




Effects of varying retention tree patterns on ground beetle (Coleoptera: Carabidae) taxonomic and functional diversity

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Abstract. Managing forests intensively for timber production can homogenize forest structure and, in turn, alter species richness and functional composition of native species communities. Retention forestry, the practice of retaining structural elements during timber harvest, can increase species diversity in recently harvested forests, but its effect on functional trait diversity is less understood. We used a broad-scale, replicated experiment to evaluate the effect of five tree retention patterns on species and functional trait diversity of ground beetles (Family: Carabidae) within early-seral production forests in the Pacific Northwest, USA. We found no evidence for differences in carabid species or functional trait richness among treatments when considering species present in retention patches and adjacent clear-cuts. However, we found evidence for lower taxonomic and functional trait variation between carabid communities present in retention patches and those present in clear-cut areas of stands when retention was allocated to several small patches. Lower levels of functional trait variation in stands with several small patches were due to specialized predators found less often in small retention patches than in aggregated or riparian retention patches. Our findings indicate that relative to single large or riparian-associated patches, small retention patches functioned similarly to clear-cuts within harvested forests and several small patches did not increase species or functional trait richness. At current levels of retention in the region, allocation of trees to a single upland patch or split between riparian and upland patches can increase variation in ground beetle taxonomic and functional composition within harvested forests.

Key words: aggregated retention; carabid beetles; functional diversity; functional dissimilarity; retention forestry; trait probability density; Pacific Northwest; forest management.

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INTRODUCTION

Intensive management to increase wood yield has homogenized forest structure in many regions globally (Lindenmayer et al. 2012, Mori et al. 2015). Typical industrial forestry practices include harvesting trees on even-aged rotations,

which reduces the diversity of tree sizes and ages and abundance of dead wood (Hayes et al. 2005, Ranius et al. 2014). Forest regeneration practices can further reduce plant diversity shortly after harvest and shorten early seral stage duration (Demarais et al. 2017, Kroll et al. 2017). Furthermore, management practices can exert effects

through vegetation composition and structure that alter the diversity and composition of animal communities present on managed forests (Martikainen et al. 1996, Root 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 and is widely implemented in many timber producing regions (Gustafsson et al. 2012, Fedrowitz et al. 2014, Mori and Kitagawa 2014). Although operational efficiency and increased wood production per unit area are the primary objectives of intensive forest management, understanding how ecological communities respond to variation in retention tree practices is critical to meet biodiversity conservation and sustainability objectives.

Intensive management of ecosystems for resource production often changes the composition of ecological communities without changing species richness (Mori et al. 2015, Hillebrand et al. 2018). Species loss as a result of intensive management is also nonrandom with respect to species traits, and declines in trait richness of communities are often steeper than declines in species richness (Flynn et al. 2009, Gámez-Virués et al. 2015, Kroll et al. 2020). Furthermore, species traits often determine their contribution to ecosystem function (Gagic et al. 2015). Hence, patterns in the functional trait composition of communities, termed functional diversity, may be more informative about management effects on biodiversity and ecosystem function than species-based (i.e., taxonomic) metrics (McGill et al. 2006). In contrast to extensive research on the effect of retention forestry on taxonomic richness and diversity (Fedrowitz et al. 2014, Mori and Kitagawa 2014), fewer studies have taken a functional trait approach to understanding biodiversity responses to alternative retention practices.

Ground beetles (Family Carabidae) are well described taxonomically and exhibit numerous 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 are not well understood, in agricultural ecosystems ground beetles can suppress both insect (Kromp 1999) and weed pests (Carbonne et al. 2020). Studies indicate that retention

forestry practices do not typically conserve later-seral ground beetle communities in harvested forests (Halaj et al. 2008, Mateveinen-Huju et al. 2009, Work et al. 2010), but retention patches can support beetle communities with a different species composition than surrounding clear-cuts (Baker et al. 2015, 2016). Although the functional diversity of ground beetle communities is sensitive to changes in the composition of ground vegetation in open habitats (Pakeman and Stockan 2014) and variation in canopy cover in managed forests (Spake et al. 2016), little information is available on the response of ground beetle functional diversity to retention forestry. Studies that relate taxonomic and functional diversity of ground beetles to retention forestry alternatives are needed to determine whether changes in species composition result in a loss of functional trait diversity, with potential impacts on their contribution forest ecosystem function.

We used an experimental design to quantify responses of ground beetle taxonomic and functional trait diversity to tree retention practices in production forests of the Pacific Northwest (PNW), USA. We compared the taxonomic and functional trait (body size, mandible morphology, and dispersal ability) composition and richness of ground beetle communities among five treatments that differed in size, number, and location of retention patches within recently clear-cut forests. We also quantified whether changes in taxonomic and functional trait composition between retention patches and clear-cut areas differed among the five treatments. When considering beetle communities present in retention patches and clear-cut areas of treatment stands, we predicted that ground beetle taxonomic and functional trait richness would be highest in treatments with a single large patch, especially those adjacent to forested riparian zones (Blanchet et al. 2013). Further, we predicted less variation in taxonomic and functional community composition between retention and clear-cuts within the treatment with several small retention patches compared to treatments containing a single large patch (Phillips et al. 2017). Both predictions are consistent with timber harvest acting as an environmental filter, where species with traits associated with older forests persist in large but not small retention patches. Our findings identify retention forestry strategies

associated with increased diversity of ground beetles in early seral production forests in the PNW and yield insights into effects of forest patch fragmentation on insect biodiversity.

METHODS

Study area

We established 10 experimental blocks on production forests in the humid conifer forests of the PNW between 122° W and 124° W, and 44.5° N and 46.5° N (Fig. 1). Experimental blocks were primarily defined by land ownership and located in the Cascade and Coast Ranges of western Oregon and Washington, USA (Fig. 1). Landscape composition

around blocks ranged from primarily commercial forest ownerships, where forests are managed intensively for timber production, to mosaics of private and public ownership. A large agricultural area (Willamette River Valley) separated the forested mountain ranges, and the Columbia River separated the two states (Fig. 1). Elevations of study treatments ranged from 43 m in southwest Washington to 1230 m in the Oregon Cascades and climate ranged from cooler and wetter in coastal Washington to warmer and drier in the southern Oregon Cascades (Appendix S1: Table S1). Forests consisted primarily of coastal Douglas fir (*Pseudotsuga menziesii*), the dominant natural and commercial species in the PNW, with western hemlock

