winter *et al.*, 2002), high-density origins of old-growth may have been an exception in some areas. Tappeiner *et al.* (1997) reported that old growth in the Oregon Coast Range commonly regenerated at much lower tree density and over longer time periods, compared to that of most young Douglas-fir stands (Tappeiner *et al.*, 1997). Low tree density and heterogeneity of growing environments promoted rapid growth and tree size differentiation characteristic of some mature and old growth forests (Tappeiner *et al.*, 1997). These findings generated interest in

investigating thinning as a management technique to encourage development of mature forest characteristics in the young, structurally simple forests.

The Young Stands Thinning and Diversity Study (YSTDS) was initiated in 1994 as a long-term study to investigate effects of thinning on development of mature forest characteristics (Davis *et al.*, 2007; Davis and Puettmann, 2009). Thinning is a tool that silviculturists traditionally use to reduce inter-tree competition during the stem exclusion stage of managed forest development (*sensu* Oliver and Larson, 1990) with the goal of accelerating growth rates of the remaining trees in order to increase future revenues (Tappeiner *et al.*, 2007). The goal of YSTDS is to test the effectiveness of thinning as an ecological restoration tool. Separate studies were initiated to address the effects of forest thinning on bird community composition and individual species response (Hagar *et al.*, 2004; Hagar and Friesen, 2009), as well as responses of arthropod communities (Yi, 2003), ground-dwelling vertebrates (Garman *et al.*, 2000; Manning *et al.*, 2012) and fungi (Pilz *et al.*, 2006).

Several Neotropical-migrant bird species that breed in North America have experienced population declines over the past forty years (Robbins *et al.*, 1989; Sauer and Droege, 1992). Shifts in landscape-level forest composition on these species' breeding grounds in the second half of the 20th century are hypothesized to be an important driver behind long-term bird population trends (Sauer and Droege, 1992; Betts, 2010). Forest thinning has the potential to restore structurally heterogeneous forests that have been diminishing in the PNW forest landscape. Managing forest structure and composition, which constitutes wildlife habitat, is the primary tool natural resource professionals have for managing wildlife. This study addresses a part of the broader question: is stand-level management of vegetation structure and composition sufficient to re-create a wildlife community of a mature forest?

Bird Response to Thinning Treatments

Both short- and relatively longer-term bird responses to forest thinning, and other forest management activities, have been studied in the PNW (Hansen *et al.*,

1995; Hagar *et al.*, 1996; Chambers *et al.*, 1999; Hayes *et al.*, 2003; Hagar *et al.*, 2004; Hagar and Friesen, 2009; Verschuyt *et al.*, 2011). Bird species have individual response patterns to thinning and some species change their response over time (Hagar and Friesen, 2009; Bayne and Nielsen, 2011). Bird responses to thinning are hypothesized to be mediated by thinning-related changes in vegetation structure and composition during the post-thinning vegetation development (Hagar and Friesen, 2009; Verschuyt *et al.*, 2011). Indeed, vegetation in thinned stands went through a rapid change in the first ten years after thinning. The canopy was opened by harvesting and then gradually closed as remaining trees expanded their crowns (Davis *et al.*, 2007). Shrub layer initially decreased due to thinning-associated mechanical damage, but low-stature shrubs recovered to initial cover levels within five to seven years after thinning, and tall shrubs did so approximately ten years after thinning and are hypothesized to benefit from thinning in the long run (Ares *et al.*, 2009; Davis and Puettmann, 2009; Wilson *et al.*, 2009). Herbaceous layers undergo compositional change resulting in increased species diversity.

The hypothesis that vegetation mediates effects of forest thinning on birds is based on the expansive number of studies relating bird community composition to characteristics of the associated vegetation community. Vegetation structure and composition at local (within home range) and landscape (> 0.5 km radius around the home range) levels have long been associated with bird species diversity and distribution patterns (MacArthur and MacArthur, 1961; James and Wamer, 1982; Orians and Wittenberger, 1991; Holmes and Sherry, 2001; Cushman and McGarigal, 2004; Lee and Rotenberry, 2005; Hewson *et al.*, 2011). As reviewed above, forest thinning has complex effects on vegetation and effects of thinning may vary with pre-thinning vegetation composition and thinning intensity (Wilson *et al.*, 2009). Relating bird response to specific vegetation characteristics may elucidate the mechanism of bird response to forest thinning and allow natural resource managers to ‘fine tune’ treatments to provide specific vegetation structures associated with bird habitat.

Most of the studies of bird-vegetation relationships are based on short-term observations (one to three years). Few long-term studies examining bird-vegetation relationships exist – they are difficult to implement financially and logistically. However, short-term studies may bias our understanding of the studied system. Wiens (1981) pointed out, short-term studies provide a ‘snapshot’ of a dynamic ecosystem and inferences made on results of short-term studies, implicitly assume that the ecosystem is in equilibrium. 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 fulfilled in a system recently disturbed by management (see the above description of vegetation developments in the first 10 years after thinning). Information about bird-vegetation relationships is fundamental to species-distribution modeling, wildlife conservation and natural resource management (Wiens, 2002; Ahlering and Faaborg, 2006). Recent modeling studies project species population change in the next 160 years with only two (Wintle *et al.*, 2005) or four (Larson *et al.*, 2004) years of bird-habitat association data. Both studies put a large effort into quantifying uncertainty of environmental stability and point out that their results hinge on how well habitat function was described (Wintle *et al.*, 2005). Variation in magnitude of vegetation effect on birds may have large effects on model predictions. Therefore, investigating possible fluctuations in the strength of bird-vegetation relationships in the long term is of great practical, as well as theoretical, interest.

The vast part of the PNW forested landscape has been managed in the past, primarily for timber production. As management priorities have recently shifted to include promotion of native species’ habitat, there is need for information about species’ response to restoration-related management activities and the mechanisms mediating that response. The temporal resolution (approximately ten years) and the management-associated disturbance of the YSTDS allows for two unique

opportunities to test: 1) the assumption of close bird-vegetation relationships in forest birds and 2) mechanisms by which forest management and the associated disturbances affect birds.

Hypotheses

It is assumed that when selecting habitat birds use proximate cues to assess availability of the resources required for reproductive success (ultimate resources from here on). Theoretically, the ultimate resources and their proximate cues should be tightly linked. However they may become decoupled if the ultimate resource itself does not serve as the proximate cue (Hilden, 1965). If birds use vegetation characteristics as the proximate cue of habitat quality, then I predict that associations between birds and vegetation characteristics will be apparent immediately after forest thinning and that the strength of those associations (size of vegetation effect on bird occurrence or abundance) will remain unchanging over time (Proximate cue Hypothesis).

Theoretical and empirical studies suggest that birds may use a variety of cues, in addition to vegetation cues, to select breeding sites (Doligez *et al.*, 2003; Ahlering and Faaborg, 2006; Betts *et al.*, 2008). Previous breeding success, social information (i.e., information about other individuals' breeding success), and density of conspecific individuals are cues that previously were found to be important in habitat selection of some bird species. Thinning introduced disturbance into a forest through tree removal and ground disturbance associated with harvesting operations. Disturbance could decouple correspondence between proximate cues and ultimate resources (e.g., Knick and Rotenberry, 2000). However, proximate cues may realign with the ultimate resources as time since disturbance progresses. I hypothesize that if weak bird-vegetation associations immediately after thinning are due to decoupling of proximate cues and ultimate resources, then the strength of bird-vegetation associations (see defined for Proximate cue Hypothesis) will increase over time as ultimate resources and proximate cues realign (Decoupling Hypothesis).

Habitat selection refers to the preference or choice that an animal has or makes, respectively. However, habitat preference is not as easily quantifiable as habitat use because one does not always get what one wants and hence, what one gets is not necessarily what one prefers. Unless an observer has full information about resources or habitat available to the observed individual, inferences about habitat preference from habitat use are uncertain (Johnson, 1980). Thus, habitat use is modified by the habitat that is available. If population size exceeds the number of high-quality breeding sites, some individuals will “spill over” into poor-quality breeding sites due to unavailability of sites in high-quality habitat patches (e.g., McPeck *et al.*, 2001). The “spill-over” may lead to an apparent homogeneous distribution of individuals across habitat or vegetation gradient (e.g., Wiens, 1976). Observed correlation between a bird species with a specific vegetation characteristic may weaken when populations exceed the size at which all sites with preferred vegetation characteristics are occupied. I hypothesize that the strength of bird-vegetation associations will be modified by population size – it will be weaker in years that the population size is more numerous than in years with small population size (Population Hypothesis).

My study offers a unique opportunity to examine whether the size of vegetation effect on birds changes (stability from here on) over ten to twelve years of vegetation development in thinned and unthinned 50-year old Douglas-fir forests. My objectives were to 1) find and quantify species-specific bird-vegetation relationships and 2) examine the stability of these relationships, if found, over the period of ten years. I did so by examining local scale, third-order *sensu* Johnson (1980), breeding-season use of habitat by eight bird species, including resident and neo-tropical migrant species.

CHAPTER 2 – METHODS

Area and Treatment Description

The study was conducted on the west slopes of the Oregon Cascade Mountains in the Willamette National Forest, between the elevations of 400 and 900 meters. The forest type is in the western hemlock zone (sensu Franklin and Dyrness, 1973). Douglas-fir (*Pseudotsuga menziesii*) was the dominant tree in the overstory; western hemlock and western redcedar were also common. Broadleaf species such as bigleaf maple (*Acer macrophyllum*) and giant chinquapin (*Chrysolepis chrysophylla*) comprised a minor component of the overstory. Common understory species in the stands included sword fern (*Polysticum munitum*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), Oregon grape (*Mahonia nervosa*) and Pacific rhododendron (*Rhododendron macrophyllum*) (Hagar *et al.*, 2004).

Mean annual precipitation in the area is 230 cm, with the majority of it falling between October and June. Average annual temperature is 10.1 °C. Soils are generally well-developed, ranging from thin shotty loams or clay loams to thin gravelly loams. (Davis *et al.*, 2007). Wildfire was the major natural landscape-level disturbance in the central-western Oregon Cascades, with fire rotation interval of 95 to 149 years (Morrison and Swanson, 1990).

The thinning study was implemented as a randomized block experiment, with four replicate blocks. Blocks had similar overstory composition, management history and size (>56 ha). The blocks consisted of 40-50 year old Douglas-fir dominated forest stands that were 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, and up to 53 ha for control stands, with the average size of control stand slightly above that of treated 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) with 250-300 tph average density that included evenly-

spaced (approximately every 2 ha) 0.2 ha circular clearcut gaps. Pre-thinning densities varied by block, see Davis *et al.* (2007) for details. Stands were thinned from below, i.e., cutting preference was given to small-diameter trees, with approximately even spacing, preferentially leaving minority tree species. Treatments were implemented from 1995 to 1997 in a staggered manner. For more details see Davis *et al.*, 2007.

Bird Sampling and Data Summary

I used data from bird surveys designed and conducted by other investigators (see Hagar, 2004). Post-treatment bird surveys were conducted during six breeding seasons (1997, 1998, 1999, 2001, 2006, and 2007). Three to five point count stations were located in each stand, depending on stand's size and geometry. Stations were spaced at least 150 meters away from each other and at least 75 meters from a road buffer, riparian buffer or forest edge. Each station was visited three times per breeding season in 1997 and 1998, and four times in other years. Standard point-count methodology was used (Ralph *et al.*, 1995). Species and distance to each detected bird were recorded during a 10-minute count period. Each point count station received at least 30 (in 1997 and 1998) or 40 (1999, 2001, 2006, 2007) minutes of observation per season. All surveys were conducted May to late June, from 30 minutes before sunrise to four hours after sunrise. No surveys were conducted during rain or strong winds.

