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Disturbance type shapes initial community assembly patterns of early seral forest ground beetles in southwest Oregon

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ABSTRACT

Forest harvests are a significant part of disturbance regimes in many temperate forest landscapes. However, variability in biodiversity between early seral stands originating from harvest versus natural disturbances like wildfire is not well understood. We used a chronosequence sampling design to compare diversity, composition, and traits of ground and tiger beetles (Coleoptera: Geadephaga, hereafter "ground beetles") between early seral stands regenerating within 20 years after clearcut harvest or stand-replacing wildfire in southwest Oregon, USA. Clearcut stands were managed with planting and herbicides whereas fire-origin stands received minimal post-fire management. We also compared ground beetle communities 6–9 years after post-fire salvage logging. Compared to young clearcut stands (2–5 yr), ground beetle communities in young fire-origin stands had 30 % higher species richness (90 % CI: 0, 60 %), distinct composition, and disturbance-adaptive traits, including small body size (90 % CI for trait-environment interaction: −1.72, −0.63) and flight ability (90 % CI: 0.39, 1.47). Communities converged in the oldest age class (16–20 yr). Salvage logging favored flight-capable species to a greater degree than unlogged fire-origin stands (90 % CI: 0.12, 1.02) up to 9 years after disturbance, suggesting prolonged early seral conditions. Ground beetle composition varied with vegetation and deadwood structure but was also likely influenced by unobserved processes, such as fire-induced beetle mortality exceeding that of timber harvest. Our results indicate an ephemeral ground beetle community inhabiting post-fire stands that differs from post-harvest environments, suggesting that fire effects on the forest floor have a distinctive role in shaping early seral forest biodiversity.

1. Introduction

Forest harvest and associated silvicultural practices shape contemporary disturbance regimes in many forest ecosystems (Betts et al., 2024; Brown et al., 2018; Cohen et al., 2002). Even-aged harvest methods create early seral conditions, which can provide important habitat for species assemblages distinct from those inhabiting mature forests (Kwit et al., 2014; Lindenmayer et al., 2019; Swanson et al., 2014), contributing to landscape heterogeneity. However, given concerns about intensive silviculture causing forest degradation and biodiversity losses (Betts et al., 2022), the conservation value of harvest-generated early seral stands requires evaluation. One way to understand the implications of forest harvest is by evaluating biodiversity responses relative to natural disturbance (Attiwill, 1994; Hunter, 1993; North and Keeton, 2008). Many natural disturbance regimes include stand-replacing disturbance effects (Lorimer and White, 2003; Reilly et al., 2022), which can serve as reference conditions for evaluating even-aged harvest methods such as clearcutting.

Clearcutting is often employed in conjunction with other intensive forest management practices, which are critical for meeting global

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demand for wood products (Peng et al., 2023). For example, timber harvested from intensively managed forest stands in the Pacific Northwest of North America contributes substantially to United States lumber production (Oregon Forest Resources Institute, 2023; Zhou and Daniels, 2018). Intensive forest management on private land in the Pacific Northwest typically includes clearcut harvests on 30–50-year rotations, herbicide treatments for site preparation and crop tree release, and planting genetically selected Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Pinaceae]) seedlings (Talbert and Marshall, 2005). Factors influencing biodiversity in young, intensively managed stands are well-documented (Arnett et al., 2010; Kormann et al., 2021; Root et al., 2017; Stokely et al., 2018) but direct comparisons with stands regenerated by natural disturbance are limited (but cf. Cobb, Langor, and Spence, 2007 in boreal Canada). Such comparisons can inform stand-scale forest management and stewardship practices, and provide insights for alternative silviculture to meet diverse objectives among land owners and managers (Butler et al., 2016; Hartley, 2002).

Additionally, temperate and boreal regions globally are experiencing increasing extent and severity of forest disturbances (Klapwijk et al., 2013; Usbeck et al., 2010), including fire regimes in the Pacific Northwest (Reilly et al., 2017). Salvage harvests may also be expected to increase to mitigate economic losses (Lindenmayer et al., 2008) and maintain timber supply (Bousfield et al., 2023). For example, the spatial extent of post-fire salvage logging has increased over the past 30 years in the Pacific Northwest (Zuspan et al., 2024), making it important to understand how biodiversity responds to this practice. Generally, removing dead or injured trees after disturbance changes early seral forest conditions, influencing species diversity and composition, but the effects of this practice vary substantially among taxa (Georgiev et al., 2020; Thorn et al., 2018). Multiple disturbances occurring in short succession, such as fire followed by salvage logging, can interact to generate unforeseen ecological responses (Paine et al., 1998). Therefore, despite extensive research on how ground beetle communities respond to forest harvest (Buddle et al., 2006; Saint-Germain et al., 2005; Sultaire et al., 2021), their responses to logging in post-fire contexts require further study.