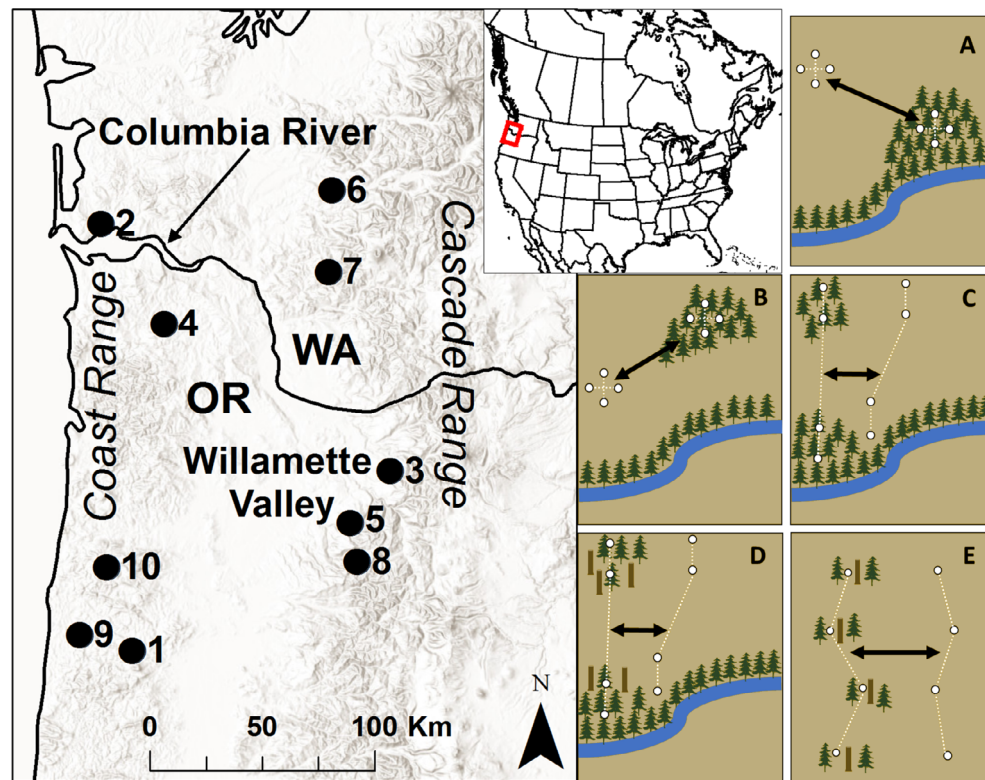


Fig. 1. Left panel: Study area in western Oregon (OR) and Washington (WA), USA, depicting 10 experimental blocks (black filled circles), each containing five structural retention treatments, where sampling of carabid beetle communities occurred in 2017 and 2018. Block numbering corresponds to Block in Appendix S1: Table S1, which summarizes climate and elevation within blocks. Right panel: Schematic of retention treatments and pitfall trap arrangements used to sample carabid beetle communities, 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-stand dissimilarity metrics (black arrows). (A) Riparian Aggregated treatment (RA), (B) Upland Aggregated treatment (UA), (C) Split treatment (S), (D) Split with Snags treatment (SS), and (E) Dispersed with Snags (DS) treatment.

(*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and noble fir (*Abies procera*) common on more mesic and higher elevation sites. 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 (Talbert et al. 2005). Forest harvesting policies require retaining approximately five trees/ha and set the maximum continuous clear-cut area at ~55 ha in Oregon (Washington Forest Practices Board 2001, Oregon Department of Forestry 2018). With the exception of Washington requirements that no part of a harvested area is >244 m from retention (Washington Forest Practices Board 2001), standard practice is to focus retention placement along riparian protection zones, as to increase stream buffering and facilitate timber harvesting logistics.

Experimental design

Our study included 5 experimental retention treatments replicated across 10 experimental blocks for a total of 50 stands (Fig. 1). Within blocks, we identified five stands scheduled for harvest and randomly assignments one of five retention treatments to each stand. The five treatments, depicted in Fig. 1, included the following:

1. Riparian Aggregated (RA): All retention trees grouped in a single patch connected to an unharvested riparian protection zone (Fig. 1A).
2. Upland Aggregated (UA): All retention trees grouped in a single patch upslope from unharvested riparian protection zones, either isolated within the stand or on the edge next to recently regenerated forest (<10 yr old; Fig. 1B).
3. Split (S): Half of 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 (Fig. 1C).
4. Split with Snags (SS): Same as the Split (S) treatment, but removed crowns of half of retention trees, leaving the lower ~8 m of trunk (Hane et al. 2019; Fig. 1D).

5. Dispersed with Snags (DS): Retention trees dispersed throughout the stand in a minimum of four patches, each containing at least 15 green trees and an equal number of created snags (Fig. 1E).

Aside from changes in spatial pattern of retention, harvesting and other silvicultural treatments of each experimental stand followed typical practices in the region. Snag creation in retention patches benefits cavity-nesting birds primarily (Hane 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. Harvesting of stands occurred between fall 2012 to spring 2015, and at the first year of sampling time since post-harvest planting of tree seedlings ranged from two to five years. In addition to treatment stands, we also sampled carabids in a rotation-aged (~50 yr old) stands in nine of the ten experimental blocks to understand how carabid communities in retention patches compared to those in closed-canopy forests in the vicinity of treatment stands.

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 (mean = 3.6, SD = 0.6) in each treatment stand between 2017 and 2018. Individual pitfall sampling periods averaged 28 d (22–35, SD = 1.7), and we sampled most treatment stands twice each summer: 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 d. We missed sampling one RA treatment in 2017 and one S treatment in 2018. The three blocks in the Oregon Cascades were sampled for a single ~28-d 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. In each treatment stand, we placed four traps in retention patch(es) and four in the clear-cut area (Fig. 1). Differences in spatial arrangement of retention patches among treatments necessitated altering the spatial arrangement of pitfall traps in the different treatments (Fig. 1). We located clear-cut 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 >200 m. We sampled rotation-aged forests in the same configuration as patches in aggregated retention treatments (Fig. 1A, B).

After each sampling period, we collected pitfall contents, separated carabid beetles from other traps contents, counted number of carabid beetles in each pitfall sample, and identified them to species using Hatch (1953). We grouped unidentified species into morphospecies that included some species of the genus *Harpalus*, two species of *Trachypachus*, and some individuals of the *Hypherpes* subgenus of *Pterostichus*. Two widespread genera that were sampled, *Omus* and *Trachypachus*, were recently reclassified outside Carabidae, but their families Cicindelinae and Trachypachidae form a monophyletic group with Carabidae and we included these widespread species in analyses. We deposited voucher specimens of each species in the Michigan State University Albert J. Cook Arthropod Research Collection.