To summarize bird count data, I collapsed counts across all visits to a station within a year, graphed the count distribution for each species and visually inspected distribution graphs. Distributions with a large number of zero counts and a small range of non-zero counts (1-3) were collapsed to Bernoulli distribution (0's and 1's only). Distributions with a large range of non-zero counts were attributed to Poisson distribution. I used species occurrence (Bernoulli-distributed counts) or abundance (Poisson-distributed counts) as the dependent variable in my models.

Vegetation Sampling

I used data from detailed vegetation surveys designed and conducted by other investigators (see Davis *et al.*, 2007; Davis and Puettmann, 2009). The year of the first post-treatment vegetation survey varied among blocks, depending on the year of thinning completion (1995-1997), three subsequent surveys were conducted in 1999, 2001, and 2006.

Stands were sampled with 0.1 ha (17.5m² radius) permanent plots randomly located along systematically laid out transects. Each stand was sampled with approximately 25 plots, so that approximately 7.5% area of each stand was sampled (Davis *et al.*, 2007). Stands with LG treatment were sampled with an equal number of plots in gaps, gap edges and the matrix between gaps (see Davis and Puettmann (2009) for further details).

Each tree within the 0.1 ha plot was identified to species, and its diameter at breast height (dbh) was measured. Five overstory canopy closure measurements were taken with “moosehorn” densitometer (Cook *et al.*, 1995), one at plot center and four in the cardinal directions, 10.25m away from plot center. Canopy lengths and heights were measured for a random subsample of trees in the study in 1999 only.

Two parallel 14.5-m transects were placed in the main plot, eight 0.1m² subplots were placed along each transect, for a total of 16 subplots per 0.1 ha plot (Fig 1). Absolute cover estimates of all understory species, excluding tall shrubs and saplings, were recorded in each subplot. Additionally, the percentage of mineral soil, and litter were determined. Tall shrubs and saplings were sampled by recording the length of the 14.5-m transects intercepted by shrub crowns.

Summary of Vegetation Characteristics

To summarize covers of forbs and low shrubs I averaged the sum of absolute covers of species attributed to the respective structural groups (i.e., forbs and low shrubs, tall shrubs) across the sixteen (16) 0.1 m² subplots within the vegetation

sampling plot (0.1 ha plot). The sum of absolute vegetation covers in structural groups was used as an explanatory variable to predict bird occurrence and abundance (see below). Tall shrub structural group was summarized by adding intercept lengths along the two 14.5m sub-transects within the vegetation sampling plot, dividing the intercept sum by the total length of the two transects (sum of TS/(14.5m*2) *100%). Tall shrub structural group included coniferous and hardwood saplings and low shrub structural group included braken and sword ferns (*Pteridium aquilinum*, and *Polystichum munitum*). Total shrub cover is a sum of low and tall shrub covers. Total tree count (dbh>8cm), including all tree species, as well as broadleaf and coniferous trees separately, was calculated for the plot and then divided by plot area to provide density per hectare.

I estimated crown lengths and tree heights for all trees using the tree's relative dominance (based on dbh distributions within the stand) and species-specific regression coefficients derived by Davis *et al.* (2007) from a limited crown length sample (see Vegetation Sampling section). Average canopy closure and coefficient of variance of canopy closure were calculated from five canopy closure measurements at each plot. Large variation in explanatory variables tended to slow down statistical software. Therefore, most vegetation variables were normalized, i.e., distribution centered on zero and divided by its standard deviation. Thus, the unit of change for vegetation characteristic is one standard error of the respective vegetation characteristic distribution, not one percent of its cover.

Correspondence of Bird and Vegetation Data

Vegetation and bird responses to thinning were not sampled at exactly the same spatial locations within each stand. To make the closest possible correspondence between the two types of data, I identified the closest vegetation plot for each point count station using GPS coordinates of both plot types. Vegetation data were used to explain bird count data in the nearest plots. The distance between point count stations

and the closest vegetation plot varied from 3 to 175 meters. Sixty nine percent (69 %) of vegetation plots fell within 75 meters of point counts, and 93% of vegetation plots were within 100 meters of point count plots. I assumed that stands were sufficiently homogeneous to result in adequate representation of vegetation characteristics near point counts despite wide spread of distances between point count and associated vegetation plots. In 1998 and 2007 bird data were collected, but not vegetation data. For these years, I used vegetation data from 1999 and 2006 respectively.

Statistical Analyses

Eight bird species were used in this study: Swainson's thrush (*Catharus ustulatus*), MacGillivray's warbler (*Oporornis tolmiei*), dark-eyed 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*). These species were selected from the full list of birds detected in the Young Stands Thinning and Diversity Study as representative of different response patterns to thinning treatments (Hagar *et al.*, 2004).

To test the Proximate Cue and the Decoupling Hypotheses I had to determine which vegetation characteristics were important in explaining occurrence or abundance of each species. To avoid missing important variable for each species I tested performance of several vegetation characteristics per species. I used the species accounts in Birds of Oregon (Marshall *et al.*, 2003) to determine vegetation characteristics likely to be associated with each species in the study. I 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 understory vegetation, Swainson's thrush and MacGillivray's warbler. Additionally, multivariate models including vegetation variables and indicator of treatment (CON

=1, else =0) were used to test for the disturbance effect on bird-vegetation associations. The models were limited to the vegetation characteristics available in the vegetation data of the YSTDS. Some important vegetation characteristics, such as downed wood and snag size or snag density were not available and, therefore, were not tested.

I was interested to see if the effect of thinning intensity (i.e., treatment type) on birds was mediated by specific vegetation characteristics. If it were, I 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. Each bird-specific model set consisted of at least four vegetation-based models, one treatment-based model and a null model, which served as a baseline reference. See Appendix A for the list of models tested for each species, and Table 2.1 for model explanations.

Both Poisson and logistic regressions require that bird observations at each point count station are independent of those at all other stations. Nested design of the experiment (point count stations are nested within stands, and stands are nested within blocks), violated that assumption. I represented the lack of independence by introducing random effects of stand and block into my 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 MacGillvray's warbler and Pacific-slope flycatcher; models for these species included random effects of block only due to the lack of variation in the dataset). I used logistic and Poisson regressions to model occurrence and abundance, respectively.

The general vegetation-based, treatment-based and null models were as follows:

$$\text{Vegetation: } Y_{ijk} = \beta_0 + \beta_1 V_{1ijk} + \beta_2 V_{2ijk} + \dots + \beta_n V_{nijk} + \eta_j + \lambda_k + \epsilon_{ijk}$$

$$\text{Treatment: } Y_{ijk} = \beta_{CON} + \beta_{HT} * HT + \beta_{LT} * LT + \beta_{LG} * LG + \eta_j + \lambda_k + \epsilon_{ijk}$$

$$\text{Null: } Y_{ijk} = \beta_{\text{constant}} + \eta_j + \lambda_k + \varepsilon_{ijk}$$

Where

Y_{ijk} represents average number of detections (Poisson species) or average occurrence probability (Bernoulli species) at site i in stand j and block k ,

$$i = 1, \dots, 58, j = 1, \dots, 16, k = 1, \dots, 4.$$

$V_{1ijk} \dots V_{nijk}$, represent the value of respective vegetation characteristics site i in stand j and block k . $i = 1, \dots, 58, j = 1, \dots, 16, k = 1, \dots, 4$.

$$\eta_j \text{ represents random effect of stand } j. j = 1, \dots, 16. \eta_j \sim N(0, \sigma_{\eta}^2),$$

$$\text{Cov}(\eta_j, \eta_j) = 0.$$

λ_k represents random effect of block k . $k = 1, \dots, 4$. $\lambda_k \sim N(0, \sigma_{\lambda}^2)$, $\text{Cov}(\lambda_k, \lambda_{k'}) = 0$

ε_{ijk} represents random variability of plot i in stand j and block k . $\varepsilon_{ijk} \sim N(0, \sigma_{\varepsilon}^2)$, and $\text{Cov}(\varepsilon_{ijk}, \varepsilon_{ijk'}) = 0$.

β_0 represents mean number of detections per site and $\beta_1, \beta_2, \dots, \beta_n$ represent coefficients to the corresponding vegetation variables. β_{con} , β_{HT} , β_{LT} and β_{LG} etc., represent coefficients for treatment types, β_{constant} represents the average species abundance or occurrence across all stands.

HT, LT and LG are indicator variables for respective treatment types.

For each year, I ranked models in each species-specific model set using Akaike Information Criterion corrected for small sample size (AICc). The model with the lowest AICc score was considered to be best-supported in the set (Burnham and Anderson, 2004) and models within two ΔAICc units of the best supported model were considered to be equally supported. Pearson residuals were examined for each model to ensure that model estimates were not heavily influenced by few unusual observations.

To examine stability of the effect of vegetation characteristics on bird occurrence or abundance I chose one vegetation-based model (most consistently-supported vegetation-based model) per species and compared magnitude of effects of

vegetation characteristics on bird occurrence or abundance among years. Before examining parameter estimates, I 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. All of the AUC values were above 0.6 and the majority of the AUC values were above 0.8. Therefore, fitted models were considered adequate.

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 I used the drop-in-deviance test after Zuur et al.’s (2009) example to confirm non-zero effect of vegetation characteristics. Approximate confidence intervals and the drop-in-deviance test results were in agreement, therefore I will refer to CI’s alone in text, although both are presented in tables. Statistical analyses were carried out in R versions 2.12 and 2.13.1.

Accounting for Imperfect Detection

Highly mobile and furtive organisms, such as birds, are not always detected, even if they are present at a site. Failure to account for imperfect detection will bias occurrence record and ultimately the study conclusions (MacKenzie *et al.*, 2002). Statistical methods have been developed to account for imperfect detection and changes in detectability with site characteristics (MacKenzie *et al.*, 2002). In addition to imperfect detection I had to account for the lack of independence between sampling stations located in the same stand and block. A mixed effects occupancy model (Kéry,

2010) would account for both issues. However, estimating occupancy and detection as well as fixed and random effects of vegetation characteristics or treatment would lead to a very low ratio of observations (58) to the number of estimated coefficients (maximum of 9). I implemented two of the simplest mixed effects occupancy models on MacGillivray's Warbler and Swainson's thrush data: a null model and a model with a single vegetation parameter. I found that the lack of variation in the data and the large number of required estimates led to nonsensical estimates of parameters. 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. When detection histories were collapsed across all within-season visits, average 'naïve' occurrence rate, i.e., when not accounting for imperfect detection, was only slightly below the estimate given by a statistical model that accounted for imperfect detection (R 2.12 package *unmarked*). Based on these findings, I decided that not accounting for the violation of independence among the sampling points could more critically bias my results than not accounting for imperfect detection.

Table 2.1. List of All Tested Models and Model Meanings

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 +Conifer_density*Control
	cStem_CRD	~ cStem+CRD+cStem*CRD
	cStem_shr	~ cStem + Shub cover
	cStem_shr_int	~ cStem + Shub cover+cStem*Shrub_cover
	cStem_TS	~ cStem+ Tall Shrubs
	forb	~ Forb cover
	GAP	~ Gap presence within 100m
	LGcon	~ Large conifer density (>20cm DBH)
	LGcon_TS	~Large conifer density+Tall shrub
	LS	~Low Shrub Cover
	LS_stemCount	~Low Shrub Cover + Tree Density
	lshr	~ Low Shrub Cover
	minSoil	~ Percent Mineral Soil
	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

CHAPTER 3 – RESULTS

Consistency of Vegetation Effect Over Time

Effects of specific vegetation characteristics or combinations of characteristics on bird occurrence or abundance were generally 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 MacGillivray's warbler, had a consistent ranking of vegetation models among years (see Appendix A).

