BIODIVERSITY RESPONSES TO ALTERNATIVE GREEN TREE RETENTION PRACTICES IN THE PACIFIC NORTHWEST: A REGIONAL FORESTRY EXPERIMENT

By

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ABSTRACT

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Conserving forest biodiversity while meeting global demand for wood products is an ongoing challenge for 21st century forest management. Naturally regenerated and regulated forests are typically heterogeneous but forest management intended to maximize wood production often homogenizes forest structure. Retaining green trees and dead wood at the time of forest harvest, termed structural retention, is a common practice for promoting biodiversity in forests managed intensively for wood production. Despite widespread implementation of structural retention and substantial body of research on effects of retention on forest biodiversity, there remains a need to evaluate alternative tree retention practices on biodiversity in specific forested regions and silvicultural systems. Further, ecologists are increasingly interested in the impacts of management actions on functional trait diversity, but few studies have quantified the effects of alternative retention practices on functional diversity of animal communities. I used a manipulative study with five experimental retention treatments to quantify effects of differing size, number, and location of retention tree patches on two animal taxa in clearcut forests within the U.S. Pacific Northwest. In my first chapter, I quantified the effects of experimental retention treatment on ground beetle species (Coleoptera: Carabidae) and functional (morphological) richness and variation in community composition between retention and clearcut areas. Although I did not find strong effects of retention treatment on either species or functional richness, I found less variation in community composition between retention and clearcut areas in the treatment that contained several small patches. This finding indicates that ground beetle communities supported by small, dispersed retention patches are redundant to those found in surrounding clearcut areas. In Chapter 2, I quantified effects of retention treatment on abundance of three common small mammal species and found that generalist and forest species were more abundant in smaller, isolated retention tree patches, and for one species this effect was related to higher levels of downed trees in small patches. In Chapter 3, I related small mammal species and functional richness to retention treatment and found that species, but not functional richness was slightly higher in patches connected to forested riparian buffers compared to isolated upland patches. I conclude from these results that retention placement does not strongly influence the number of small mammal species present or their contribution to forest ecosystem function, but small increases in species richness can be obtained by grouping all trees adjacent to riparian zones. In Chapter 4, I analyzed abundance data from eleven small mammal species to look for evidence of competitive interactions between species, finding that when the effects of retention treatment and environmental variation were accounted for, most species abundances were positively correlated, suggesting that environmental factors and not inter-specific competition structured small mammal communities in early seral forest plantations. Results from my research indicate that no single retention strategy is optimal among taxa for biodiversity conservation in clearcut forests of the Pacific Northwest, and implementing a combination of retention treatments favors diversity and abundance of the two animal groups I studied. My results further indicate that community responses to fragmentation of retained forest patches in clearcuts differs between taxonomic groups, highlighting the importance of clearly articulated biodiversity objectives (as opposed to a broad goal of conserving biodiversity).

This dissertation is dedicated to all the animals who endured long nights in traps, unwanted ear piercings, and at times paid the ultimate sacrifice in the name of conservation science. Hopefully the information in this dissertation will help make intensively managed forests a more hospitable place for your species going forward.

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PREFACE

Each chapter within this dissertation was drafted as a stand-alone manuscript for publication in a peer-reviewed journal. Chapter 1 is currently in revision with *Ecosphere*. Chapter 2 is in revision in *Forest Ecology and Management* and Chapter 3 is formatted for *Forests*. As such, I use the pronouns “we” and “our” throughout these chapters. Although I am listed as the sole author and use the pronoun I in Chapter 4 of this dissertation, this chapter was also collaborative and associated manuscripts will include one or more co-authors when submitted for peer-review.

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INTRODUCTION

Maintaining native species diversity in forests managed for wood production is an increasingly important management consideration. In forests around the world, intensive management for wood production has homogenized components of forest structure, which changes species composition compared to unmanaged forests (Martikainen et al. 1996) and can reduce ecological variation across space (Mori et al. 2015). Even-aged harvesting often reduces heterogeneity of early seral forest conditions, which is typically the most diverse stage of forest succession (Swanson et al. 2011), and mechanical and chemical preparation on harvested sites for replanting can act as an environmental filter, reducing occurrence of species typically found in young forests (Kroll et al. 2017). Several alternative management practices have been proposed to alleviate the impacts of intensive forest management on native species diversity. These practices, such as green tree retention and dead wood creation at the time of forest harvest, aim to mimic conditions created by natural disturbances and have become standard practice in many timber producing regions (Gustafsson et al. 2012, Sandström et al 2019). Studies spanning local to global scales indicate that retention forestry can be effective at increasing diversity in harvested forests (Fedrowitz et al. 2014, Mori and Kitigawa 2014, Baker et al. 2016). However, regional scale studies that assess the relative effectiveness of alternative retention practices, implemented in the context of existing forest harvesting regimes, are needed to maximize retention effectiveness and understand potential conservation tradeoffs between alternatives.

In addition to maintaining native species diversity, resource managers and conservation biologists are increasingly interested in maintaining functional diversity of species communities (McGill et al. 2006). Within ecological communities, species differ in their contributions to ecosystem function, and those contributions can be described using measures of functional trait diversity (Tilman 2001, Petchey and Gaston 2006). Understanding the effects of management practices on functional diversity can reveal changes in community composition that species-based approaches do not, important because functional diversity is often more sensitive than taxonomic diversity to intensive management of ecosystems (Flynn et al. 2009). Comparing patterns of functional diversity and species diversity can also provide insights into the factors structuring ecological communities and whether impacts on species richness are likely to influence ecosystem function. Hence, studies on the impacts of forest management on ecological diversity are increasingly focused on patterns of functional diversity (Spake et al. 2016, Curzon et al. 2020).

Conifer forests of the U.S. Pacific Northwest are highly productive, with old growth forests in the region containing more biomass per unit area than almost any other forests globally (Franklin and Waring 1981). Due to these high levels of productivity, these forests have been heavily exploited for timber, with over 70% of the historical old growth logged after European settlement (Strittholt et al. 2006). In response to the decline of species that require mature forest conditions, most commercial logging ceased on federally-owned lands in the region, while private timber companies continue to manage secondary forests intensively for wood production (OFRI 2017). These managed forest landscapes are losing important structural elements associated with ecological diversity (Hayes et al. 2005, Linden and Roloff 2013), and private forest managers are altering harvesting practices to meet sustainability requirements and forest harvesting regulations. Retention forestry is one conservation practice implemented in wood producing forest landscapes to alleviate negative impacts of even-aged forest management on forest biodiversity (Lindenmayer et al. 2012). Retention forestry is required by forest harvesting regulations in the Pacific Northwest. Specific goals of retention forestry include allowing forest interior species to persist following harvest, increasing structural diversity of early seral forests, and creating uneven-aged forest structure later in succession (Rosenvald and Lohmus 2008). Several experimental studies in the Pacific Northwest measured the effectiveness of alternative retention practices at achieving these goals (Aubry et al. 2009, Gustafsson et al. 2012), but these studies have not evaluated the effects of retention on forest biodiversity at lower proportions of trees retained (i.e., <10% of original basal area). Retrospective studies on retention in the region indicated that larger retention patches have higher bird species richness (Linden et al. 2012) but effects of retention patch size on diversity are not well understood for most taxonomic groups (Fedrowitz et al. 2014). Lack of data on retention patch sizes and biodiversity leads to decisions on placement of retention trees that are often based on timber harvesting logistics rather than biodiversity conservation outcomes.

In this dissertation, I use a manipulative experiment to evaluate the relative benefits of five alternative structural retention patterns at increasing the diversity and abundance of two indicator taxa in recently logged Pacific Northwest forests; small mammals and ground beetles. In Chapter 1, I used taxonomic and functional approaches to understand how five retention alternatives influenced ground beetle diversity and variance in community composition across recently harvested forest stands. In Chapter 2, I use a spatially explicit analysis to quantify how population density of common small mammal species responds to retention alternatives and how small mammal density varies in response to measures of structural complexity within retention patches. In Chapter 3, I quantified the effects of retention pattern on small mammal species and functional richness. Similar to my first chapter this analysis provided insights into the effects of patch size and number on ecological diversity as well as the importance of riparian forests for conserving small mammal diversity. In Chapter 4, I used a joint species distribution model to quantify levels of residual correlation between small mammal species abundance at two spatial extents. In the Conclusion, I identify useful future research to further our understanding of biodiversity responses to structural retention and the effect of retention patch size on forest biodiversity in the U.S. Pacific Northwest and other wood producing regions.

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CHAPTER 1

CARABID BEETLE FUNCTIONAL AND TAXONOMIC DIVERSITY RESPOND CONSISTENTLY TO SPATIAL ARRANGEMENT OF RETENTION TREES

Co-authors on the manuscript resulting from this chapter include: Andrew J. Kroll, Jake Verschuyl, Douglas A. Landis, and Gary J. Roloff

1.1 **Abstract**

Managing forests intensively for wood production can homogenize components of forest structure, which can alter species richness and functional composition of native species communities. Retention forestry, the practice of retaining structural elements of forests during timber harvest, has been shown to increase species diversity in recently harvested forests but its effect on functional diversity is less understood. We implemented an experimental study that manipulated retention tree patch size and location at a constant proportion of retention within harvested areas. We evaluated the effectiveness of five retention patterns at increasing the species and functional diversity within early seral, production forests in the Pacific Northwest U.S.A. Within these treatments, we tested effect of retention treatment on ground beetle (Family: Carabidae) taxonomic and functional richness and community dissimilarity. We found no evidence for differences in carabid species or functional richness among treatments when considering species present in both retention and clearcut areas of harvest units. However, within harvest units, we found evidence for lower taxonomic and functional variation between carabid communities present in retention and clearcut areas when retention was allocated to several small patches. Furthermore, the lower levels of functional variation between carabid communities in retention and harvested areas in the treatment containing several small retention patches was

primarily driven by lower abundances of specialized predators in small retention patches compared to aggregated or riparian-associated retention patches. We found that relative to single large or riparian-associated patches, small retention patches function similarly to clearcuts within harvested forests and several small patches does not increase species or functional richness. At levels of retention currently required in the Pacific Northwest, retention trees should be allocated to a single upland patch or split between riparian and upland patches to increase variation in ground beetle taxonomic and functional composition within clearcut forests.

1.2 **Introduction**

Intensive management to increase wood yield has homogenized components of forest structure in many regions of the world (Lindenmayer et al. 2012, Mori et al. 2015). Harvesting trees on short, even-aged rotations can reduce important resources such as the diversity of tree sizes and ages and abundance of standing and downed woody debris (Hayes et al. 2005, Ranius et al. 2014). Also, regeneration practices may reduce plant diversity shortly after harvest and shorten duration of the early seral stage (Demarais et al. 2017, Kroll et al. 2017). Structural retention, in which forest elements such as live and dead trees are retained during timber harvest, can increase ecological diversity within intensively managed forests (Gustafsson et al. 2012, Fedrowitz et al. 2014, Mori and Kitagawa 2014). Although operational efficiency and wood production per unit area are the primary objectives of intensive forest management, understanding how ecological communities respond to variation in retention tree patterns is critical to meet sustainability objectives.

Management of ecosystems often changes the composition of ecological communities without changing species richness (Hillebrand et al. 2018). Quantifying variation among ecological communities based on differences in species identities, known as taxonomic dissimilarity, can indicate if management practices shift species composition (Socolar et al. 2016). However, species within assemblages exhibit varying degrees of functional differentiation, an aspect of community composition that taxonomic dissimilarity does not capture. Diversity in morphological, physiological, and life history traits (collectively termed functional diversity) provides a different perspective on community diversity and assembly processes (McGill et al. 2006). For communities organized by competition among species, differences in species composition (i.e., taxonomic dissimilarity) may not reflect changes in functional capacity if species replacement is by functionally similar, competing species (Smith et al. 2013). In contrast, environmental filtering, whereby environmental factors (e.g., climate, habitat structure) inhibit species with certain traits, can result in consistent responses between taxonomic and functional community composition (Smith et al. 2013). Intensive management of ecosystems often acts as an environmental filter, excluding species with traits that depend on components of the ecosystem that are lost (Flynn et al. 2009, Gámez-Virués et al. 2015, Kroll et al. 2017). Therefore, functional and taxonomic richness and dissimilarity measures provide complementary insights into mechanisms structuring ecological communities and effect of management practices on ecological diversity (Flynn et al. 2009).

Carabid beetles are taxonomically well-described and exhibit a variety of habitat and diet specializations, making them a useful indicator taxon for effects of forest management practices on biodiversity (Pearce and Venier 2006, Hoekman et al. 2017). Although the ecosystem level effects of ground beetles in forests is not well understood, in agricultural systems ground beetles are associated with control of both animal (Krompe 1999) and plant pests through granivory (Carbonne et al. 2020). The functional diversity of ground beetle changes in relation to the functional composition of ground vegetation in open vegetation conditions (Pakeman and

Stockan 2014), and variation in canopy cover in managed forests (Spake et al. 2016). Studies indicate that retention forestry in the Pacific Northwest alters the taxonomic composition of ground beetle communities (Halaj et al. 2008, Baker et al. 2016), but information on whether retention practices also influence functional composition of carabid communities is lacking. Measuring the response of functional and taxonomic diversity of carabids to retention forestry can yield mechanistic insights into processes driving responses of this taxon to size and configuration of retained forest patches (Ding et al. 2013).

We measured responses of ground beetle (Family Carabidae) taxonomic and functional diversity to tree retention practices in forests of the U.S. Pacific Northwest managed for wood production. We compared carabid beetle taxonomic and functional richness, and levels of taxonomic and functional dissimilarity between retention patches and clearcut areas within harvest units in five different retention configurations implemented at a constant level of retention. When considering beetle communities pooled between retention and clearcut patches in treatment harvest units, we predicted that ground beetle taxonomic and functional richness would be highest in aggregated retention treatments, particularly the treatment with retention adjacent to riparian protection zones. When comparing ground beetle communities in retention and clearcut patches within treatments, we predicted lower taxonomic and functional dissimilarity in treatments with multiple, dispersed retention patches (Blanchet et al. 2013, Phillips et al. 2017). Both predictions are consistent with forest harvest acting as an environmental filter, where species with traits associated with older forests persist in large but not small retention patches. Alternatively, if interspecific competitive interactions are more important than environmental filtering in structuring post-harvest carabid communities, we predict higher taxonomic richness in multiple dispersed patches, but similar levels of functional richness across treatments, because dispersing retention throughout the harvested area allows functionally similar, competing species to coexist (Smith et al. 2013).

1.3 Methods

1.3.1 *Study Area*

We established 10 experimental blocks on production forestlands in the humid conifer forests of the Pacific Northwest (PNW), USA, between 122°W and 124°W, and N44.5° and N46.5° (Fig. 1.1). We sampled conifer plantations in the Cascade and Coast Ranges of western Oregon and Washington, USA (Fig. 1.1). The landscapes around blocks ranged from mostly commercial forest ownerships, where forests are primarily managed intensively for wood production, to mosaics of private and public ownership. In this region, forests managed intensively for wood production are in second or third tree harvest rotations. Public lands ranged from a mixture of conservation and wood production objectives (e.g., state-owned lands in Oregon) to federally protected (e.g., Wilderness Areas in Oregon). A large agricultural area (Willamette River Valley) separated the forested mountain ranges, and the Columbia River separated the two states (Figure 1.1). Elevations of study treatments ranged from 43 m in southwest Washington to 1,230 m in the Oregon Cascades and climate ranged from cooler and wetter in coastal Washington to warmer and drier in the southern Oregon Cascades (Table 1.1). Forests consisted primarily of coastal Douglas fir (*Psuedotsuga menziesii*), the dominant natural and commercial species, with western hemlock (*Tsuga heterophylla*) and western red cedar occurring on more mesic sites, and noble fir (*Abies procera*) at higher elevations. Bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubrum*) were the most common deciduous trees.

Intensive silviculture in the PNW generally employs clearcutting and subsequent planting of desirable native tree species after site preparation (e.g. herbicide application, burning) to temporarily control competing plants (Demarais et al. 2017). At the time of this research, forest harvesting policies in the region required retaining approximately 5 trees/ha and set the maximum continuous area that could be clearcut to ~55 ha in Oregon (Washington Forest Practices Board 2002, Oregon Department of Forestry 2018). Retention trees were intended to provide structure for wildlife, protect water quality and sensitive soils, and improve aesthetics of clearcut areas. With the exception of requirements in Washington that no part of a harvested area was >244 m from retention (Washington Forest Practices Board 2002), standard practice was to focus placement of retention patches along riparian protection zones, in large part because stream buffering and harvesting logistics are of primary focus when designing forest harvests.

1.3.2 *Experimental Design*

Within each of the 10 experimental blocks, we made random assignments of five treatments, with each harvest unit receiving only one treatment:

1. Riparian Aggregated (RA): All retention trees grouped together in one patch connected to an unharvested riparian protection zone.
2. Upland Aggregated (UA): All retention trees grouped together in one patch upslope from unharvested riparian protection zones that was either isolated within the harvest unit or on the edge next to recently regenerated forest (<10 years old).

3. Split (S): Half the retention trees grouped in a patch connected to unharvested riparian protection zone, and half in the upland portion of the stand, isolated within the harvest unit or on the edge next to recently regenerated forest.
4. Split with Snags (SS): Same as the Split (S) treatment but removed tops of half of retention trees, leaving the lower ~8m of the tree.
5. Dispersed with Snags (DS): Retention trees dispersed throughout the harvest unit in a minimum of four patches, each containing at least 15 green trees and an equal number of created snags.

Aside from changes in spatial pattern of retention, harvesting and other silvicultural treatments of each experimental unit followed typical practices in the region. Snag creation in retention patches primarily benefits cavity-nesting birds (Kroll et al. 2012), but also reduces canopy cover of retention patches and modifies ground cover used by ground-dwelling species like carabid beetles. Retention patches in the DS treatment initially had ≥15 trees per patch, based on previous studies of bird community responses to retention patch size (Linden et al. 2012), but extensive post-harvest tree mortality resulted in many DS retention patches containing <5 standing trees by the time sampling commenced. At the first year of sampling, time since post-harvest planting of tree seedlings ranged from two to five years.

1.3.3 *Carabid Sampling and Identification*

We sampled carabid beetles using pitfall traps from late May through early September (the dry season in the PNW) 1-4 times between 2017 and 2018. Although timing of trap deployment varied among treatments, we sampled each treatment once early (before June 1) and once later (after July 1). We deployed traps in treatments within a block during the same sampling period within 2-3 days. We sampled all 50 stands for at least one 28-day period. We missed sampling one RA treatment in 2017, and one S treatment in 2018. We sampled the three blocks in the Oregon Cascades for a single 28-day period in 2017 due to logistical constraints. We constructed pitfall traps from 5 cm diameter by 8 cm depth plastic storage cups, with a square cover suspended 1 cm above the cup to keep out rain and debris (Hoekman et al. 2017). We filled cups halfway with a 50:50 mix of propylene glycol and water and opened traps for two 28-day periods each summer. In each treatment harvest unit, we placed four traps in a retention patch(es) and four in the clearcut area (Figure 1.2). Because the spatial arrangement of retention patches varied by treatment, spatial arrangement of pitfall traps also varied by treatment (Figure 1.2). In RA and UA treatments, we located four traps 10 m from patch center in cardinal directions (Figure 1.2A). In S and SS treatments, we located two traps 10 m from patch center, 180° from one another in each of the two retention patches (resulting in 20 m spacing; Figure 1.2B). In DS, we placed one trap at the center of four small (~15 trees) retention patches (Figure 1.2C). In each treatment, we placed four traps in the clearcut area of each harvest unit in the same arrangement as the patch traps: in a grid of four in the aggregated treatments, paired in the two split treatments, and singly in the dispersed treatment (Figure 1.2). We located clearcut plots at a random distance and bearing from patch center; distances varied from 12 to 212 m (average=49.50, SD=27.50) with only one distance < 20 or > 200m.

After approximately 28 days (22-35, average=28, SD=1.7), we collected pitfall contents and separated carabid beetles from other traps contents. We quantified number of carabid beetles in each pitfall sample and identified them to species. We grouped unidentified species into morphospecies that included some species of *Harpalus* genus, two species of *Trachypachus*, and some individuals of the *Hypherpes* subgenus of *Pterostichus*. Although two widespread genera sampled, *Omus* and *Trachypachus*, were recently reclassified outside Carabidae, their families Cicindelinae and Trachypachidae form a monophyletic group with carabids and we included these in analyses. We deposited voucher specimens of each species in the Michigan State University Albert J. Cook Arthropod Research Collection.

Given that little life history information is available for most species of carabids in the PNW, we quantified the functional niche occupied by each species based on three morphometric traits that reflect their food resources: body length, mandible length, and width between mandibles at their base (Deroulers and Bretagnolle 2019). We randomly sampled five individuals from each collected species to measure traits, and for species represented by <5 individuals we measured all individuals collected. Using a Nikon stereomicroscope (Model SMZ1270, Nikon Instruments Inc., Melville, NY, USA), we measured body length (mm) as the longest distance from the base of the mandibles to anterior of the elytra, or abdomen, whichever extended further, excluding genitalia. We quantified mandible length (mm) by measuring the length of one mandible, defined as hinge of attachment to the tip, and mandible width, defined as the width (mm) between mandibles at the hinge of attachment. Quantifying mandible length and width at the hinge attachment point ensured that these measurements were not sensitive to position of the mandible at the time of measurement. To simplify the number of traits used, we combined mandible length and width into one trait value, the ratio of individual mandible length to the width between mandibles. A higher index value represented beetles with more elongated mandibles that are typically specialized predators such as members of the genera *Scaphinotus*, *Cychrus*, and *Promecognathus*, whereas lower index values typically represent more generalist feeders of the genera *Harpalus*, *Amara*, and *Pterostichus*.

1.3.4 *Vegetation Surveys*

In addition to estimating treatment effects on ground beetle communities we also related vegetation characteristics within treatment experimental units for a more mechanistic understanding of how the retention treatments influenced ground beetle communities. Botany field crews conducted surveys of ground vegetation and overstory canopy cover in each treatment in retention patches and adjacent clearcuts May -September 2018. Our beetle sample locations occurred at the approximate center of vegetation sampling arrays. Within 1m^2 plots spaced every 5-10 m along 21-48 m long transects (depending on treatment) oriented in cardinal directions from a center location, crews classified the area of each herbaceous species into 7 cover classes with midpoints of 0.5, 3, 15, 37.5, 62.5, 85, 97.5 percent. We grouped all fern and graminoid species into fern and grass functional groups, respectively. Crews measured overstory canopy cover with a spherical densiometer at each plot in four cardinal directions. Using these data, we calculated mean patch level canopy cover and Bray-Curtis dissimilarity of ground vegetation between separately pooled patch and clearcut vegetation plots for each treatment harvest unit (averaging cover class scores for each plant species).

1.3.5 *Analysis*

As an initial step, we characterized carabid community patterns at the harvest unit extent using non-metric multidimensional scaling and species presence-absence, because differing effort among harvest units prohibited abundance comparisons among these units. This NMDS procedure allowed us to visualize broad variation in carabid community composition among harvest units by treatment. We performed this ordination with all species captured >10 times and used Jaccard distance to quantify community dissimilarity.

Harvest Unit-extent Taxonomic and Functional Richness Indices – To account for varying effort in harvest units within sampling periods due to trap failure from vertebrate disturbance and to adjust for undetected species, we used the Chao1 species richness estimator (Chao 1987). To calculate harvest unit-level Chao1 estimates, we pooled all samples collected from a treatment harvest unit for a given sampling period (early or late) in a given year. This analysis yielded a taxonomic richness estimate for each harvest unit in each sampling period. We performed harvest unit-level NMDS and taxonomic richness estimation in the package Vegan version 2.5-6 (Oksanen et al 2019) in the R statistical computing platform version 3.6.1 (R Core Team 2019).

To quantify harvest unit-level functional richness for each collection period, we constructed a dendrogram of all sampled carabid species based on body length and mandible length to width ratio (Figure 1.3). We constructed the dendrogram from a matrix that represented pairwise functional dissimilarity among species using Gower's distance (Laliberte and Legendre 2010). We then used this dissimilarity matrix to construct a dendrogram with UPGMA clustering (Podani and Schmera 2006), and calculated harvest unit-level functional richness as total branch length connecting all species sampled from a harvest unit in a given sampling period (Flynn et al. 2009). Consistent with taxonomic richness, this yielded a functional richness estimate for each harvest unit in each sampling period. We calculated functional richness using the R package BAT version 2.1.1 (Cardoso et al. 2015).

We used harvest unit level taxonomic and functional richness as response variables in mixed effects regression models with retention treatment as an explanatory variable and harvest unit identity as a random effect to account for repeated measures from harvest units. For taxonomic richness, we rounded Chao1 species richness estimates to the nearest integer and fit the rounded estimates as a Poisson distributed response variable. We fit functional richness values as a Gaussian-distributed response. We included number of pitfall samples used to estimate harvest unit-level functional richness as an explanatory variable in the functional richness models because the functional richness estimates were not adjusted for effort. We also included sampling year and Julian date of pitfall deployment as explanatory variables.

Within-harvest unit Taxonomic and Functional Dissimilarity Indices –To calculate within-harvest unit taxonomic and functional dissimilarity between patches and clearcuts by treatment, we separately pooled patch and clearcut pitfalls collected from a harvest unit for a 28 day period (Figure 1.2), after subsampling to ensure that pooled samples were based off the same number of traps (in several instances, individual trap failure occurred). We then calculated Bray-Curtis dissimilarity (Bray and Curtis 1957) between these pooled retention patch and clearcut samples using the package Betapart version 1.5.1 (Baselga and Orme 2012). We used Trait Probability Density (TPD) to quantify functional dissimilarity of carabid communities within harvest units. TPD represents probability of observing specific traits when sampling a community, and accounts for relative abundances of species when calculating the functional volume that a community encompasses (Carmona et al. 2016). We derived TPDs from our beetle trait measurements of body length and mandible length to width ratio, a proxy for the foraging niche of each species. We quantified within-harvest unit functional dissimilarity by creating a TPD for the same pooled patch and clearcut samples used to calculate within-harvest unit taxonomic dissimilarity and calculated dissimilarity as one minus the overlap of pooled patch and clearcut TPDs (Carmona et al. 2019).

We fit within-harvest unit taxonomic and functional dissimilarity as beta-distributed response variables in mixed effects regression models with a logit link function, as these values ranged between 0 and 1 (Ferrari and Cribari-Neto 2004). Consistent with richness models, we included retention treatment, date of trap deployment, and sampling year as explanatory variables with a harvest unit level random effect. To explore how differences in vegetation characteristics between treatments affect carabid community responses to retention treatments, we assessed the effect of canopy cover and understory vegetation variables on carabid community dissimilarity in beta regression models independent of retention treatment. In beta-distributed models we also fit the number of samples pooled as a dispersion parameter.

Sampling Trait Values from TPDs–To assess how differences in trait values affect within-harvest unit functional dissimilarity patterns, we sampled trait values from TPDs and related sampled traits to treatment and cover type (patch or clearcut). When sampling a TPD, the probability of sampling a specific trait is proportional to abundance of that trait in the community (Carmona et al. 2019). To perform trait sampling, we generated a TPD for each individual pitfall that contained carabids and randomly drew a body length and mandible ratio value from the resultant TPD. In addition to treatment harvest units, we also derived TPDs and sampled trait values from carabid community samples collected from nine rotation-aged (~50 years old) forests in 9 of the 10 experimental blocks to understand how trait values from treatments compared to those from closed-canopy forests in the vicinity of treatment harvest units. We sampled these rotation-aged forests in the same configuration as patches in aggregated retention treatments (Figure 1.2A). We fit sampled trait values as Gaussian distributed responses in mixed effects regression models with retention treatment, cover type (i.e., patch or clearcut), and an interaction between treatment and cover type as explanatory variables with a harvest unit level random effect. We also included trap deployment date and year as explanatory variables.