Species trait data

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) and two traits that reflect their dispersal ability: rear leg length and wing type. To quantify these traits for each species, we drew random samples of 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, Melville, New York, USA), we measured body length (mm) as the longest distance from the base of the mandibles to posterior 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 (the joint) of attachment to the tip, and mandible width, defined as the width (mm) between mandibles at the hinge (joint) of attachment. Quantifying mandible length and width at the hinge (joint) attachment point ensured that these measurements were not sensitive to position of the mandible. To capture the dispersal ability of each species, we measured rear femur and tibia length on each individual. To simplify the number of traits used, a necessity for our analysis functional trait dissimilarity, 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*. Species dispersal abilities represent an important aspect of their functional niche. Most carabid species are flightless and disperse by walking, but some species have functional wings or are wing dimorphic (i.e., winged and wingless individuals). We created a quantitative variable to represent species dispersal abilities from rear leg length (femur and tibia combined) and wing type using principle coordinates analysis (Carmona et al. 2016) and Gower's distance (Laliberte and Legendre 2010). Wing type for each species was defined as an ordinal factor with 1 = brachypterous species (no wings), 2 = wing dimorphic species, and 3 = winged species (macropterous) from (Larochelle and Lari-vière 2003).

Analysis

To assess stand-scale differences in carabid species and functional trait composition among treatments, we used redundancy analysis (RDA) and distance-based RDA (db-RDA), respectively. Both RDA and db-RDA are constrained ordination techniques that allow testing of relationships between community data and experimental factors. For both ordinations, we included data on species captured >10 times. For the species-based RDA, we performed Hellinger's transformation on the species count data, which allows the

Table 1. Carabid community metrics used in mixed-effects models, statistical method used to quantify them, range of values, model distribution, and sample size.

Metric	Method	Range	Distribution	Sample size
Taxonomic richness	Chao1	2.00–33.00	Poisson	178
Functional richness	Dendrogram	0.53–2.32	Gaussian	178
Taxonomic dissimilarity	Bray-Curtis	0.04–1.00	Beta	178
Functional dissimilarity	TPD	0.09–0.99	Beta	178
Body size	TPD	2.97–25.9	Gaussian	1269
Mandible length/width	TPD	0.59–2.17	Gaussian	1269
Dispersal PCoA	TPD	–0.47–0.52	Gaussian	1269

analysis of community data collected across long gradients with many zeros using techniques such as RDA that are based on Euclidean distance (Legendre and Gallagher 2001). Because Hellinger's transformation relativizes species abundances, this transformation also helped account for differences in sampling effort among stands.

To quantify differences in functional composition of carabid communities among treatments for use in db-RDA, we used trait probability density (TPD, Carmona et al. 2016). Trait probability density represents probability of observing specific trait values 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 generated a TPD of the carabid community present in each stand based on species-specific trait measurements and calculated pairwise functional dissimilarity as one minus the overlap of stand-scale TPDs (Carmona et al. 2019). We then used pairwise dissimilarity values in db-RDA (Legendre and Anderson 1999). We fit a second species-based RDA and trait-based dbRDA that included the effect of climate (annual mean precipitation and maximum temperature) in addition to treatment, to account for the effect varying climate on carabid community composition when estimating treatment effects across a broad study area. We tested for the significance of the RDA and dbRDA axes using permutation tests with 999 permutations, and we constrained the permutations to only reshuffle samples within blocks. Climate variables mean annual precipitation and mean maximum annual temperature were 30-year averages sourced from PRISM at a 400-m resolution (PRISM Climate Group 2004).

To further investigate how the configuration of retention tree patches influenced carabid community diversity and composition within-stands, we calculated four stand-level community variables for each sampling period: (1) taxonomic (species) richness, (2) functional trait richness, (3) taxonomic community dissimilarity between patches and clear-cuts, and (4) functional community dissimilarity between patches and clear-cuts (Table 1). Taxonomic richness was quantified using the Chao1 species richness estimator, which accounts for varying effort due to trap failure and undetected species (Chao 1987). We quantified functional trait richness by constructing a dendrogram of all sampled carabid species based on their pairwise dissimilarity with regard to functional traits using Gower's distance (Laliberté and Legendre 2010) and the UPGMA clustering algorithm (Appendix S1: Fig. S1, Podani and Schmera 2006). Using this dendrogram, functional richness was quantified as total branch length connecting all species sampled from a stand in a given sampling period (Flynn et al. 2009).

To calculate within-stand taxonomic and functional dissimilarity between patches and clear-cuts by treatment, we separately pooled patch and clear-cut pitfalls collected from a stand each sampling period (Fig. 1), 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 clear-cut samples. Consistent with how we quantified functional dissimilarity among-stands, we quantified functional dissimilarity of carabid communities between patches and clear-cuts within

stands using TPD. We created a TPD for the same pooled patch and clear-cut samples used to calculate taxonomic dissimilarity within-stands and calculated dissimilarity as one minus the overlap of pooled patch and clear-cut TPDs (Carmona et al. 2019). To understand how differences in trait values (i.e., body size, mandible characteristics, and dispersal ability) were associated with differences in functional trait composition between patches and clear-cuts among treatments, we sampled trait values from each generated TPD. The probability of sampling a specific trait from a TPD is proportional to abundance of species with that trait in the community (Carmona et al. 2019). For this portion of the analysis, we also included carabid data collected from rotation-aged forests. We generated a TPD for each sample collected, yielding multiple values for each trait from each treatment stand.

We used each of the four stand-level community variables and sampled trait values as response variables in mixed-effects regression models with retention treatment as a categorical explanatory variable and stand identity as a random effect to account for repeated measures from stands (sampling periods). We also included Julian date and year of each sampling period as additional explanatory variables. We considered effects of retention treatment or other regression parameters on a community variable significant if 95% confidence intervals excluded zero. We fit mixed effects models in R package lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017). We assessed residuals of fitted models using nonparametric simulation tests in R package DHARMA (Hartig 2019). We generated all TPDs, calculated functional dissimilarity metrics, and sampled trait values from TPDs using the R package TPD (Carmona et al. 2019). We performed RDA, db-RDA, and taxonomic richness estimation in the package Vegan (Oksanen et al. 2019) in the R statistical computing platform (R Core Team 2019).