The treatment-based model (see Table 2.1 and Methods for explanation) was a reliable predictor of bird occurrence or abundance for Hammond's flycatcher (AICc $w_{\text{treatment}'97-'99, '07} > 0.9$), Pacific wren (AICc $w_{\text{treatment}'97-'07} > 0.9$), MacGillivray's warbler (AICc $w_{\text{treatment}'98, '06, '07} > 0.5$), and dark-eyed junco (AICc $w_{\text{treatment}'97-'99, '06-'07} > 0.7$). The treatment-based model emerged most frequently as the best-supported model for these species (see Appendix A).

Effect of Vegetation Characteristics on Bird Occurrence or Abundance

As expected, species varied widely in the vegetation characteristics that best predicted their distributions. For all bird species, I examined magnitudes of vegetation effect from one vegetation-based model (see Methods for selection criteria). The direction of the relationship between various vegetation characteristics and bird abundance or occurrence remained consistent for all species across years. However, the magnitude of vegetation effects on bird occurrence or abundance, expressed by the slope of logistic or Poisson regression curve, varied greatly from year to year, which is consistent with the AICc results. The degree of annual fluctuation in the magnitude of the effects was highly variable across species and year. However, estimates were not statistically different from each other, with the exception of stem density effect on MacGillivray's Warbler occurrence (see Table 3.1), due to wide confidence intervals. Three general patterns of variation emerged: 1) Vegetation remained an important predictor of bird occurrence or abundance across years, but the magnitude of its effect varied among years; 2) The magnitude of vegetation effect gradually declined over

time; and 3) None of the tested vegetation characteristics had an effect on species occurrence or abundance.

Consistent vegetation effect, with non-directional year-to-year variation

Occurrence of three species (MacGillivray's warbler, Pacific-slope flycatcher, and Hammond's flycatcher) varied along gradients of vegetation characteristics, but the size of the effect of the vegetation characteristics on occurrence of these species changed from year to year, without an apparent trend. Effect of vegetation characteristics on bird occurrence or abundance may become greater or lesser in sampling period T+1 than in T. See Figs 3.1A-3.1F for a visual example of variation in bird-vegetation associations.

Occurrence of MacGillivray's warbler was negatively associated with tree density and positively associated with shrub cover. The negative effect of tree density on occurrence varied in magnitude over the 10 year study but CI's never overlapped zero (Table 3.1). Mean odds of occurrence for MacGillivray's warbler varied by a factor of ten (10) among years (from 0.01 in 1998 to 0.13 in 2007). Despite large variation, MacGillivray's warbler response to tree density remained highly negative across years – mean odds of occurrence diminish by a factor of 100 to a factor of, approximately, ten (10) for every additional 300 trees per hectare (Table 3.1, Fig 3.1A). Note that tree density, and other vegetation characteristics, were measured at the scale of 0.1 ha vegetation plot and tree density and cover values were scaled up to per hectare base. While highest average tree density in the study was 750 tph (in Control stands), local densities, measured at 0.1 ha plot level, ranged from 0 tph to an equivalent of 1600 tph.

Mean odds of MacGillivray's warbler occurrence increased with greater shrub cover, after accounting for the effect of tree density. Size of the shrub cover effect varied among years and was not always statistically different from zero (Table 3.1, Fig 3.1A).

Pacific-slope flycatcher was positively associated with density of large (>20cm dbh) trees (Table 3.2). Hammond's flycatcher was negatively associated with conifer density (Table 3.3), with mean odds of occurrence approaching one at tree densities near zero (Fig 3.1D), suggesting species' preference for small (0.1 ha) forest openings or vicinities of small forest openings (distances between bird and vegetation plots were variable).

Decreasing vegetation effect over time

Effects of vegetation characteristics on abundance of two species, Swainson's thrush, dark-eyed junco, and occurrence of golden-crowned kinglet decreased over time (Figs. 3.1C, 3.1E, 3.1F).

Abundance of Swainson's thrush was positively associated with tall shrub cover in the first three years post-thinning (1997-1999) and did not respond to tall shrub cover in 2001, 2006 and 2007 (Fig. 3.1C, Fig 3.2, Table 3.4). This apparent decrease in the effect of tall shrub cover on Swainson's thrush abundance was statistically significant (slope = - 0.06, $p=0.04$, adjusted $R^2=0.60$).

Abundance of dark-eyed junco was negatively associated with total tree density but the magnitude of the effect decreased over time (slope=0.25, $p=0.049$, adjusted $R^2=0.58$). The slope of the negative relationship between tree density and dark-eyed junco abundance diminished, hence slope for the regression on diminishing magnitude of effect is positive (Fig. 3.1E, Table 3.6).

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. 3.1F). However, in the subsequent years (1998, 1999, 2001, 2006, and 2007) this species was almost uniformly distributed along the conifer density gradient (Table 3.5).

Lack of detected vegetation effect

Two species, Pacific wren and hermit warbler did not respond to any of the tested vegetation characteristics (Appendix A). However, Pacific wren responded strongly to treatment type in all six sampling periods: $\Delta\text{AICc}_{\text{treatment}} = 0$, $\Delta\text{AICc}_{\text{next_best_model}} \geq 3$ for all six years (see Appendix A). The effect of treatment, however, was not explained by tree density effect: CI's for estimates of the stem density effect overlap zero for all six years (Table 7). Pacific wrens were less abundant in treated stands compared to Control stands. Ratio of abundance in Heavy Thin stands compared to Control in 1997 was 0.6, CI (0.43, 0.98), in. This ratio decreased even further in the subsequent years. Pacific wrens are known to nest in downed wood and forage in dead foliage. Quantitative information on these characteristics was not available for this study, which is one of the possible reasons why I did not find a strong effect of a specific vegetation characteristic on Pacific wren's abundance.

The abundance of hermit warbler also did not correlate consistently with any of the vegetation characteristics tested nor with any of the treatment types (Appendix A, Table 7). 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.

Experimental disturbance of the forest stands in the study offered the opportunity to test whether management-related disturbance produces a decoupling between ultimate resources (Decoupling Hypothesis), which may be expressed by or correlated with vegetation characteristics, and proximate habitat cues. I found bird-vegetation associations in the first sampling year after forest thinning (as well as subsequent years) for six out of eight examined species, suggesting that decoupling between ultimate resources and proximate cues was unlikely. 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 potential decoupling between vegetation characteristics and proximate cues difficult.

To ensure that the observed variation in the magnitude of vegetation effects was not a statistical artifact of poorly fitting models I 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 ($AUC_{0.97-1.07} > 0.85$, $AUC_{cumulative} > 0.85$ for both species). AUC scores fluctuated among years for Pacific-slope flycatcher ($0.67 < AUC < 0.86$, $AUC_{cumulative} > 0.73$) and golden-crowned kinglet ($0.57 < AUC < 0.91$, $AUC_{cumulative} > 0.67$). Thus three out of four models had at least "acceptable" discrimination power (Hosmer and Lemeshow, 2000).

I considered bird response to vegetation characteristics biologically meaningful, if mean abundance of a species changed at least by one bird, or mean odds of occurrence at least doubled, along the gradient of a vegetation characteristic. Overall, mean abundance or mean odds of occurrence of each of the six species at least doubled along the examined gradient of vegetation characteristics (see Figs. 3.1A-3.1F). Additionally, the magnitude of vegetation effect was mostly statistically different from zero (Tables 3.1-3.6). Therefore, I consider observed effect of vegetation on bird occurrence or abundance biologically significant.

Post-hoc Hypotheses

The high amount of inter-annual variation in effect sizes of vegetation characteristics on bird occurrence or abundance across all species prompted me to develop post-hoc hypotheses addressing potential reasons for the observed variation. I explored whether 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).

Population Size Hypothesis: Under ideal despotic distribution (IDD) (sensu Fretwell, 1972) individuals will settle the highest-quality habitat first. If populations are large enough to fill all of high-quality habitat, individuals settle in low-quality

territories (McPeck *et al.*, 2001). Therefore, bird density gradients or occurrence patterns may not be representative of the habitat quality gradients at high population density. Under this hypothesis, the strength of bird-vegetation associations varies with conspecific population size; at low population numbers only the best sites are occupied and bird density matches habitat quality gradient. However, at high population numbers, density ceases to reflect the habitat quality gradient because individuals spill over into low quality habitat.

The ratio of vegetation effect size to its standard error has been used previously as an indicator of the strength of bird-vegetation associations (Betts *et al.*, 2010). I assumed that abundance was an indicator of population size and used prevalence, defined as percent of sites where a species was detected across all point count sites, as an estimate of abundance for Bernoulli-distributed species and total number of detections divided by the number of site visits, for Poisson-distributed species. If population size influenced the strength of bird-vegetation relationships as a result of IDD, I expected to observe a negative relationship between the strength of the bird-vegetation association and abundance. To test the population size hypothesis, I regressed the strength of bird-vegetation associations (see definition above) on indices of abundance. I performed this regression for 1) individual species and for 2) pooled Bernoulli and 3) pooled Poisson species.

Threshold Hypothesis: Several types of resources are required for reproductive success and survival, the ultimate measures of habitat quality. Birds likely establish breeding territories along the gradient of the most limiting resource (Hilden, 1965). If the initially limiting resource develops and reaches levels at which it is no longer limiting, birds will no longer respond to the increase in the resource, i.e., they reach a response “threshold” (Betts *et al.* 2007). Under this hypothesis, initial positive response to increase in limiting vegetation characteristic will become zero when these vegetation characteristics become sufficiently abundant.

Abundance data of Swainson's thrush, a known shrub associate (Marshall *et al.*, 2003; Ellis *et al. in review*), exhibited a pattern of declining response to tall shrub

cover over time. Tall shrubs were initially damaged by thinning operations, but gradually recovered in thinned stands (Davis and Puettmann, 2009). Declining response of Swainson's thrush to tall shrub cover coincided with an increase of tall shrub cover in thinned stands. If declining response to tall shrub cover was due to resource saturation, I expected to see a threshold in abundance response to increase of tall shrub cover.

I 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.

Disturbance Hypothesis: Forest thinning not only removed trees, but 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). Thus, initially, tree density may be negatively correlated with the intensity of disturbance. As time since thinning progresses, disturbance effects may dampen as secondary succession occurs and disturbance effects disappear. Dark-eyed junco is a forest-floor associated species, whose response to tree density decreased over time (Fig. 3.1E). This response pattern suggests that dark-eyed junco was responding to an ephemeral resource associated with disturbance. Under this hypothesis the strength of association between dark-eyed junco's abundance and tree density should decrease over time. I also expected a lack of tree density effect on dark-eyed junco's abundance in Control stands, since those stands were not disturbed. To test these predictions I regressed the ratio of the estimate to its standard error against the sequential number of sampling period (one through six) and examined the effect of tree density on dark-eyed junco's abundance in Control stands only.