To characterize forest succession and biodiversity response to stand-replacing harvest and fire, we focused on ground beetles and tiger beetles (Coleoptera: Geadephaga, including Carabidae, Cicindelidae, and Trachypachidae; hereafter, "ground beetles"). Ground beetles have proven useful for understanding biodiversity responses to forest disturbance and management (Niemelä et al., 2007; Pearce and Venier, 2006) and complement our parallel studies of bird and bee communities in the same study area (Frank et al., 2025a,b). Ground beetles are abundant in forest ecosystems, can influence plant and arthropod populations in their roles as consumers, and are functionally diverse in their ecological roles and tolerances (Alalouni et al., 2013; Lövei and Sunderland, 1996).

The influences of environmental filtering, disturbance-induced-mortality, and dispersal-colonization are likely important components of community assembly in ground beetles, with logical connections to metacommunity theory (Leibold et al., 2004). Ground beetle community responses to forest disturbance and succession often show high turnover along gradients in forest structure (Heyborne et al., 2003; Koivula et al., 2002; Kriegel et al., 2021; Work et al., 2010), suggesting that species may have distinct "successional niches" driven by environmental filtering (Pacala and Rees, 1998). Specifically, both downed dead wood and ground-layer vegetation can structure ground beetle communities in disturbed forests (Perry et al., 2018; Skłodowski, 2017; Ulyshen and Hanula, 2009) and vary both among disturbances and with early successional development. For example, total dead wood biomass is typically higher after fire than harvest (Dymond et al., 2010), though most of this biomass is initially in standing snags after fire and transitions to downed logs as snags fall (Dunn and Bailey, 2015). After harvest, silvicultural herbicides can reduce plant cover and diversity for several years compared to unmanaged vegetation (Stokely et al., 2021).

Generally, ground beetle species inhabiting open environments are distinguished from those adapted to closed-canopy forests by small body size and flight capability, and sometimes by robust body shapes, strong pushing abilities, and herbivory (Barton et al., 2011; Ng et al., 2018; Ribera et al., 2001, 1999a; Sultaire et al., 2021). Of these traits, flight ability is an important component of dispersal power for ground beetles and facilitates colonization (Den Boer, 1970). Additionally, ground beetles experience high mortality rates in the combustion of organic layers during intense fires but can survive at higher rates through harvest disturbance events (Paquin and Coderre, 1997). Consequently, species adapted to closed-canopy forests are often more abundant in post-harvest stands than post-fire stands (Buddle et al., 2006; Saint-Germain et al., 2005), and colonization through dispersal may be more important to community assembly after fire than harvest.

To evaluate responses of ground beetle biodiversity to forest management, we studied ground beetles and their habitat in early seral forest stands of the Klamath Mountains of southwest Oregon, USA. The intersection of a commercially harvested land base and widespread fire activity within this region provides a rare opportunity to assess biodiversity responses to the early seral forest stands generated by these disturbances. We used a trait-based framework to infer life history strategies and inform our interpretation of biodiversity responses. We asked: (1) How do the composition and diversity of ground beetles and their traits vary among early seral fire-origin, salvage-logged, and clearcut stands? (2) How do comparisons in ground beetle communities between fire-origin and clearcut stands vary with stand age across a two-to-20-year chronosequence? and (3) How does variation in habitat characteristics among disturbance types and stand ages explain patterns in ground beetle communities in this early seral forest context?

2. Methods

2.1. Study area and sampling framework

We studied ground beetles as one component of a broader multi-taxa biodiversity study that also included bee, bird, and plant communities. This study was conducted in early seral forest stands mapped as Douglas-fir or Douglas-fir/tanoak (*Notholithocarpus densiflorus* [Fagaceae]) potential vegetation types in the Klamath Mountains of southwest Oregon, USA (Henderson, unpublished report). This study area is primarily on the ancestral territory of the Cow Creek Band of the Umpqua Tribe of Indians, who have stewarded these lands for millennia. The Klamath Mountains historically experienced a mixed-severity fire regime (Spies et al., 2018; Taylor and Skinner, 1998), with high-severity fire effects increasingly prevalent in recent decades due to a warming climate and a century of fire suppression (Knight et al., 2022; Taylor et al., 2021).