RESULTS

We deployed 664 and 784 pitfall traps 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 1184 pitfall samples for two ~28-d periods each year: 512 from 2017 and 672 from 2018

(Appendix S1: Table S2). The average number of pitfall traps collected per stand across all sampling sessions was 23.7 (range = 5–30; SD = 5.1), and after each 28-d period, an average of 6.6 pitfalls were collected per stand out of the original eight deployed.

We collected 10,538 individuals of 47 species (5 morphospecies) from 21 identifiable genera (Appendix S1: Table S3). The genera *Harpalus*, *Omus*, *Pterostichus*, *Scaphinotus*, and *Trachypachus* dominated our samples (Appendix S1: Table S3). Average number of individual carabids in a pitfall trap was 8.95, with an average of 3 species per pitfall trap (Appendix S1: Table S2). Average abundance of a beetle species in a pitfall trap was 2.85 individuals, and species occurred in 67 pitfall traps and 6.7 stands on average. For functional traits, average body length by species was 11 mm and mean mandible length to width ratio was 1.03 (Table 1).

For among-stand comparisons, only the first axis was significant in the test for shifts in species composition between treatments ($F = 5.33$, $P < 0.001$). This axis indicated a shift in species composition from the DS treatment to rotation-aged forests, with the 4 other treatments typically having intermediate scores (Fig. 2A, B). The results obtained for variation in stand-scale functional-trait composition from db-RDA were similar; only the first axis was significant ($F = 3.32$, $P < 0.001$) and indicated a shift in the functional-trait composition of carabid communities between the DS treatment and rotation-aged stands (Fig. 2A, B). However, the first axes explained a relatively small proportion of the variation in community composition (Fig. 2A, B). The inclusion of temperature and precipitation variables increased the explanatory power of both the taxonomic RDA and functional db-RDA (Fig. 2C, D). For the taxonomic RDA including climate, permutation tests indicated both the first ($F = 11.23$, $P < 0.001$) and second axes ($F = 6.36$, $P < 0.001$) were significant. Likewise, both the first ($F = 5.03$, $P < 0.001$) and second axes ($F = 3.57$, $P < 0.001$) from the db-RDA ordination with climate explained a significant amount of variation in the functional-trait composition of carabid communities. The explanatory power of the constrained ordinations with climate was higher for taxonomic than functional community composition, suggesting that in our study area,

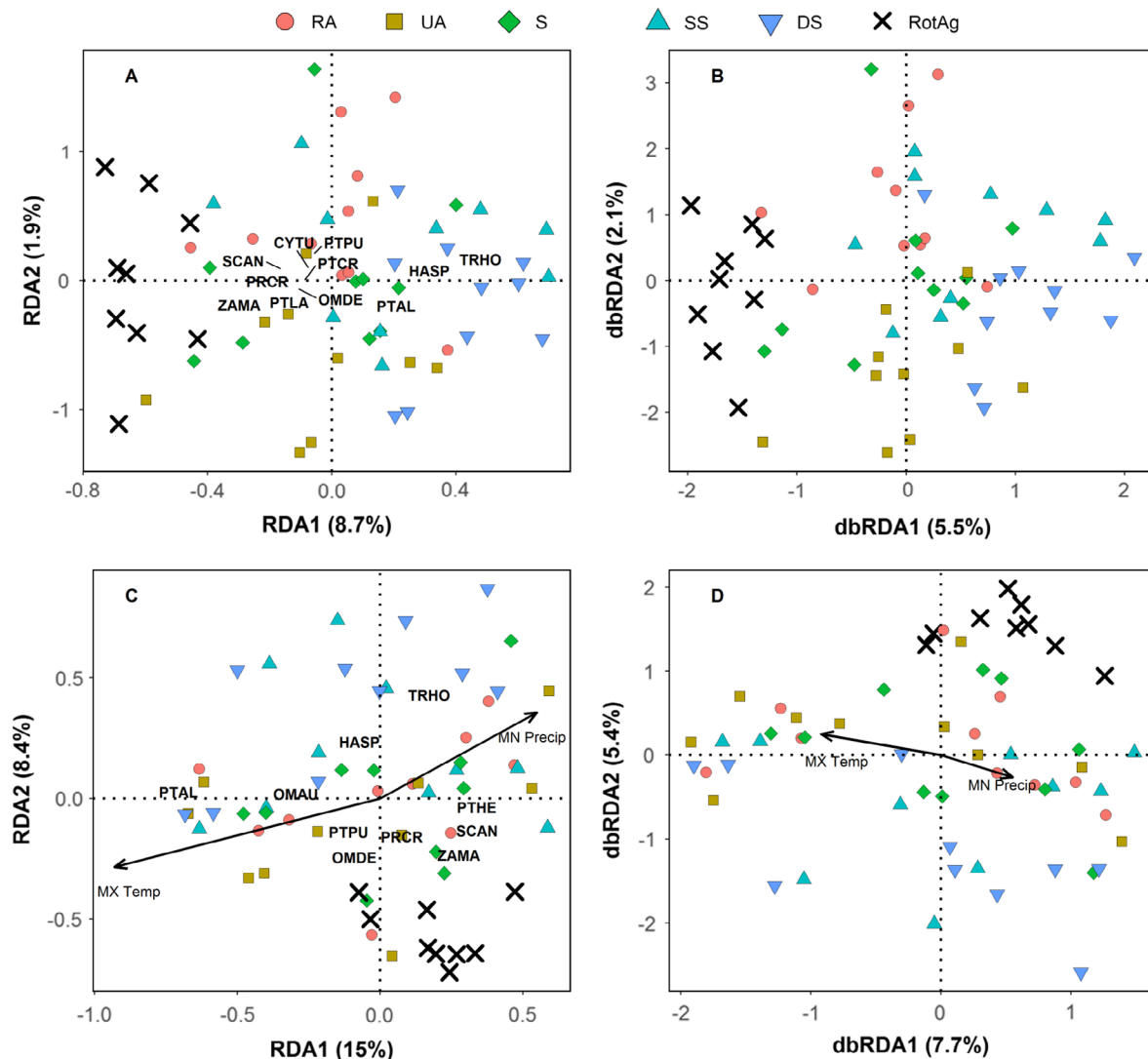


Fig. 2. Species-based RDA (A and C) and functional trait-based db-RDA (B and D) constrained ordination plots of carabid species relative abundance within 50 treatment stands and nine rotation-aged forest forests, northwest Oregon and southwestern Washington, USA, 2017–2018. Panels A and B include only the effect of retention treatment on carabid community composition, whereas panels C and D also include the effect of temperature and precipitation. The percent of variance explained by each ordination axis is included in the axis labels. The first axes were significant in A and B; the first and second axes were significant in C and D. Only species with scores approximately >0.1 or <-0.1 on either axis are displayed for readability. Species acronyms are located in Appendix S1: Table S3. RA, Riparian Aggregated; UA, Upland Aggregated; S, Split; SS, Split with Snags; DS, Dispersed with Snags; and RotAge, Rotation-aged Forest.

the species composition of carabid communities is more sensitive to changes in temperature and precipitation than functional trait composition.