Post-hoc Results

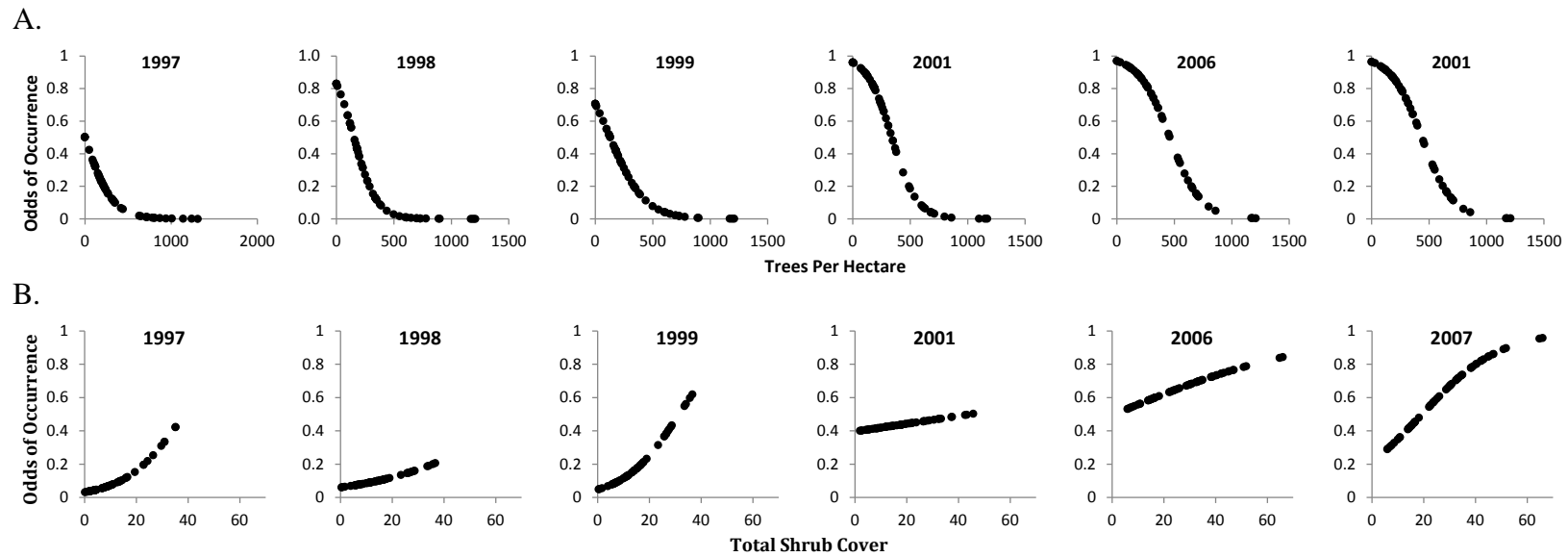
The Population Size hypothesis received only weak support. Strength of bird-vegetation associations was weakly (not statistically significant for any given species) related to species prevalence (Table 8 and 9) and did not relate to time since thinning (data not shown) for both “rare” (<150 detections/year), and “common” (>150 detections/year) species when each species was examined individually. When pooled, there was a significant negative relationship between strength of association and relative abundance for common species (slope = -0.01, $p < 0.002$, $R_{adj}^2 = 0.19$) driven by among-species differences (Fig. 3.3). No statistically significant association was found for rare species when they were pooled (slope = -0.01, $p = 0.36$) (Fig 3.4).

The Threshold hypothesis was supported for Swainson’s thrush ($AIC_{no_threshold} - AIC_{threshold} = 13.4$). Segmented regression suggested a threshold at 9 % cover of tall shrubs, CI (5.5, 13.9). Abundance of Swainson’s thrush increased with higher tall shrub cover up to the threshold value and was flat for additional tall shrub cover increases above the threshold value. The mean number of Swainson’s thrush detections increased by a factor of 1.07, CI (1.01, 1.14), for every 1% increase in tall shrub cover. Above the 9 % threshold, average probability of detecting additional individuals increased by a factor of 1.001, CI (0.995, 1.018) (Fig. 3.5). This response pattern is indicative of resource saturation.

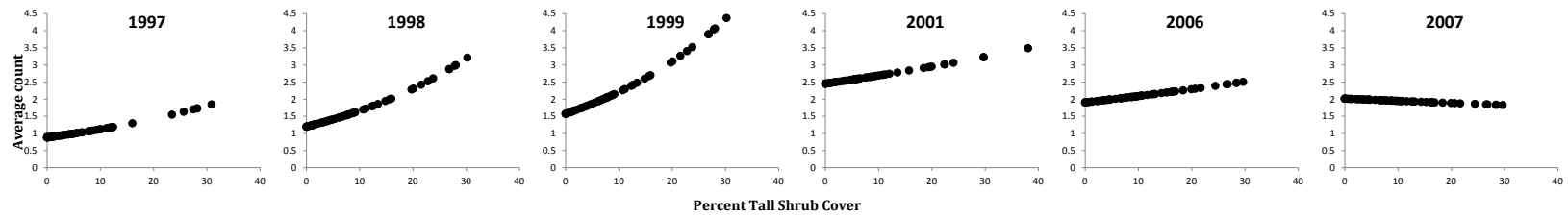
The disturbance hypothesis was supported for dark-eyed junco. Abundance of this species did not respond to variation in tree density in Control stands. Confidence intervals for the effect of tree density in Control stands included zero in all six seasons (CI’s not shown). Strength of association (ratio of vegetation effect estimate to its standard error) between dark-eyed junco abundance and conifer density decreased over time (analysis included data from both treated and control stands): slope = -0.25, $p = 0.049$, $R_{adj}^2 = 0.58$ (Fig 3.6). Strength tree density effect also increased with the overall abundance of dark-eyed junco’s (slope = -0.03, $p = 0.08$, $R_{adj}^2 = 0.47$), contradictory to the trends predicted by IFD, IDD or IPD hypotheses. However, this

trend could be an artifact of a decrease in dark-eyed junco's abundance over time. Thus, both strength of tree density effect and dark-eyed junco's abundance decreased with time (cor= -0.72). The two trends are not necessarily related, suggesting that positive relationship between abundance and strength of tree density effect may be spurious.

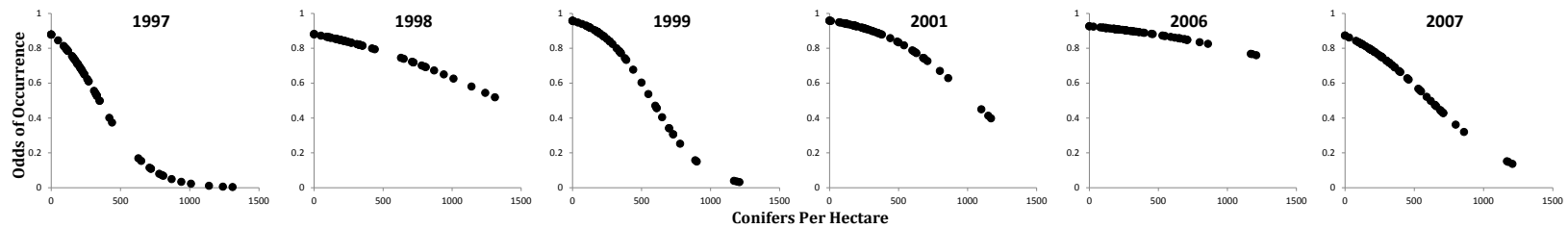
Figure 3.1 Relationships between vegetation gradients and species occurrence or abundance. Note different independent variables on the x-axes. (A) MacGillivray's warbler and tree density (after accounting for the effect of shrubs) and (B) MacGillivray's warbler and shrub cover (after accounting for the effects of tree density); (C) Swainson's thrush and tall shrub cover; (D) Hammond's flycatcher and conifer density; (E) dark-eyed junco and tree density; (F) golden-crowned kinglet and conifer density.



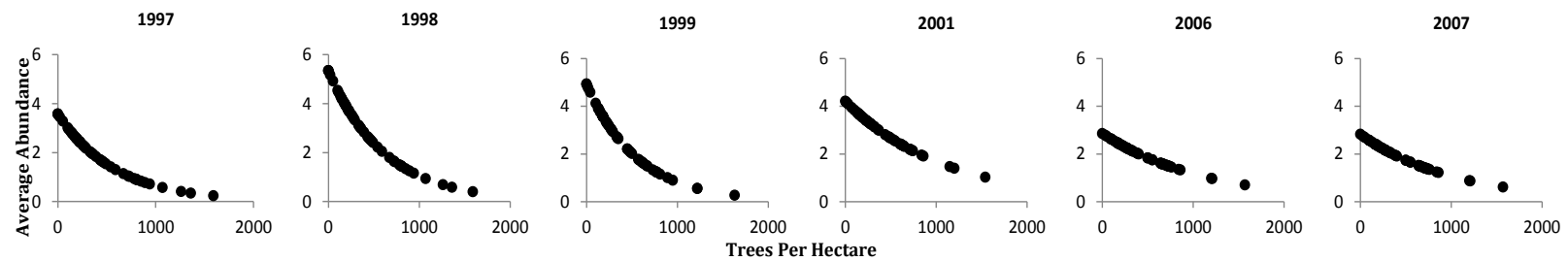
C.



D.



E.



F.

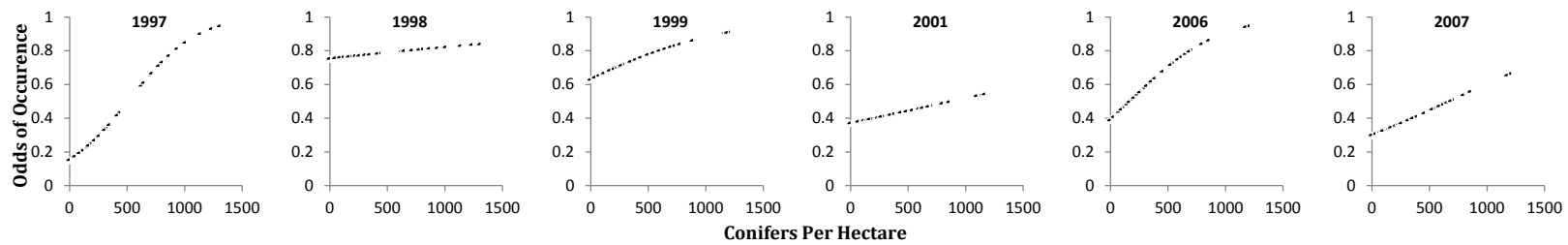


Figure 3.2. Average sizes and confidence intervals for the multiplicative effect of tall shrubs (log (increase in abundance) per one standard deviation increase in tall shrub cover) on abundance of Swainson's thrush.

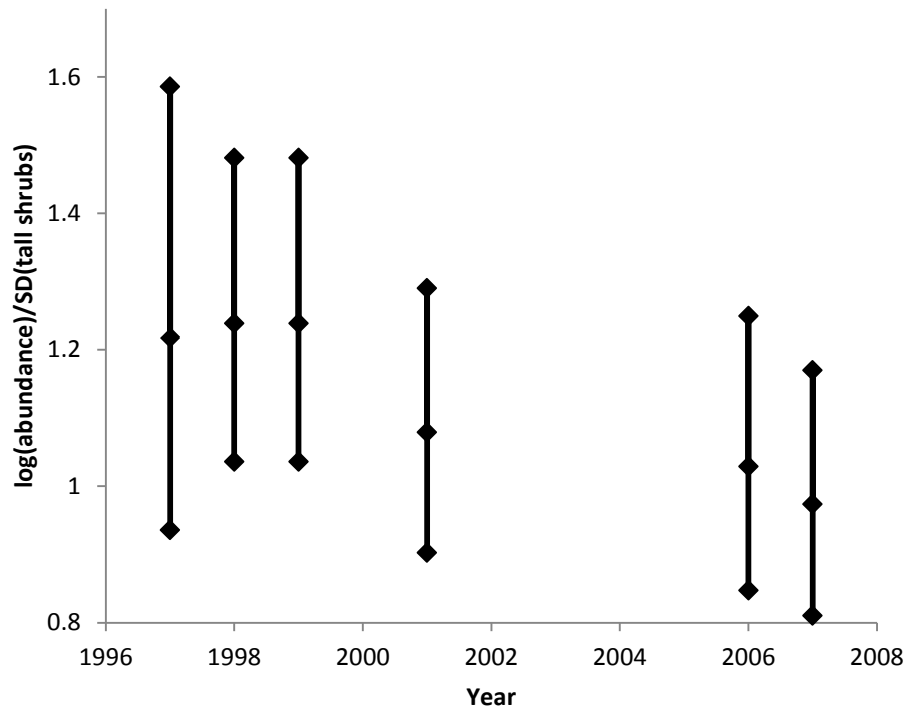


Figure 3.3. Population size hypothesis (Poisson species): relationship between total abundance and strength of vegetation effect (expressed as ratio of effect estimate to its standard error or EST/SE). For species with asterisk (*) symbols on the graph represent strength of association with the Heavy Thin stands.