We deemed effects of retention treatment or other regression parameters on a beetle community variable significant if 95% confidence intervals excluded zero. We fit Gaussian and Poisson distributed models in R package lme4 version 1.1.23 (Bates et al. 2015), beta regression models in R package glmmTMB version 1.0.2.1 (Brooks et al. 2017) and assessed the residuals of fitted models using nonparametric simulation tests in R package DHARMa version 0.3.2 (Hartig 2019). We generated all TPDs, calculated functional dissimilarity metrics within and among harvest units, and sampled trait values from TPDs using the R package TPD version 1.1.0 (Carmona et al. 2019).

1.4 Results

We deployed 664 and 784 pitfall traps in 49 harvest units in 2017 and 2018, respectively. After accounting for 12% trap failure rate and removing 61 traps that did not collect carabids, our beetle community data included 1,184 pitfall samples for two 28-day periods each year; 512 from 2017 and 672 from 2018 (Table 1.2). The average number of pitfall samples per treatment across all sampling sessions was 23.7 (range = 5-30; SD = 5.1), and after each 28-day period an average of 6.6 pitfalls were collected per harvest unit out of the original eight deployed.

We collected 10,538 individuals of 47 species (5 morphospecies) from 21 identifiable genera (Table 1.3). The genera *Harpalus*, *Omus*, *Pterostichus*, *Scaphinotus*, and *Trachypachus* dominated our samples (Table 1.3). Average number of individual carabids in a pitfall sample was 8.95, with an average of 3 species per pitfall sample (Table 1.2). Average abundance of a beetle species in a pitfall sample was 2.85 individuals, and species occurred in 67 pitfall samples and 6.7 experimental harvest units on average. Captures included five non-native species, and most were uncommon: *Nebria brevicollis* (16 individuals, 10 harvest units), *Calathus fuscipes* (69 individuals, 8 harvest units), *Carabus nemoralis* (10 individuals, 2 harvest units), *Anisodactylus trinotatus* (18 individuals, 7 harvest units) and *Harpalus aeneus* (75 individuals, 4 harvest units). For functional traits, average body length by species was 11 mm (range = 2.77 - 23.30), and mean mandible length to width ratio was 1.03 (range = 0.56 - 1.82; Table 1.3). The first axis of the species-level NMDS ordination indicated a transition from mostly smaller-bodied open area species (*Amara spp*., *Harpalus spp*., *Syntomus americanus*) to mostly larger-bodied species more common in closed canopy forests, while the second axis captured variation in community composition across a temperature and elevation gradient (Figure 1.4). Rotation-aged forests tended to separate from treatment harvest units by having a greater proportion of larger-bodied forest species (Figure 1.4).

Sample size for all harvest unit-level mixed effects models of taxonomic and functional richness and dissimilarity was 178 (out of a potential 200, if we sampled all harvest units evenly). We did not find a difference in Chao1 taxonomic or functional richness among treatments (Fig 1.5A, B). Effect sizes, using the RA treatment for comparison, were low and highly variable for both taxonomic and functional richness (Table 1.4). Taxonomic richness within harvest units was not affected by sampling date (β = -0.04, 95% CI = -0.09—0.01) or sampling year (β = -0.07, 95% CI = -0.16—0.03), whereas functional richness declined later in the sampling (dry) season (β = -0.15, 95% CI = -0.19 — -0.11) and in the second year of sampling (β = -0.11, 95% CI = -0.19 — -0.03).

Within-harvest unit taxonomic dissimilarity (Bray-Curtis) for each 28-day sampling period ranged from 0.09 to 0.99, and functional dissimilarity ranged from 0.04 to 0.99. We found low variation in within harvest unit taxonomic and functional dissimilarity among treatments except for DS, which had consistently lower within-harvest unit taxonomic and functional dissimilarity compared to other treatments ($\text{Tax}_{\text{dissim}}$ β = -0.66, 95% CI = -1.11— -0.21; $\text{Fun}_{\text{dissim}}$ β = -0.68, 95% CI = -1.19 — -0.17; Table 1.4). The negative effect of DS treatment indicates that carabid communities, on average, were more taxonomically and functionally homogeneous between patches and clearcuts in several small isolated patches compared to samples collected from other treatments (Fig 1.5C, D). Taxonomic dissimilarity between patches and clearcuts within harvest units declined later in the sampling season (β = -0.15, 95% CI = -0.28—0.-02) but not across years (β = -0.04, 95% CI = -0.30—0.22). Functional dissimilarity was not associated with date (β = -0.09, 95% CI = -0.22—0.04) or year (β = -0.23, 95% CI = -0.49—0.02). We found that average canopy cover of retention patches had a weak but positive effect on taxonomic dissimilarity of carabids (β = 0.29, 95% CI = 0.09—0.50, Figure 1.6) within harvest units whereas dissimilarity of herb species had no effect (β = 0.14, 95% CI = -0.09—0.36; Table 1.4). This same pattern occurred for functional dissimilarity, which increased marginally with increasing canopy cover of patches (β = 0.30, 95% CI = 0.13—0.47, Figure 1.7) but did not respond to herbaceous communities (β = 0.15, 95% CI = -0.03—0.33, Table 1.4). Our within-harvest unit dissimilarity analyses revealed that carabid communities in the DS treatment were more redundant between patches and clearcuts, both taxonomically and functionally, when compared to levels of dissimilarity found in other treatments; and that this relationship was at least partly driven by lower patch canopy cover.

Our analysis of changes in trait values among treatments included 1,269 TPDs generated from each pitfall sample collected, 1,184 in the 50 treatment harvest units and 85 samples collected in 9 rotation-aged forests. We generally found higher estimated trait values in retention patches compared to clearcuts within harvest units, but this relationship was only consistent for mandible length to width ratio (β = 0.11, 95% CI = 0.06—0.16, Figure 1.7B), not body length (β = 0.38, 95% CI = -0.92:1.68:, Fig. 1.7a). Mandible length to width ratios among harvest units were lower in the DS treatment compared to other treatments (β = -0.08, 95% CI = -0.15—-0.01, Figure 1.7B), and the 95% CI for the interaction between plot type (patch or clearcut) and the DS treatment on mandibular characteristics narrowly included zero (β = -0.06, 95% CI = -0.14—0.00, Fig. 7b). This result indicates that mandible length to width ratios were lower in the DS treatment and not different in retention patches compared to clearcut plots in this treatment (Figure 1.7B). The effect was similar but not as strong for body size (Figure 1.7A). Hence, lower levels of functional dissimilarity between retention patches and clearcuts in the DS treatment were primarily driven by lower variation in mandible characteristics.

1.5 Discussion

Intensive management of forests, where trees are often managed on short, even-aged rotations, often reduces ecological variation (Mori et al. 2015). Forest managers may use structural retention during forest harvests to achieve conservation outcomes, including creating structural heterogeneity within harvest units. Community diversity metrics can assess effects of forest management practices on spatial variation in ecological communities (Baker et al. 2015), with trait-based approaches yielding more insights on process and ecosystem function (McGill et al. 2006). We evaluated how carabid beetle communities responded to multiple spatial patterns of retention trees and contrary to our expectations, did not find support for higher ground beetle species or functional trait richness in harvest units containing larger aggregated patches of retention trees compared to other retention patterns. However, at the harvest unit scale we found strong evidence for taxonomically and functionally homogenized carabid communities in the treatment containing several small, isolated retention patches compared to aggregated and split retention treatments. Carabid communities in these dispersed retention patches were more redundant with surrounding clearcuts, whereas larger upland and riparian-associated patches supported ground beetle communities that differed from surrounding clearcuts. These findings indicate that aggregated retention can increase spatial variation in carabid beetle communities within clearcut forests throughout the Pacific Northwest, one of the major wood producing regions of the world.

The discrepancy between our findings for richness (no treatment effect) and dissimilarity (evidence of a treatment effect) metrics highlights the importance of metric choice for inference on the effects of management on community diversity. Unlike richness estimates, taxonomic and functional community dissimilarity measures we used incorporated species abundances (Carmona et al. 2016). Our results indicate that while retention patches shared species with adjacent clearcuts, changes in the relative abundances of species with varying functional traits affected differences in beetle community composition, with dispersed retention providing the least heterogeneity between patches and clearcuts. This finding is consistent with previous studies relating ground beetle communities to woody debris retention, where the abundance of species within different functional groups varied in response to levels of coarse woody debris retention but species richness and diversity did not vary (Grodsky et al. 2020). Thus, our results underscore the shortcomings of species richness as a single measure of diversity because it fails to capture abundance-based variations in community composition (Hillebrand et al. 2018). However, our approach of using richness and dissimilarity metrics together demonstrated not only that retention and clearcut carabid communities were more similar for treatments with dispersed, small retention patches (<15 trees), but also that distributing patches throughout the harvest unit to create spatial heterogeneity did not result in higher species or functional richness in harvested forests.

Lower variation in the carabid beetle community in the dispersed treatment was not surprising given that overstory canopy cover of retention patches was <10%. Our regression models relating ground beetle community composition to vegetation suggested that differences in canopy cover in retention patches were related to taxonomic and functional variation in ground beetle communities, but variation in this relationship was high (Figure 1.6). This weak relationship indicates that differences in canopy cover alone not not a reliable indicator of ground beetle community composition. However, this relationship is consistent with studies that found functional diversity of ground beetles more strongly related to canopy cover variation than understory vegetation characteristics in managed forests (Spake et al. 2016). Studies from western North American boreal forests found combinations of dispersed and aggregated retention resulted in more diverse saproxylic beetle and plant communities than dispersed retention alone (Lee et al. 2017, Franklin et al. 2018), further emphasizing the importance of using retention forestry practices to create variation in canopy cover. Using mean patch size within the UA retention treatment as a guide, retention patches with ~90 trees maintained sufficient canopy cover to increase variation in ground beetle community composition in clearcut forests. Our results further suggest that upland patches with 44 trees, the mean number of trees per patch in the two split retention treatments, may increase diversity of carabid beetles in upland areas of clearcuts, but we caution that this finding is confounded by potential contributions of riparian associated retention to species composition in split retention treatments.

Our NMDS ordination suggested differences in carabid community composition between riparian and upland retention treatments, with overlap between larger upland and split retention patches and rotation-aged forest communities (Figure 1.4). This result suggests that limiting the location of retention practices adjacent to riparian buffers alone may not conserve the complete ground beetle community in the Pacific Northwest, consistent with studies from other timber producing regions of the world (Baker et al. 2006). Other studies noted importance of structural connectivity of retention patches in driving variation in ground beetle community composition across managed forest landscapes (Blanchet et al. 2013). Connectivity with riparian buffers may have contributed to similar levels of dissimilarity in riparian-associated treatments observed in our study. However, comparable levels of dissimilarity in upland aggregated retention to riparian associated retention suggest that patches do not need to be connected to adjacent forest to support ground beetle communities with different composition from nearby clearcut areas. From a functional diversity perspective, our results indicate that aggregated and riparian associated retention supported carabid beetle species with traits more similar to closed-canopy forests (Figure 1.7). Hence, although retention forestry in clearcuts does not conserve late seral carabid communities in the Pacific Northwest even at higher levels of retention (Halaj et al. 2008), our results suggest that some functional and taxonomic characteristics of later seral carabid communities, like specialized carnivores, can be conserved with aggregated retention.

Previous studies focused on taxonomic dissimilarity between ground beetle communites in retention patches and surrounding clearcuts in the Pacific Northwest regardless of patch size (Baker et al. 2015, 2016). Our results demonstrate that functional dissimilarity within harvest units is lower for several small patches compared to more aggregated configurations at low retention levels (>15% basal area). We generally interpret dissimilarity between retention patches and clearcuts as an indication of retention patch ability to ‘lifeboat’ forest carabid species into the next forest rotation, with higher dissimilarity indicating higher capacity to lifeboat.

However, larger retention patches may also influence species composition of clearcuts surrounding patches (termed forest influence, Baker et al. 2013), which could reduce dissimilarity between patches and clearcuts. Higher dissimilarity in aggregated treatments suggests that lifeboating of retention patches contributes more to carabid diversity at the retention levels we investigated, but functional trait values for carabid communities in clearcuts differed slightly across treatments (Figure 1.7). This pattern suggests that larger and riparian associated retention patches may influence functional composition of carabid communities in nearby clearcuts, meaning that larger retention patches may have a larger effect on carabid diversity in recent clearcuts than indicated by our dissimilarity measures.

A consistent response of both taxonomic and functional diversity, as we observed, is suggestive of an environmental filter that inhibits species with certain functional traits from persisting in clearcuts and dispersed treatments (Smith et al. 2013). In our study system, specialized feeders with longer mandibles occurred in larger retention patches, whereas species with more widely spaced mandibles occurred in clearcuts and dispersed retention patches (Figure 1.4B). Although the functional niche of carabids is not typically quantified using body size and mandible structure alone (Spake et al. 2016, Pakeman and Stockan 2014), species with shorter mandibles that are broad basally (such as those of the genus *Amara* and *Harpalus*) include more seeds in their diet (Forsythe 1982). Species with longer mandibles are typically specialist carnivores (such as members of the genus *Scaphinotus*, *Cychrus*, and *Promecognathus*). Hence, carabid responses to retention may reflect distribution of food resources, with dispersed patches supporting generalists and seed feeders that are also common in clearcuts, and larger patches supporting different feeding specializations. In this sense, our conclusions follow the broader interpretation of an environmental filter, which can act indirectly on a species by altering food resources, as opposed to directly through physiological tolerance to abiotic conditions (Cadotte and Tucker 2017). Other studies found this relationship between retention patch area and trophic level for beetles (Bouchard and Hébert 2016) and more specifically for predaceous beetles (Lee et al. 2015), suggesting that such filters are common on managed forest landscapes. One caveat to our conclusions is that pitfall trapping is more effective at sampling larger-bodied, predaceous species (Knapp et al. 2020), but this bias would only affect our inference regarding functional variation in carabid communities if detection of species differed between patch and clearcut areas.

Although our results suggest that aggregated retention can support a different carabid beetle community than that found in clearcuts, this study occurred within five years following tree planting in harvested areas, limiting our ability to detect longer-term treatment effects. Other studies demonstrated a time-lagged response of carabid beetle communities to logging, where presence of forest interior species declined in retention aggregates with increasing time since logging (3-5 years), even in larger patches (Matveinen-Huju et al. 2009). However, other more regional studies demonstrated that carabid community dissimilarity between patches and clearcuts remained high, even 20 years following harvest (Baker et al. 2015), although patch size was not considered. The large decline in functional richness between years in our study could indicate that the functional composition of carabid species in larger retention patches could be ephemeral. Monitoring of carabid community responses to retention strategies through time will provide a better understanding of how retention pattern affects community composition beyond the early seral stage. Furthermore, although carabid beetles are considered an indicator taxon (Pearce and Venier 2006), quantifying responses of other animal taxa to retention strategies is essential for a more complete understanding of how retention forestry contributes to the biodiversity on managed forests in the Pacific Northwest.

In addition to retention pattern, other processes likely affect levels of community dissimilarity between retention patches and clearcuts. Factors such as landscape composition (Barbaro et al. 2007) and land use history (Neumann et al. 2017) influence forest carabid beetle communities and likely contribute to the large within treatment variability we observed in this study. We sampled a wide range of environmental conditions present on managed forests in the Pacific Northwest and landscape composition, climate, and topography strongly varied across blocks and forest harvest units. Despite the presence of these potentially confounding factors, we identified consistently more homogeneous ground beetle communities in dispersed upland retention and thus, managers should aggregate retention when given a choice to promote carabid diversity. For landscape-level biodiversity, decisions on retention practices may be most important for landscapes lacking late seral forests, where the only opportunity to conserve closed canopy carabid species in upland areas is in larger patches embedded in a matrix of forests continuously managed on short, even-aged rotations. As functional diversity responded similarly to taxonomic diversity, aggregated retention strategies may not only conserve native carabid species diversity, but also promote varied functions they perform in forest ecosystems.

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APPENDIX

Table 1.1

Mean climate and elevation (m) for each experimental block (see Figure 1.1), northwest Oregon and southwestern Washington, USA, 2017-2018. Climate variables are PRISM 30-year annual averages of precipitation in mm (MeanPrecip), and maximum (MaxTemp) and minimum (MnTemp) temperatures in °C.

Block	**MeanPrecip**	**MaxTemp**	**MnTemp**	**Elevation**
1	1893.19	16.37	10.83	296.83
2	2646.71	15.07	10.1	74.01
3	1939.23	14.2	9.27	606.14
4	1834.91	14.82	9.71	335.79
5	2493.58	13.15	8.37	785.61
6	1797.8	15.01	9.6	431.96
7	2733.67	12.54	8.18	758.57
8	2552.58	13.52	8.35	868.27
9	1989.52	15.71	10.94	159.05
10	3525.35	14.12	9.32	646.13

Table 1.2

Pitfall trapping effort and carabid beetle captures by retention treatment and year, northwest Oregon and southwestern Washington, USA, 2017-2018. Traps = number of pitfall traps collected (average), Individuals = number of individual carabids collected (average), Species = number of carabid species collected (average), Species/Trap Sample = average carabid species per collected trap, and Individuals/Trap Sample = average number of individuals per collected trap.

	Traps		Individuals		Species		Species/Trap Sample		Individuals/Trap Sample	
Treatment[a]	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
RA	104 (10.4)	141 (14.1)	865 (96)	858 (86)	31 (12)	27 (10)	3.2	2.5	8.3	6.1
UA	108 (10.8)	140 (14.0)	1,030 (103)	1,357 (135)	32 (10)	30 (11)	3.2	2.9	9.5	9.7
S	98 (9.8)	115 (11.5)	650 (65)	836 (92)	30 (10)	30 (11)	3.0	2.7	6.6	7.2
SS	98 (9.8)	138 (13.8)	1,129 (112)	916 (91)	33 (11)	31 (12)	3.5	2.7	11.5	6.6
DS	104 (10.4)	138 (13.8)	1,130 (91)	1,767 (176)	36 (11)	31 (10)	3.5	2.7	10.9	12.8
Total	512 (10.2)	672 (13.4)	4,804 (98)	5,734 (117)	42 (11)	41 (11)	3.3	2.7	9.4	8.5

[a] RA= Riparian Aggregated, UA = Upland Aggregated, S = Split, SS = Split with Snags, DS = dispersed with snags

Table 1.3

Traits and capture summaries for the 48 species of carabid beetles captured in pitfall traps, northwest Oregon and southwestern Washington, USA, 2017-2018. Individuals are the total number of individuals sampled, and the last three columns are the number of blocks, stands, and samples in which the species were detected, respectively.

Species	**Body length (mm)**	**Mandible length (mm)**	**Mandible width (mm)**	**Ratio of length to width**	**Indiv-iduals**	**Blocks**	**Stands**	**Samples**
Agonum muelleri	8.28	0.87	0.76	1.15	4	2	3	4
Amara conflata	9.95	1.12	1.31	0.86	181	10	24	67
Amara impuncticollis	7.79	0.77	0.97	0.79	245	8	18	55
Amara obesa	11.57	1.44	1.39	1.03	2	1	1	1
Amara patruelis	7.97	0.86	1.00	0.85	68	9	17	27
Amara sanjuanensis	7.64	0.79	0.84	0.94	12	5	7	10
Amara spp	6.06	0.69	0.70	0.98	5	2	2	2
Anisodactylus binotatus	11.65	1.37	1.66	0.83	18	5	7	11
Calathus fuscipes	11.87	1.24	1.14	1.06	69	5	8	21
Carabus nemoralis	22.83	2.89	2.28	1.29	10	2	2	4
Carabus taedatus	20.38	2.41	2.02	1.19	162	2	10	84

Table 1.3 Continued

Cychrus tuberculatus	20.97	3.04	2.25	1.42	243	10	41	171
Harpalus aeneus	11.02	1.78	1.99	0.89	75	2	4	13
Harpalus animosus	12.78	1.93	2.29	0.84	63	4	8	37
Harpalus cordifer	8.39	1.19	1.46	0.82	168	10	28	94
Harpalus spp	9.40	1.28	1.49	0.86	467	10	44	245
Lebia viridis	4.00	0.48	0.51	0.95	1	1	1	1
Leistus virginiosus	8.96	0.77	1.38	0.56	10	5	8	9
Microlestes nigrinnis	2.83	0.33	0.40	0.81	1	1	1	1
Nebria brevicollis	11.31	1.23	1.56	0.80	16	9	10	12
Notiophilus sylvaticus	4.88	0.52	0.59	0.89	19	9	15	18
Omus audouini	15.13	2.88	2.66	1.09	940	4	10	90
Omus dejeani	19.52	4.26	4.01	1.07	1050	8	33	383
Platynus ovipennis	10.89	1.22	1.18	1.04	7	5	6	7
Promecognathus crassus	11.77	3.01	2.03	1.49	127	9	24	90

Table 1.3 Continued

Pterostichus adstrictus	11.49	1.33	1.19	1.12	6	1	2	5
Pterostichus algidus	13.08	1.63	1.59	1.03	2296	10	37	421
Pterostichus amethystinus	12.93	1.60	1.64	0.98	45	6	20	43
Pterostichus crenicollis	17.29	2.39	2.10	1.14	46	7	9	31
Pterostichus herculaneus	14.06	1.86	1.88	0.99	666	6	23	272
Pterostichus infernalis	9.17	1.21	1.12	1.08	384	3	14	147
Pterostichus lama	23.30	3.62	3.60	1.03	529	10	44	336
Pterostichus nigracaeruleus	11.02	1.37	1.15	1.19	1	1	1	1
Pterostichus pumilis	8.41	1.12	0.99	1.13	523	7	34	246
Pterostichus rothi	10.16	1.50	1.28	1.17	2	2	2	2
Pterostichus spp	12.63	1.49	1.39	1.07	19	8	13	16
Scaphinotus angulatus	17.54	2.89	1.59	1.82	9	5	7	9

Table 1.3 Continued

Scaphinotus angusticollis	19.88	2.35	1.66	1.42	940	8	20	152
Scaphinotus marginatus	12.73	1.73	1.04	1.67	124	8	24	78
Syntomus americanus	2.91	0.33	0.35	0.96	54	10	20	39
Tanystoma sulcata	10.67	1.13	1.10	1.02	2	1	2	2
Trachypachus holmbergi	4.61	0.41	0.59	0.71	1230	10	39	268
Unknown2	3.03	0.22	0.22	0.98	2	1	1	1
Unknown3	5.64	0.64	0.70	0.91	3	1	1	2
Unknown4	2.77	0.27	0.25	1.07	1	1	1	1
Unknown5	4.85	0.44	0.51	0.86	1	1	1	1
Zacotus mathewsi	15.13	1.70	1.73	0.99	367	10	35	186

Table 1.4

Pitfall trapping effort and carabid beetle captures by retention treatment and year, northwest Oregon and southwestern Washington, USA, 2017-2018. Traps = number of pitfall traps collected (average), Individuals = number of individual carabids collected (average), Species = number of carabid species collected (average), Species/Trap Sample = average carabid species per collected trap, and Individuals/Trap Sample = average number of individuals per collected trap.

Response	UA	S	SS	DS	MnCan	d_{herb}
SRich	-0.05 (0.17)	-0.08 (0.17)	0.00 (0.17)	-0.09 (0.17)	-	-
FRich	-0.03 (0.13)	-0.03 (0.13)	-0.01 (0.13)	-0.13 (0.13)	-	-
Tax_{dissim}	-0.08 (0.23)	0.11 (0.24)	-0.11 (0.23)	-0.66 (0.23)*	0.26 (0.07)*	0.14 (0.08)
Fun_{dissim}	0.05 (0.25)	0.21 (0.26)	0.03 (0.26)	-0.68 (0.26)*	0.25 (0.09)*	0.12 (0.09)

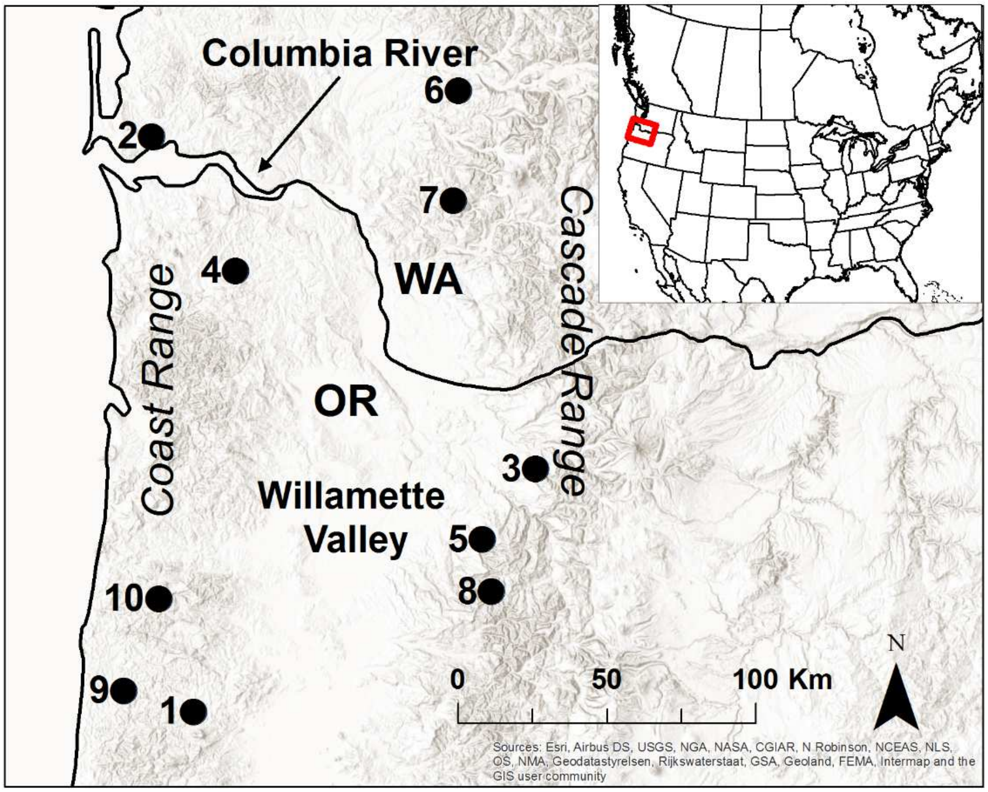

Figure 1.1

Study area in western Oregon (OR) and Washington (WA), USA, depicting 10 experimental blocks (black filled circles), each containing five structural retention treatments, where sampling of carabid beetle communities occurred in 2017 and 2018. Block numbering corresponds to Block in Table 1.1, which summarizes climate and elevation within blocks.