We did not find differences in Chao1 species richness or functional trait richness among

treatments and effect sizes, using the RA treatment for comparison, were low and highly variable for taxonomic and functional richness (Table 2). In addition, sampling date did not have an effect on species richness ($\beta = -0.04$, 95% CI =

–0.09 to 0.01) but functional trait richness declined later in the sampling (dry) season ($\beta = -0.11$, 95% CI = –0.15 to –0.08). Similarly, functional trait richness declined in the second sampling year ($\beta = -0.15$, 95% CI = –0.19 to –0.04) but species richness did not ($\beta = -0.06$, 95% CI = –0.19 to 0.03). Hence, functional trait richness in stands was more variable across time than species richness.

Comparing variation in community composition within stands, the DS treatment had consistently lower within-stand taxonomic and functional dissimilarity (Table 2). The negative effect of DS treatment indicated that carabid communities in several small retention patches were more similar to carabid communities found in clear-cuts than carabid communities in patches in the four other treatments (Fig. 3). Taxonomic dissimilarity between patches and clear-cuts within-stands also declined later in sampling season ($\beta = -0.15$, 95% CI = –0.28 to –0.02) but not across years ($\beta = -0.04$, 95% CI = –0.30 to 0.22). Functional dissimilarity was not associated with date ($\beta = -0.09$, 95% CI = –0.22 to 0.04) or year ($\beta = -0.23$, 95% CI = –0.49 to 0.02).

Our analysis of changes in functional trait values among treatments included 1269 TPDs generated from each pitfall sample collected, 1184 in the 50 treatment stands and 85 samples from nine rotation-aged forests. For body length and mandible characteristics, sampled trait values were generally higher in retention patches compared to clear-cuts within-stands, but this relationship was only consistent for mandible characteristics (Table 3). Sampled mandible length to width ratios were lower in the DS treatment compared to other treatments but body length did not differ (Table 3). Sampled body

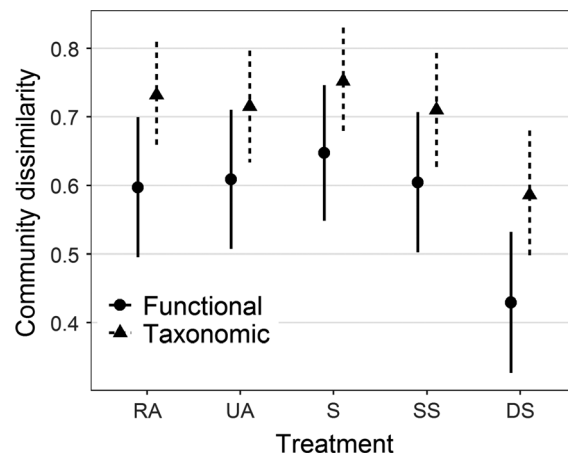


Fig. 3. Predicted (mean and 95% confidence interval) taxonomic and functional dissimilarity of carabid beetles between retention patches and clear-cuts by retention treatment from beta-distributed mixed effects models. Year and Julian date of sampling were included in each model and for predictions year 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. Abbreviations are RA, Riparian Aggregated; UA, Upland Aggregated; S, Split; SS, Split with Snags; and DS, Dispersed with Snags.

lengths, however, were significantly larger in rotation-aged stands than retention stands (Table 3), indicating carabid communities in retention patches across all treatments did not resemble closed-canopy carabid communities with respect to species body size. The first principal coordinate axis derived from species leg length and wing type explained 76% of variation

Table 2. Coefficient estimates (and 95% CIs) from mixed-effects models testing the effect of retention treatment on taxonomic and functional richness (stand-scale) and within-stand community dissimilarity (between patch and clear-cut).

Response	UA	S	SS	DS
SRich	–0.05 (–0.39, 0.29)	–0.08 (–0.43, 0.26)	0.00 (–0.34, 0.34)	–0.09 (–0.43, 0.25)
FRich	–0.06 (–0.17, 0.29)	0.00 (–0.24, 0.22)	0.04 (–0.19, 0.26)	–0.04 (–0.26, 0.18)
TDissim	–0.08 (–0.54, 0.38)	0.11 (–0.37, 0.59)	–0.11 (–0.57, 0.35)	–0.66 (–1.12, –0.20)
FDissim	–0.05 (–0.46, 0.56)	0.21 (–0.31, 0.74)	0.03 (–0.49, 0.54)	–0.68 (–1.20, –0.16)

Notes: SRich is the Chao1 species richness estimate, FRich is functional richness calculated from dendrogram length, TDissim is Bray-Curtis dissimilarity, and FDissim is the nonoverlap of the trait probability distributions as calculated by Carmona et al. 2016. Bold indicates treatment effects for which the 95% confidence interval did not overlap zero.

Table 3. Coefficient estimates (and 95% CI) from mixed-effect models for the effect of retention treatment and cover type (patch/rotation age or clear-cut) on carabid functional traits body size, mandible characteristics, or dispersal.

	Body length	Mandible ratio	Dispersal PCoA†
UA	0.69 (−1.02, 2.40)	−0.05 (−0.11, 0.00)	0.02 (−0.06, 0.09)
S	0.78 (−0.96, 2.54)	−0.02 (−0.08, 0.03)	0.02 (−0.06, 0.09)
SS	−0.52 (−2.24, 1.20)	−0.07 (−0.12, 0.01)	−0.03 (−0.11, 0.05)
DS	−0.56 (−2.28, 1.16)	−0.13 (−0.19, −0.07)	−0.08 (−0.16, −0.01)
RotAge	2.23 (0.27, 4.20)	0.01 (−0.06, 0.08)	0.09 (0.00, 0.18)
CoverType‡	1.58 (0.99, 2.17)	0.07 (0.05, 0.09)	0.11 (0.08, 0.13)

Notes: Coefficients are in comparison with the RA treatment. Bold values indicate covariate effects with 95% CIs that do not include 0.