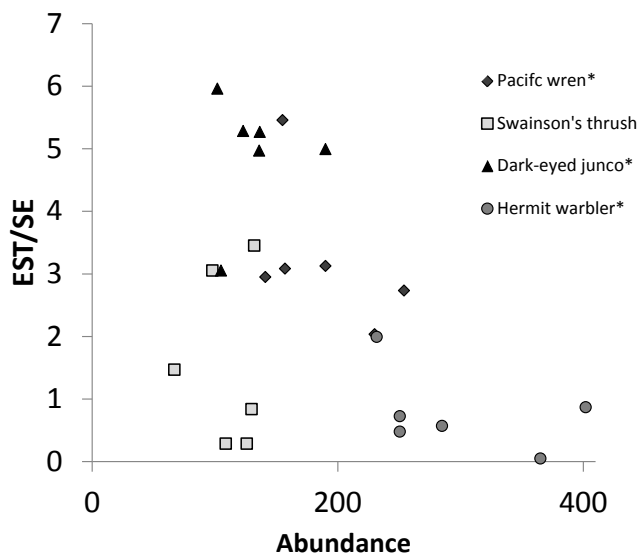


Figure 3.4. Population size hypothesis (Bernoulli species): relationship between prevalence and strength of vegetation effect (ratio of the effect estimate to its standard error or EST/SE).

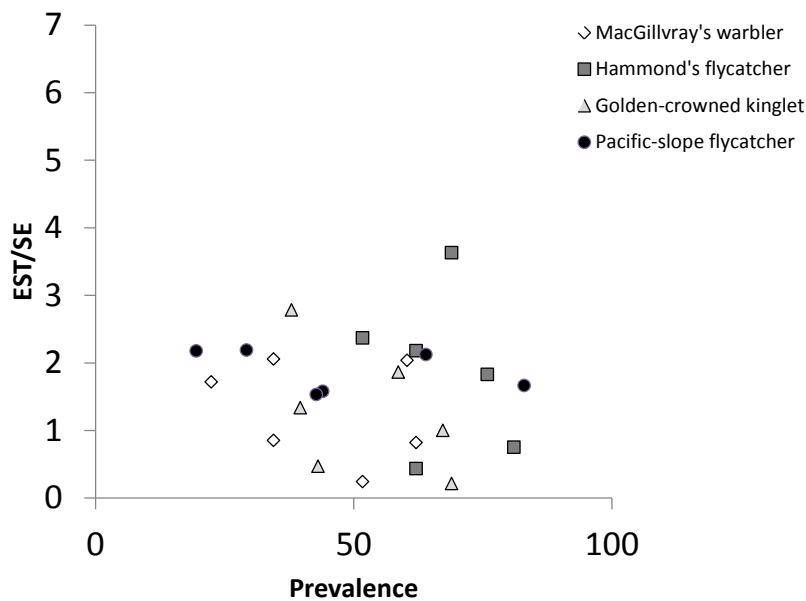


Figure 3.5. Threshold hypothesis: segmented regression of abundance of Swainson's thrush on tall shrub cover.

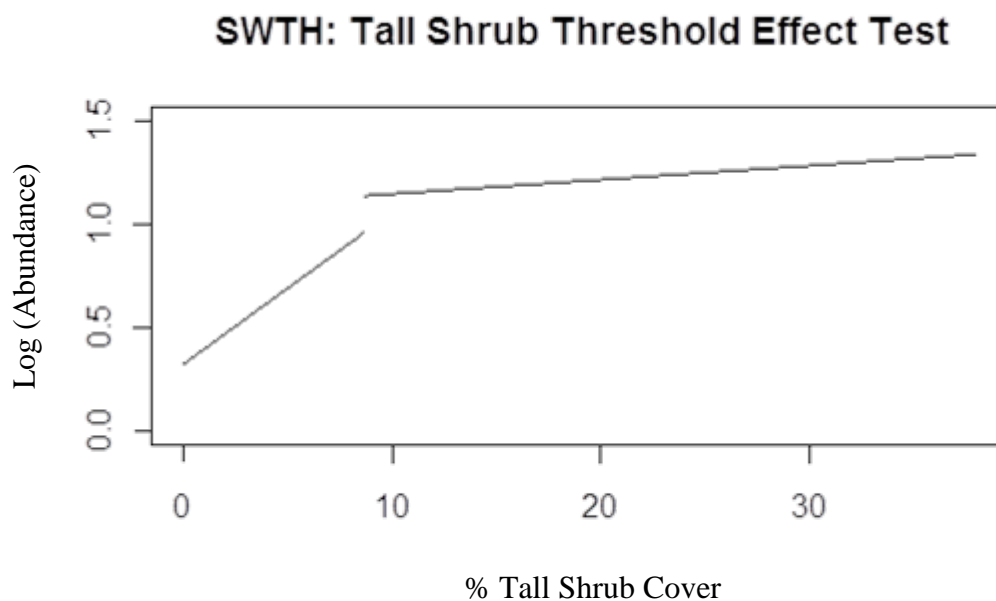


Figure 3.6. Relationship between the strength of tree density effect (ratio of estimate to its standard error or EST/SE) on the abundance of dark-eyed junco and time since thinning.

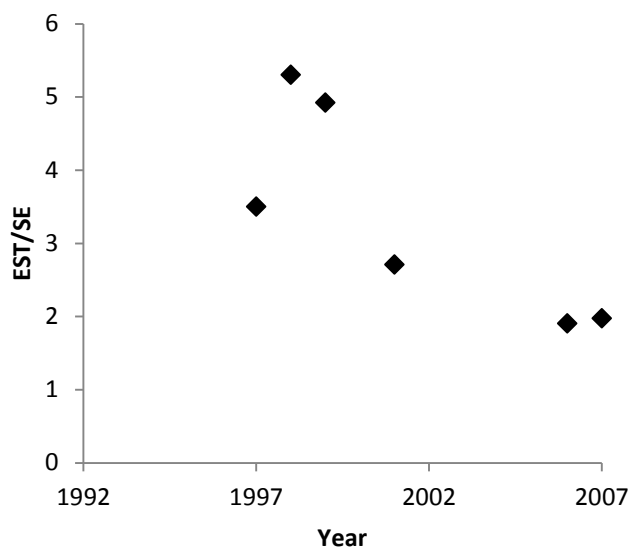


Table 3.1. Estimates for the effects of tree density and shrub cover on mean odds of occurrence of MacGillivray's warbler.

Year	Shrub Effect Size	~95% CI [#]	Chi ² (Pr(>Chi ²))*	Stem Density Effect Size (±SE)	~95% CI [#]	Chi ² (Pr(>Chi ²))*
1997	3.35	(0.84, 13.3)	2.86(0.09)	0.09	(0.01, 0.59)	12.9 (0.0003)
1998	2.50	(0.49, 12.8)	1.16(0.28)	0.01	(0.001, 0.20)	26.1 (p<0.0001)
1999	3.64	(1.06, 12.4)	4.61(0.03)	0.13	(0.03, 0.52)	13.5 (0.0002)
2001	1.14	(0.40, 3.21)	0.05(0.82)	0.06	(0.01, 0.33)	21.0 (p<0.0001)
2006	1.42	(0.62, 3.27)	0.68(0.41)	0.13	(0.04, 0.44)	18.1 (p<0.0001)
2007	2.46	(1.04, 5.84)	4.73(0.03)	0.13	(0.039, 0.44)	18.2 (p<0.0001)

* 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))

Confidence intervals are “approximate” and given for ease of interpretation.

Table 3.2. Estimates for the effect of large conifers on mean odds of occurrence of pacific-slop flycatcher.

Year	Estimate	~95%CI	Chi ² (Pr(>Chi ²))*
1997	2.79	(1.17, 6.60)	6.29 (0.012)
1998	1.84	(0.93, 3.64)	1.87 (0.172)
1999	2.78	(0.92, 8.38)	5.04 (0.024)
2001	2.04	(1.10, 3.80)	4.92 (0.027)
2006	2.77	(1.42, 5.38)	8.09 (0.004)
2007	2.84	(1.23, 6.59)	6.09 (0.014)

Table 3.3. Estimates for the effect of conifer density on mean odds of occurrence of Hammond's flycatcher.

Year	Estimate	~95%CI	Chi²(Pr(>Chi²))*
1997	0.94	(0.90, 0.99)	15.91 (6.64E-05)
1998	0.99	(0.95, 1.03)	8.45 (0.003)
1999	0.95	(0.92, 0.98)	18.98(1.32E-05)
2001	0.97	(0.94, 1.002)	7.13 (0.007)
2006	0.99	(0.96, 1.018)	1.36 (0.24)
2007	0.97	(0.94, 0.99)	3.80 (0.05)

Table 3.4. Estimates for the effect of tall shrub cover on mean abundance of Swainson's thrush.

Year	Estimate	~95%CI	Chi²(Pr(>Chi²))*
1997	1.22	(0.94, 1.59)	2.048 (0.152)
1998	1.24	(1.01, 1.48)	7.501 (0.006)
1999	1.32	(1.13, 1.55)	9.627 (0.002)
2001	1.08	(0.90, 1.29)	0.657 (0.418)
2006	1.03	(0.85, 1.25)	0.081 (0.776)
2007	0.97	(0.81, 1.17)	0.079 (0.778)

Table 3.5. Estimates for the effect of conifer density on mean odds of occurrence of golden-crowned kinglet.

Year	Estimate	~95%CI	Chi²(Pr(>Chi²))*
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)

Table 3.6. Estimates for the effects of conifer density on mean abundance of dark-eyed junco.

Year	Estimate	~95%CI	Chi ² (Pr(>Chi ²))*
1997	0.57	(0.414, 0.780)	7.68 (0.01)
1998	0.58	(0.479, 0.713)	13.95 (<0.01)
1999	0.55	(0.437, 0.701)	12.29 (<0.01)
2001	0.74	(0.593, 0.919)	4.24 (0.04)
2006	0.74	(0.549, 1.009)	3.38 (0.07)
2007	0.72	(0.526, 0.998)	3.04 (0.08)

Table 3.7. Estimates for the effects of conifer density on mean abundance of hermit warbler.

Year	Estimate	~95%CI	Chi ² (Pr(>Chi ²))*
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)

Table 3.8. Regression of strength of association between birds and vegetation characteristics on abundance index (Bernoulli species).

Species	Intercept	Slope	R ² _{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 3.9. Regression of strength of association between birds and vegetation characteristics on abundance index (Poisson species).

Species	Intercept	Slope	R ² _{adj}
Pacific wren	4.82(1.29), p=0.02	-0.01(0.001), p=0.26	0.12
Dark-eyed 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

CHAPTER 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 my knowledge, this is one of the first long-term 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). Therefore, variation of vegetation effects on birds documented in this ten-year study may have important implications for 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 a range of bird responses to vegetation characteristics and thus create an impression of an unchanging relationship between birds and vegetation. Accounting for variability in any ecological relationship is important. Scientists projecting population dynamics in the future already do so, when variability is quantifiable, and point out the influence of environmental variability on modeling outcomes (Wintle *et al.*, 2005). Taking variability of bird-vegetation relationships into account when planning for the effects of management may encourage managers to “hedge their bets” by diversifying management approaches.