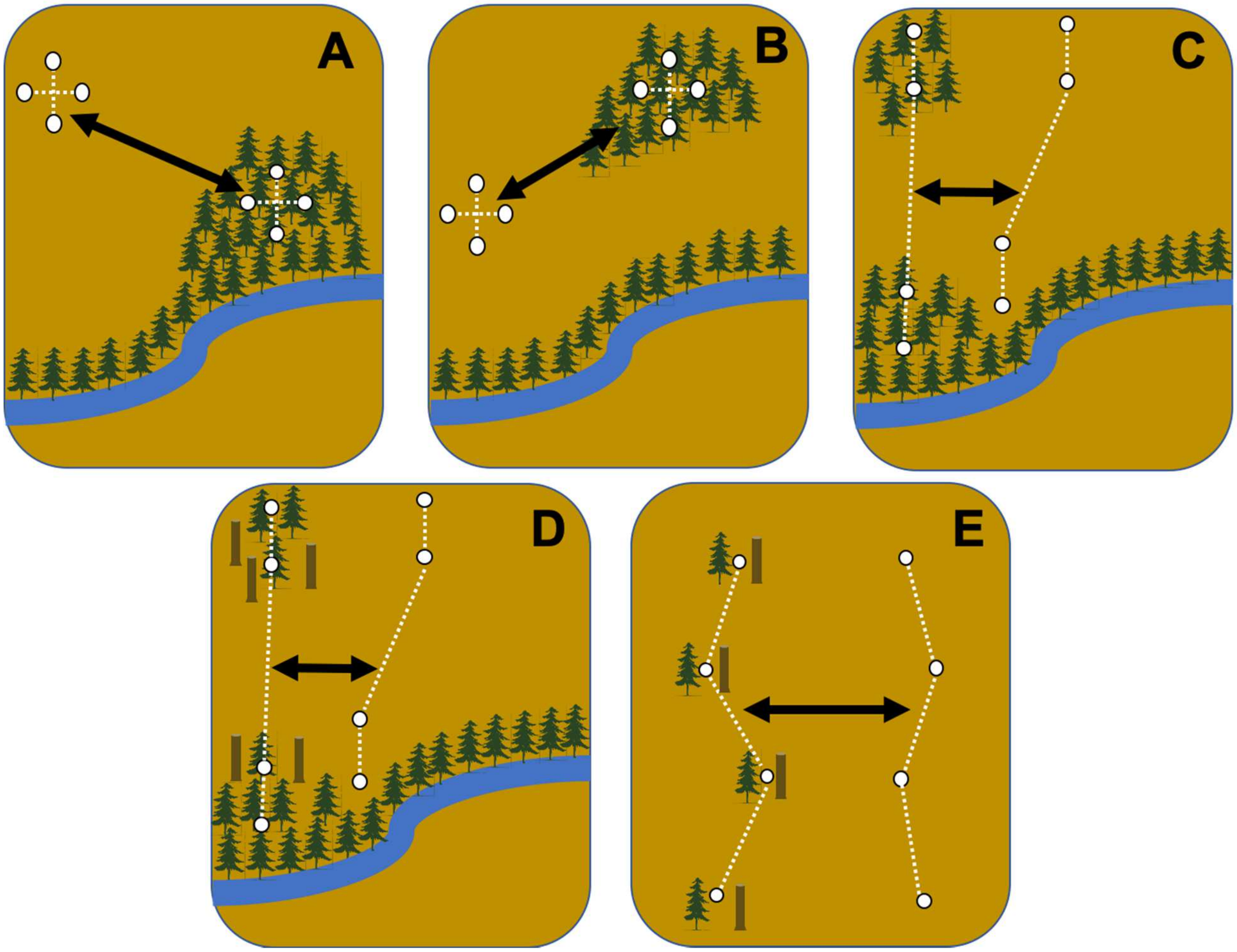

Figure 1.2

Schematic of pitfall trap arrangements used to sample carabid beetle communities in structural retention treatments in clearcut area of northwest Oregon and southwestern Washington, USA, 2017-2018. White filled circles depict pitfall trap sites and dashed white lines denote pooling of samples for calculating within-harvest unit dissimilarity metrics (black arrows). (A) Riparian Aggregated (RA), (B) Upland Aggregated (UA), (C) Split (S), (D) Split with Snags (SS) treatments, and (E) Dispersed with Snags (DS). Treatments with only upland retention (UA and DS) did not always contain riparian zones if not streams were present.

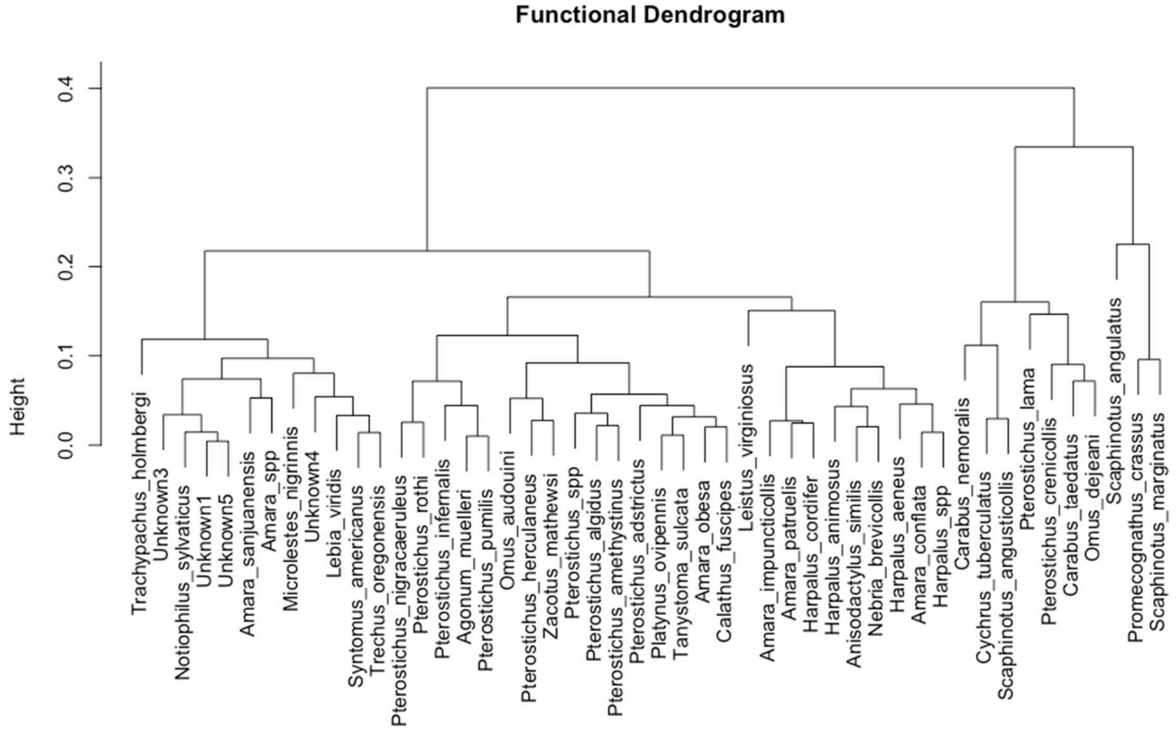

Figure 1.3

Functional dendrogram for all carabid species and morphospecies collected in 50 clearcut harvest units with varying structural retention in northwest Oregon and southwestern Washington, USA, 2017-2018. Dendrogram is constructed from pairwise dissimilarity between each species based on body size and mandible length to width ratio using Gower's distance and the UPGMA clustering algorithm. Height = branch length of dendrogram.

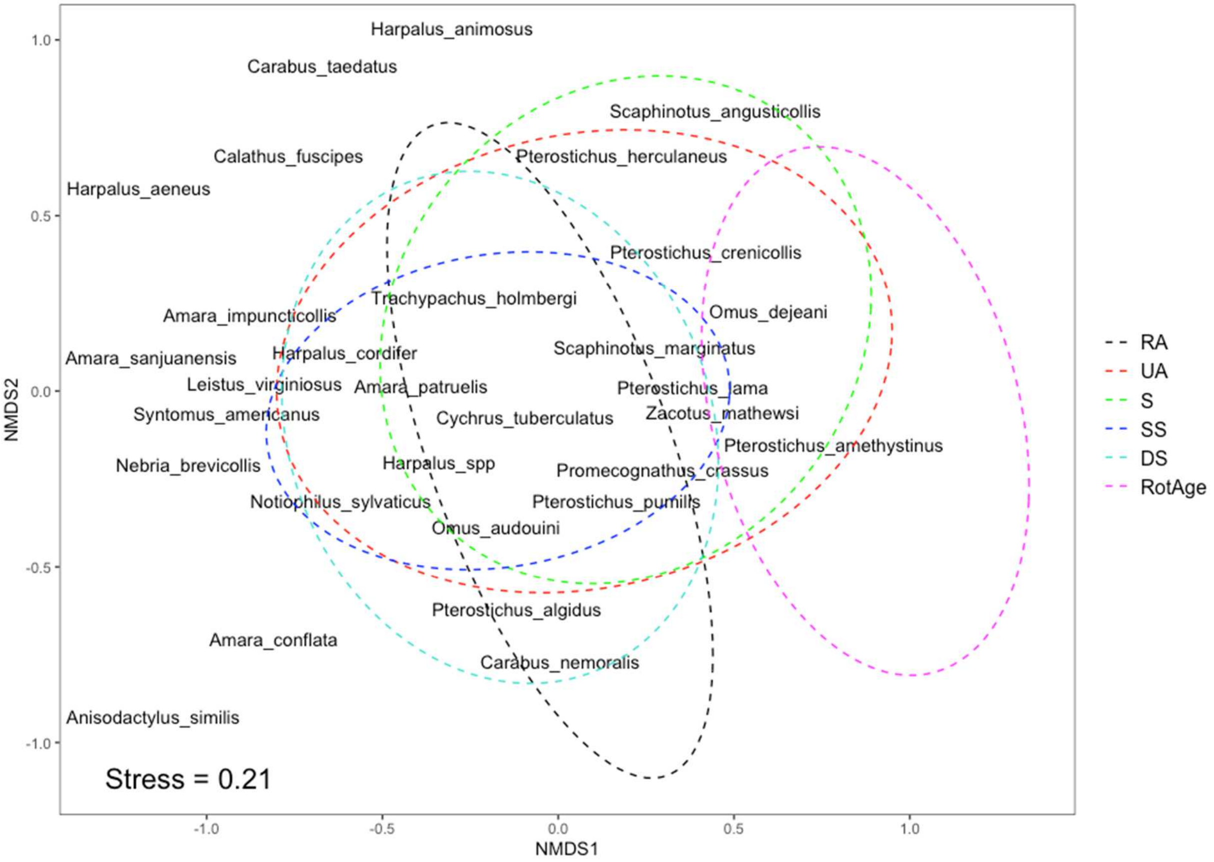

Figure 1.4

Nonmetric multidimensional scaling ordination plot of carabid species occurrence within 50 clearcut forests containing different levels of structural retention and 9 rotation-aged forest forests, northwest Oregon and southwestern Washington, USA, 2017-2018. Ellipses represent location of retention treatments within ordination space (95% ellipses) and species names represent the location of species with jittering for readability. RA = Riparian Aggregated, UA = Upland Aggregated, S = Split, SS = Split with Snags, DS = Dispersed with Snags, and RotAge = Rotation-aged Forest.

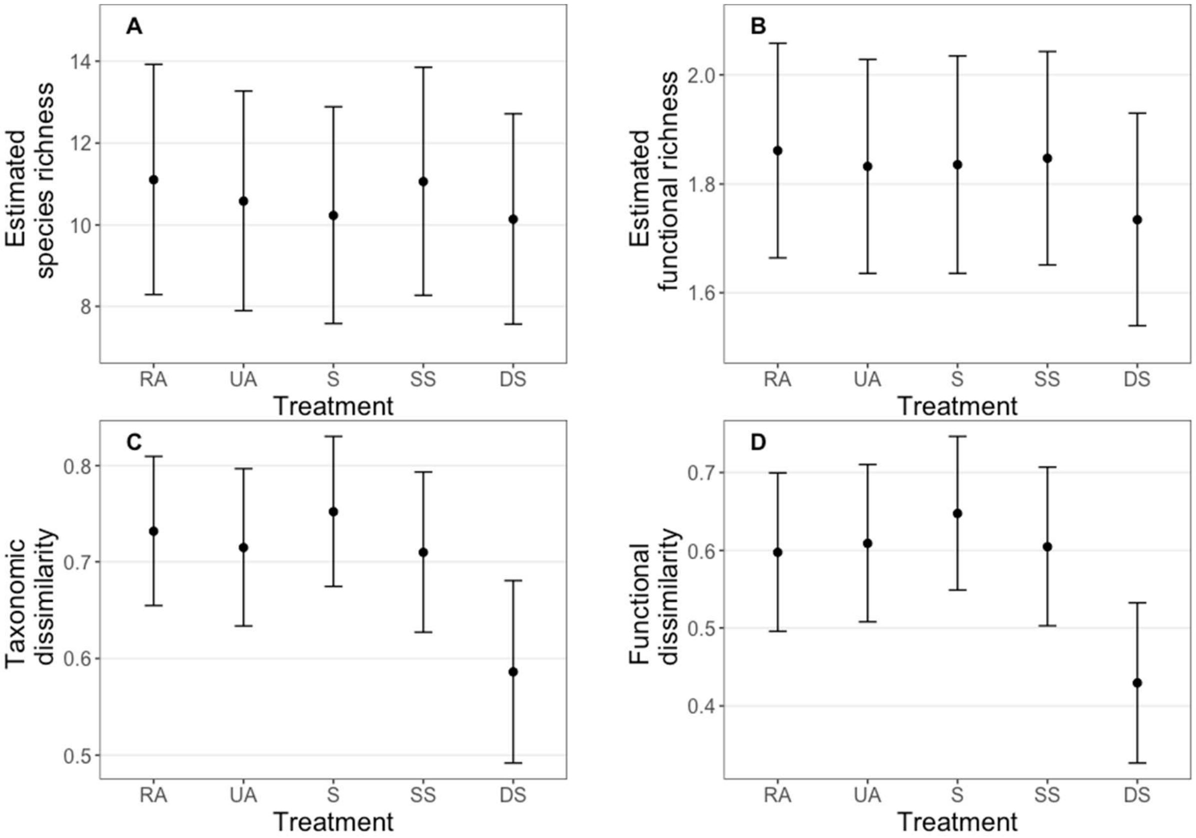

Figure 1.5

Predicted (mean and 95% confidence interval) clearcut harvest unit-level of species (A) and functional richness (B) of carabid beetles by structural retention treatment. Predicted (mean and 95% confidence interval) taxonomic (C) and functional (D) dissimilarity of carabid beetles between retention patches and clearcuts within harvest units by retention treatment. Year and Julian date of sampling were included in each model, and year was set to 2018 and Julian date to 136 for predictions (136 represented the earliest value for all sample collection periods). Sampling conducted in western Oregon and Washington retention treatment harvest units, 2017 and 2018. RA = Riparian Aggregated, UA = Upland Aggregated, S = Split, SS = Split with Snags, and DS = Dispersed with Snags.

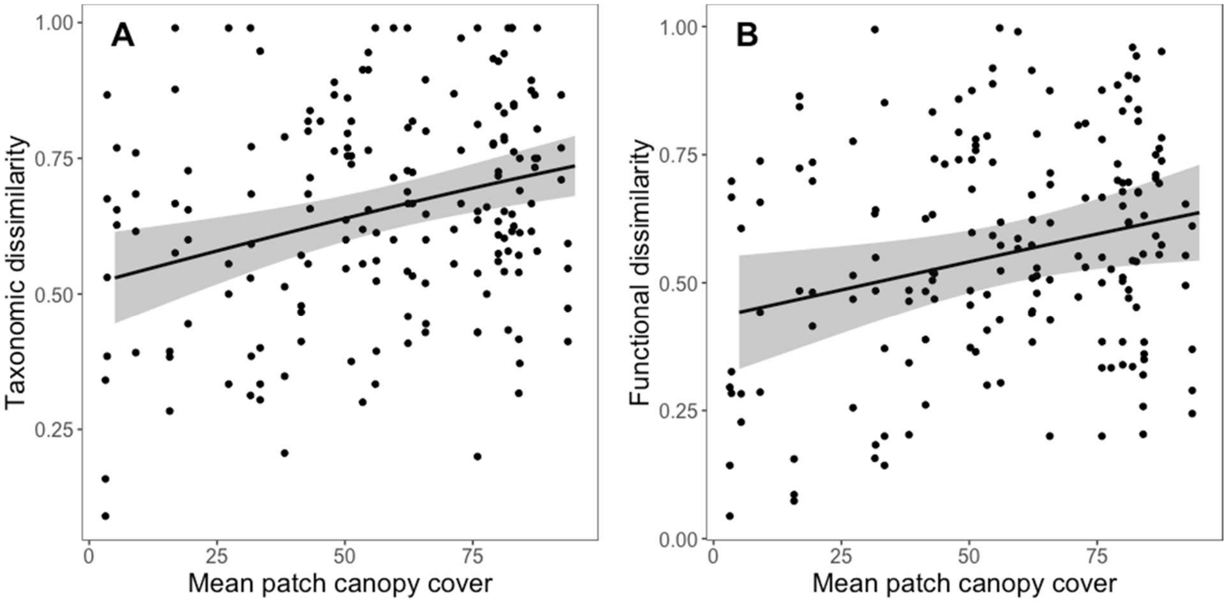

Figure 1.6

Predicted relationship between ground beetle (A) taxonomic dissimilarity and (B) functional dissimilarity and mean retention patch canopy cover from a beta-distributed mixed effects regression model. Both dissimilarity measures are calculated between ground beetle communities present in retention patches and clearcuts within harvest units. Shaded region represents 95% confidence interval for predictions and points represent measured dissimilarity at a given patch canopy cover value. Other variables in the model include Julian date of the beginning of the sampling period which was set to 136, the earliest value for all sample collection periods, and sampling year, which was set as 2018 for the predictions.

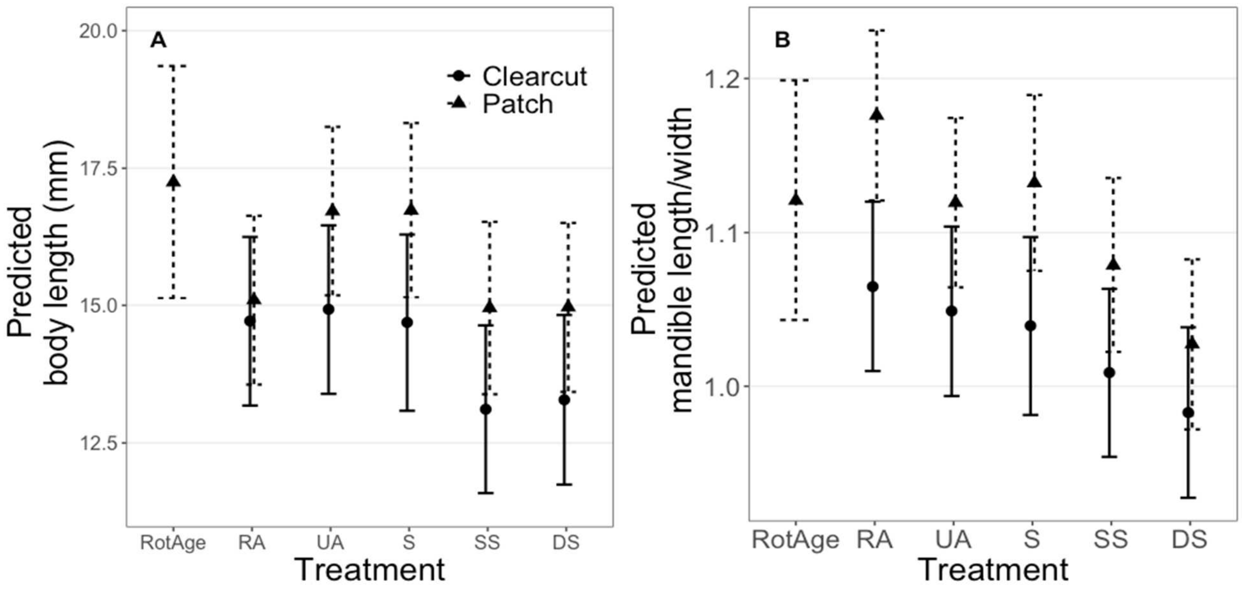

Figure 1.7.

Mean (and 95% confidence interval) predicted trait values for (A) body length and (B) ratio of mandible length to width between the mandibles for carabid beetles by retention treatment for clearcut areas (solid circles) and retention patches (solid triangles), northwest Oregon and southwestern Washington, USA, 2017-2018. Year and Julian date of sampling were included in each model and for predictions year was set to 2018 and Julian date was set to 136, the earliest value for all sample collection periods. Sampling conducted in western Oregon and Washington retention treatment harvest units, 2017 and 2018. RotAge = rotation-aged forests, RA = Riparian Aggregated, UA = Upland Aggregated, S = Split, SS = Split with Snags, and DS = Dispersed with Snags.

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CHAPTER 2:

STAND-SCALE RESPONSES OF FOREST-FLOOR SMALL MAMMAL POPULATIONS TO VARYING SIZE, NUMBER, AND LOCATION OF RETENTION TREE PATCHES

Co-authors on the manuscript resulting from this chapter include: Andrew J. Kroll, Jacob Verschuyl, and Gary J. Roloff

2.1 Abstract

In forests harvested on even-aged rotations, retention forestry is commonly practiced to structurally enrich production forests and meet biodiversity conservation goals. However, the relative effectiveness of different retention strategies at increasing structural complexity and populations of dependent wildlife species is not well understood. We used an experimental study to evaluate changes in population density of three small mammal species in response to different size and location (riparian or upland) of retention tree patches within clearcut harvested forests in the Pacific Northwest, U.S.A. We also assessed whether small mammal densities varied in relation to measured structural complexity within retention patches. Within experimental treatment stands, deer mice (*Peromyscus* spp) population density did not differ between retention and clearcut areas (β = -0.05, SE = 0.06), Townsend's chipmunk (*Neotamias townsendii*) density was higher in retention compared to clearcut areas (β = 1.61, SE = 0.10), and creeping vole (*Microtus oregoni*) density was highest in clearcut areas (β = -0.68, SE = 0.10). At the scale of experimental treatment stand, the lowest deer mouse densities occurred in stands with large, isolated upland patches of retention (mean = 83, SD = 28 trees) and was highest in stands with several small patches of upland retention (mean = 8, SD = 2 trees). Creeping vole density followed the opposite pattern, highest in stands with large isolated upland patches and lowest in stands with multiple small isolated patches. Densities of each species were intermediate in treatments where at least a portion of the retention trees were connected to forested riparian buffers. We found that Townsend's chipmunk density increased with increasing retention tree blowdown in the patches, a proxy for downed wood resources, whereas creeping vole density decreased. Deer mice density did not change consistently in response to tree blowdown. Furthermore, retention tree mortality was highest in the treatment with several small isolated patches (mean = 0.49 down, SD = 0.21) and lowest in the treatment with a single large patch (mean = 0.10 down, SD = 0.09). Our results demonstrate that smaller, dispersed retention increases abundances of small mammals in recently clearcut, early seral forests (3-6 years after tree planting) in the Pacific Northwest. This relationship is at least partly mediated through higher levels of structural complexity within small retention patches caused by increased retention tree blowdown compared to larger patches.

Keywords: Aggregated retention, Forest structural complexity *Microtus oregoni*, *Neotamias townsendii*, Pacific Northwest, *Peromyscus*, Retention forestry, Small mammals

2.2 Introduction

Forest management intensity has increased to meet global demand for timber products (Brockerhoff, 2008; FAO, 2016). Intensive management often simplifies the structure of production forests, with important consequences for forest biodiversity (Hayes et al., 2005; Demarais et al., 2017). Retention forestry, the practice of retaining green trees and other stand legacies at harvest, is implemented in many timber producing regions to increase the conservation value of production forests (reviewed by Gustafsson et al., 2012; Kroll et al., 2012; Mori and Kitigawa, 2014). Retention forestry may increase plant and animal species richness of harvested areas, resulting in a more diverse early seral forest community compared to clearcut areas without retention (Fedrowitz et al., 2014). Also, retention tree patches may serve as ‘lifeboats’ by promoting persistence of forest dependent species in harvested areas until mature forest conditions develop (reviewed by Rosenvald and Lõhmus, 2008). Despite widespread research on the benefits of retention forestry and the impacts of retention level on forest species (Franklin et al., 2019), less information is available on how the spatial arrangement of retention trees influences biodiversity (Kroll et al., 2012; Fedrowitz et al., 2014).

Retention forestry experiments have compared biodiversity responses between aggregated retention, where trees are retained in distinct patches, to dispersed retention patterns, where individual trees are retained throughout the harvested area (Aubry et al., 2009). However, stand scale responses of forest biodiversity to different patch sizes of aggregated retention is not well-understood (Fedrowitz et al., 2014), especially under constant stand-level retention density (trees/ha). Although support for an effect of retention patch size and number on forest biodiversity is limited (Lindenmayer et al., 2010, 2015), creating either a single large or several small retention patches at a constant proportion of retention may have implications for species-specific responses to retention. Aggregating all retention trees in one patch may conserve species dependent on forest interior conditions (e.g., ‘lifeboating’). However, early seral or generalist species may benefit from the additional edge created by multiple, smaller patches (Betts et al., 2019) and access to resources in harvested and retention areas (Fahrig, 2017). Retention tree mortality through blowdown varies based on size of retention patches, with increased blowdown in small patches (Xing et al., 2018), which may influence species dependent on structural complexity and downed wood. In addition to informing retention practices during forest harvest, studies of different patch configurations (i.e., single large vs several small patches) at constant stand-level retention density can also illuminate whether forest species respond to habitat fragmentation independent of habitat amount, a topic that continues to be debated in the conservation literature (Fletcher et al., 2018; Fahrig, 2018).

Small mammals are sensitive to changes in forest structure (Carey, 1995), likely in related to predation pressure, and their populations can be monitored with mark-recapture techniques. As a result, these species are ideal study subjects to evaluate effects of retention practices on wildlife (Sullivan and Sullivan, 2001; Sullivan et al., 2017). Importantly, small mammals disperse spores of ectomycorrhizal fungi (Maser et al., 1978; Stephens et al., 2017) in addition to serving as prey for forest carnivores of conservation concern (Jacobs and Luoma, 2008). Hence retention practices that increase abundance of small mammals are likely to benefit other components of forest ecosystems (Jacobs and Luoma, 2008; Sullivan et al. 2017). The abundance of many forest-associated small mammal species is often related to microhabitat components associated with structural complexity of forests, such as downed wood and understory shrub cover (Carey 1995; Waldien et al. 2006; Gray et al. 2016, 2019). Retention forestry can increase prevalence of these structural elements in intensively managed forests (Linden and Roloff, 2013; Hane et al., 2019), but information on whether certain retention practices create higher structural complexity and increase abundance of small mammals at stand scales is needed for more effective retention implementation.

We conducted an experimental study to understand how population densities of common small mammal species vary in relation to size and placement of retention tree patches within recently clearcut forests of the Pacific Northwest (PNW). Our study included five retention treatments, representing alternative retention strategies, using the constant density of green trees required by current forest harvesting regulations in the region. Using this design, we tested for treatment effects on population density of three small mammal species that demonstrate different levels of forest specialization. We also tested whether species-specific responses to retention treatment varied through time. Lastly, we quantified whether small mammal densities varied with levels of tree blowdown and shrub cover within retention patches. We predicted that species responses to retention treatment would relate to species-specific responses to structural complexity (i.e., shrub cover, downed wood) associated with different treatments, with forest associated species responding positively to increases in structural complexity. Our results demonstrate how size and location of retention patches influences small mammal populations independent of retention amount and the role of structural complexity in moderating these responses. Based on these findings, we provide recommendations for implementation of retention requirements that are likely to increase small mammal abundance within early seral production forests.

2.3 Methods

2.3.1 *Study Design*

We conducted a randomized complete block experiment in managed forest landscapes in northwest Oregon and southwest Washington, U.S.A. (Figure 2.1). Forest practices rules in both states set maximum clearcut harvest size to ~55 ha, require unharvested forested stream buffers, and require retention of ~5 green trees or snags/ha of the harvested area (Washington Forest Practices Board 2002; Oregon Department of Forestry 2018). Oregon does not provide rules on retention tree placement (Oregon Department of Forestry 2018), whereas Washington requires that all locations within a clearcut harvest area are <244m from retention (Washington Forest Practices Board 2002). Our experimental design included five retention treatments in each of seven blocks in Oregon and three blocks in Washington (five blocks each in the Cascade and Coast Mountain Ranges). The retention treatments included:

1. **Riparian aggregated treatment (RA):** All required retention trees placed adjacent to an unharvested riparian buffer.
2. **Upland Aggregated Treatment (UA):** All retention trees grouped together in the upland portion of a harvested stand, either isolated or on the edge of the stand adjacent to recently regenerated forest (<15 years old).
3. **Split Treatment (S):** Half of the retained trees placed adjacent to an unharvested riparian buffer and half in the upland portion of the harvested stand, either isolated or on the edge of the stand adjacent to regenerating forest.
4. **Split with Snags Treatment (SS):** Identical to the Split Treatment but half of the green trees were turned into snags (standing dead wood, ~8m tall) with a mechanical harvester.
5. **Dispersed with Snags Treatment (DS):** Retention trees grouped into at least four small patches, each with nine green trees and an equal number of created snags, distributed throughout the harvested stand and isolated from riparian buffers or stand edge.