† First principal coordinate axis of leg length and wing type.

‡ Binary variable indicating closed canopy (retention or rotation-aged) or clear-cut.

in these traits between species. Lower PCoA values indicated species with high dispersal ability (i.e., developed wings but short legs), intermediate, positive values corresponded to species with low dispersal ability (i.e., no wings, short legs), and high positive values corresponded to moderate dispersers (i.e., no wings, long legs). We found that carabid communities present in the DS treatment were characterized by species with lower PCoA values and hence, better dispersal ability (Table 3). Thus, smaller shifts in functional trait composition between retention patches and clear-cuts in the DS treatment were primarily driven by lower variation in mandible

characteristics and dispersal ability of carabid species present in this treatment (Fig. 4).

DISCUSSION

Our study represents the first in the literature to link different retention forestry practices to both taxonomic and functional dimensions of ground beetle diversity, an important indicator taxonomic group. Contrary to our predictions, we did not find higher ground beetle species or functional trait richness in harvested stands containing a single large patch of retention trees compared to stands with several smaller patches.

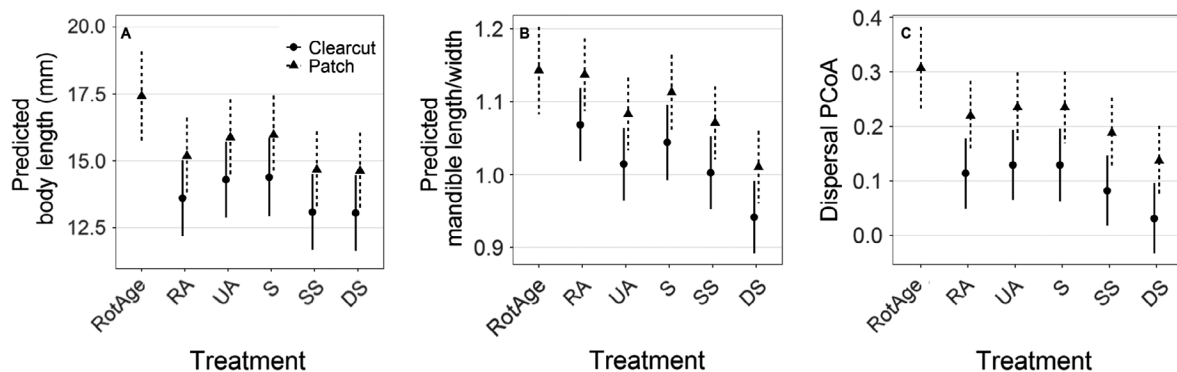


Fig. 4. Mean (and 95% confidence interval) predicted trait values for (A) body length, (B) ratio of mandible length to width between the mandibles and (C) dispersal ability for carabid beetles by retention treatment for clear-cut areas (solid circles) and retention patches (solid triangles). Dispersal PCoA is a first principal coordinate axis derived from leg length and wing type of each species, and lower values indicate species with better dispersal ability. 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.

However, we found evidence for taxonomically and functionally homogenized carabid communities in clear-cut stands with several small retention patches compared to aggregated and split retention configurations, when species relative abundances within communities were accounted for. These results demonstrate that retention and clear-cut carabid communities were more similar to each other in stands with several small retention patches (<15 trees). Furthermore, distributing small patches throughout harvested stands to create spatial heterogeneity did not result in higher species or functional trait richness. The latter finding contrasts with general responses of communities to patch fragmentation (Fahrig 2020). Instead, our results suggest that, under a certain patch size threshold, a higher number of patches does not support more species than a single large patch, particularly when accounting for the community present outside of patches.

We interpreted dissimilarity between carabid communities in retention patches and clear-cuts to suggest that patches served as a lifeboat (sensu Rosenvald and Lohmus 2008) for forest carabid species through the early-seral stage, with higher dissimilarity indicating higher capacity of the patches to lifeboat. Previous studies investigated the lifeboating potential of retention patches using taxonomic dissimilarity of ground beetle communities between retention patches and surrounding clear-cuts in the PNW regardless of patch size (Baker et al. 2015, 2016). Our study provides more explicit information on the size of retention patches required to create variation in carabid community composition across space in recently harvested forests. Using mean patch size within the upland aggregated retention treatment as a guide, retention patches with ~90 trees can increase variation in ground beetle community composition in harvested forests. Upland patches with 44 trees, the mean number of trees per patch in the two split retention treatments, may be sufficient to increase diversity of carabid beetles in upland areas. However, we caution that riparian-associated retention likely influenced levels of variation in community composition in split retention treatments. Other studies noted importance of structural connectivity of retention patches for conserving forest ground beetle communities in managed forest landscapes (Blanchet et al. 2013). Connectivity with

riparian buffers likely contributed to levels of community dissimilarity within riparian-associated treatments but comparable levels of dissimilarity in upland aggregated retention suggested that patches do not need to be connected to adjacent forest to support ground beetle communities that differ compositionally from nearby clear-cut areas. Hence, although retention forestry does not conserve late seral carabid communities in the PNW even at higher levels of retention (Halaj et al. 2008), our results indicate that aggregated retention can conserve some functional and taxonomic characteristics of later seral carabid communities (such as specialized carnivores).

These conclusions are further supported by our stand-scale ordination analyses, which showed all retention patterns evaluated, with the exception of DS, supported carabid communities with species composition similar to rotation-aged forests in at least some replicates (Fig. 2). The species that dominated carabid communities in small retention patches in the DS treatment were typically early-seral specialists including species in the genera *Amara*, *Harpalus*, and *Trachypachus* (Heyborne et al. 2003). These species have high dispersal abilities that enable them to colonize newly disturbed areas. In contrast, the species most abundant in larger retention patches are forest species with lower dispersal abilities (e.g., *Zacotus mathewsi*, *Scaphinotus angusticollis*), and rather than colonizing recent clear-cuts they persist at higher abundances if conditions remain suitable (Halaj et al. 2008). Hence, although we found differences in carabid community composition among treatments with respect to species dispersal characteristics (Fig. 4C), we concluded that species responses to the environmental conditions in clear-cuts is a more important driver of their response to retention patch size than their ability to colonize patches after harvest. Consistent with these findings, retention studies elsewhere also found carabid species typical of open habitats dominate carabid communities in small forest patches (Halme and Niemela 1993, Blanchet et al. 2013). Our study builds on these results by demonstrating that taxonomic homogenization of ground beetle communities in clear-cut stands with small patches also results in more functionally homogeneous carabid communities.