On the other hand, despite fluctuations in the size of estimate, the direction of the effect of vegetation on bird response remained consistent over time for most species in this study. Additionally, estimates, although different numerically, often were not statistically different among sampling periods, as they had overlapping confidence intervals. Despite the variation in the magnitudes of estimates, model fits remained consistently good for three out of four species modeled with logistic regression (see Results). For species in this study these results suggest that short-term studies are likely to capture the important vegetation variables and the direction of the

effect, but may misrepresent the overall size of the effect. The danger, then, is in interpreting absence of a vegetation effect on bird occurrence. My results show, birds that respond strongly (statistically and biologically significantly, see definition of biological significance in Results) to vegetation characteristics in one year may not have a strong response in the previous or subsequent years (e.g., MagGillvray's warbler). Absence of response in the short-term, therefore, is not necessarily representative of the bird-vegetation associations over the longer-term.

Observed variation of vegetation effects on bird occurrence or abundance raised the question of what could be causing it. I ruled out three potential methodological causes: inappropriate vegetation variables, poor model fit and poor data quality. I believe vegetation variables were ecologically significant to birds because they were supported by the literature and examined vegetation-based models performed better than null models. I used appropriate statistical methods to ensure that models fit the data (see AUC paragraph in Results). I 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 I discuss possible ecological causes of variation in the strength of bird-vegetation relationships.

Population Size Effects on Bird-Vegetation Associations

Theoretically, strong bird-vegetation associations should result if individuals have an “ideal” knowledge of habitat quality, are free to settle at the site of their choice and settle best-quality habitat first. These are the assumptions of ideal free distribution (IFD) (Fretwell and Lucas, 1969). Bird density is not indicative of habitat preference when individuals that have settled high-quality habitat prevent others from settling there, and density of individuals in low quality habitat therefore increases faster than in high-quality habitat (ideal despotic distribution, IDD) (Fretwell, 1972). Alternatively, a habitat quality gradient may become decoupled from population density under ideal preemptive distribution (IPD). If breeding territories are of fixed

size, can only be settled by one individual or breeding pair at a time, and individuals settle them sequentially, choosing “best” quality habitat first, apparent bird-habitat association will dissipate with increasing population pressure as more individuals “spill over” into poor-quality sites (Pulliam and Danielson, 1991; McPeck *et al.*, 2001) (Fig 4.1).

I found that the strength of bird-vegetation associations within a species was only weakly related to population density of that species, providing little support for the IFD hypothesis. For rare species (Bernoulli-distributed), perhaps, populations are not large enough to saturate available habitat. If habitat is not saturated I would expect consistently high bird-vegetation associations under IFD, IDD or IPD assumptions, as nothing precludes individuals from settling in high-quality habitat. However, at very low population densities, proximity to conspecifics may play an important role in reproductive success, the ultimate measure of habitat quality (Fretwell and Lucas, 1969). This phenomenon of increased individual fitness with increasing population size is termed Allee effect and can be mediated by several mechanisms (Stephens *et al.*, 1999). Distribution of individuals, therefore, may deviate from that predicted by IFD – the positive effects of settling close to other conspecific individuals outweigh marginal benefit of settling in a higher-quality vegetation site (Greene and Stamps, 2001). Additionally, at low population size 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 example, if the total number of individuals in a population is small then death of a single individual occupying a high-quality patch may significantly alter observed bird-vegetation associations. Some of the species in the study, such as MacGillivray’s warbler, were scarce at the beginning of the study (only 13 of 58 examined sites were occupied), and highest bird density estimated was 7.5, 95 % CI (3.7, 15.4), birds/40 ha (Hagar *et al.*, 2004) in Heavy Thin stands. Low densities of MacGillivray’s warbler, and therefore small population size, suggest that

the Allee effect and stochastic events could have a disproportionately large effect on observed occurrence patterns of this and other low-population species.

The variation I observed in the strength of associations between the occurrence or uncommon species (by definition, small populations) and vegetation characteristics was inconsistent with predictions by IPD, IFD, or IDD. My results suggest that at low population numbers, 1) vegetation preference signal may be relatively weak due violation of the ideal habitat knowledge assumption (this violation is especially likely in a recently disturbed stands where resources may be in flux) and Allee effects; 2) the effect of stochastic events may be strong compared to the effect of vegetation. Therefore, observed bird-vegetation associations were weak and fluctuated in time.

For each common (Poisson-distributed) species, the strength of vegetation effect decreased slightly, but not significantly, abundance. However, within the common species group, more abundant species had a weaker relationship to vegetation than the less abundant species (Fig 3.3 in Results). This negative relationship between effect size and population size suggests a decreasing affinity for specific habitat features with increasing bird abundance. This trend may be interpreted as evidence supporting the IPD or IDP. However, there are several potential drivers behind this multi-species pattern that are not mutually exclusive.

Abundance of common species did not overlap among years, nor did abundance of each species fluctuate much among years (Fig 3.3 in Results). The stability of abundance of common species suggests that it may be regulated by one of several potential mechanisms: available habitat (Rodenhous *et al.*, 1997), density of con-specifics (Rodenhous *et al.*, 2003) or another factor (e.g., predation, disease, winter events). Strength of bird-vegetation associations was also relatively unchanging for these species (see Fig. 3.3 in Results) over time and did not fluctuate with abundance. The weak relationship between bird-vegetation associations and population 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 and that bird-vegetation associations within species were at their lowest value and could not erode any further.

On the other hand, the decrease in the strength of the relationships between vegetation characteristics and bird occurrence or abundance with increasing abundance index across species suggests a difference in the way species perceived and used forest stands in the study. For example, dark-eyed juncos had consistently high strength of association with vegetation characteristics, which indicated that this species perceived the forest stands as a heterogeneous environment and had a coarse-grained response (*sensu* Wiens, 1976). Hermit warbler, on the other hand, had a consistently low strength association with vegetation characteristics, which indicates that hermit warbler perceived the used the stands as a homogeneous habitat, and had a fine-grained response in the examined environment. Note that the above discussion of fine- and coarse-grain response is scale-specific. On the larger scale, dark-eyed juncos appear across a wider range of habitats than hermit warblers, but in young Douglas-fir forest dark-eyed juncos appear to be more selective about their habitat than hermit warblers. If hermit warbler perceives the forest as a homogeneously good habitat because its habitat needs are fulfilled by young Douglas-fir forests, it may have a homogeneous or random distribution in the forest at any population density. If dark-eyed junco perceives the forest as a heterogeneous habitat, it may use higher quality patches preferentially and, thus, have an uneven distribution in the forest (see Fig. 4.2 for a visual example). Hermit warbler potentially had a greater area of habitat to exploit, compared to dark-eyed junco. Abundance differences among dark-eyed junco and hermit warbler, therefore, could be a result of site-dependent population regulation (Rodenhouse *et al.*, 1997) and, thus, be the cause of the negative relationship between species abundance and strength of bird-habitat association across species. Alternatively, abundances of the two species may have been limited by other resources or events (e.g., high post-fledgling mortality, winter mortality, migration-associated mortality etc.) and the observed negative trend, therefore, would be spurious. I suggest that for common species life history traits, such as response grain, as well as

demographic processes regulating population size modify observed bird-vegetation relationships.

Recent studies attempted to relate species life and biological traits to the accuracy of distribution models for that species (McPherson and Jetz, 2007; Riffell and Gutzwiller, 2009). Resident (vs migratory) (McPherson and Jetz, 2007) and abundant (vs rare) species (Riffell and Gutzwiller, 2009) were found to be more accurately-predicted in their distributions. However, no clear distinctions in the strength of association between birds and vegetation characteristics emerged between residents and migrants or rare and abundant species in my study, perhaps due to small sample size.

Vegetation Threshold Hypothesis

Variation in the strength of vegetation effect on Swainson's thrush was consistent with the Threshold Hypothesis. Thresholds in population processes in relation to amount of habitat at the landscape level 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, *in press*, Marshall et al, 2003) at the stand level. Thus, a positive association of Swainson's thrush with tall shrubs, a structural group that includes broadleaf tall shrubs, conifer saplings and young hardwoods, supports previous findings.

Forest thinning has been found to have a positive effect on relative cover of hardwood species, including tall shrubs (Bailey and Tappeiner, 1998; Ares *et al.*, 2009; Davis and Puettmann, 2009; Wilson *et al.*, 2009). However, damage to tall shrubs resulting from thinning operations can cause initial reduction in their cover. Tall shrubs recover to pre-thinning level approximately ten years post thinning. Though recovery time varies by pre-thinning conditions and thinning intensity (Wilson *et al.*,

2009). The threshold I observed in Swainson's thrush's response to tall shrubs was consistent with these post-thinning tall shrub dynamics.

The threshold value found in this study should be used with caution. Threshold values have been found to vary by region for other species (Betts et al 2010) and may be influenced by landscape-level vegetation composition, which was not considered in this study, as well as broader population processes.

Thinning-associated Disturbance Effects

My results did not support the Decoupling Hypothesis, which suggested that forest thinning may disturb bird-vegetation relationships immediately after thinning due to site fidelity (e.g., Knick and Rotenberry, 2000) and that the decoupling effect, if found, would diminish with time. Counter to this hypothesis, I did not find strengthened bird-vegetation associations with time. Two species seemed to respond to disturbance, but not in the hypothesized way. Dark-eyed junco's response was consistent with the species tracking ephemeral, disturbance-related, resources. Abundance of this species was highest at point-counts nearest to vegetation plots with very low tree density (0-20 tph) the first few years after thinning but then declined in low-density areas as time since thinning progressed. Similarly, golden-crowned kinglets showed evidence of avoiding vicinities of low-density forest areas immediately after forest thinning, but returned to approximately homogeneous use of the forest, including low density areas, after the first year. Forest dwelling species examined in this study appear to follow habitat fluctuations closely, compared to shrub-steppe birds where time-lags were found in response to habitat alteration (Wiens *et al.*, 1986).

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; Hagar and Friesen,

2009), and that response of some species may change over time (Hagar and Friesen, 2009). Treatment effects on bird abundance were hypothesized to be mediated by vegetation developments after thinning (Hagar and Friesen, 2009; Verschuyt *et al.*, 2011). My results show that thinning intensity was a more reliable predictor of bird abundance and occurrence than individual vegetation characteristics or their combinations.

Thinning treatments introduced differences in horizontal (i.e., 0.2 ha gaps in the Light Gap treatment) and vertical (with shrub layer development) structure, as well as differences in understory plant community composition to forest stands (Davis *et al.*, 2007; Davis and Puettmann, 2009). Treatment type implicitly included not only all of the vegetation characteristics that were tested independently, but also indirectly captures structural heterogeneity and floristics. Treatment type is a variable that captured a large spatial extent. The smallest treatment unit in the study was 15 hectares, whereas individual vegetation characteristics were measured at the scale of 0.1 ha vegetation plots. Spatial scale of thinning treatments is likely to be more relevant to the patch-level (*sensu* Johnson, 1980) habitat selection process than the characteristics of vegetation measured at the fine scale of plots. The geographical extent of treatment type, as well as its integrative nature, makes it a more complete and ecologically-relevant descriptor of habitat explaining its superior AICc performance compared to local-scale vegetation characteristics.