Aside from these retention criteria, harvests followed typical operations (e.g., regeneration practices including herbicide applications and conifer planting; see Kroll et al., 2017 for representative example) to make inferences broadly applicable to clearcutting harvesting within the region. Average treatment stand size was 33 ha (SD = 10.3 ha). In both states, forest practice rules require retention of approximately five trees per hectare during timber harvest (Oregon Department of Forestry 2018; Washington Forest Practices Board 2002). Our retention treatments represented different spatial arrangements of these trees. Assignment of stands within a block was not completely randomized, as three treatments required a riparian zone in or adjacent to the harvested stand. The created snags included in SS and DS, although created primarily to benefit cavity-nesting birds, reduced overstory canopy cover of patches and affected ground vegetation relevant to ground-dwelling and semi-arboreal mammals studied here.

2.3.2 *Field Methods*

Within recently clearcut stands (2-6 years after trees were planted), we established 96 permanent live trap sites, half in retention patches and half in adjacent clearcuts. As the pattern and configuration of retention among treatments varied, we modified the configuration of trap grids to coincide with retention placement. In the aggregated treatments (i.e., RA and UA), we set two 48-trap grids, one within the retention patch and one in the adjacent clearcut. In the split retention treatments (i.e., S and SS), we set four 24-trap grids, one in each retention patch (riparian and upland) and in the clearcut adjacent to each retention patch. For the dispersed treatment (i.e., DS), we set eight 12-trap grids; four each in retention patches and adjacent clearcut areas. Considerable variation in patch size between stands of the same treatment resulted in minor variation in grid sizes between treatments, and considerable variation in grid configuration due to patch shape. Trap sites within the grid were spaced 5 m from each other. We established clearcut grid locations on a random bearing and distance from the center of sampled patches. Distances of clearcut grids to paired retention patch grids ranged from 12—212 m (mean = 49 m, SD=27.5).

We live-trapped using a combination of Sherman (Model LFA, 7.6 x 8.9 x 22.9 cm; H. B. Sherman Traps Inc., Tallahassee, Florida) and Tomahawk (Model 202, 48.3 x 15.2 x 15.2 cm, Tomahawk Live Trap Co., Tomahawk, Wisconsin) traps. We placed Sherman traps at every trap site (5m spacing) and Tomahawk traps at every-other trap site (10 m spacing), resulting in half the number of Tomahawk traps deployed per grid as Sherman traps. We used a lower density of Tomahawk traps to accommodate lower densities and longer movements of larger-bodied mammal species. We baited Sherman traps with a combination of black oiled sunflower seeds, whole oats, and fresh apple. We baited Tomahawk traps with peanut butter, rolled oats, and apple. We also placed polyester batting in each trap to help captured animals thermoregulate, and we covered traps with bark and debris to provide cover.

We trapped patches and clearcut areas of each treatment stand for one, 4-day period between late May/early June and late August/early September from 2017-2019, resulting in three sampling periods per treatment stand (one in each year). Among years, we rotated the timing of trapping in a given block to avoid confounding variation in species densities across the study area with seasonal trends in density. We set traps in the morning or afternoon and then checked in the morning or early afternoon the following day. During each trap check, we identified all captured animals to species and tagged each individual with two unique ear tags (National Band and Tag Company, Style 1005-1, Monel), one in each ear, except for voles which received a single ear tag to reduce handling related stress. For recaptures, we only recorded tag numbers and the location of recapture. The Institutional Animal Care and Use Committee at Michigan State University approved all animal trapping, handling, and tagging procedures (AUF #04-16-040-00).

In summer 2018, botanical survey crews measured cover of shrubs >1m tall that intercepted transects established within retention patches, with transect length varying among treatments to ensure that sampling did not extend into the adjacent clearcut. In the two aggregated treatments (RA and UA) shrubs were measured along four, 48m transects beginning at patch center and oriented in each cardinal direction. For the two split retention treatments (S and SS), shrubs were measured on four, 35m transects oriented in each cardinal direction from riparian and upland patch centers. For the DS treatment, 2 patches were chosen for shrub measurements and within each of these patches proportion shrub cover was measured on 4, 20m transects oriented in each cardinal direction from patch center. To quantify the proportion of retention tree mortality in each treatment, which typically resulted from blowdown, each retention tree was numbered with an aluminum tag within 1-2 years of forest harvest. We assessed tree survival in 2019 (4-6 years after forest harvest) and used these data to calculate proportion of retention tree mortality within each treatment stand.

2.3.4 *Analysis*

We captured >20 small mammal species during the three years of sampling but most species were rare and patchily distributed, with few recaptures (see Chapter 3). For this reason, we estimated density for the three most commonly captured species that occurred in all 10 experimental blocks: Townsend's chipmunk (*Neotamias townsendii*), creeping vole (*Microtus oregoni*), and deer mice (*Peromyscus* spp.). In the seven Oregon blocks, *Peromyscus maniculatus* is the only deer mouse species that occurs, but in the three Washington blocks, *P. maniculatus* and *P. keeni* occur sympatrically (Figure 2.1). These two species cannot be identified definitively in the field, so we pooled them for density estimation where they co-occurred. Although our three focal species represent a small subset of small mammal diversity in the region, they represent three different levels of habitat specialization. Townsend's chipmunk is a forest specialist that prefers forests with abundant woody debris (Waldien et al., 2006) and primarily consumes fungi (Maser et al., 1978; Jacobs and Luoma, 2008). Creeping voles are typically an open habitat species that occurs at highest densities in forest openings with abundant herbaceous vegetation and at lower densities in closed canopy forests (Carraway and Verts, 1985). The two species of *Peromyscus* are habitat generalists that can occur at high densities in a variety of habitats (Verts and Carraway, 1998), although *Peromyscus keeni* in Washington has a stronger affinity for forests (Lehmkuhl et al., 2008).

We analyzed our data in a spatially explicit capture-recapture (SECR) framework (Borchers and Efford, 2008). Spatially explicit capture-recapture models use the spatial distribution of individual recaptures to estimate three parameters: detection probability for an individual at their center of activity (g0), the spatial scaling of detection (sigma), and population density, each of which can be modeled as a function of covariates. In the SECR framework, each animal is assumed to have an activity center where space use is concentrated. The sigma parameter describes how quickly individual detection probability declines as distance of a trap from the activity center of an individual increases. Activity center (population) density is a derived parameter from g0 and sigma and estimated as a homogeneous Poisson point process, or inhomogeneous when density covariates are included (Efford et al., 2009). Unlike traditional mark-recapture analysis frameworks where the spatial scale of abundance estimates is unclear, the effective sampling area of a SECR model yields spatially explicit estimates of abundance (i.e., density). Likelihood estimation in the SECR framework does not account for trap competition among individuals at high levels of trap success, but in our study trap saturation for all species captured was 10.3% across treatments, well below the level of saturation that Efford et al., (2009) found to cause bias in density estimates.

Our SECR models estimated the influence of each retention treatment, sampling year, and an interaction between retention treatment and year on density of the three focal species at the stand level. In addition to treatment at the stand level, we included a patch covariate that estimated variation in density between retention patches and clearcut areas within a stand. Spatially explicit capture-recapture models require that the grain and extent, known as the state space, are specified for the analysis. For each species, we specified a 100 m buffer around traps as the extent, and 10 m spacing within those buffers as the grain for density estimates. A 100m buffer was greater than four times the estimate of sigma for the largest-bodied species (see Results), indicating that our state space should encompass home ranges of most individuals sampled. Specifying a grain of 10 meters allowed us to estimate fine scale variation in density but also maintain computational efficiency compared to smaller grain sizes. When fitting a SECR model to estimate spatial variation in density (i.e., between treatments), all areas of the state space must have covariate values. Given the state space in some instances extended past the boundaries of clearcut stands, we included a sixth treatment factor representing surrounding habitats.

We implemented a multi-session analysis, where each block-year combination was a different session (30 sessions total). Parameters in a multi-session SECR are estimated by maximizing the product of the session-specific likelihoods (Efford et al., 2009). Multi-session SECR analyses are different from open-population capture-recapture models in that the sessions are assumed independent from one another. Although we violated this assumption with repeat surveys of treatment stands across years, point estimates for treatment effects remain unbiased (Efford, 2019). Additionally, and sampling was balanced and all stands contributed equally to the likelihood, with the exception of missing one UA treatment in 2019. We also used a conservative significance threshold (95% confidence intervals around the parameter estimates exclude 0) for interpreting treatment effects.

Before fitting models to estimate treatment effect on small mammal density, we fit a suite of detection models. For each species, we fit a: 1) null (constant) detection model, 2) time dependent model that estimated trends in individual detection from trap nights 1 through 4, and 3) behavioral model that allowed heterogeneity in capture probability based on whether an individual was previously captured. We also independently tested two different detection functions; half-normal and exponential decay functions (Efford, 2019). With the exponential function, detection probability initially declines more rapidly with increasing distance from the activity center of an individual, but the distribution also asymptotes toward 0 more slowly at large distances to accommodate occasional long-distance movements. We ranked detection models based on AICc and used the top-ranked detection function in our density models. Year was included as a density covariate in detection models (given issues with model convergence due to large inter-annual fluctuations in captures). After selecting the highest ranked detection model for each species, we ran one density model for each species based on the experimental design (i.e., treatment by year interaction).

In addition to the treatment by year interaction model for each species, we fit models assessing relationships between each species density and structural complexity variables. For these models, we only used capture-recapture data from 2018 to avoid pseudoreplication within treatment stands because structural complexity variables were only measured once within stands and hence did not vary among years as the effect of treatment was allowed to in the design model. Furthermore, our design was not balanced with respect to structural complexity variables as it was for retention treatment, potentially leading to larger influence of stands with extreme covariate values when the effect of repeated measures is not accounted for. Using the 2018 data, we ran a model that included linear and quadratic terms for average proportion of retention tree mortality within a stand, and for average proportion shrub cover in retention patches on each species density. For small mammals, patches are more complex when they contain a combination of standing and downed trees and patchy shrub cover. SECR analysis was performed in the R statistical computing platform version 3.6.1 (R Core Team, 2019) using the secr R package version 4.0.2 (Efford, 2019).

2.4 Results

Over three years and 81,534 trap nights, we captured 5,145 individual small mammals with 9,017 total captures, including 4,427 of our focal species: 1,354 Townsend's chipmunks, 2,423 deer mice, and 650 creeping voles (Table 2.1). We completed sampling in all treatment stands in each of the three years with the exception of one UA treatment in 2019 due to logistical constraints. On average, an individual chipmunk was captured 1.92 times, a deer mouse 2.14 times, and creeping vole 1.35 times per 4-day trapping session. For all three species, the exponential detection function was better supported than the half-normal detection function (Table 2.2). For individual detection probability, a model that included time dependent detection received the most support for chipmunks and creeping voles, whereas the model with behaviorally modulated detection received the most support for deer mice (Table 2.2). Chipmunk ($\beta = 0.38$, 95% CI = 0.34—0.42) and creeping vole ($\beta = 0.55$, 95% CI = 0.48—0.62) detection increased later in trapping sessions and deer mouse detection increased after initial capture ($\beta = 1.77$, 95% CI = 1.60—1.94).

Population density of each of the species responded differently to retention patches within treatments. Townsend's chipmunks occurred at higher densities in patches compared to the clearcut portion of stands (β = 1.61, 1.41—1.81, Figure 2.2A), deer mice densities did not differ between patches compared to clearcuts (β = -0.06, -0.17—0.06, Figure 2.2B), and creeping vole densities were higher in clearcuts compared to retention patches (β = -0.68, -0.88— -0.49, Figure 2.2C). Estimated densities varied as expected given body sizes, with maximum estimates being lowest for chipmunks, intermediate for deer mice, and highest for creeping voles (Figure 2.2). Sigma estimates showed chipmunks moving larger distances than smaller bodied species (Figure 2.3).

The 95% confidence intervals for the main effect of each retention treatment on population density of the three species all overlapped zero, with the exception of a negative effect of the UA treatment on chipmunk density and negative effect of the DS treatment on creeping vole density (Table 2.3). In the first year of sampling, population densities of chipmunks were 32% lower in the UA treatment compared to the RA (Figure 2.2A), and densities of creeping voles were 57% lower in the DS treatment compared to the RA treatment (Figure 2.2C) The estimated density of chipmunks in areas surrounding treatment stands was negative compared to the RA but the 95% CI included 0 (β =-0.37, -0.88—0.14), indicating the contribution of individuals from areas outside of treatment stands was low for this species. Estimates of density in areas surrounding treatments were negative for deer mice (β = -0.45, -0.90—-0.01) and positive but not different from the RA treatment for creeping voles (β = 0.31, -0.28—0.90). However, estimates of sigma for these species indicate a negligible chance of detecting individuals from outside the treatment stands (Figure 2.3).

Treatment by year interactions were not significant for chipmunks (Table 2.3), indicating that chipmunk responses to retention treatment were consistent over time (Figure 2.2A). For deer mice, we found that the UA treatment interacted with year (Table 2.2), with deer mouse density decreasing in UA relative to RA over time (Figure 2.2B). For creeping voles, we found that the two treatments with created snags had positive treatment by year interactions (Table 2.2). Chipmunk densities increased in all treatment types over time, ranging from one (UA clearcut in 2017) to 22 (DS patches in 2019) individuals per hectare (Figure 2.2C). Predicted deer mouse densities ranged from 7 (UA patch in 2019) to 30 (S clearcut in 2017) individuals per hectare and decreased in all treatments over time (Figure 2.2C). Creeping vole densities ranged from 2 (DS patch in 2017) to 44 (UA clearcut in 2019) individuals per hectare without strong trends in density through time except for SS and DS treatments, where creeping vole density increased (Figure 2.2C).

Proportion of retention tree mortality within treatment stands varied from 0.00 to 0.89, and proportion shrub cover within retention patches varied from 0.02 to 0.94. We found evidence for a quadratic relationship between retention tree mortality and Townsend’s chipmunk density (Table 2.4), with density of chipmunks peaking at intermediate levels of retention tree mortality (Figure 2.4A). We also found evidence for a quadratic relationship between creeping vole density and retention tree mortality (Table 2.4), with creeping vole density lowest at intermediate levels of retention tree mortality (Figure 2.4B). However, the increase in density at high levels of retention tree mortality was primarily driven by one SS treatment stand. Across the range of retention tree mortality within treatments, estimated chipmunk density increased by 150 percent (Figure 2.4A) and estimated creeping vole density decreased by 160 percent (Figure 2.4B). Creeping vole density also increased with increasing shrub cover (Table 2.4) with evidence for a quadratic relationship, but few stands had proportion of shrub cover within patches greater than 0.50 (Figure 2.4C). As proportion of shrub cover within patches increased from 0.02 to 0.50, estimated creeping vole density increased by more than 200 percent (Figure 2.4C). We did not find support for a relationship between deer mouse density and either shrub cover or retention tree mortality (Table 2.4).

2.5 Discussion

Under contemporary forest harvesting practices in the Pacific Northwest, retention is often placed along riparian buffers to accommodate harvest and subsequent silvicultural operations. Lack of retention in upland areas, however, reduces structural complexity in the regenerating harvest unit. Structural complexity, typically the presence of green trees, snags, downed logs, and understory shrub cover, is an important factor affecting abundance of forest small mammals in forests of the Pacific Northwest (Carey and Johnson, 1995; Carey et al., 1995; Gray et al., 2016), but the relative importance of upslope retention for small mammal populations is largely unknown. In early seral conifer plantations (i.e., 2-6 years post planting) we found that, densities of Townsend’s chipmunks and deer mice were lower in aggregated upland patches and higher in stands containing multiple small patches compared to densities observed in riparian associated retention patches. Densities of creeping voles, an early seral species closely linked to herbaceous vegetation (Carraway and Verts, 1985), followed the opposite pattern with higher densities observed in the treatment with a single large upland patch of retention and lowest in the treatment with multiple small patches. Furthermore, we found that density of Townsend’s chipmunks and creeping voles differed due to blowdown of retained trees (i.e., increasing horizontal complexity), which varied by treatment. These findings supported our prediction that small mammal responses to retention pattern are related to different levels of structural complexity resulting from forest harvest treatments. For the ground active study species we studied, direct effects of retention trees (i.e., vertical complexity) on small mammals appear less important than indirect effects of downed wood and shrub cover (i.e., horizontal complexity) in retention areas. In this sense, dispersed retention at levels investigated here effectively creates more structurally complex early seral conditions, and the ability of large upland patches to 'lifeboat' uncommon late seral species (e.g., *Myodes californicus, Glaucomys oregonensis*) appears limited (see Chapter 3).

Townsend's chipmunk densities were 5 times higher in retention patches compared to surrounding clearcuts (Figure 2.2A). This species associates with structurally complex forests across all seral stages (Gashwiler, 1970; Rosenberg and Anthony, 1993). Retention, regardless of patch size and location, appears to increase habitat quality of recently clearcut areas in intensively managed forests. Positive responses of Townsend's chipmunks to higher horizontal complexity, in the form of downed wood, corresponds with chipmunk densities being highest in the DS treatment that experienced the highest retention tree mortality, and lowest in the UA treatment, which had lowest average retention tree mortality (Table 2.5). Downed wood is an important component of Townsend's chipmunk habitat, providing movement pathways and potential protection from predators (Waldien et al., 2006). As a result, increased retention tree blowdown in small (<15) retention tree groups benefits this species. In contrast, retention tree mortality in the RA treatment was generally low yet estimated chipmunk densities in this treatment were similar to the DS treatment. Hence, factors besides downed wood appear to affect chipmunk density in the RA treatment, and this finding is consistent with riparian buffers acting as refugia for this species in harvested forests (Cole et al., 1998). Collectively, our findings indicate that riparian associated retention generally supports high densities of chipmunks, but allocating retention to multiple small patches in upland areas results in high chipmunk densities distributed over a larger area within clearcut stands.

Deer mice densities did not differ between retention patches and clearcuts, consistent with the generalist life history strategy of this species. Deer mice populations increase in response to timber harvest (Gitzen et al., 2007; 2018) and are more abundant in areas with exposed soil that is common in recent clearcuts (Gray et al., 2016). Lack of a deer mouse density response to patches in our study may result from favorable habitat conditions that are ubiquitous throughout clearcut harvest areas. We also found a temporal trend in deer mice densities, with densities not differing among treatments initially, but then declining after the first year of sampling, with largest declines in UA and lowest in DS treatments (Fig. 2.2). By the end of the study, this resulted in patterns of deer mouse densities among treatments similar to those found for chipmunks. In contrast to chipmunks, we did not find a relationship between deer mouse density and structural complexity, although deer mice are positively associated with downed wood (Manning and Edge, 2004) and shrub cover (Weldy et al., 2019) in Pacific Northwest forests. Deer mice abundance typically increases at forest edges (Bayne and Hobson, 1998) and in small patches (Robinson et al., 1992) so our observed lower densities in larger upland patches may relate to lower levels of edge compared to several small patches. Given similar densities of deer mice between patches and clearcuts, lower densities in the UA treatment likely reflects small-scale reductions in density within aggregated patches rather than lower stand scale abundance. Hence, lower densities of deer mice in the UA treatment has fewer implications for this species abundance on intensively managed forest landscapes compared to the negative effect of larger patches on chipmunks, which are more abundant in retention than clearcut areas.

Creeping vole densities were lower in retention patches compared to clearcuts, consistent with their affinity for forest disturbance and abundant herbaceous vegetation (Carraway and Verts, 1985). This suggests that retention has little value to this species in early seral forest plantations. However, our sampling ended before the stem exclusion phase (*sensu* Oliver and Larson, 1996) of forest development in the clearcuts, and herbaceous and non-tree woody cover remained common during our study. We predict that as succession of clearcuts continues and stands reach the stem exclusion stage, the value of retention to creeping voles, and potentially deer mice and chipmunks, will increase relative to less structurally complex regenerating forests surrounding patches. The negative relationship between creeping vole density and retention tree mortality is consistent with documented lower survival in conifer forests with higher levels of downed wood (Manning and Edge, 2004), but the mechanism driving this relationship is unclear. The increase in creeping vole density in the two treatments with snags over time suggests that patches with low canopy cover resulting from snag creation may favor open habitat species as forest succession progresses.

Despite our focus on population density, it can be a misleading measure of habitat quality if immigration sustains high densities in low quality habitats (Van Horne, 1983). For Townsend's chipmunks, previous research suggests that habitat structure, rather than immigration drives population density patterns (Carey, 1995). In addition, our highest density estimate for Townsend's chipmunks in DS treatment patches (20/ha, Fig. 2.2) is near the highest densities reported in the literature from old growth forests in western Oregon (24/ha; Hayes et al., 1995), and higher than reported from second growth forests (10/ha; Rosenberg and Anthony, 1993). However, our highest density estimates were for relatively small (<0.1 ha) patches and it is unclear if these high estimates are scale dependent. Our maximum estimate of deer mouse density (30.3/ha) also closely aligns with a previous maximum estimate of 31.6/ha in western Oregon clearcuts (Gashwiler, 1970) and our maximum creeping vole density (44/ha) is well above density estimates previously reported for western Oregon (13.3/ha; Gashwiler, 1970).

A persistent question in landscape ecology and conservation biology is whether habitat fragmentation affects species after controlling for habitat amount (Fahrig, 2017, 2018; Haddad et al., 2017). Although our study was not a fragmentation experiment, we standardized retention amount proportionally to clearcut area, providing an opportunity for inference on the effects of forest fragmentation on small mammal density. The two upland retention treatments, UA and DS represent low and high fragmentation of retention trees, respectively. By the end of our study, 95% CIs for predicted density of each focal species in these two treatments did not overlap, suggesting that the small mammals we studied responded significantly to forest fragmentation in upland areas. Deer mice and chipmunks occurred at higher densities in more fragmented retention patterns, whereas creeping vole densities were higher in less fragmented upland patterns (Figure 2.2). These findings align with previous experiments that demonstrated generally positive population responses of small mammals to habitat fragmentation (Dooley and Bowers, 1998), but also variable responses by species (Robinson et al., 1992). For our study species, changes in habitat structure between small and large patches appears to mediate their responses to fragmentation of retained forests patches.

2.3.6 **Management Implications**

Decisions on the spatial arrangement of retention trees have important implications for small mammal densities in recently clearcut forests. Adopting riparian-associated retention or a combination of upland and riparian-associated retention strategy will result in moderate densities of Townsend's chipmunks, deer mice, and creeping voles. However, we also found benefits to dispersed upland retention as chipmunks occurred in higher densities in these retention patches compared to clearcuts. Thus, adopting dispersed retention strategies will distribute high densities of this important ectomycorrhizal dispersing species over a larger area of clearcut stands. The positive relationship between chipmunks and downed wood provided by retention tree mortality is new evidence supporting the value of retaining trees or downed wood upslope from riparian zones, and indicates that moderate levels of retention tree mortality is desirable for forest small mammal conservation. Aggregating all retention trees into larger upland forest patches should be avoided as this strategy mainly benefits creeping voles, which are most abundant in surrounding clearcut areas. However, a potential tradeoff exists between increasing small mammal abundance and increasing diversity of taxa sensitive to patch size of standing retention trees such as birds (Linden and Roloff, 2013). If increasing the abundance of small mammals in post-clearcut forests is a management objective, our findings demonstrate that harvesting operations should retain multiple upland patches of retention, which creates more structurally diverse early seral conditions in recently clearcut forests in the Pacific Northwest.

APPENDIX

Table 2.1

Number of new captures (and recaptures) for small mammal species by year in clearcut harvest areas with retention, southwest Washington and northwest Oregon, 2017-2019.

Species	**2017**	**2018**	**2019**	**Total**
Townsend’s Chipmunk	312 (208)	390 (291)	652 (490)	1354 (989)
Deer Mouse	1391 (1103)	326 (307)	706 (652)	2423 (2062)
Creeping Vole	179 (38)	174 (44)	297 (45)	650 (127)

Table 2.2

Model selection results for the detection function (i.e., Null-Exponential and Null-Half Normal) and detection covariates (i.e., Time Dependent and Behavioral) for focal small mammal species captured and recaptured in southwest Washington and northwest Oregon, 2017-2019. Candidate models were ranked by Akaike information Criteria, corrected for small sample sizes (AICc), where ΔAICc is the difference in AICc score for each model compared to the top ranked model for that species.

Species	**Model**	**AICc**	**ΔAICc**
Townsend's chipmunk	Time Dependent[a]	22241.97	0.00
	Behavioral[b]	22558.62	316.64
	Null-Exponential	22573.29	531.79
	Null-Half Normal	22777.94	535.69
Deer Mouse	Behavioral	37631.66	0.00
	Time Dependent	37795.54	163.88
	Null-Exponential	38295.25	663.59
	Null-Half Normal	38396.68	765.02
Creeping Vole	Time Dependent	8395.26	0.00
	Behavioral	8563.36	168.10
	Null-Exponential	8631.46	236.20
	Null-Half Normal	8663.72	268.50

[a] Time Dependent detection model allows individual detection to vary linearly within trapping sessions, for trap nights 1-4.

[b] Behavioral detection allows individual detection to vary after initial capture

Table 2.3

Coefficient estimates (95% CI) for each retention treatment, sampling year, and interaction between retention treatment and sampling year for three small mammal species in summer 2017-2019, southwest Washington and northwest Oregon. UA = Upland aggregated, S = Split between upland and riparian, SS = Split with mechanically created snags, and DS = Dispersed with created snags. All treatment coefficients are in comparison to the riparian aggregated (RA) treatment and on the log scale. Bold values indicate treatment effects that the 95% confidence did not include zero. Not shown is coefficient for the density of individuals in areas surrounding treatments, which is included in all models.

	Townsend's Chipmunk	**Deer Mouse**	**Creeping Vole**
UA	**-0.54 (-0.98, -0.11)**	0.05 (-0.16, 0.25)	0.14 (-0.24, 0.52)
S	0.05 (-0.30, 0.40)	0.13 (-0.07, 0.35)	-0.26 (-0.69, 0.16)
SS	0.16 (-0.18, 0.49)	-0.07 (-0.27, 0.14)	-0.25 (-0.68, 0.17)
DS	0.16 (-0.17, 0.48)	0.04 (-0.16, 0.23)	**-1.32 (-1.91, -0.75)**
Year	**0.45 (0.28, 0.61)**	**-0.21 (-0.33, -0.09)**	0.06 (-0.15, 0.27)
UA*Year	0.01 (-0.28, 0.30)	**-0.39 (-0.59, -0.19)**	0.18 (-0.10, 0.47)
S*Year	-0.17 (-0.41, 0.07)	-0.09 (-0.27, 0.18)	0.10 (-0.22, 0.41)
SS*Year	-0.15 (-0.38, 0.07)	-0.31 (-0.31, 0.05)	**0.32 (0.03, 0.61)**
DS*Year	0.09 (-0.12, 0.30)	0.04 (-0.12, 0.20)	**0.53 (0.15, 0.91)**

Table 2.4

Estimates and 95% confidence intervals for the relationships between small mammal density and measures of structural complexity within retention patches in summer 2017-2019, southwest Washington and northwest Oregon. TreeMort = linear effect of retention tree mortality, TreeMort^2 = quadratic effect of retention tree mortality, ShrubCover = linear effect of shrub cover, and ShrubCover^2 = quadratic effect of retention tree mortality. Bold values indicate variables with 95% confidence intervals that do not overlap zero.