The similar responses of both taxonomic and functional trait diversity we observed is suggestive of an environmental filter that inhibits species with certain functional traits from persisting in clear-cuts and dispersed retention treatments (Smith et al. 2013). Carabid 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 specialized carnivores that prey on snails in the case of *Scaphinotus* spp. and *Cychrus tuberculatus*, or larger millipedes for *Promecognathus crassus*, and these species were more abundant in larger patches compared to clear-cuts. Hence, carabid responses to retention may reflect distribution of food resources, with dispersed patches supporting generalists and seed feeders that are also common in clear-cuts, and larger patches supporting species with 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 a 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. In contrast, among-stand comparisons revealed that taxonomic carabid community composition varies more strongly in relation to broad-scale climatic gradients than functional community composition. This result suggests that species with similar functional traits replace each other (e.g., *Omus audoini* replacing *Omus dejeanii*), or that functionally unique species (e.g., *Promecognathus crassus*) do not vary substantially in abundance along the climate gradient in our study area.

One caveat to our conclusions regarding functional composition of carabid communities is that pitfall traps more effectively sample larger-bodied, predaceous species (Knapp et al. 2020). However, this bias would only affect our inference if the detection of species differed between patch and clear-cut areas. Furthermore, this study occurred within five years following tree planting in the harvested area. Previous

studies demonstrated a time-lagged response of carabid beetle communities to logging, where the presence of forest interior species declined in retention aggregates with increasing time since logging (3–5 yr), even in larger patches (Matveinen-Huju et al. 2009). However, other studies demonstrated that compositional shifts in carabid communities between patches and clear-cuts remained high even 20 yr after harvest in the PNW (Baker et al. 2015). 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 carabid community responses to retention strategies through time and comparing the response of this taxon with other taxonomic groups will provide a better understanding of how retention forestry contributes to the biodiversity in PNW managed forests (e.g., Linden et al. 2012, Sultaire et al. 2021).

In addition to retention pattern, other processes likely affect levels of carabid community dissimilarity between retention patches and clear-cuts. Factors such as landscape composition (Barbaro et al. 2007), land use history (Neumann et al. 2017), and climate (Marrec 2021) 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 PNW and landscape composition, climate, and topography strongly varied across blocks and stands. Despite the presence of these potentially confounding factors, our study design enabled us to identify consistently more homogeneous ground beetle communities in stands with small (<15 tree) upland retention patches. When considering biodiversity at landscape scales, decisions on retention placement may be most important in landscapes lacking late seral forests, where the only opportunity to conserve closed canopy carabid species in upland areas is in aggregated retention patches embedded in a matrix of younger regenerating forests. As functional diversity responded similarly to taxonomic diversity, aggregated retention strategies may conserve native carabid species diversity and promote the varied functions they perform in forest ecosystems.

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LITERATURE CITED

- Baker, S. C., et al. 2015. Short- and long-term benefits for forest biodiversity of retaining unlogged patches in harvested areas. *Forest Ecology and Management* 353:187–195.
- Baker, S. C., et al. 2016. A cross-continental comparison of plant and beetle responses to retention of forest patches during timber harvest. *Ecological Applications* 26:2493–2504.
- Barbaro, L., J. P. Rossi, F. Vetillard, J. Nezan, and H. Jactel. 2007. The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. *Journal of Biogeography* 34:652–664.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Blanchet, F. G., J. C. Bergeron, J. R. Spence, and F. He. 2013. Landscape effects of disturbance, habitat heterogeneity and spatial autocorrelation for a ground beetle (Carabidae) assemblage in mature boreal forest. *Ecography* 36:636–647.
- Bouchard, M., and C. Hébert. 2016. Beetle community response to residual forest patch size in managed boreal forest landscapes: Feeding habits matter. *Forest Ecology and Management* 368:63–70.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325–349.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378–400.
- Cadotte, M. W., and C. M. Tucker. 2017. Should environmental filtering be abandoned? *Trends in Ecology and Evolution* 32:429–437.
- Carbonne, B., D. A. Bohan, and S. Petit. 2020. Key carabid species drive spring weed seed predation of *Viola arvensis*. *Biological Control* 141:104148.
- Carmona, C. P., F. Bello, N. W. H. Mason, and J. Lepš. 2019. Trait probability density (TPD): measuring functional diversity across scales based on TPD with R. *Ecology* 100:1–8.
- Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. Traits without borders: integrating functional diversity across scales. *Trends in Ecology and Evolution* 31:382–394.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43:783–791.
- Demarais, S., J. P. Verschuyt, G. J. Roloff, D. A. Miller, and T. B. Wigley. 2017. Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the U.S. *Forest Ecology and Management* 385:308–330.
- Deroulers, P., and V. Bretagnolle. 2019. The consumption pattern of 28 species of carabid beetles (Carabidae) to a weed seed, *Viola arvensis*. *Bulletin of Entomological Research* 109:229–235.
- Fahrig, L. 2020. Why do several small patches hold more species than few large patches? *Global Ecology and Biogeography* 29:615–628.
- Fedrowitz, K., et al. 2014. Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology* 51:1669–1679.
- Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12:22–33.
- Forsythe, T. G. 1982. Feeding mechanisms of certain ground beetles (Coleoptera: Carabidae). *Coleopterists' Bulletin* 36:26–73.
- Gagic, V., et al. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences* 282:20142620.
- Gámez-Virués, S., et al. 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications* 6:1–8.
- Gustafsson, L., et al. 2012. Retention forestry to maintain multifunctional forests: a world perspective. *BioScience* 62:633–645. <http://dx.doi.org/10.1525/bio.2012.62.7.6>