Poor performance of vegetation-based models compared to the treatment-based model raises the question of whether vegetation-based models were too simple to adequately represent variation in habitat quality. Most, though not all, of my vegetation-based models were univariate. Hansen *et al.* (1995) successfully modeled abundance of bird species using tree density measurements by dbh classes and found that most of their bird species, including eight species in the present study, responded to total density of trees ≥ 10 cm dbh. Thus, simple vegetation descriptors have been previously used successfully in modeling species distributions. Hilden (1965) suggested that birds recognize a gestalt of suitable habitat, the “right” combination of

several habitat characteristics. Hansen *et al.* (1995) noted that tree density was likely correlated with other important vegetation characteristics that make up high-quality habitat. A single vegetation characteristic, such as tree density, may implicitly represent several other vegetation characteristics, if the correlation between them is consistent. For example, in a forest without recent (10-20 years) disturbances shrub cover is likely to be negatively correlated with tree density (e.g., Bailey *et al.*, 1998). However, in the plots examined for this study, the relationship between low shrub cover and tree density changed from positive to negative within 10 years after thinning (data not shown) as shrubs recovered after disturbance. Therefore, a single vegetation characteristic is likely carrying less associated information in recently disturbed stand compared to a stand without recent disturbances, which may explain lesser success of my univariate models (three quarters of observations come from ‘disturbed’ stands), compared to those of Hansen *et al.* (1995) (two out of five examined studies are thinning studies).

Issues of Scale

Dependence of result on observation scale is a classic idea in ecology (Wiens, 1989). The variability of small-scale bird-vegetation associations in this study compared to stable associations with treatment type may be an example of the principle. Both vegetation characteristics and bird occurrence or abundance were measured at small 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 was not evident when vegetation values were averaged at the stand scale. Mean tree densities in examined stands varied from approximately 200 tph to 750 tph, local tree densities ranged from an equivalent of 0 tph to 1600 tph. Three bird species showed a preference for vicinities of low-density areas, with highest occurrence (MacGillivray’s warbler and Hammond’s flycatcher) or abundance (dark-eyed junco) in the vicinity of vegetation

plots where tree or conifer density was near zero. Pacific-slope flycatcher showed preference for vicinity of the densest patches of conifers, and golden-crowned kinglet showed avoidance of vicinities of low-density areas in the first year post-thinning. Birds' response to small-scale variations in vegetation characteristics were not evident on the stand (same as treatment) scale, there was no statistical difference found between bird responses to Light with Gaps and Heavy Thins (Hagar and Friesen, 2009), even though bird's preference or avoidance of gaps in clear in the small-scale observations.

Dark-eyed junco is a species, for which I found both, a strong and unchanging association with the most intensive thinning treatment (Fig. 3.3 in Results) but a diminishing association with tree density (Fig. 3.6 in Results). The two patterns seem contradictory, but in fact, support the above-proposed hypothesis of the sensitivity of fine-scale sampling to local processes. If dark-eyed junco's association with low tree density was driven by ground disturbance, a fine-scale characteristic, then fine-scale sampling is more likely to capture such an association than coarse-scale sampling/descriptor such as treatment type. At the treatment level dark-eyed juncos were still associated with intense thinning ten years after thinning, while at plot-scale level they were not found near low-density vegetation plots anymore, likely due to attenuating disturbance effects. Birds' response to small-scale changes in vegetation characteristics emphasizes the importance of small scale horizontal variation in vegetation structure. A forest stand with variable tree density may have the potential to support a greater diversity of bird species in a small area.

Study Limitations

I assumed that greater odds of occurrence or greater abundance coincided with greater habitat quality for birds. While numeric response of birds may be suggestive of habitat quality, the two measures may be decoupled, especially in human-altered landscapes (e.g., Van Horne, 1983). When proximate cues do not coincide with the

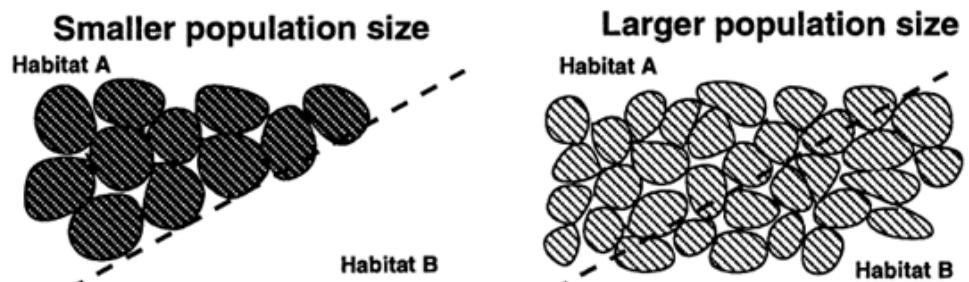
expected habitat quality, an ecological trap may be created (see Schlaepfer *et al.*, 2002). Habitat quality and presence of an ecological trap for birds can be determined by measuring birds' reproductive success, along the vegetation gradient. However, no such information was collected in this study. Tewksbury *et al.* (1998) suggested that nest parasitism and predation are the two main mechanisms mediating the effect of human-related habitat alteration on birds' reproductive success. Effects of predation and parasitism depend on the predator and parasite community, landscape context (agricultural matrix vs. forested matrix) as well as species sensitivity to both of these processes. Hagar *et al.* (2004) reported sightings of brown-headed cowbirds in thinned stands close to pastureland, suggesting potential for increased parasitism rate for cup-nested birds in thinned stands. While it may be reasonable to assume that bird occurrence frequency or bird abundance coincides with quality habitat, the possibility of an ecological trap for some species has to be acknowledged.

The YSTDS was a manipulative experiment by design. However, my study is correlative because I related various responses to thinning treatments and the levels of responses are not controlled. Correlation between specific vegetation characteristics and bird occurrence or abundance does not imply that those characteristics have a causative effect on respective bird species. Local vegetation characteristics, such as tree density and shrub cover may imperfectly correlate with other vegetation characteristics, floristics, food abundance, predation, heterospecific aggression or conspecific attraction, as well as landscape-level population processes, all of which are likely contributing to observed bird occurrence or abundance at the local level and could be, individually or as an aggregate, the driving forces behind observed occurrence and abundance patterns.

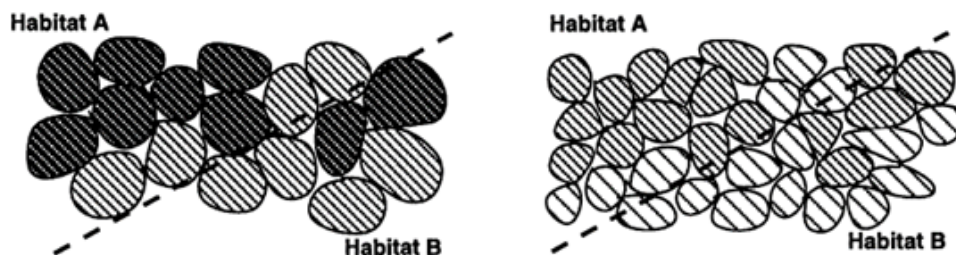
Habitat selection by birds is a multi-scale process (e.g., Johnson, 1980; Orians and Wittenberger, 1991). Both local vegetation characteristics and landscape-level composition have been found important in explaining forest bird community composition in the PNW (Cushman and McGarigal, 2004). I did not account for the effects of landscape composition on the local-level species occurrence. 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, more and more of adjacent stands were thinned (Klaus Puettmann – personal communication). I cannot discount the influence of landscape-level vegetation composition nor the increasing amount of disturbed (thinned) forest as unimportant. Results of this study have to be interpreted with the understanding that I did not account for landscape composition around the study blocks.

Figure 4.1. Distribution of individuals at various population sizes under ideal free and ideal despotic hypotheses. Copied from Rodenhouse *et al.*, 1997



Scenario 1. Ideal-free distribution of territory suitability. Increased population size results in individuals on all sites experiencing increased density, smaller territory size, and decreased site suitability (high suitability on the left becomes medium on the right), whether habitat suitability is high (to the left of the dashed line, labelled Habitat A) or low (Habitat B).

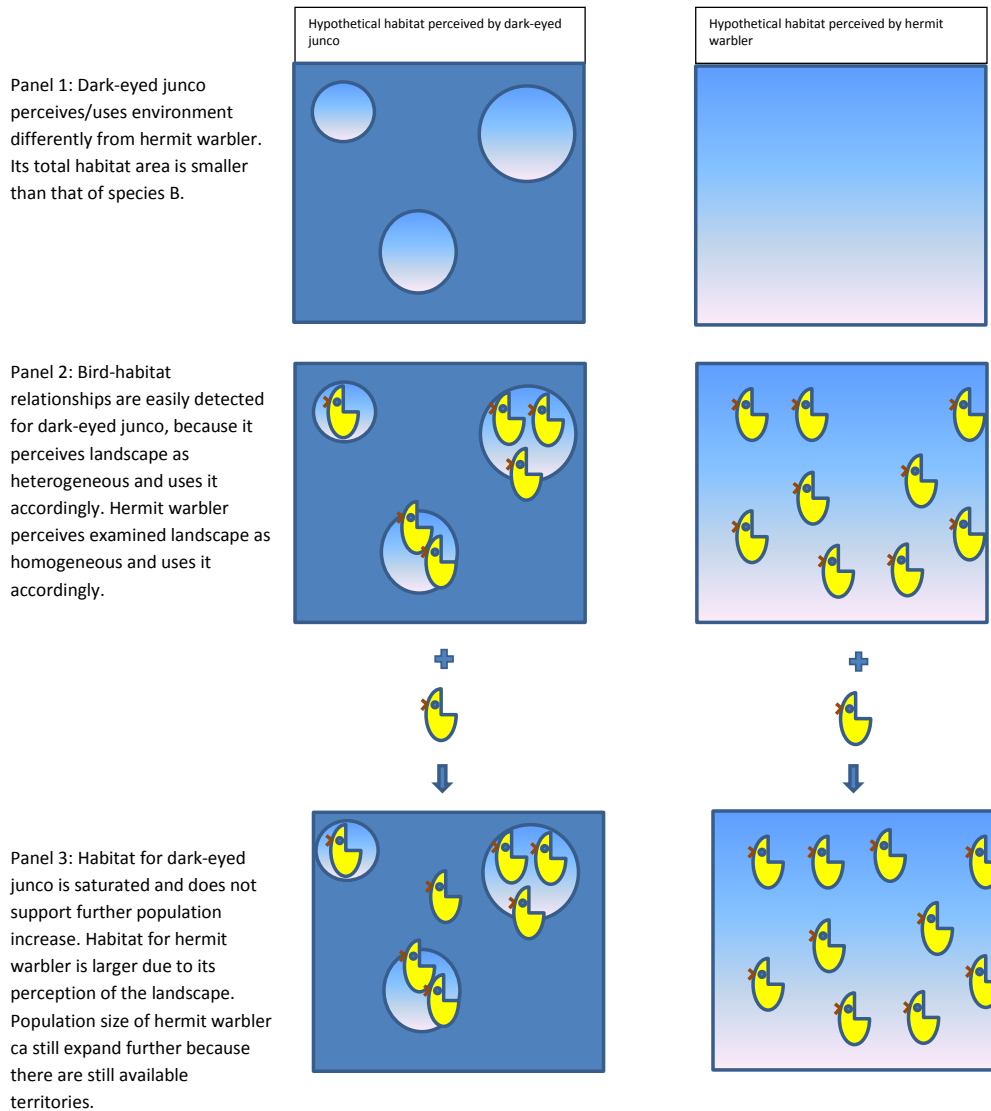


Scenario 2. Ideal-despotic distribution of territory suitability. Increased population size results in individuals on all sites experiencing increased density, smaller territory size, and decreased site suitability. Unlike scenario 1, however, despotism results in some individuals experiencing higher suitability than others, in this particular case, at both smaller and larger population sizes. Like scenario 1, suitability declines for all site holders as population size increases.