	Townsend's Chipmunk	Deer Mouse	Creeping Vole
TreeMort	**0.39, (0.23, 0.54)**	0.00, (-0.15, 0.16)	**-0.51, (-0.74, -0.27)**
TreeMort^2	**-0.1, (-0.19, -0.01)**	0.00, (-0.09, 0.10)	**0.22, (0.08, 0.35)**
ShrubCover	0.0, (-0.13, 0.15)	-0.03, (-0.18, 0.12)	**0.62, (0.38, 0.85)**
ShrubCover^2	0.03, (-0.04, 0.11)	-0.03, (-0.11, 0.06)	**-0.29, (-0.43, -0.15)**

Table 2.5

Mean and SD of the proportion of retention tree mortality (TreeMort), the proportion of shrub cover >1m tall (ShrubCov), retention trees per patch (Trees/Patch), and proportion herbaceous cover (HerbCover) across different retention treatments where small mammal population density was measured in summer 2017-2019, southwest Washington and northwest Oregon, USA. RA = Riparian aggregated, UA = Upland aggregated, S = Split between upland and riparian, SS = Split with mechanically created snags, and DS = Dispersed with created snags.

	TreeMort	**ShrubCover**	**Trees/Patch**	**HerbCover**
Riparian aggregated	0.14 (0.13)	0.27 (0.28)	76 (38)	0.67 (11)
Upland aggregated	0.10 (0.09)	0.22 (0.17)	74 (26)	0.65 (0.23)
Split	0.20 (0.18)	0.28 (0.18)	35 (17)	0.65 (14)
Split with snags	0.37 (0.20)	0.16 (0.11)	18 (12)	0.72 (16)
Dispersed with snags	0.49 (0.21)	0.24 (0.16)	5 (2)	0.54 (0.18)

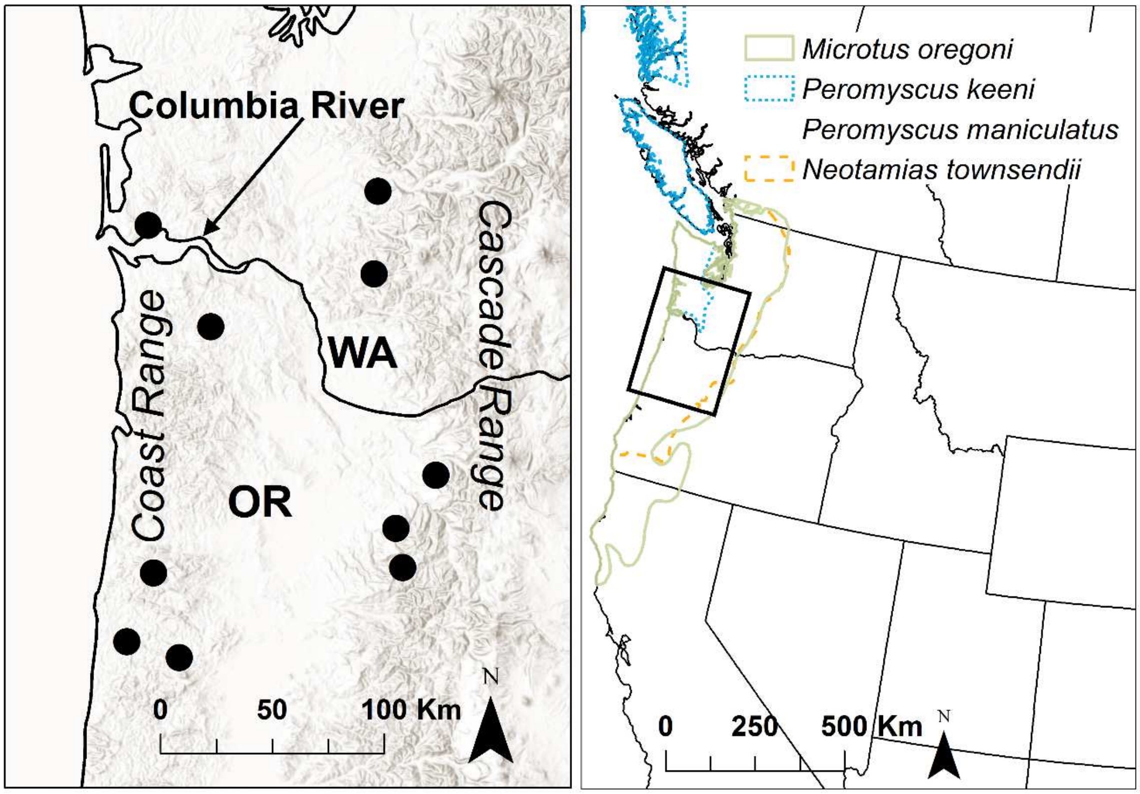

Figure 2.1

Study area map (left panel) depicting location of 10 experimental blocks (solid black circles) in southwest Washington (WA) and northwest Oregon (OR), each containing five retention treatments. Blocks equally distributed between Coast and Cascade Mountain Ranges, and the Columbia River separates WA and OR. Distribution of small mammal species (right panel) that are the focus of this study (IUCN). The distribution of *P. maniculatus* (not shown) covers all terrestrial areas shown and extends to northeastern North America and boreal forest. Distribution of *P. keeni* extends to coastal south-central Alaska.

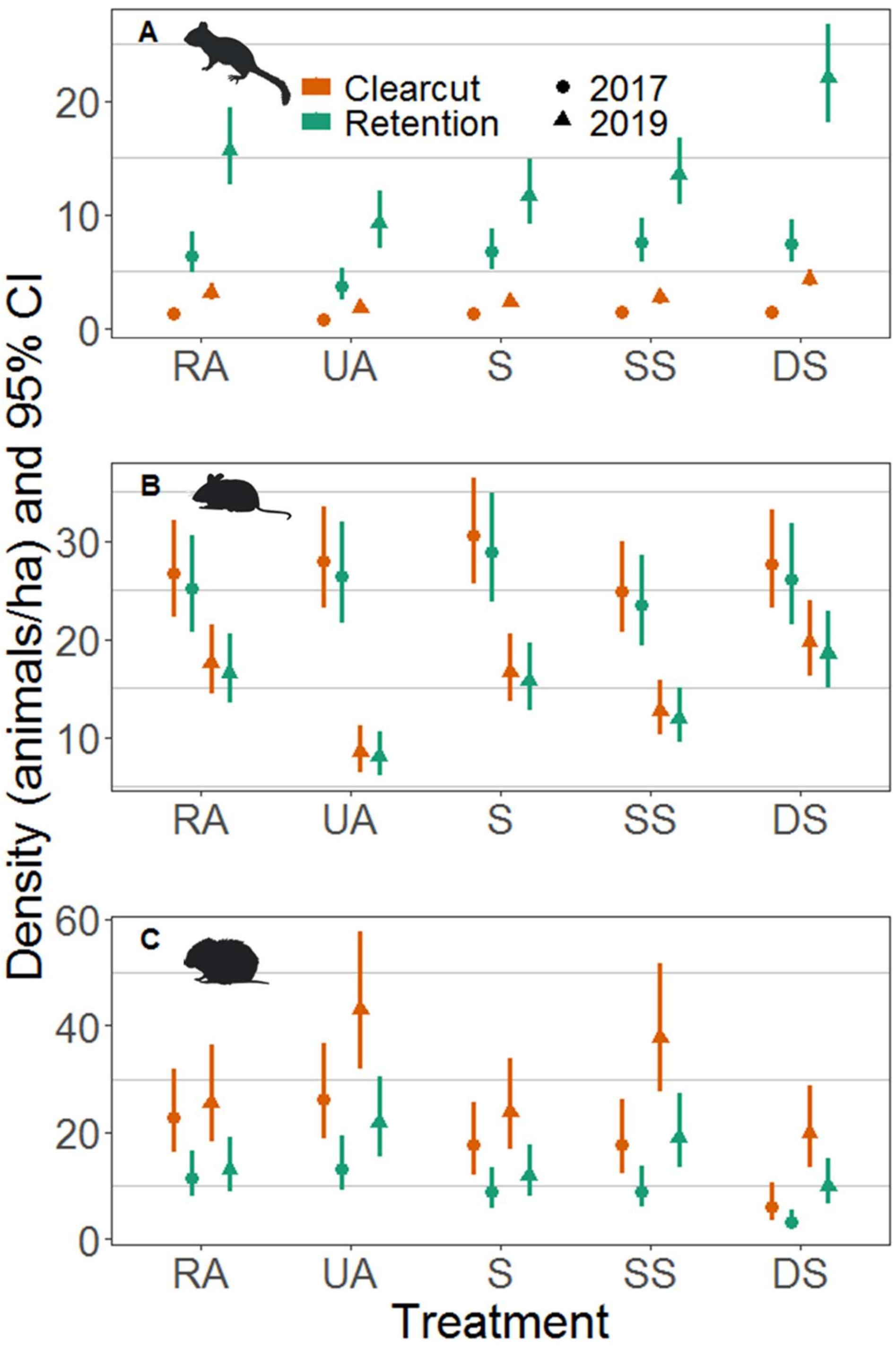

Figure 2.2

Predicted population density from spatially explicit capture-recapture models including retention treatment, within stand cover type, year, and a retention treatment by year interaction. For (A)

Figure 2.2 Continued

Townsend's chipmunks, (B) deer mice, and (C) creeping voles in clearcut forests of northwestern Oregon and southwest Washington, USA, 2017-2019. RA = Riparian aggregated, UA = Upland aggregated, S = Split between upland and riparian, SS = Split with mechanically created snags, and DS = Dispersed with created snags.

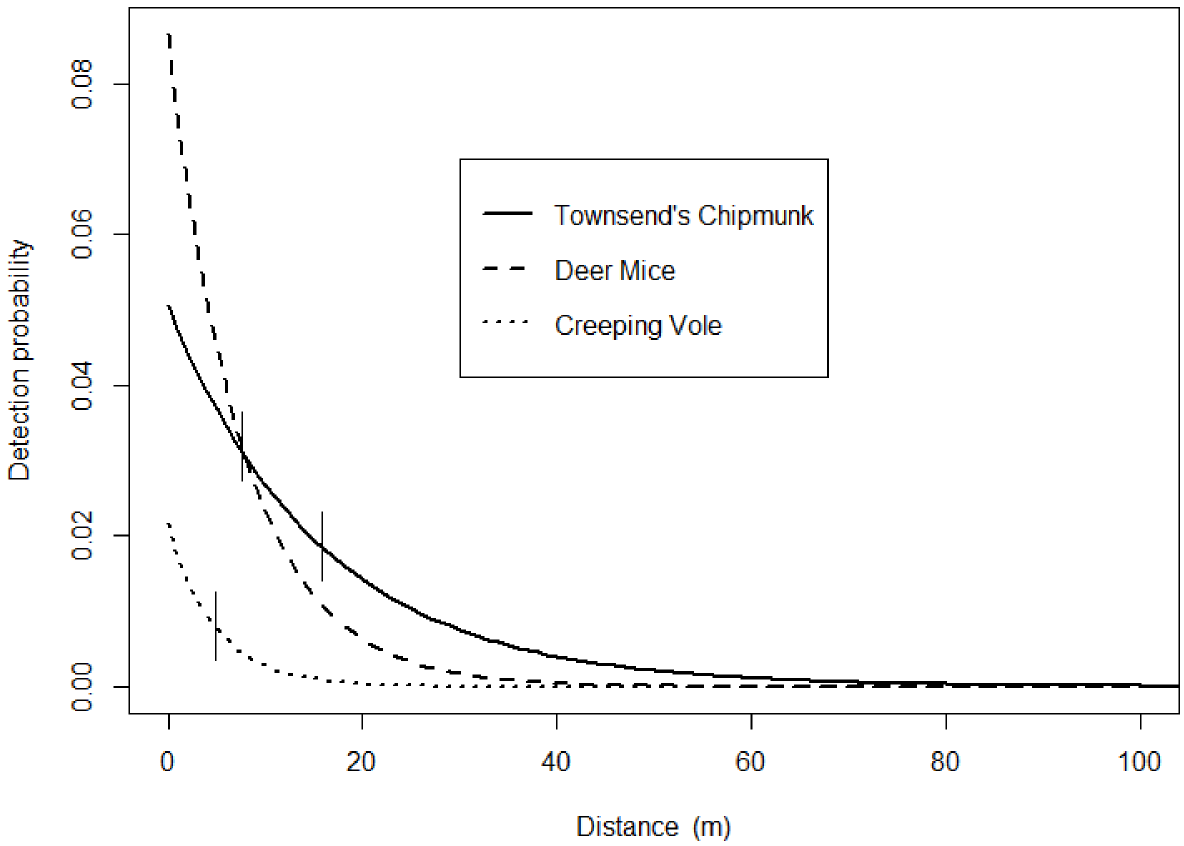

Figure 2.3

Distance decay of detection probability by focal species, with estimated value of sigma from the exponential detection model (vertical line) used in spatial mark recapture models. The relationship between detection probability and distance from activity center for the exponential decay function is g(d) = g0 * exp(- d / σ), where σ = sigma, g = detection probability and d = distance.

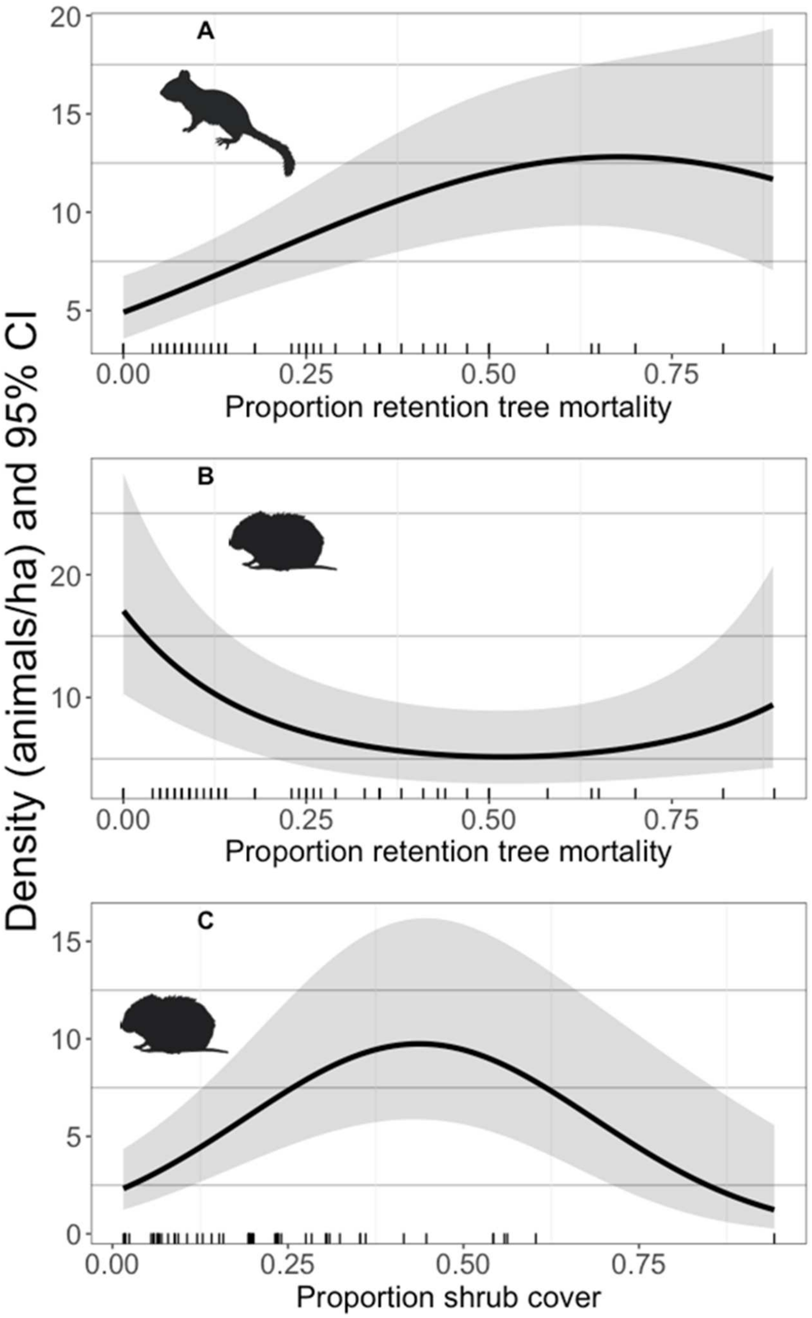

Figure 2.4

Predicted relationship between proportion of retention tree mortality within treatment stands and population density for (A) Townsend’s chipmunk, (B) creeping voles, and (C) between creeping vole populations density and proportion shrub cover >1m in clearcut forests of northwestern

Figure 2.4 Continued

Oregon and southwest Washington, USA, 2018. Predictions are from a spatially explicit capture recapture model that contained proportion retention tree mortality, proportion shrub cover in retention patches, and quadratic terms for each variable. Shrub cover was set at its mean value within stands for plots (A) and (B), and proportion retention tree mortality was set at its mean value for plot (C). Shaded region represents 95% confidence intervals for the predictions and ticks on x-axis depict actual covariate values within the 50 treatment stands

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CHAPTER 3

THE EFFECT OF AGGREGATION AND LOCATION OF RETENTION TREE PATCHES ON SMALL MAMMAL SPECIES AND FUNCTIONAL RICHNESS IN EARLY-SERAL CONIFER PLANTATIONS

Co-authors on the manuscript resulting from this chapter include Andrew J. Kroll, Jacob Verschuyl, and Gary J. Roloff

3.1 Abstract

Green tree retention during forest harvesting is a common practice for biodiversity conservation in wood producing regions globally. Yet, experimental evaluations of different retention patch configurations, at a consistent proportion of trees retained, are lacking for many regions and taxonomic groups. We implemented an experimental study that manipulated the size, number, and location (riparian or upland) of retention patches in five different experimental treatments, using a constant level of retention among treatments, replicated across the Pacific Northwest, USA. Within these experimental treatments, we measured small mammal (<1kg) species and functional trait (i.e., body size, diet, activity stratum) richness in both retention areas, surrounding clearcuts, and in closed-canopy forests. We captured 21 species of small mammals, and found limited effects of treatment on species richness. We also found no differences in small mammal functional trait richness among treatments. Species richness was highest in the treatment where all retention trees were aggregated into one patch that was connected to a forested riparian buffer (mean = 6.6, SE = 0.46), and lowest in the treatment containing one retention patch isolated in the upland portion of early seral (2-6 years after harvest) conifer plantations (mean = 4.7, SE = 0.47). Furthermore, estimates of species richness within only

retention areas (i.e., not considering species in the surrounding early seral plantation) did not differ among treatments, indicating that the slightly elevated species richness in riparian-associated retention results from 1-2 species in these patches that do not occur in adjacent regenerating forest areas. Species and functional richness were both lower in unharvested closed-canopy forests. Our results indicate that at retention levels currently required in the Pacific Northwest, decisions on where to allocate retention trees are not overly consequential for small mammal species or functional richness in early seral conifer plantations, but local increases in species richness can be achieved by connecting all retention trees to riparian buffers.

3.2 Introduction

Society is increasingly reliant on intensively managed even-aged rotations of forest plantations to meet demand for wood and other forest products (Brockerhoff et al. 2008, Demarais et al. 2017). Consequently, area of these plantation forests is increasing despite decreases in total forest cover globally (Brockerhoff et al. 2008), creating opportunities for forest species conservation. However, wildlife habitat structure in tree plantations is simplified compared to less intensively managed forests (Stephens and Wagner 2007) and early seral conditions following forest harvest are often less diverse than forests resulting from natural, stand-replacing disturbance (Swanson et al. 2011). Retention forestry aims to increase native species diversity in plantation forests by leaving behind a proportion of trees during timber harvest (Lindenmayer et al. 2012). Green tree retention typically increases native species richness of wildlife communities within harvested forests compared to older forest interiors and harvested forests without retention (Aubry et al. 2009, Linden et al. 2012, Fedrowitz et al. 2014, Mori and Kitagawa 2014). However, in the context of aggregated retention where forest harvesting operations leave trees in distinct patches, the effect of retention patch size and location on wildlife communities is less clear (Fedrowitz et al. 2014).

Whether conserving a single-large or several-small (SLOSS) patches of habitat conserves more species for equal amounts of habitat has been debated for decades (Diamond 1975, Simberloff and Abele 1976, Fahrig 2020). However, the effect of patch size and number at a constant level of retention is rarely assessed in experimental retention forestry studies. The few manipulative studies showed no effects of retention patch size or number on species diversity and abundance within harvested areas (Lindenmayer et al. 2010, 2015), but these studies were limited in geographic scope. Distributing retention patches throughout a forest harvest area may increase biodiversity within retention patches, either by competitive release between more similar species that use patches, or by encompassing different microhabitats across the harvest area. Alternatively, aggregating retention into larger patches may maintain conditions necessary for forest interior species, whose persistence following forest harvest would influence species richness at the scale of the entire harvested area (Lee et al. 2017, Franklin et al. 2019). The function of retention areas is also influenced by connectivity to adjacent forest (Blanchet et al. 2013), but experimental studies typically do not assess connectivity when evaluating the benefits of different retention strategies to biodiversity.

Patch level species richness can be a misleading measure of patch contributions to broader scale species richness as species present in small patches are often redundant with those occurring in the matrix surrounding patches (Phillips et al. 2017; see Chapter 1). Hence, studies that quantify species richness in retention patches and the surrounding harvested area can indicate whether species in small patches are redundant with the surrounding matrix and if larger patches are required to increase species richness. Species traits can influence their responses to habitat patch size, and functional richness (the diversity of traits species in a community possess) can be more informative than species richness about the effects of patch size and fragmentation on a community (McGill et al. 2006, Ding et al. 2013). Comparing patterns of species and functional richness in response to retention practices provides insight into whether species traits moderate responses to changes in forest patch size. Stronger or consistent responses of functional richness compared to species richness to retention forestry alternatives suggests that changes in patch size disproportionately affects certain functional groups (Flynn et al. 2009). This is important because the traits that species within a community possess are more strongly related to the contribution of that community to ecosystem function than species richness (Hooper et al. 2005, Gagic et al. 2015). In contrast, greater changes in species richness compared to functional richness in response to patch size suggests that changes in patch size only reduce levels of functional redundancy within a community (Farneda et al. 2019).

We implemented a manipulative study to test how the size, number, and location of retention patches influences species and functional richness of small mammals (<1 kg) within early seral conifer plantations (2-6 years post planting) in the Pacific Northwest, U.S.A. The study included five retention treatments, each containing different combinations of isolated upland retention and retention connected to riparian zones. Treatments contained a relatively constant proportion of tree retention, but patch size and number differed. We predicted that harvested areas containing aggregated retention would provide habitat for forest interior and open habitat species and functional groups present in clearcuts, thereby resulting in small mammal communities with higher species and functional richness for the entire harvested area, compared to harvests with smaller patches of retention. We further predicted that the positive effect of aggregating retention would be strongest in the treatment containing aggregated riparian-associated retention due to connectivity with forested riparian buffers. Alternatively, small mammal species richness in harvested areas may be higher in more dispersed treatments if multiple small patches intercept different abiotic conditions or allow competing species to coexist (Fahrig 2017), but functional richness would be similar across treatments because competing species are often functionally similar (Smith et al. 2013). This study fills key knowledge gaps on effects of retention placement on an understudied ecological community in the Pacific Northwest and contributes to understanding the effects of forest patch pattern and connectivity on small mammal communities.

3.3 Methods

3.3.1 *Study Design*

We conducted this study in the mesic conifer forests of northwest Oregon and southwest Washington, U.S.A., in the Coast and Cascade Mountain Ranges (Figure 3.1). Our experimental design included five retention treatments replicated in 10 blocks (Fig. 3.1). More detailed descriptions of the five retention treatments are in Chapter 1 of this dissertation. Briefly, each treatment represents different locations and aggregations of a relatively constant proportion (i.e., retention trees/area of harvest unit) of retention trees as required by regulation. Treatments included riparian aggregated retention (RA), upland aggregated retention (UA), two types of split (S) retention (half riparian and half upland), one with created snags (SS), and retention dispersed throughout the harvest area in small, isolated patches that contained created snags (DS). All forest harvesting restrictions were followed that included protection of waterbodies, threatened or endangered species locations, and special ecological or cultural sites, avoidance of unstable slopes, and soil conservation. Hence, our experimental design reflects typical site- and landowner-specific variability in clearcut harvest practices in the region. Mean harvest stand size was 33.6 ha (SD = 10.6 ha) and number of retained structures per harvest area ranged from 51 to 227 (mean = 82, SD = 35). In addition to sampling treatment sites, we sampled one rotation-aged forest (RotAge, ~50 years old) in 9 of 10 blocks to compare small mammal communities occurring in managed, closed canopy forests to those found in the different retention treatment stands.

3.3.2 *Field Methods*

To sample small mammal communities in treatment stands we used two live traps models: Sherman (Model LFA, 7.6 x 8.9 x 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) and Tomahawk (Model 202, 48.3 x 15.2 x 15.2 cm, Tomahawk Live Trap Co., Tomahawk, Wisconsin) traps. For each stand, we allocated 96 trap sites; half in retention patches and half in the surrounding early-seral clearcut area (distances of clearcut grids from patches varied from 12-213m (mean = 49m). We deployed a Sherman trap at each trap site, and a Tomahawk trap at every other trap site. Details on size and configuration of live trapping grids are in Chapter 2 of this dissertation. We sampled rotation-aged stands with a 48-trap grid (24 Tomahawk), consistent with effort in aggregated retention patches of experimental treatment stands.

We annually live-trapped each treatment for three consecutive summers (2017-2019) between late May and early September. Due to logistical constraints, we were unable to trap 1 UA treatment in 2019, and 1 Split treatment for only 3 nights in 2019. We trapped 7 of 9 rotation-aged stands in 2019 because 2 of the areas were logged between 2018 and 2019 as part of routine harvest schedules. We opened traps in the morning or afternoon and then checked the following morning or early afternoon for 4 consecutive days. During each trap check we identified captured animals to species, recorded weight, and tagged each ear with unique ear tags (National Band and Tag Company, Style 1005-1, Monel). We only used one ear tag on vole species. For recaptures, we only recorded tag numbers and location of capture.

For shrews, we collected morphological measurements to aid in species identification but did not ear tag them; we considered all captured shrews to be new individuals. As we did not bait traps to attract shrews, and >60% of shrews we captured died in our traps, we believe this is a reasonable assumption. We collected dead shrews for lab identification except for the most common and easily identified species, *Sorex trowbridgii*. Aside from *Sorex trowbridgii* and the diminutive *Sorex vagrans*, we classified all other shrews caught and released in the field as *Sorex* species. These include individuals of *Sorex bairdii, Sorex monticolus, Sorex pacificus, and Sorex sonomae* that are not possible to differentiate in the field, and for the most part have allopatric distributions in western Oregon. We differentiated between the 2 species of *Peromyscus* at the Washington sites by measuring tail length. Individuals with tail lengths ≥95mm were classified as *Peromyscus keeni*, and those <95mm were classified as *Permomyscus maniculatus* which separates adults of each species with 94% accuracy (Zheng et al. 2003). Animal capture, handling and tagging procedures were approved by the Institutional Animal Care and Use Committee at Michigan State University (AUF 04-16-040).

3.3.3 *Analysis*

We included species captured >1 time, but excluded non-native Virginia opossum (*Didelphis didelphis*; two captures) in the richness analyses. We excluded four species captured once because our trapping protocol did not reliably detect these widespread species (*Mephitis mephitis*, *Sylvalagus bachmanii, Aplodontia rufa*, *Microtus richardsoni*). Observed species richness at a location is usually lower than true richness and to account for potential under-sampling of species we used the Chao 1 species richness estimator (Chao 1987, Gotelli and Chao 2013). The Chao1 estimator adjusts observed species richness at a location upwards based on number of species represented by 1 or 2 individuals, under the assumption that rare species contain most of the information about number of undetected species. We estimated species richness at 2 extents; treatment stand (i.e., stand extent), and for retention patch and early-seral clearcut area separately within a treatment stand (i.e., cover type extent). Comparing estimates at both these extents yields insights into levels of redundancy between retention patch and clearcut communities, and if this redundancy varies by treatment. For example, if species richness estimates for stand and cover type extents are similar, we can infer that most species are redundant between retention patches and clearcuts. We implemented the Chao1 estimator in R package vegan version 2.5.6 (Oksanen et al 2019).