- Halaj, J., C. B. Halpern, and H. Yi. 2008. Responses of litter-dwelling spiders and carabid beetles to varying levels and patterns of green-tree retention. *Forest Ecology and Management* 255:887–900.
- Halme, E., and J. Niemela. 1993. Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici* 30:17–30.
- Hane, M. E., A. J. Kroll, J. R. Johnson, M. Rochelle, and E. B. Arnett. 2012. Experimental effects of structural enrichment on avian nest survival. *Forest Ecology and Management* 282:167–174.
- Hane, M. E., A. J. Kroll, A. Springford, J. Giovanini, M. Rochelle, and E. B. Arnett. 2019. Survival dynamics of mechanically topped Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) snags in Douglas-fir plantations, Oregon, USA. *Forest Ecology and Management* 433:105–110.
- Hartig, F. 2019. DHARMA: Residual diagnostics for hierarchical (multi-level /mixed) regression models. R package version 0.2.4. <https://CRAN.R-project.org/package=DHARMA>
- Hatch, M. H. 1953. The beetles of the Pacific Northwest: Part 1: Introduction and aedeophaga. University of Washington Press, Seattle, Washington, USA.
- Hayes, J. P., S. H. Schoenholtz, M. J. Hartley, G. Murphy, R. F. Powers, D. Berg, and S. R. Radosevich. 2005. Environmental consequences of intensively managed forest plantations in the Pacific Northwest. *Journal of Forestry* 103:83–87.
- Heyborne, W. H., J. C. Miller, and G. L. Parsons. 2003. Ground dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA. *Forest Ecology and Management* 179:123–134.
- Hillebrand, H., et al. 2018. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. *Journal of Applied Ecology* 55:169–184.
- Hoekman, D., et al. 2017. Design for ground beetle abundance and diversity sampling within the National Ecological Observatory Network. *Ecosphere* 8:e01744.
- Knapp, M., J. Knappová, P. Jakubec, P. Vonička, and P. Moravec. 2020. Incomplete species lists produced by pitfall trapping: How many carabid species and which functional traits are missing? *Biological Conservation* 245:108545.
- Kroll, A. J., A. Springford, and J. Verschuyt. 2020. Conservation and production responses vary by disturbance intensity in a long-term forest management experiment. *Ecological Applications* 30:e02148.
- Kroll, A. J., J. Verschuyt, J. Giovanini, and M. G. Betts. 2017. Assembly dynamics of a forest bird community depend on disturbance intensity and foraging guild. *Journal of Applied Ecology* 54:784–793.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems & Environment* 74:187–228.
- Laliberte, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305.
- Larochelle, A., and M.-C. Larivière. 2003. A natural history of the ground-beetles (Coleoptera: Carabidae) of America North of Mexico. Pensoft, Sofia-Moscow, Russia.
- Lee, S. I., J. R. Spence, D. W. Langor, and J. Pinzon. 2015. Retention patch size and conservation of saproxylic beetles in boreal white spruce stands. *Forest Ecology and Management* 358:98–107.
- Legendre, P. and M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69:1–24.
- Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280.
- Linden, D. W., G. J. Roloff, and A. J. Kroll. 2012. Conserving avian richness through structure retention in managed forests of the Pacific Northwest, USA. *Forest Ecology and Management* 284:174–184.
- Lindenmayer, D. B., et al. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters* 5:421–431.
- Marrec, R., et al. 2021. Multiscale drivers of carabid beetle (Coleoptera: Carabidae) assemblages in small European woodlands. *Global Ecology and Biogeography* 30:165–182.
- Martikainen, P., J. Siitonen, L. Kaila, and P. Punttila. 1996. Intensity of forest management and bark beetles in non-epidemic conditions: a comparison between Finnish and Russian Karelia. *Journal of Applied Entomology* 120:257–264.
- Matveinen-Huju, K., M. Koivula, J. Niemelä, and A. M. Rauha. 2009. Short-term effects of retention felling at mire sites on boreal spiders and carabid beetles. *Forest Ecology and Management* 258:2388–2398.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- Mori, A. S., and R. Kitagawa. 2014. Retention forestry as a major paradigm for safeguarding forest biodiversity in productive landscapes: a global meta-analysis. *Biological Conservation* 175:65–73.
- Mori, A. S., A. T. Ota, S. Fujii, T. Seino, D. Kabeya, T. Okamoto, M. T. Ito, N. Kaneko, and M. Hasegawa. 2015. Biotic homogenization and differentiation of

- soil faunal communities in the production forest landscape: taxonomic and functional perspectives. *Oecologia* 177:533–544.
- Neumann, J. L., G. J. Holloway, A. Hoodless, and G. H. Griffith. 2017. The legacy of 20th century landscape change on today's woodland carabid communities. *Diversity and Distributions* 23:1447–1458.
- Oksanen, J., et al. 2019. *vegan: Community Ecology Package*. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>
- Oregon Department of Forestry. 2018. Oregon Forest Practices Act. Oregon revised statutes: ORS 527.610-992. Oregon Department of Forestry, Salem, Oregon, USA.
- Pakeman, R. J., and J. A. Stockan. 2014. Drivers of carabid functional diversity: Abiotic environment, plant functional traits, or plant functional diversity? *Ecology* 95:1213–1224.
- Pearce, J. L., and L. A. Venier. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecological Indicators* 6:780–793.
- Phillips, H. R. P., J. M. Halley, J. N. Urbina-Cardona, and A. Purvis. 2017. The effect of fragment area on site-level biodiversity. *Ecography* 41:1220–1231.
- Podani, J., and D. Schmera. 2006. On dendrogram-based measures of functional diversity. *Oikos* 115:179–185.
- PRISM Climate Group, Oregon State University. <http://prism.oregonstate.edu>
- R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ranius, T., A. Caruso, M. Jonsell, A. Juutinen, G. Thor, and J. Rudolphi. 2014. Dead wood creation to compensate for habitat loss from intensive forestry. *Biological Conservation* 169:277–284.
- Root, H. T., J. Verschuyt, T. Stokely, P. Hammond, M. A. Scherr, and M. G. Betts. 2017. Plant diversity enhances moth diversity in an intensive forest management experiment. *Ecological Applications* 27:134–142.
- Rosenvald, R., and A. Lohmus. 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management* 255:1–15.
- Smith, A. B., B. Sandel, N. J. B. Kraft and S. Carey. 2013. Characterizing scale-dependent community assembly using the functional-diversity–area relationship. *Ecology* 94:2392–2402.
- Spake, R., N. Barsoum, A. C. Newton, and C. P. Doncaster. 2016. Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations. *Forest Ecology and Management* 359:300–308.
- Sultaire, S. M., A. J. Kroll, J. Verschuyt, and G. J. Roloff. 2021. Stand-scale responses of forest-floor small mammal populations to varying size, number, and location of retention tree patches. *Forest Ecology and Management* 482:118837.
- Talbert, C., and D. Marshall. 2005. Plantation productivity in the Douglas-fir region under intensive silvicultural practices: results from research and operations. *Journal of Forestry* 103:65–70.
- Washington Forest Practices Board. 2002. *Forest Practices Rules*. Title 222 WAC Washington State Department of Natural Resources, Olympia, Washington, USA.
- Work, T. T., J. M. Jacobs, J. R. Spence, and W. J. Volney. 2010. High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests. *Ecological Applications* 20:741–751.

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