Scenario 3. Site dependence by the addition of noncontiguous sites of low suitability. Increased population size results in decreased *average* suitability per site by the addition of noncontiguous sites, which are of relatively reduced (medium rather than high) suitability, and which do not affect the suitability of previously occupied sites such as the site marked with an x.

Figure 4.2. An illustration of a hypothetical site-regulated population size for a coarse-grained (dark-eyed junco) and a fine-grained (hermit warbler) species, assuming neither of the species is limited by movement among habitat patches.



CHAPTER 5 - CONCLUSIONS

Study-specific Conclusions

My results suggest that while vegetation characteristics partially mediate birds' local-level response to forest management, birds' responses to vegetation characteristics are likely modified by species-specific demographic processes, species-specific life traits and change in limiting resources due to rapid development of vegetation after thinning. At the very least, my results warn that short-term estimates of vegetation effects on bird occurrence or abundance are likely to be either too high or too low (although, some of them are likely to be in line with a long-term average). Therefore, inferences and projections made with short-term information should be made cautiously. Including information about the variation in the magnitude of vegetation effects explicitly into a predictive model or using an averaged magnitude of vegetation effect on birds over a long period of time may allow for less uncertain modeling results. Variability in response to management is especially alarming in the face of drastic decreases in populations of some bird species in the last forty years, combined with the environmental uncertainty associated with changing climate. Providing habitat for a species whose population is very low, may not be as effective in increasing population size, on average, as suggested by short-term studies due to large influence of demographic and environmental stochasticity on habitat associations. Therefore, species of management interest may warrant intensive management efforts, such as landscape-level habitat creation efforts, before their populations get even lower.

This study is an important contribution to the forest and wildlife management literature and knowledge base. As federal forest managers in the PNW are transitioning to managing for native species' habitat and biodiversity, detailed information about the mechanisms of species response to management is necessary. My 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. However, the magnitude of birds' response should be assessed for several years after management implementation to account of variability observed in this study. Consistent direction of vegetation effect on bird response together with biologically significant bird response to gradients of vegetation characteristics indicates that vegetation characteristics examined here could be used as general guidelines for species-specific wildlife management in young Douglas-fir forests in the PNW.

Fluctuating strength of association between vegetation and occurrence of rare species, for which high-quality habitat patches are likely unsaturated, raises the question of how weak correspondence to vegetation gradients affects that species' reproductive success. If a vegetation gradient indeed represents a gradient in habitat quality for a species, then the population may have a lower average reproductive success than that predicted by habitat availability because high-quality sites may remain unoccupied (Rodenhouse *et al.*, 1997). Quantifying differences between expected, based on habitat availability, and actual, based on habitat occupancy, reproductive success of a population will further improve accuracy of model predictions.

Bird species examined in the study responded to different vegetation characteristics and had individual response patterns within and across years. Individuality of species response is in agreement with previous studies (e.g., Hansen *et al.*, 1995; Hagar and Friesen, 2009), and re-iterates previously stated premise that no single management treatment can benefit all species simultaneously. Species responsiveness to small-scale variations in vegetation structure within a stand suggests that maintaining variable-density stands may encourage bird species diversity within a stand.

While examining effectiveness of thinning treatments as habitat management tool was not my primary objective, my results indicate that bird responses to thinning treatment were more easily detected than responses to individual vegetation characteristics. The success of treatment type in predicting bird occurrence or

abundance suggests that the spatial scale of thinning treatment and its vegetation 'gestalt' are appealing to breeding forest birds. Assuming bird abundance reflects habitat quality, forest thinning at spatial scales of 10's of hectares has potential use as an effective technique in 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, my results suggest, that long-term monitoring of management effects is crucial despite the practical and financial difficulties associated with it. My study highlights two main reasons for long term monitoring of the effects of management efforts. First, after studying correlations between bird occurrence and vegetation characteristics in thinned forests, I cannot claim that the studied vegetation characteristics are the causation of birds' response to thinning. Experimental studies that control for vegetation composition may be difficult to implement due to natural variability of vegetation composition and structure in thinned stands. Therefore, an accumulation of evidence from several long-term studies may be a way to support or reject effects of examined vegetation characteristics and their role in the temporal trends in birds' response identified in this study. Second, variability in the effect of vegetation characteristics on bird occurrence or abundance is an important finding that has concrete implications for wildlife management and for modeling management scenarios. Quantification of uncertainty in bird-vegetation relationships may allow managers and conservation planners to better assess management risks, and therefore make better management and conservation decisions.

Inferences and Generalizations

Structure-Function Analogy

The conceptual framework underlying my study was the search for the relationship between structure and function. The question was whether a change in forest structure brings on or enhances the function of habitat provision for bird

species. The metaphor of structure facilitating function is applicable and useful in the case of forest structure and habitat function. My results, though correlational, support this statement. Altering forest structure by thinning correlated with immigration of MacGillvray's warblers into the thinned forest stands, a species that was extremely scarce or absent in the stands before thinning. The observed correlation supports the hypothesis that altered forest structure allowed for the function of habitat for MacGillvray's warbler.

However, when considering the structure-function concept and its application to forests and habitat function, one has to recognize multiple levels of forest or vegetation structure and their respective role in facilitating the function of habitat provision. Physical characteristics of birds, such as bill size, body mass and shape, toe lengths etc., that affect birds' interaction with their environment (Hilden, 1965). Vegetation characteristics at several spatial scales influence and limit species' activity. At the micro-scale, plant architecture, such as petiole lengths affect foraging efficiency of insect gleaning birds (Hilden, 1965; Holmes, 2011). Plant species composition will influence the insect community on which bird forage. Local-level vertical and horizontal structure affect bird community composition (MacArthur and MacArthur, 1961) and landscape composition influences accessibility and use of local-level habitat patches (e.g., Frey *et al.*, 2011). Finally, bird presence and reproductive success in a created habitat is required to test whether altered forest structure provides the habitat function. Therefore, testing of the hypothesis is contingent on a sufficiently large bird population to find and fill the habitat at the landscape scale. My study examines local-level breeding season habitat, which is necessary but not sufficient to fulfill successful reproduction and survival of a population. Winter mortality due to low temperatures and food availability for resident species (Virkkala, 1991; Jones *et al.*, 2003) and migration-associated mortality for Neotropical migrants (Van Horne, 1983; Holmes, 2011) have a significant effect on population size, and therefore, bird presence at a given location.

My study addresses only one aspect of the structure that creates the function of habitat provision. My results have to be interpreted with the understanding of the greater landscape composition around the study stands – largely forested and scarcely developed landscape of the Oregon Cascades. Following the structure-function discussion above, I conclude that my results are likely transferable to systems that fulfill the following conditions: 1) similar floristic composition, as well as vertical and horizontal structure at the local and landscape scales; 2) similar physical and life-history trait characteristics of the bird species to the ones examined in this study.

Do Thinned Forests Provide for a More Stable Habitat Function than Unthinned Forests?

One of the questions currently asked of thinned forests in the PNW is whether forest thinning can create a forest that reliably provides ecological functions in the face of disturbances and uncertain climatic conditions (Neill, 2012) by diversifying response type traits of plants within a functional group. My study addresses a small part of that question. My results indicate that bird occurrence or abundance correlates with vertical and horizontal structure of the forest. Diversifying response types within a structural group (e.g., mid-story structural level) will theoretically ensure the function of cover or nest-site provision for bird species that use mid-story vegetation structures. Ensuring sufficient amount of a structural characteristic required for a species' habitat at the landscape level may also facilitate species stability in the face of disturbance events that may destroy part of the previously available habitat. Besides providing cover and nesting sites, vegetation houses insect communities that are a major food source for forest birds (Hagar, 2004). Recent studies of the impacts of climate change on bird species suggest earlier spring onset may decouple the reproduction timing of a migrant species and the peak of the species' main food supply, which leads to population declines of this bird species (Both *et al.*, 2006). Matthew Betts (*pers comm*) suggested that the decoupling of insect emergence and bird breeding season onset could be reduced or mitigated in ecosystems with diverse vegetation composition, which would potentially foster diverse insect communities

with varying emergence timings. My study did not address birds' response to floristic composition, functional or response type plant groups. Future studies examining emergence timing of insect communities in relation to substrate's response type will further clarify the link between the diversity of response types of plant species and the stability of the food provision function.

Young Thinned Forests, Old Growth and Habitat Provision

Forest thinning did encourage horizontal, vertical and floristic heterogeneity (not examined in my study) in the YSTDS forest stands (Davis *et al.*, 2007; Davis and Puettmann, 2009). The above characteristics are typical of old-growth forests (Franklin *et al.*, 1981). My study suggests that birds are sensitive to small-scale changes in vegetation characteristics and, therefore, a greater diversity of these vegetation characteristics in thinned stands may encourage a greater diversity of bird species compared to an unthinned young stand (also examined in Hagar and Friesen, 2009). However, onset of other important characteristics of old-growth forests cannot be brought on in thinned forests in the near future. Large living trees, large standing dead trees and large fallen trees are missing in the young thinned stands and will take a long time to develop. None of the species examined in my study were obligate cavity nesters, which could be affected by the above vegetation characteristics. However, Hagar and Friesen (2009) report greater abundance of cavity-nesting birds in thinned stands after snags were artificially created. Nevertheless, old-growth forests support vegetation structures unique to old forests that may support ecological functions that are outside of the scope of this study. My study did not directly address the importance of large alive and dead trees. However, the importance of those vegetation characteristics cannot be discounted. Therefore, preservation of old-growth forests is ecologically justified, even as managers create more structurally and floristically diverse young and mature forest.

Thinned Forests and Ecosystem Goods and Services

My results suggest that birds respond quickly and significantly (statistically and biologically, see discussion of biological significance in Results) to changes in forest structure. Previous studies also suggest that small changes in the amount of broadleaf vegetation at the local and landscape level may have a strong effect on bird community composition and abundance of individual species in an industrial forest landscape (Ellis and Betts, 2011). Therefore, encouraging structural and floristic heterogeneity on private forest lands (federal land managers are mandated to do so by law) by instituting a system of payments for habitat credits may be an efficient way of promoting bird habitat availability in otherwise hostile environments. Assuming the ability of birds to find and colonize new habitat is great, treating small islands of habitat in an unsuitable environment may have a disproportionately large positive effect on species richness (DeMars *et al.*, 2010). However, small patches of suitable habitat surrounded by an unsuitable environment are likely to become ecological traps (Van Horne, 1983; Schlaepfer *et al.*, 2002), see discussion of ecological traps in the Discussion section. Further assessment of costs and ecological benefits of habitat creation on private forest lands is required to form a well-informed recommendation regarding institution of habitat credits.

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APPENDICES

Appendix A. AICc Tables

Dark-eyed Junco

Year	Model Name	$\Delta AICc$	wt
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

Golden-crowned kinglet

Year	Model Name	$\Delta AICc$	wt
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
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

Hammond's flycatcher

Year	Model Name	$\Delta AICc$	weight
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
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

Hermit warbler

Year	Model Name	$\Delta AICc$	wt
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
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

MacGillivray's warbler

Year	Model Name	$\Delta AICc$	wt
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
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

Pacific-slope flycatcher

Year	Model Name	$\Delta AICc$	wt
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

Pacific wren

Year	Model Name	$\Delta AICc$	wt
1997	trtmt	0.00	0.78
1997	null	4.33	0.09
1997	stemCount	6.39	0.03
1997	CC	6.62	0.03
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

Swainson's thrush

Year	Model Name	$\Delta AICc$	wt
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
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