We estimated functional richness using a dendrogram constructed from mean body mass (grams), diet guild, and activity stratum (arboreal, semi arboreal, ground dwelling or fossorial) using Gower's distance and the unweighted pair group method with arithmetic mean clustering algorithm (Figure 3.2; Laliberte and Legendre 2010). We calculated mean body mass for all individuals captured, including juveniles. For species that we did not weigh in the field (i.e., *Mustela erminea*, *Mustela frenata*, *Lepus americanus*) we sourced mean body mass from a regional mammal guide (Verts and Carraway 1998). We grouped species into diet guilds based on whether they are primarily carnivorous (3 species), insectivorous (4 species), or granivorous/mycophagous (14 species). This functional trait was also phylogenetic at the order level as we grouped carnivores, insectivores, and rodents (including one lagamorph). Although we do not assert that these 3 traits entirely represent functional niches for these species in forest ecosystems, body size determines a large part of species ecology within a guild (Peters 1986). Using the dendrogram constructed from these three traits, we quantified functional richness for treatment areas as the total branch length of a tree linking all species captured in a treatment stand during a given sampling session (Petchey and Gaston 2002). Although a Chao1 correction is available for functional richness, we only modeled observed functional richness because of the highly variable estimates of functional richness produced by this method. We performed functional richness calculations in R package BAT version 2.1.1 (Cardoso et al. 2015).

We used species and functional richness estimates for each treatment area as response variables in linear mixed effects models to quantify how retention pattern influences mammalian diversity in and adjacent to retention patches. Although count data (like species richness) are typically analyzed using Poisson regression models, Chao1 species richness estimates are not always integers and at the stand-extent, our sampled species richness estimates were normally distributed. Hence, we used models with a Gaussian response for both estimated species and functional richness. Species richness estimates for cover types within stands were left-skewed so we fit this variable as a Poisson distributed response, after rounding the Chao1 estimates to the nearest integer.

We structured our models using Helmert contrasts with the RA treatment as the intercept, and the coefficients for remaining treatments representing deviations in richness from that treatment. We also included sampling year as a numeric covariate. We fit a second model for each response variable that included an interaction between retention treatment and sampling year to test whether the effect of retention treatment on species and functional richness changed over the course of sampling. Our data included sampling from the same sites across multiple years, so for each model we included a stand-level random effect to account for dependency among observations from the same stand, in addition to a block-level random effect. The treatment by year interaction model did not converge with a block-level random effect so we did not include a dependency at this level in the model. To understand how variation in sampling among treatments influenced the number of individuals captured we fit a Poisson mixed model with total number of individuals captured per trapping period as a response variable and treatment, year, and sampling week as dependent variables. We square root transformed the number of individuals captured to aid in model convergence. Mixed effects modeling was performed in R package lme4 version 1.1.23 (Bates et al. 2015). We assessed regression assumptions of all mixed-effects models using residual plots from the R package DHARMa version 0.3.2.0 (Hartig 2019).

3.4 Results

We captured 5,150 individual mammals of 24 species and, typical for small mammal studies, the distribution of abundances skewed heavily towards a few common species (Figure 3.3). Four species accounted for over 85% of captures: *Peromyscus maniculatus* (2,063 individuals), *Neotamias townsendii* (1,434 individuals), *Microtus oregoni* (655 individuals), and *Sorex trowbridgii* (252 individuals). Number of individual animals captured over 4-day trapping sessions ranged from 3 to 123 (median = 29). Observed species richness at the stand scale ranged from 1 to 9 species (median = 5), Chao1 estimates ranged from 1 to 14 species (median = 5), and stand scale functional richness (dendrogram length) ranged from 0.62 to 2.09 (median = 1.25). Observed mammal species richness for the cover type extent ranged from 1 to 8 species (median = 4), and Chao1 estimates for this scale ranged from 1 to 13 species (median = 4).

For the treatment main effects model coefficient estimates for the effect of retention treatment on species richness at the stand extent were negative relative to RA (Table 3.1), but effect sizes were small. Species richness for the 2 treatments with only upland retention were lower than RA (Table 3.1). On average, UA and DS treatments had 1.8 and 1.4 fewer small mammal species, respectively, than the RA treatment (Figure 3.4a). Rotation-aged forest had the lowest species richness relative to RA (Figure 3.4a). Although this may have been related to lower sampling effort in the Rotation-aged forest treatment (i.e., half the effort of other treatment stands), Chao1 estimates are typically robust to variation in sampling effort (Chao 1987). Functional richness did not differ among treatments, however functional richness was lower in rotation-aged forests (Figure 3.4b). We did not find statistical support for year by treatment interactions on species or functional richness (Table 3.2).

We did not find a difference in species richness at the cover type extent (i.e., retention patch and early-seral plantations) among treatments (Table 3.1). Similar species richness estimates within retention patches indicates that the slightly elevated stand extent richness in the RA treatment likely resulted from less redundancy in species composition between patches and young plantations, not more species in the RA patches compared to patches in other treatments. Coefficient estimates from the Poisson mixed model indicated that total individuals captured were highest for the DS treatment and lowest for the UA treatment on average, but 95% CI for all parameter estimates overlapped each other and 0 (Table 3.2).

3.5 Discussion

Retention forestry is a widely implemented conservation practice to increase species diversity in managed forests but experimental studies of different retention strategies while controlling for amount of retention are rare. Our study revealed that small mammal species richness was lower in aggregated and dispersed upland patches in young conifer plantations, containing 1-2 fewer species on average compared to aggregated retention connected to unharvested riparian forests. This finding partially supported our prediction that aggregating retention into large patches should increase small mammal diversity compared to more dispersed retention patterns, because aggregated patches not connected to riparian corridors had the lowest species richness of all patch types. Median species richness across all sites was low (5), and loss of 1-2 species in the UA treatment represented a ~25% reduction in species richness compared to the RA treatment. Higher species richness in riparian aggregated retention compared to upland retention treatments indicates that unharvested riparian forests are important locations of small mammal diversity within young conifer plantations in the Pacific Northwest. The fact that the two treatments that contained upland and riparian-associated retention did not support higher small mammal species than the RA treatment richness further suggests that upland retention does not conserve unique species compared to riparian retention.

Quantifying species richness in retention patches and surrounding early seral conifer portions of treatment stands enabled us to demonstrate a slight increase in species richness in riparian aggregates compared to other retention patterns (Figure 3.4a). As small forest patches are susceptible to incursion from open habitat species, comparing species richness estimates among patches without considering species occurring in the surrounding environment can be misleading (Blanchet et al. 2013, Phillips et al. 2017). Species richness estimates for retention areas within treatments were more similar among treatments than stand extent estimates (Figure 3.4a), and for most treatments, stand extent species richness was not significantly higher than species richness in retention. This indicates that species are mostly redundant between retention patch and young plantations within stands. However, this redundancy was lower in aggregated patches connected to unharvested riparian buffers, as the RA treatment was the only treatment where the stand extent species richness was significantly higher than species richness in retention patches (Figure 3.2a). Other studies have taken a different approach and estimated richness for forest and non-forest species separately, finding greater influence of forest fragment area on forest species than all species combined (Matthews et al. 2014, Bueno et al. 2018). However, we found that species of small mammals classified as forest specialists in other studies (e.g. *Sorex trowbridgii*, *Tamiasciurus douglasii*, Perault and Lomolino 2000) can also occur in early seral conifer plantations.

In contrast to species richness in our study, functional richness (quantified by body size and broad diet guilds) did not vary consistently by treatment, suggesting that lower species richness in aggregated upland patches is not resulting from loss of functionally unique species, but from reduction of species that are functionally similar (Farneda et al. 2019). Hence, while green tree retention patterns do not consistently alter small mammal functional groups present in young conifer plantations, upland aggregates likely have less functional redundancy. We acknowledge that under-sampling and imperfect detection of species potentially affected our functional richness estimates (Roth et al. 2018), and that we used only limited trait information to define functional identity of species. Importantly, our field sampling based on baiting traps placed on the ground with seeds may not effectively sample certain functional groups (i.e., arboreal species, insectivores, carnivores). This may in part explain why we did not find an effect of retention treatment on small mammal functional richness.

Species richness patterns arise from varied processes, commonly associated with environmental heterogeneity (Stein et al. 2014). Environmental heterogeneity increases availability of potential niches (Tews et al. 2004), and can stabilize predator-prey or competitive interactions between species (Kotler and Brown 1988). The species-area relationship predicts that sampling a larger area increases the likelihood of encountering more species (Preston 1960), potentially because more heterogeneity in habitat is intersected as sampling area increases (Kallimanis et al. 2008). Another proposed mechanism for the species area relationship is the "more individuals hypothesis", where number of individuals sampled increases with sampling area, thereby increasing the likelihood of encountering new species (Hill et al. 1994). In our study system, habitat heterogeneity appears more strongly related to variation in species richness across space than number of individuals encountered. The number of individuals captured was highest in the DS treatment and lowest in the 2 aggregated treatments (Table 3.2), but the RA treatment supported higher estimated richness than DS. This suggests that the environment across upland portions of young conifer plantations is relatively homogenous and only riparian zones create sufficient levels of habitat heterogeneity to increase small mammal species richness. At broader spatial extents, small mammal species richness is associated with primary productivity (McCain et al. 2018), offering another potential explanation for our results as primary productivity in riparian zones tends to be higher compared to upland areas (Naiman et al. 1998).

Our results are consistent with previous studies in the region based on pitfall traps that targeted smaller-bodied species, finding that small mammal species richness was higher in riparian zones with only one species occurring at higher abundances in upland forests (Gomez and Anthony 1998, Lehmkuhl et al. 2008). The only species more common in upland forests, *Myodes californicus*, was rare in our data (4 individuals) and its scarcity on intensively managed forest landscapes may in part explain why larger upland patches in our study failed to increase small mammal richness. *M. californicus* (and *M. gapperi* in WA) is a dominant component of old growth forests in the region and its absence at our sites likely reflects lack of structural complexity in intensively managed forests (Carey and Johnson 1995). Whether green tree retention as currently practiced in the region can increase structural complexity of later seral production forests for the benefit of late seral species (Tallmon and Mills 1994, Carey et al. 1999) is an important question for future research.

3.6 Conclusions

Across the range of young conifer plantation sizes we evaluated higher small mammal richness corresponded to retaining groups of trees connected to unharvested riparian corridors. If increasing small mammal diversity in upland areas of young conifer plantations is a management objective, or in plantations without riparian zones, dispersing trees in multiple small patches throughout the harvest appears to result in slight increases in species richness compared to retaining a single large, isolated patch. Within the constraints of how we quantified functional richness, retention pattern had minimal effect on functional richness of the small mammal community. Hence, retention placement decisions are most consequential for small mammal species richness as opposed to presence of particular functional groups in early seral conifer forests of the Pacific Northwest, USA.

APPENDIX

Table 3.1

Coefficient estimates and 95% confidence intervals from linear mixed effects models (Gaussian response) predicting small mammal species (SppRichness) and functional (FunRichness) richness by structural retention treatment in early seral conifer plantations. Also, coefficient estimates and 95% confidence intervals for a linear mixed effect model (Poisson response) predicting small mammal species richness by cover type (retention patch or clearcut; CoverTypeSppRich) within structural retention treatment areas. Reference treatment for all models is Riparian Aggregate (RA). Data for models collected in southwest Washington and western Oregon, 2017-2019.

	Model		
Treatment	SppRichness	FunRichness	CoverTypeSppRich
Upland Aggregated	**-1.84, -3.08 – -0.59**	-0.19, -0.51 – 0.11	-0.12, -0.38 – 0.14
Split	-0.41, -1.64 – 0.82	-0.10, -0.41 – 0.21	0.06, -0.19 – 0.31
Split with Snags	-0.74, -1.96 – 0.50	-0.12, -0.43 – 0.18	0.01, -0.26 – 0.24
Dispersed with Snags	**-1.46, -2.66 – -0.19**	-0.13, -0.44 – 0.17	-0.10, -0.36 – 0.15
Rotation-aged	**-3.41, -4.70 – -2.13**	**-0.58, -0.89 – -0.26**	-

Table 3.2

Coefficient estimates and 95% confidence intervals from linear mixed effects models (Gaussian response) predicting small mammal species (SppRichness) and functional (FunRichness) richness by structural retention treatment with treatment by sampling year interaction in early seral conifer plantations. Reference treatment for all models is Riparian Aggregate (RA). Data for models collected in southwest Washington and western Oregon, 2017-2019.

	Model	
Treatment	SppRichness	FunRichness
Upland Aggregate (UA)	**-2.09, -3.80 – -0.40**	-0.15, -0.54 – 0.24
Split (S)	-0.01, -1.72 – 1.68	0.08, -0.31 – 0.47
Split, Created Snags (SS)	-1.19, -2.89 – 0.51	-0.14, -0.53 – 0.24
Dispersed (DS)	-1.42, -3.11 – 0.28	-0.04, -0.43 – 0.35
Rotation-aged	**-3.34, -5.09 – -1.59**	**-0.44, -0.85 – -0.04**
Year	-0.03, -0.87 – 0.81	0.09, -0.08 – 0.26
Upland Aggregate * Year	0.27, -0.93 – 1.47	-0.05, -0.29 – 0.20
Split * Year	-0.47, -1.58 – 0.79	-0.18, -0.42– 0.61
Split with Snags * Year	0.36, -0.73 – 1.64	0.02, -0.22 – 0.26
Dispersed with Snags * Year	0.04, -1.19 – 1.18	-0.09, -0.33 – 0.15
Rotation-aged * Year	-0.09, -1.36 – 1.18	-0.14, -0.40 – 0.12

Table 3.3

Coefficient estimates and 95% CI from a linear mixed effects model (Poisson response) predicting the relationship between each retention treatment (and year) and number of individual small mammal captures, relative to the RA control in early seral conifer plantations. Number of individuals captured was square root transformed. Data collected in southwest Washington and western Oregon, 2017-2019.

Treatment	Beta	Lower2.5%	Upper97.5%
Upland Aggregated	-0.35	-1.32	0.62
Split	0.50	-0.47	1.46
Split with Snags	0.40	-0.57	1.37
Dispersed with Snags	0.85	-0.11	1.82
Rotation-aged	-2.52	-3.53	-1.51
Year	0.12	-0.11	0.35

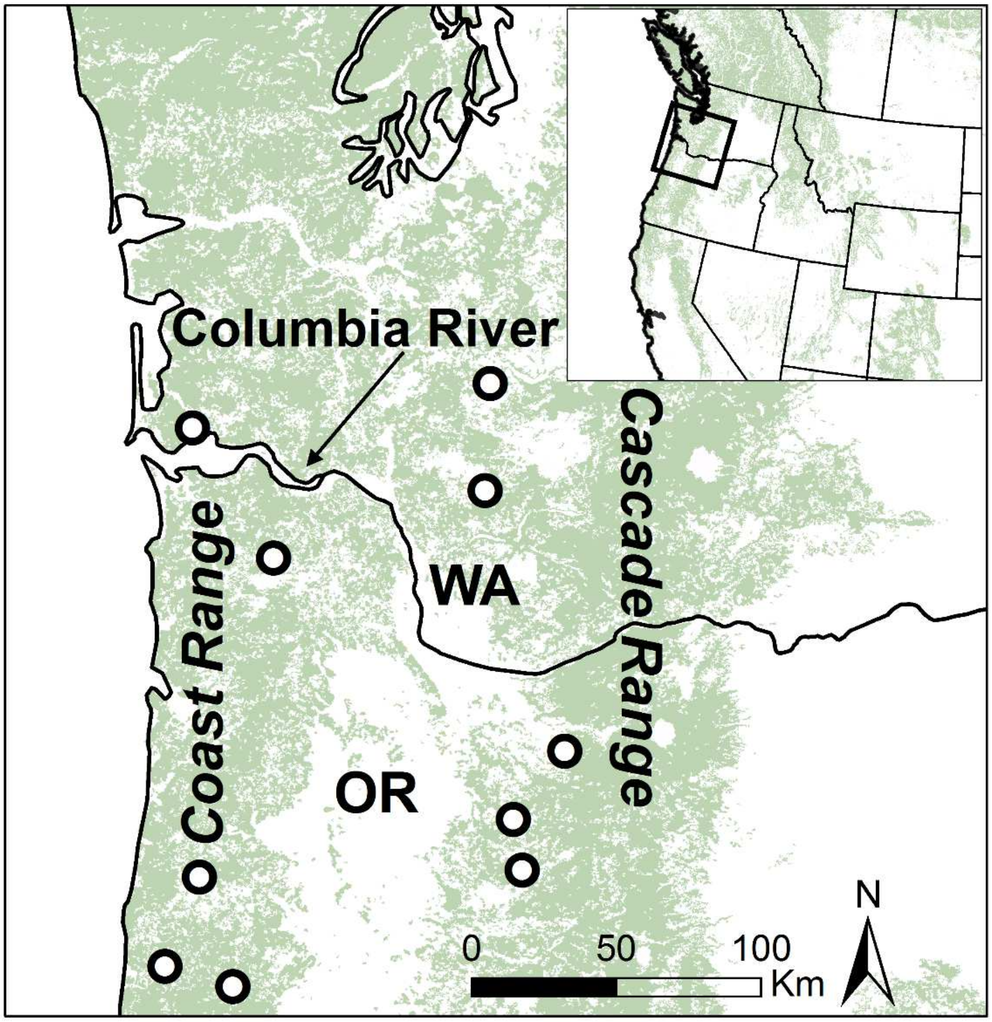

Figure 3.1

Study area in the Pacific Northwest, U.S.A., depicting 10 experimental blocks (open circles) each containing 5 treatment early-seral conifer plantations with retention sampled for small mammals in summers 2017-2019. Green depicts approximate forest cover at 250m resolution (North American Land Cover 2005 Data Release).

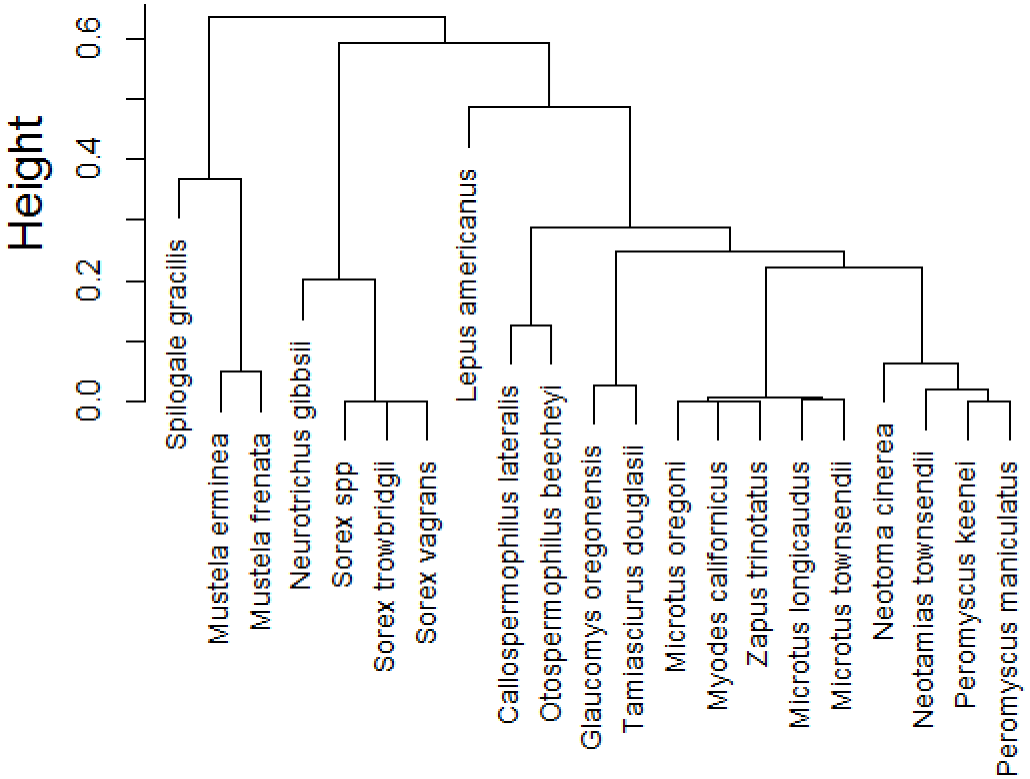

Figure 3.2

Functional dendrogram for 21 small mammal species used to calculate functional richness within 50 early-seral conifer plantations with retention and 9 rotation aged forests in northwest Oregon and southwest Washington USA during summers 2017-2019. Dendrogram was constructed from the UPGMA clustering algorithm and Gower's distance derived from the functional traits body size, diet, and activity stratum.

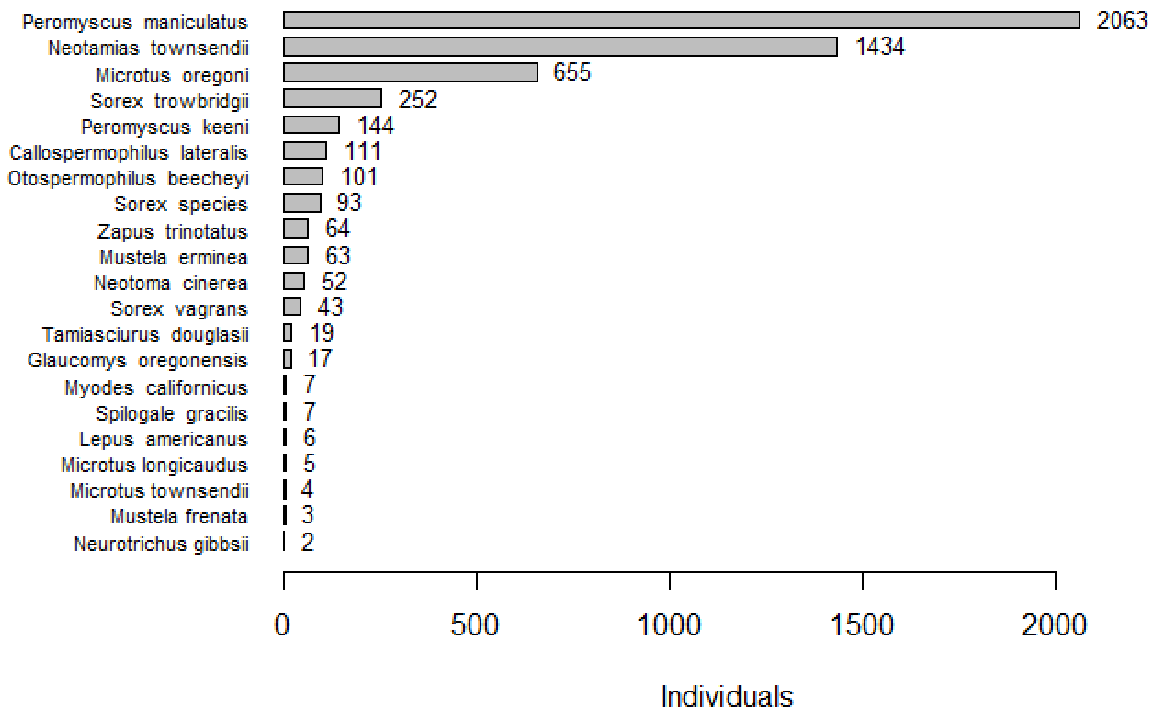

Figure 3.3

Number of individuals captured for each of 21 small mammal species captured >1 time in 50 early-seral conifer plantations with retention and 9 rotation aged forests in northwest Oregon and southwest Washington, USA, during summers 2017-2019.

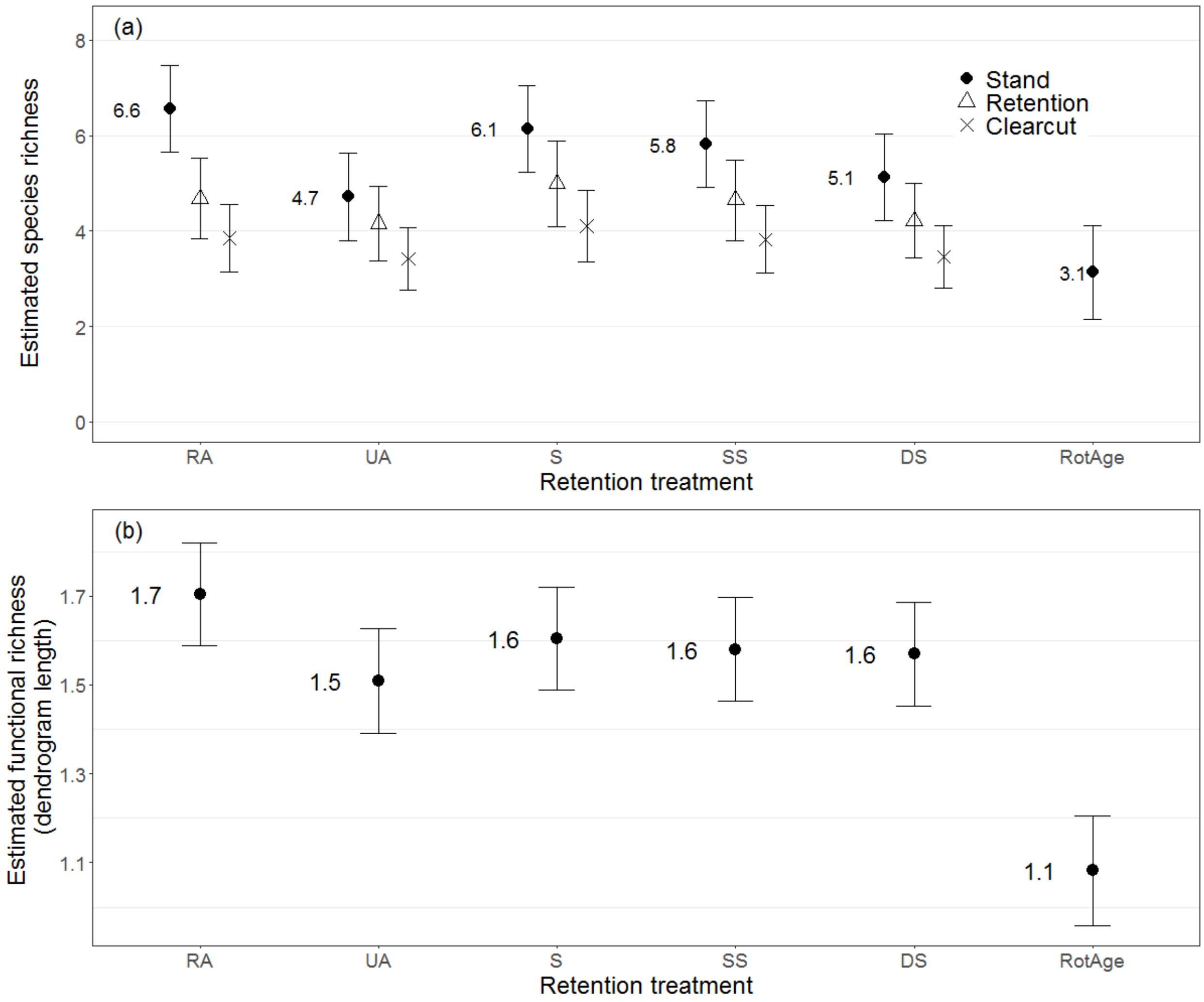

Figure 3.4

(a) Chao1 species richness estimates at the stand extent (black circles), within retention (white triangles) and within early-seral conifer plantations surrounding retention (X), and (b) stand extent functional richness estimates. Estimates represent unconditional predictions from mixed effects models for 2018 sampling year. Estimates derived from small mammal live trapping in in northwest Oregon and southwest Washington, USA, during summers 2017-2019.

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CHAPTER 4

ABIOTIC AND BIOTIC CORRELATES OF SMALL MAMMAL ABUNDANCE ACROSS SCALES: INSIGHTS FROM A JOINT SPECIES DISTRIBUTION MODEL

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4.1 Abstract

The distribution and abundance of species within ecological communities are influenced by both abiotic conditions, such as climate, and biotic interactions with other species, with importance of each potentially varying across spatial scales. Joint species distribution models (JSDMS) can estimate the effects of environmental variation on multiple species, and subsequently infer biotic interactions between species from residual correlations, with the inclusion of species traits aiding in interpretation of residual correlation between species. We related count data collected on eleven small mammal species in early seral forest plantations in the U.S. Pacific Northwest with forest management and environmental covariates using a JSDM at two spatial extents. After accounting for relevant environmental factors, we expected to find negative residual correlation between functionally similar species at more local spatial extents, which might reflect interspecific competition. Contrary to this expectation we found that most statistically supported species associations were positive at the local spatial extent, while other species pairs were negatively associated at a larger (i.e., multiple stands within an experimental block) extent. This pattern suggests that rather than competition between species, shared responses to resources within and broad scale environmental filters underlie community abundance patterns of small mammals in early-seral temperature forests.

4.2 Introduction

A central focus of community ecology is determining the relative influences of internal and external drivers of community composition (HilleRisLambers et al. 2012). Geographic distributions of species and ecological communities reflect both internal biotic drivers, such as predation or competition, and external (often abiotic) drivers, such as climate and habitat structure (Wiens 2011). Importantly, relationships between species and environmental conditions are scale dependent (Wiens 1989, Belmaker et al. 2015). Generally, ecologists predict that abiotic conditions such as climate or geomorphology are important at structuring communities at broader extents (Pearson and Dawson 2003), with species interactions becoming increasingly important at more local extents (McGill 2010). However, highly mobile taxa like birds, the imprint of biotic interactions on community structure is detectable at fairly broad, regional extents (Gotelli et al. 2010, Belmaker et al. 2015). Although observational data on community composition alone cannot differentiate abiotic and biotic community assembly processes (Blanchet et al. 2020), identifying scale dependent species associations provides insights into potential biotic interactions, particularly if higher levels of residual correlation among species are detected at more local spatial extents.

Species distribution models (SDMs) are widely used to estimate abiotic correlates of species occurrences but have been criticized because they tend to focus on one species and ignore biotic interactions among species (Wisz et al. 2013). Joint species distribution models (JSDMs, Pollock et al. 2014) address these pitfalls by estimating abiotic correlates of occurrences or abundances for multiple species, and estimating residual correlation between two or more species (Warton et al. 2015, Ovaskainen et al. 2017). Although JSDMs and SDMs are parameterized with observational data, the residual correlation among species in JSDMs may signal biotic interactions among species, but cautious interpretation is required (Dormann et al. 2018). The ability of JSDMs to portray interactions among species that influence community-level patterns is uncertain as processes driving a species response to environmental variation or other species can result in similar patterns of species covariation (Blanchet et al. 2020). For example, if two species have contrasting responses to unmeasured variation in the environment then their occurrence or abundance will be negatively correlated even in the absence of competition (Letten et al. 2015). To improve interpretation of how communities are structured by external and internal drivers (particularly biotic interactions), JSDMs can be paired with data at varying spatial extents and species functional traits that reflect the degree of shared niche space and degree of competition between species (Read et al. 2018).

Species that are behaviorally or morphologically similar are more likely to compete for resources, so species trait data can provide important insights into signals of biotic interactions between species in observational community data (Dormann et al. 2018). Observing negative associations between species that are similar to one another is potential evidence for competition, whereas presence of positive correlations between functionally similar species suggests that shared responses to resources underlie community co-occurrence patterns (McGill et al. 2006). For animal taxa, body size is a key trait that reflects degree of shared niche space and degree of competition at the community level (Read et al. 2018). Furthermore, competition among functionally similar species may reduce abundances without resulting in complete exclusion (Ritchie et al. 2009), and source-sink dynamics can lead to species occurrence in low-quality habitat (Shmida and Wilson 1985). Multispecies abundance data may reflect factors influencing species distributions better than presence-absence data (Howard et al. 2014). However, because community-wide estimates of abundances are less common, fewer studies use abundance data in JDSMs to assess residual correlation between potentially interacting species.

Small mammals (<1kg), particularly rodents, are an important study group for community assembly processes (Fox and Brown 1993). Although the presence of nonrandom co-occurrence patterns in rodent communities due to competition is debated (Brown et al. 2000, Stone et al. 2000), interspecific competition can be strong among species (Abramsky et al. 1991), potentially leading to negative associations among species across space. However, time series data often indicate high levels of synchrony among small mammal species within a community and this synchrony can occur across trophic levels (Stephens et al. 2017), suggesting that bottom up forces or extrinsic factors are more important than competition for driving population dynamics. Despite synchronous dynamics among species across years, species abundance patterns often show little broad-scale spatial structure (i.e., distances of >1km; Bowman et al. 2000), suggesting that small mammal populations are mostly structured by local scale habitat features. However, these small mammal studies occurred across relatively small geographic extents and within relatively homogeneous landscapes with limited variation in abiotic conditions. Measuring community-wide patterns of small mammal abundance at multiple spatial extents across large geographic areas can provide stronger inference into the role of species interactions in community assembly (Püttker et al. 2019). Furthermore, similarity among body sizes between species can be used to guide interpretation of species association patterns.

We used joint species distribution modeling and species-specific body sizes to investigate the roles of biotic interactions and habitat structure in driving variation in small mammal abundance at different spatial extents in early seral forests. In this dispersal limited group, we interpret higher support for associations between species abundances at larger extents as indicative of abiotic or geographic factors acting as an environmental filter (Kohli et al. 2018). Conversely, higher levels of local correlation between species abundances suggests that microhabitat components or species interactions are more important determinants of species abundance patterns. We predicted that after accounting for important environmental factors that influence small mammal abundances (e.g., vegetation, elevation, forest patch size), significant residual correlation would exist between species and that the correlation would be higher at smaller spatial extents. We also predicted that residual associations between species would be more apparent when considering count data for each species compared to presence-absence, due to the more detailed information contained in abundance data (Howard et al. 2014). Finally, we predicted that evidence for competitive processes between ecologically similar species would exist, indicated by significant negative correlation between species more similar in body size. In contrast, positive correlation between species would suggest shared responses of species to resources as a more important driver of small mammal abundance patterns than competition between species.

4.3 Methods

4.3.1 *Study Area*

I conducted this study on forest landscapes managed primarily for wood production in northwestern Oregon and southwestern Washington, U.S.A., from latitudes 44.51 to 46.42ºN and longitudes 122.06 and 123.92ºW (see Chapter 2: Figure 2.1). Study sites were located in the Coast and Cascade mountain ranges with elevations ranging from 57 to 1172 m. Although historically dominated by old growth conifer forests, most managed forests in these landscapes are harvested on even-aged forest rotations of approximately 50 years, with planting of native conifer species after harvest. Douglas fir (*Pseudotsuga menzeii*) is the dominant native and commercial tree species in the region, with western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) occurring on wetter sites, and noble fir (*Abies procera*) at higher elevation sites. Red alder (*Ulnus rubrum*) and bigleaf maple (*Acer macrophyllum*) comprise the minor deciduous component of forests throughout the region. Common understory shrubs include salmonberry (*Rubus spectabilis*), vine maple (*Acer circinatum*), Pacific rhododendron (*Rhodendrom macophyllum*), and *Vaccinium* spp. Understory herbaceous vegetation includes sword fern (*Polystichum munitum*) and *Oxalis oregana* with fireweed (*Chamaenerion angustifolium*), grasses, and several exotic forbs being common in harvested areas.

4.3.2 *Study Design*

I summarize site selection and experimental treatment elements here; more detailed information on can be found in Chapter 2 of this dissertation. Fifty forested stands within ten experimental blocks were selected for sampling, each assigned to one of five experimental harvest treatments. Experimental treatments consisted of a early seral conifer plantation (2-6 years after forest harvest) with varying distribution of retained green trees. Green trees were retained at a constant proportion of approximately ~5 trees per hectare of harvested area. Importantly, although location (upland or riparian) or number of retention patches differed among treatments, each study site was a young conifer plantation (within 2-6 years) with a small portion of standing trees retained. Mean size of these experimental sites was 33.6 ha (SD=10.6) with an average of 82 (SD = 35) retained trees.

4.3.3 *Small Mammal Sampling*

We sampled small mammals annually from May through early September, in 2017, 2018, and 2019. Sampling in one experimental site was not conducted in 2020 resulting in a total of 149 sampling sessions. We used two types of live traps: Tomahawk traps (Model 202, 48.3 x 15.2 x 15.2 cm, Tomahawk Live Trap Co., Tomahawk, Wisconsin) that capture larger-bodied species (e.g., squirrels) and Sherman traps (Model LFA, 7.6 x 8.9 x 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) that capture smaller-bodied species (e.g., mice, voles, and shrews). We placed live trap grids both within retention tree patches and adjacent harvested areas, with equal effort between the two cover types. Number of trap sites was constant but trapping grid configuration varied by treatment. Details on the trapping process and grid configurations can be found in Chapter 2 of this dissertation.

Each site was sampled for one, four-day period in each of the three sampling years and the dates of sampling at individual sites rotated between years. We marked all rodent species captured with a unique ear tag. Shrews and weasels were not tagged, and we considered each captured shrew and weasel to be a new individual. This is a reasonable assumption as we did not bait traps specifically for these species, and for shrews capture related mortality was >60%, leaving reduced opportunities for recaptures. Repeat detections within sampling sessions were uncommon for weasels. We collected dead shrews to verify species identity. Oregon has three closely related endemic shrew species that have largely allopatric distributions not possible to definitively differentiate in the field. We classified these species as *Sorex spp.*, and *S. trowbridgii or S. vagrans* for confirmed identifications. (Table 4.1). We also pooled the two species of

Peromyscus (*P. maniculatus and P. keeni*) that co-occur in the Washington portion of the study area north of the Columbia River.

4.3.4 *Vegetation Sampling*

To quantify the effect of ground vegetation on abundance of small mammal species, a botanical crew measured two vegetation characteristics at study sites: average proportion of vegetation ground cover and proportion of shrub cover > 1 m tall. Both variables are associated with small mammal abundance in Pacific Northwest forests (Gray et al. 2019; Weldy et al. 2019). Vegetation transects were established and surveyed in each cardinal direction in retention patches and adjacent plantation areas in the summer of 2018, co-located with small mammal trapping grids. Along these transects, proportion of herbaceous ground cover was recorded in $1m^2$ plots spaced every 5-10 m along the transect and proportion of shrub cover was recorded as the length of transect intersected by shrubs >1m tall. Proportion of herbaceous ground cover was averaged across all plots in both retention patches and surrounding plantations yielding a site level value of herbaceous ground cover. Shrub cover from the transects in plantation areas was not included in the site-level proportion shrub cover values because shrubs >1 m tall were rare outside of retention areas due to site preparation for forest replanting.

4.3.5 *Analysis*

We implemented a lognormal-Poisson distributed joint species distribution model in the Hierarchical Modelling of Species Communities framework (HMSC, Ovaskainen et al. 2017).

HMSC is a latent variable modelling approach that jointly estimates responses to environmental (or experimental) covariates and latent variables for multiple species in a community. Residual correlation between species pairs is assessed as the correlation between the average latent factor loadings for each species pair. This residual correlation results from either interactions between species or unmeasured environmental predictors affecting the community (Warton et al. 2015). Importantly, latent factors can be estimated at different hierarchical levels to assess whether associations between species are scale dependent (Ovaskainen et al. 2016). In our study design, we estimated species associations at two extents: landscape (i.e., experimental block) and local (i.e., forest stand).

We captured 11 species > 20 times (Figure 4.1a) and these species comprised our community data for the JDSM. For each species, we used the number of unique individuals captured as an index of species site level abundance (i.e. minimum number known alive, Kelt et al. 2013). These abundance estimates were not corrected for detection at either the individual or species level, and hence the count data is only an index of abundance within sites. We assumed that individual-level detection did not vary considerably among sites as capture and handling techniques were standardized. As sampling occurred throughout summer across years, we also included sampling date in the model to account for potential seasonal trends in detection or abundance. We assumed that detection of one species was not influenced by presence of another species (~10% of traps were occupied during trap checks). With these assumptions, the index should be sufficient to evaluate residual correlation between species. The eleven focal species are primarily ground active, increasing efficacy of ground traps for detection and probability they will interact with each other, given similar diet and body size between species.

Given design-based differences among treated areas, we included treatment as a forest stand level variable, with one treatment specified as the intercept and the remaining four as factors. We also included sampling year as a factor, sampling week as numeric, elevation, proportion herbaceous ground cover, and proportion shrub cover. All continuous covariates were standardized to a mean of zero and standard deviation of one. We specified a Poisson-lognormal distribution for the distribution of species counts to better handle over dispersion in count data relative to the mean (compared to standard Poisson), which is common for species count data (Figure 4.2, Williams and Ebel 2012). We included a random effect for experimental block (landscape) and forest stand (local) levels to estimate associations between species through the latent factor loadings at each of these hierarchical levels. We also fit a presence-absence model to the small mammal data with a probit link function to compare levels of residual correlation among species when considering the two data types and examine whether factors that related to the occurrence and abundance of small mammal species were similar.

We used R package Hmsc version 3.0.6 (Tikhonov et al. 2020) to implement both models in a Bayesian framework. We specified default priors for each model parameter and did not constrain the number of latent factors estimated at each hierarchical level (Landscape and Local). To estimate regression parameters, we ran three MCMC chains for 500,000 iterations, a 250,000 iteration burn-in and a thinning rate of 50, resulting in 5,000 MCMC iterations for each chain and a total of 15,000 iterations. For both models, we assessed convergence of the three MCMC chains using the Gelman-Rubin statistic. We assessed the predictive ability of the count model by calculating Pearson's rank correlation between the observed count of each species at each study site and count predicted by the model, termed pseudo-R2 (in-sample validation). We also calculated pseudo-R2 conditional on species presence for the count model, not considering sampling sessions where a species was not detected for the count model. We considered residual correlations between species that had support at $\alpha = 0.95$ to be evidence for nonrandom associations between species at the either of the two spatial extents (Block and Stand) and potential evidence for species interactions.

4.4 Results

We captured 4,885 individual small mammals from the eleven focal species (Table 4.1), and these eleven species collectively represented 98.9% of total captures within sites. For these eleven species, the total number of individuals sampled ranged from 42 for *Sorex vagrans* to 2,135 for *Peromyscus spp* (Figure 4.1a). During the study ~10% of the traps were occupied on a given day, indicating that competition for traps among individuals was low and trap availability was high.

For the lognormal Poisson count model, correlation between observed and predicted counts (pseudo-R^2) by species ranged from 0.14 to 0.82 (mean = 0.36, sd = 0.21); correlations between predicted and observed counts were highest for the two most abundant species (Figure 4.1B). Pseudo-R^2 conditional on presence ranged from 0.08 to 0.80 and was generally higher for less common species (Figure 4.1B). Overall, abundance of the 11 species did not vary strongly in response to experimental retention treatments, with 95% CI for only six of 44 species-specific treatment effects not overlapping zero (Figure 4.3). Species abundances tended to be higher in treatments with more dispersed retention trees and sampling configurations compared to treatments where sampling was more concentrated in larger and more aggregated retention patches (Figure 4.3).

Based on pseudo-R^2 values, explanatory power of the experimental treatment and habitat model was low (Figure 4.1b) and for five species either block or stand level random effect explained the most variance in counts (Table 4.2). Vegetation explained the most variance for an additional three species, followed by elevation for two species, and temporal effects for one species (Table 4.2). For each species, 95% CI for at least one environmental covariate was significant (Figure 4.4). We observed a sampling year effect on abundances for five species (i.e., SOVA, MUER, ZATR, CALA, NETO, and PESP), whereas sample week was only significant for ZATR (Figure 4.4a,b,c). Counts of ZATR consistently declined later in the sampling season, likely related to catchability (S. Sultaire, personal observation). The small mammal community responded most to the amount of vegetation ground cover, with counts of 6 species positively associated with ground cover and counts of the most abundant species, *Peromyscus spp*, negatively correlated with ground cover (Figure 4.4d). Counts of 4 species were positively associated with shrub cover (Figure 4.4e), and 4 positively with elevation (Figure 4.4f). Except for *Peromyscus* which occurred in all but 2 of the 149 sampling sessions, covariate estimates from the presence-absence model were similar to those estimated from the count model (Figure 4.5).

After accounting for the fixed treatment and environmental effects, the count model estimated ten non-random species associations at the landscape extent (i.e., block); four positive and six negative (Figure 4.6a). The presence-absence model estimated three significant pairwise correlations at the landscape extent; one positive and two negative (Figure 4.7a). At the local extent (i.e., stand), the count model estimated seven statistically supported correlations between species, all positive (Figure 4.6b), whereas the presence-absence model identified two positive correlations with statistical support, both not identified in the count model (Figure 4.7b). In the count model, the pairwise residual correlations between species at the stand extent was concentrated among smaller bodied species, whereas the significant correlations at the block extent tended to include larger bodied species (Figure 4.6).

4.5 Discussion

Investigating variation in the direction and magnitude of species associations across scales can give insights into the mechanisms structuring species distributions and communities (Leibold et al. 2004). In the small mammal community present in early-seral conifer forests, we expected to find more evidence for associations between species at local spatial extents than landscape extents, reflecting a stronger influence of local environment and species interactions on community structure. We also expected negative associations between species that were more similar in body size, which is a proxy for niche competition. In contrast, we found evidence for more positive correlations between species abundances at the broader, landscape extent than at the smaller, local extent. Also contrary to predictions, counts of several species were positively associated at the smaller spatial extent, with the only negative associations occurring at the larger landscape extent. Although the two extents included in this analysis are not rigorously controlled (sizes of blocks and stands differed), positive residual correlations at the local extent suggests interspecific competition between similar species is not a strong determinant of species abundances within early seral conifer forests. Instead, this pattern suggests shared positive responses to resources and habitat structure within forest stands. These positive associations were strongest between rodent species, and I did not observe strong residual correlations between shrew species, suggesting they occur independently after accounting for environmental differences. I also observed no positive residual correlation between the number of weasel captures and any potential prey species. This suggests that the amount of prey is not the primary driver of abundance for this small carnivore, but this conclusion does not take into account the potential of a lagged response of weasels to small mammal population changes.

There are several local scale factors that could drive the observed correlation in abundance between small mammals at the local extent. Vegetation variables included in the JSDM represented vegetation structure but positive associations between species may have resulted from shared responses to changes in vegetation composition. For example, the abundance of most small mammal species studied on managed forests in northern California were influenced by the composition of ground vegetation (i.e., grasses vs. forbs; Gray et al. 2016) but these vegetation categories were grouped in our analysis. Small mammals are also responsive to the presence of forest structural elements such as standing and downed dead wood (Carey 1995) and presence of these habitat elements varies considerably across managed forest landscapes in the Pacific Northwest (Linden and Roloff 2013).

Interestingly, all significant residual associations between species at the local spatial extent were between relatively small bodied species, whereas several significant landscape extent residual associations included larger bodied species. This result suggests that while abundances of smaller bodied species covary in relation to local habitat elements, abundances of larger-bodied species such as ground squirrels are correlated with habitat or abiotic conditions at landscape extents. Although evidence exists that competitive interactions structure communities at broad spatial scales (Gotelli et al. 2010), the negative landscape extent correlations we observed were often detected between ecologically distinct species (i.e., large differences in body size), and the strongest positive associations were detected at this extent between ecologically similar species (e.g., ground squirrel species). Hence, broad-extent residual correlation observed between species appears related to broad-scale unmodelled differences in early seral forest conditions (e.g., forest management regime, climate) or dispersal barriers that prevent species from colonizing certain landscapes. Two large river valleys (the Columbia and Willamette Rivers) fragment the study area, likely functioning as dispersal barriers for some small mammal species (e.g., *Callospermophilus lateralis, Otospermophilis beecheyi*) as indicated by range boundaries.

JSDMs are increasingly used to assess associations between species and the potential for interspecific interactions, but because they are based on observational data their results cannot prove that species within communities interact (Blanchet et al. 2020). We took several steps, such as including count data and multiple spatial extents in the analysis, to strengthen inference on the presence of biotic interactions between small mammal species (Wisz et al 2013). As predicted, the count-based JSDM allowed us to detect more significant associations between species pairs compared to the presence-absence model. This finding supports the idea that abundance information improves inference on associations between species (Blanchet et al. 2020), especially when dominant species occur within all communities sampled (e.g., *Peromyscus* in this study). On the other hand, our model lacked predictive power for abundance of all species (most species pseudo-R^2 values <0.5), reducing the ability to interpret residual correlation as evidence for species interactions. However, it is also possible that the covariates included in the JSDM (i.e. vegetation cover) mediate interactions between species (Morris et al. 2000), in which case covariate effects would mask residual correlation that signals competition between species (Godsoe et al. 2017). For example, small mammal species and functional richness often increase with more structurally complex vegetation (Dorph et al. 2020), suggesting that increasing ground and shrub cover creates more niche space or allows coexistence of similar species. My results support this possibility as six of the eleven species, across three trophic levels (herbivores, insectivores, carnivores) responded positively to increases in ground vegetation, and the four significant abundance relationships with shrub cover were positive. Deer mice, the species with highest recorded counts, was the only species negatively associated with ground cover, further suggesting that increases in the complexity of vegetation could mediate competitive interactions between species. This potential for environmental factors to mediate interactions between species suggests that JSDMs might be most successful at detecting biotic relationships when the mechanistic effect of covariates on species within the community of interest are well understood.

The limited direct evidence for negative interspecific interactions found here is consistent with previous small mammal studies, many conducted in fragmented landscapes comparable to experimental retention stands in our study. Experimental studies in hardwood forests that focused on chipmunk and deer mice species suggest that competitive processes between these species are not strong drivers of abundance (Brunner et al. 2013). Our results build on these findings by demonstrating limited evidence for competition between small mammal species in early seral, post-disturbance forests; which are typically resource rich compared to mid- and late-seral forests (Swanson et al. 2011). Forest small mammal population dynamics often synchronize with masting (Wolff 1996, Stephens et al. 2017), further suggesting that bottom up forces are most important for regulating small mammal populations in temperate forests. Populations from different trophic levels can fluctuate synchronously, suggesting the importance of abiotic factors such as weather (Stephens et al. 2017). Our observed unsynchronized changes in deer mouse and chipmunk populations are consistent with contrasting responses of these species to winter climate in the region (Weldy et al. 2019) and lower synchrony between species with different overwintering strategies (i.e., hibernating vs. non-hibernating; Stephens et al. 2017). The observed trends in species counts over time could also be related to successional processes. Although early seral plant abundance is reduced in intensively managed forests by herbicide applications to control vegetation competing with crop trees (Root et al. 2017), ground vegetation rapidly recovers (i.e., within 3-5 years; Ulappa et al. 2020) and is typically more extensive in early seral forests compared to later stages of succession (Swanson et al. 2011). Deer mice likely responded to changing vegetation by decreasing in abundance both over time and with increasing ground vegetation between sites (Gray et al. 2019); while other species responded positively to increases in vegetation.

One of the few studies to investigate co-abundance patterns of small mammals at multiple spatial extents found evidence for competition between species within forest patches (Püttker et al. 2019). However, this study occurred in tropical forests where biotic interactions between species are more prevalent compared to temperate zones (Schemske et al. 2009). Other observational studies of competitive effects in small mammal communities suggest that competition is stronger at the individual level (e.g., survival, body condition) than at the population level (Sozio and Mortelliti 2015), an effect that would not be detected in our population level analysis. More explicitly incorporating functional traits such as body size into future analyses of small mammal community patterns could better identify individual-level effects of species interactions and the role of body size in structuring interactions between species (Read et al. 2018).

Despite limitations of observational data, our results provide further evidence that interspecific competition, if present in small mammal communities, does not impart a large effect on species abundance patterns. Instead, the overwhelmingly positive residual associations between species at the local spatial extent suggests shared responses to unmeasured environmental variation among forest stands. The shared responses of species to vegetation characteristics suggests that maintaining higher levels of ground vegetation and shrub cover within areas recently harvested for wood will increase abundance of less dominant species within the community and support more complex trophic structure. These localized vegetation factors appear more important than spatial arrangement of retention trees or location of forest patches within logged forests for this group of mostly ground active species. Our results also suggest that even coarse data on abundance (i.e., counts) are more useful than presence-absence data when using correlative approaches like JSDMs to detect associations between species. However, divergent responses of species to between-year variation may mask the effect of competition between species that is moderated by environmental conditions and highlight the difficulty of using correlative JDSMs to infer biotic interactions. The strongly asynchronous population dynamics observed over the three sampling years for the two most abundant species suggests that compensatory dynamics (Ernest and Brown 2001) may stabilize community level abundance patterns during the early years of forest succession. Further investigations into community abundance patterns in later successional forests, where food resources are typically lower than early seral forests (Swanson et al. 2011), will help determine the extent that these findings are generalizable to forest small mammal communities.

APPENDIX

Table 4.1

Species from Coastal and Cascade mountain ranges, Washington and Oregon, U.S.A., included in joint species distribution model analysis of small mammal count data. Mean body size was calculated from all individuals of the species captured, including juveniles (except for *Mustela erminea*, see Methods).

Species	**Species Code**	**Mean Body Size (g)**	**Guild**
Sorex vagrans	SOVA	4.7	Insectivore
Sorex trowbridgii	SOTR	4.8	Insectivore
Sorex spp.	SOSP	7.4	Insectivore
Microtus oregoni	MIOR	17.0	Rodent
Peromyscus spp.	PEMA	18.5	Rodent
Zapus trinotatus	ZATR	22.5	Rodent
Mustela erminea	MUER	54.7	Carnivore
Neotamias townsendii	NETO	73.2	Rodent
Callospermophilus lateralis	CALA	133.0	Rodent
Neotoma cinerea	NECI	218.0	Rodent
Otospermophilus beecheyi	OTBE	494.8	Rodent

Table 4.2

Proportion of variance explained in species (see Table 1 for acronyms) count data by different fixed effects groupings and random effects from a lognormal Poisson count model. Treatment includes five experimental treatment categories, temporal includes the effects of year and sampling date, and vegetation includes proportion ground vegetation and proportion shrub cover. Bold numbers indicate the covariate that explained the highest proportion of variance for each species. Species are ordered by their mean body size increasing from SOVA. Small mammals were sampled in 50 early-seral conifer plantations (2-6 years after forest harvest) with green tree retention within northwest Oregon and southwest Washington, USA during summer 2017-2019.

	Fixed Effects					Random Effects		
Species	Treatment	Temporal	Vegetation	Elevation	Subtotal	Block	Stand	Subtotal
SOVA	0.18	0.22	0.20	0.05	0.65	**0.32**	0.02	0.34
SOTR	0.12	0.09	**0.35**	0.21	0.77	0.08	0.16	0.24
SOSP	0.05	0.06	0.15	0.03	0.29	0.02	**0.68**	0.70
MIOR	0.13	0.12	**0.42**	0.12	0.79	0.06	0.15	0.21
PESP	0.12	**0.68**	0.06	0.04	0.90	0.07	0.04	0.11
ZATR	0.05	0.32	0.22	0.07	0.65	0.01	**0.33**	0.34
MUER	0.23	0.23	**0.45**	0.04	0.95	0.02	0.03	0.05
NETO	0.11	0.14	0.06	0.09	0.40	0.15	**0.44**	0.59
CALA	0.14	0.14	0.08	**0.33**	0.69	0.28	0.03	0.31
NECI	0.15	0.13	0.17	**0.41**	0.86	0.04	0.10	0.14
OTBE	0.14	0.13	0.24	0.04	0.55	**0.39**	0.07	0.46

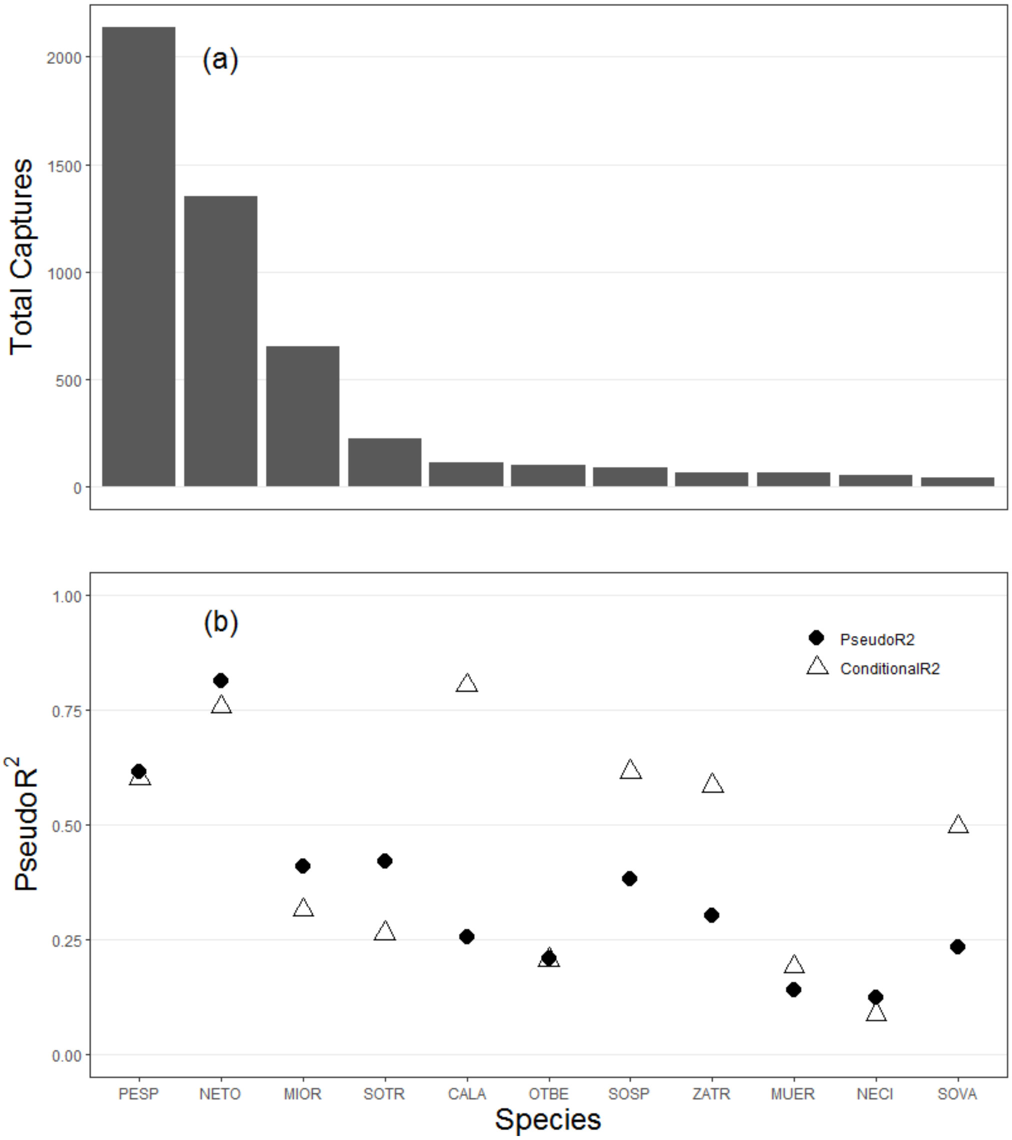

Figure 4.1

(a) Total captures of small mammals. (b) PsuedoR^2 values (correlation between observed and predicted counts for each sampling session) for all locations (filled circles) and conditional on species presence (open triangles) from the lognormal Poisson count model and the total number of individuals captured for each of eleven small species included in the joint species distribution models (bottom panel). Small mammals were sampled in 50 early seral conifer plantations (2-6 years after forest harvest) with green tree retention within northwest Oregon and southwest Washington, USA during summer 2017-2019.

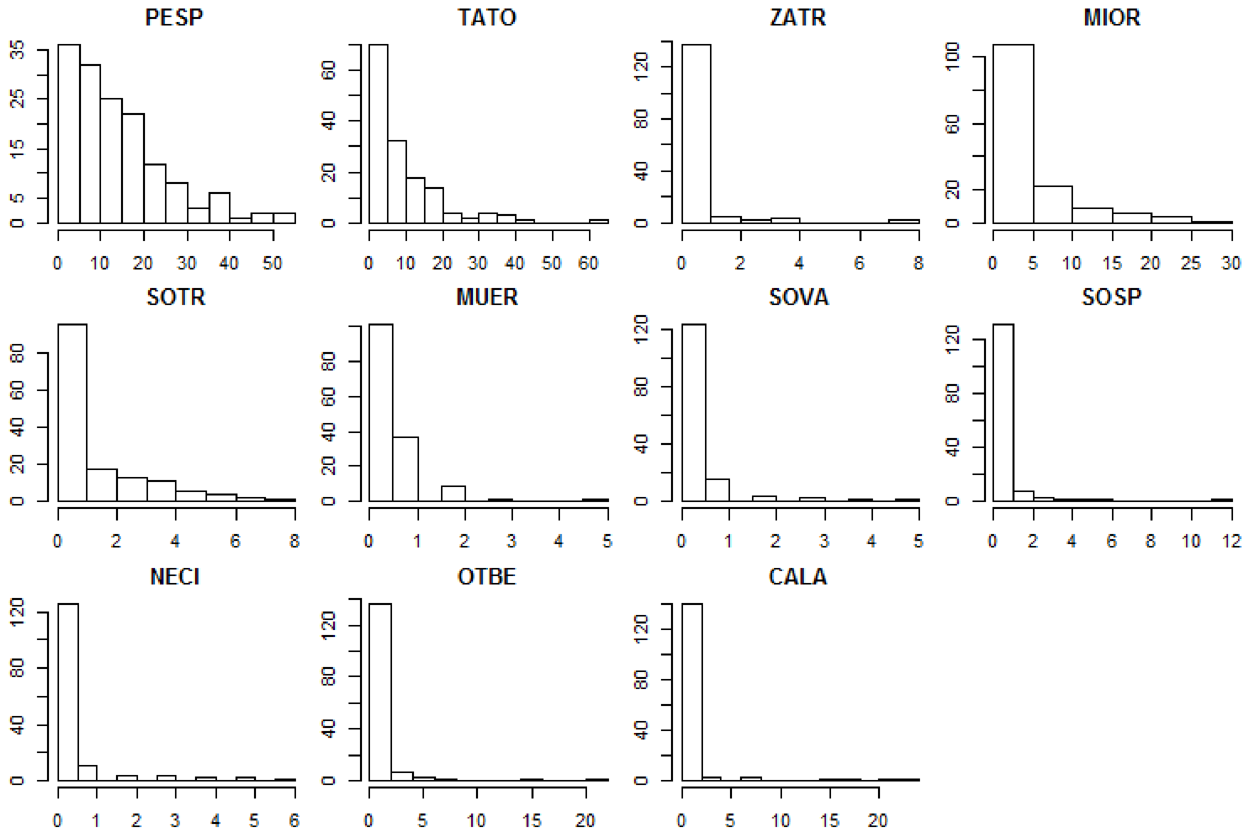

Figure 4.2

Distribution of raw counts for each of 11 small mammal species (see Table 4.1 for acronym definitions) used in joint species distribution models captured during 2017-2019 in early seral conifer plantations with green tree retention patches in the Coastal and western Cascade Mountain Ranges, Washington and Oregon, U.S.A.

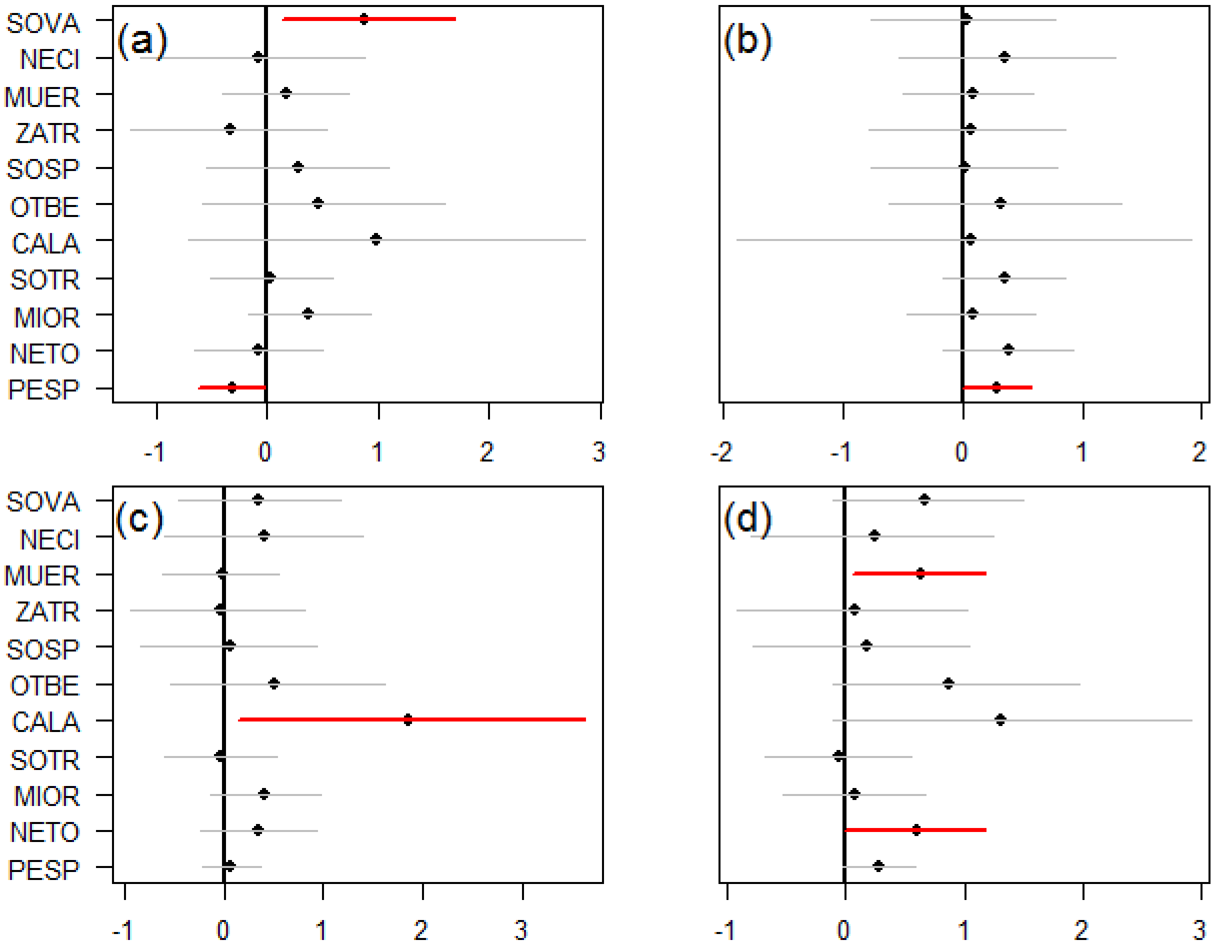

Figure 4.3

Effects of 4 experimental retention treatments on the abundance of 11 small mammal species relative to a control treatment where all retention trees were grouped and connected to a forested riparian buffer. (a) is a treatment where all retention trees are grouped into one upland patch, (b) is a treatment where retained trees are split between a riparian and an upland patch of retention, split retention but with created snags, retention dispersed in four patches in upland area with created snags. Small mammals were sampled in 50 early seral conifer plantations (2-6 years after forest harvest) with green tree retention within northwest Oregon and southwest Washington, USA during summer 2017-2019.

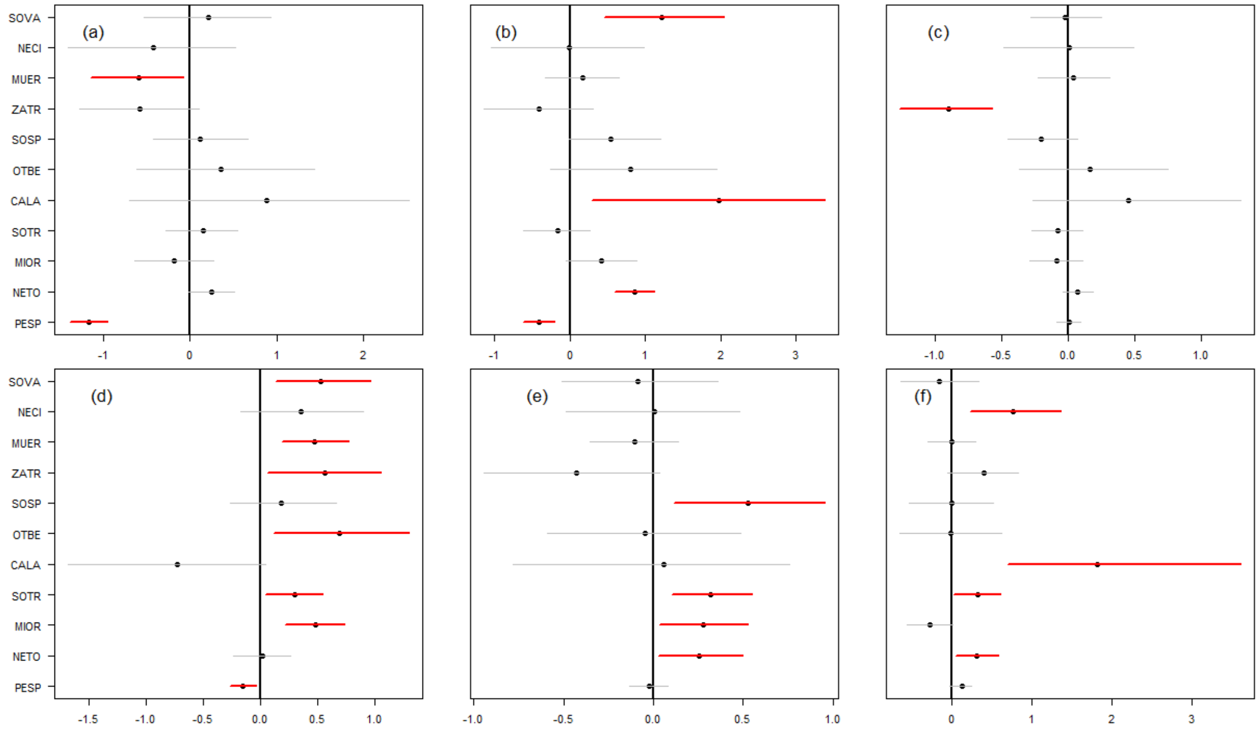

Figure 4.4

Coefficient estimates for the relationship between the abundance of eleven small mammal species and (a) year 2018, (b) year 2019, (c) sampling week, (d) proportion vegetative ground cover, (e) proportion shrub cover >1m tall, and (f) elevation (m). Horizontal bars represent 95% Bayesian credible interval with red lines indicating credible intervals that do not include zero. Species codes can be found in Table 4.1. Small mammals were sampled in 50 early-seral conifer plantations with retention within northwest Oregon and southwest Washington, USA during summer 2017-2019.

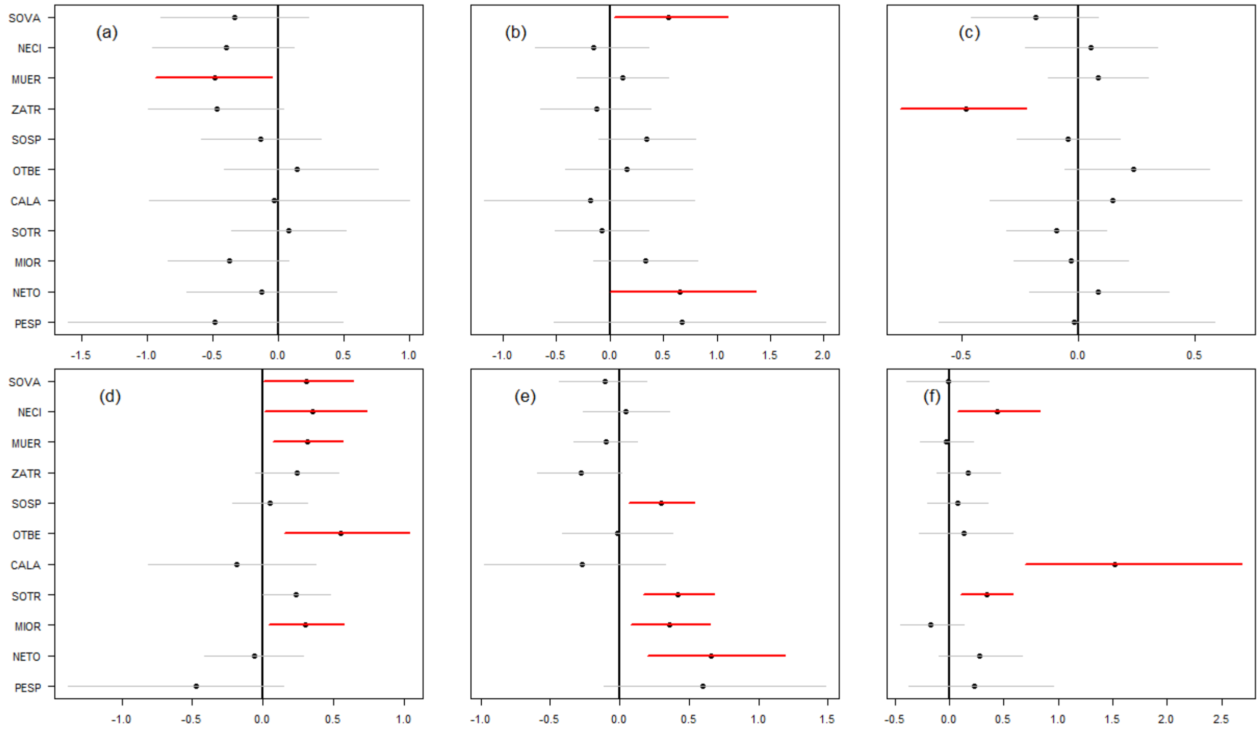

Figure 4.5

Coefficient estimates for the relationship between presence of 11 small mammal species and (a) year 2018, (b) year 2019, (c) sampling week, (d) proportion vegetative ground cover, (e) proportion shrub cover >1m tall, and (f) elevation (m). Horizontal bars represent 95% Bayesian credible interval with red lines indicating credible intervals that do not include zero. Species codes can be found in Table 4.1. Small mammals were sampled in 50 early-seral conifer plantations with retention within northwest Oregon and southwest Washington, USA during summer 2017-2019.

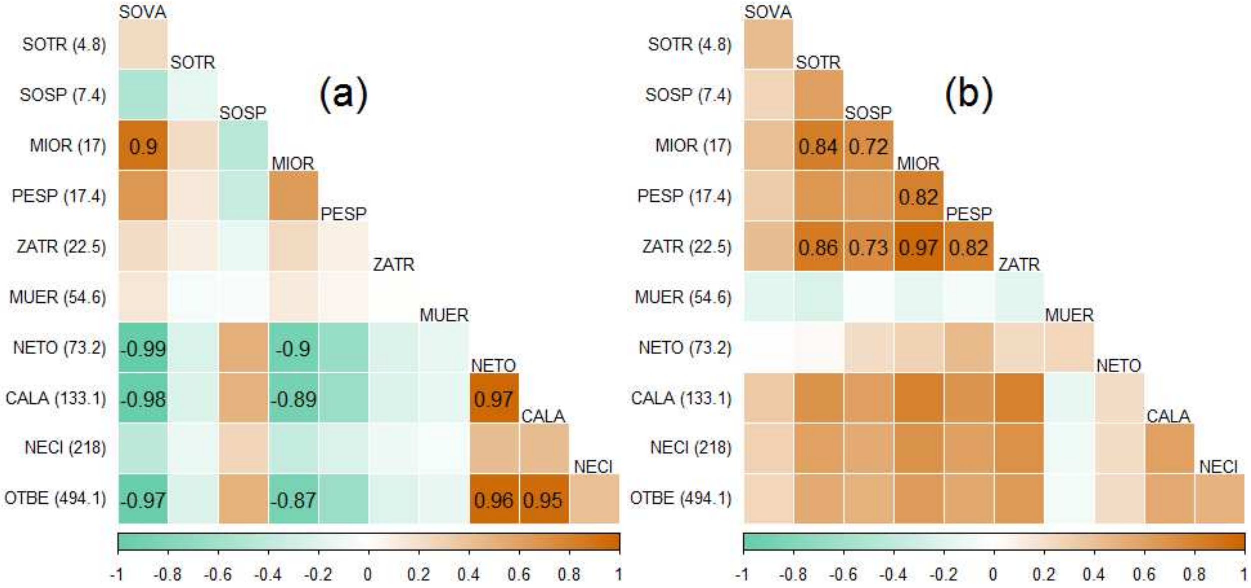

Figure 4.6

Residual correlation matrices based on the small mammal species loadings with latent factors from the Poisson lognormal count model at the (a) experimental block scale and (b) forest stand scale. Species are ordered according to their body size with body size in grams indicated in parentheses (SOVA = 4.2 g). Tiles with numbers indicate residual correlations with support at α=0.05 threshold, with numbers representing the mean correlation of factor loadings between the species pair at the given scale. All other correlations are nonsignificant. Species codes can be found in Table 4.1. Small mammals were sampled in 50 early-seral conifer plantations with retention within northwest Oregon and southwest Washington, USA during summer 2017-2019.

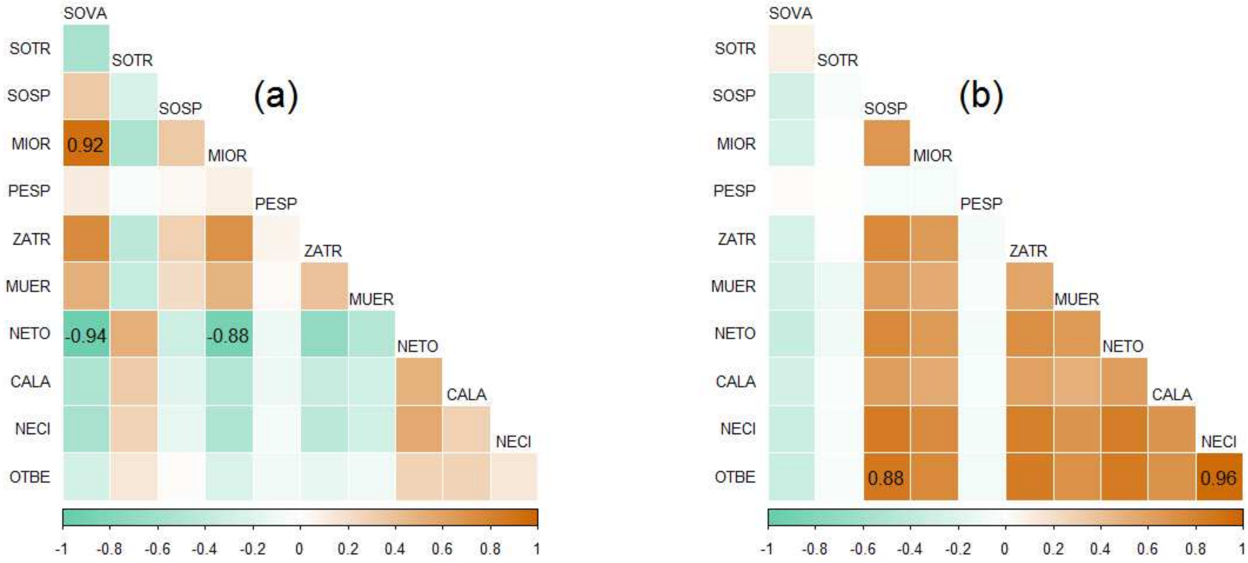

Figure 4.7

Residual correlation matrices based on the species loadings with latent factors from the presence-absence probit model at the experimental block (a) and forest stand scale (b). Species are ordered according to their body size (descending bottom to top). Tiles with numbers indicate residual correlations with support at α=0.05 threshold, with numbers representing the mean correlation of factor loadings between the species pair at the given scale. All other correlations are nonsignificant. Species codes can be found in Table 4.1. Small mammals were sampled in 50 early-seral conifer plantations with retention within northwest Oregon and southwest Washington, USA during summer 2017-2019.

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CONCLUSION

In this dissertation, I used taxonomic and functional approaches to understand how retention forestry impacts diversity and abundance of two animal groups considered indicator taxa for the effects of forest management on biodiversity. Importantly, conclusions regarding the most effective pattern of retained trees varied depending on taxon and response variable considered. Small mammals were most abundant in logged forest stands with multiple small patches of dispersed retention, but the small mammal species richness was highest in stands where all retention trees were connected with forested riparian buffers. Variation in ground beetle community composition across space was lowest in stands containing multiple small patches of retention, and differences in community composition between riparian and upland retention patches were detected. Collectively, these results suggest that a combination of stand-level retention alternatives evaluated here should be implemented in Pacific Northwest clearcuts to promote diversity and abundance of focal taxonomic groups on managed forest landscapes.

In Chapter 1, I investigated ability of retention patches across the different experimental treatments to create heterogeneity in ground beetle community composition across space and promote ground beetle communities with different functional traits than surrounding clearcut areas. I found that allocating retention trees to multiple small patches dispersed throughout clearcut areas resulted in ground beetle communities within patches that are more similar to those that occur in logged areas. This retention pattern also does not increase species or functional richness of ground beetles.

In Chapter 2, I quantified whether abundance of common small mammal species differed across retention treatments and the role that structural complexity played in this relationship. I found that two of the three species were most abundant in small, dispersed patches of retention and for one species, this appeared to be driven by increased structural complexity in small patches resulting from retention tree blow down. This analysis suggested that species responses to forest patch size is mediated by variation in structural complexity between large and small patches.

In Chapter 3, I used the experimental design to investigate whether small mammal species and functional richness varied in response to size and location of retention patches. I found that small mammal species richness was highest in riparian-associated retention but that this effect was only apparent when species present in the clearcut areas surrounding the patches was accounted for. This finding and those from Chapter 1 demonstrated the importance of considering the community that occurs in areas surrounding forest patches when assessing conservation value of retention forestry.

Finally, in Chapter 4 I used small mammal community abundance data in a joint species distribution model (JSDM) to look for competition between species at different spatial extents. This analysis did not yield evidence for competitive interactions between ecologically similar small mammal species, although these results should be cautiously interpreted as they are based on observational data from experimental treatment stands. This result indicated that environmental factors (e.g., elevation, vegetation structure) are more influential than inter-specific competition at structuring small mammal communities in recent clearcuts with retention.

Future research on retention forestry should focus on effects of retention pattern on biodiversity as surrounding early-seral conifer plantations undergo succession into later stages of forest development. Across the wide body of retention literature, few studies evaluated the effects of retention on animal communities past the early seral stage and there is strong reason to predict that functionality of retention patches changes with succession. Although I took a functional approach to understanding the effect of retention alternatives on biodiversity, further research would benefit from more explicitly measuring the contribution of animal taxa to forest ecosystem function among varying retention practices. Small mammals in particular function as dispersers of ectomycorrhizal fungi, which facilitate establishment and growth of commercially valuable conifers. Additionally, the interplay between retention patch size, location and structural complexity of habitat elements on animal communities warrants further research, particularly as understories in surrounding plantations simplify as tree canopies close. The robust experimental design employed here is ideal for answering these questions in the context of Pacific Northwest forest management. As has been the case for the past century, forest landscapes in the Pacific Northwest will continue to change in response to climate and the needs of human society. A continued emphasis on evaluating effectiveness of retention alternatives across forest successional stages and the contribution of this practice to forest ecosystem function will help ensure that future forest management conserves forest biodiversity and meets the resource demands of human society.