We sampled ground beetles and habitat characteristics across three disturbance types and three stand age classes. Disturbance types included: stand-replacing fire on federal forest lands (fire-origin stands), post-fire salvage logging on federal forest lands (salvage-logged stands), and clearcut timber harvest with intensive management on private forestland (clearcut stands). Stand age (i.e., time since disturbance) classes included: 2–5 yr (young), 6–9 yr (intermediate), and 16–20 yr (advanced). We only sampled salvage-logged stands in the intermediate age class, as additional fires during site selection limited availability of young and advanced candidate stands. We selected stands to match distributions of elevation and topographic heat load (McCune and Keon, 2002) as much as possible among combinations of disturbance × stand age (Table A.1). Our final study design included 69 sampled stands (i.e., forest patches) from seven disturbance × stand age categories: young, intermediate, and advanced fire-origin and clearcut stands, and intermediate salvage-logged stands. For additional study area and site selection details, refer to parallel studies on bird and bee responses (Frank et al., 2025a,b).

2.2. Field sampling

We sampled ground beetle communities and habitat variables for each stand in one of three years: 2019, 2021, or 2022. Within each stand, we established three plots at least 100 m apart from one another and at least 50 m from an identifiable stand edge such as a road, harvest edge, or lower burn severity (< 75 % basal area mortality).

We sampled ground beetles using pitfall traps, set for six weeks beginning April 24 – May 6. In three stands with late snowfall in spring 2022, we delayed trap deployment to May 17–18. We installed four pitfall traps at each plot (three plots per stand, 12 traps per stand), with three traps 12 m from plot center at 0°, 120°, and 240° azimuths, and a fourth trap 3 m from plot center at 60°, 180°, or 300°. We collected samples two weeks after deployment, and again four weeks later. Pitfall traps consisted of plastic collection cups (11.75 cm diameter, 473 ml volume) filled with propylene glycol as a preservative liquid (diluted 50 % for two-week sampling round). Traps also included a second cup with drainage holes, nested beneath the collection cup, to facilitate sample collection. We placed plywood covers over the traps, elevated 2 cm above the opening, to reduce evaporation, rainwater intrusion, wildlife disturbance to traps, and vertebrate bycatch (Hoekman et al., 2017). Nonetheless, traps experienced extensive wildlife disturbance in some stands. To maximize sampling intensity, we reset disturbed traps when visiting stands for other purposes during the four-week sampling round.

We characterized vegetation within 25 m^2 circular subplots adjacent to each pitfall trap, with subplot centers located 6 m beyond each trap and on the same azimuths relative to plot center. In each subplot, field crews visually estimated vegetation cover by species using ordinal cover classes to reduce variability among observers (Peet et al., 1998). To account for the vertical structure of vegetation, crews estimated separately for four vertical strata: below 0.5 m, 0.5–2 m, 2–5 m, and above 5 m. Field crews also estimated bare ground cover. We converted ordinal cover estimates into percent cover by taking the midpoint of each cover class.

We quantified downed dead wood volume using line intercept transects. Field crews measured the diameter (cm) of all logs > 7.62 cm at the point of intersection along three 35 m transects at each plot (nine per stand), extending 5–40 m from plot center along 0°, 120°, and 240° azimuths.

2.3. Ground beetle identification

We separated ground beetles from pitfall trap debris and invertebrate bycatch and identified specimens to species or morphospecies (Frank et al., 2025c; Table B.1). We deposited a voucher collection with the Oregon State Arthropod Collection (accession record: OSAC_AC_2024_08_07–001).

2.4. Trait measurements

We measured elements of ground beetle morphology (traits) related to life history characteristics including foraging niche, microhabitat use, and dispersal ability (Table 1). We derived all traits from linear measurements of ground beetle body parts recorded to the nearest μm using a digital microscope (VHX-1000 with 20–200X VH-Z20W zoom lens, KEYENCE, Itasca, IL). For some traits, we summed values from multiple measurements (antennae length, tarsi length, leg length, and body length; Table C.1). For species captured at least six times, we measured six randomly selected specimens, and we measured all specimens of species with fewer individuals.

2.5. Data analysis

2.5.1. Development of composite traits

Prior to analysis, we developed interpretable, composite trait metrics from ground beetle morphology data because many morphological measurements are highly correlated. To develop these composite trait metrics, we first calculated the mean measurement value across specimens within each species/morphospecies. Then, we controlled for the influence of body size on each trait (i.e., allometric scaling) by regressing log-transformed trait values against log-transformed body length, and extracting the residuals of these regressions (Barton et al., 2011; Ribera et al., 1999b). In the allometric regression for mandible length, we included mandible width as an additional predictor to generate a metric of mandible shape independent of mandible size. We then conducted principal components analysis on the correlation matrix of these trait residuals, including varimax rotation to improve the interpretability of each axis in terms of the original input variables. We extracted a subset of the resulting axes that accounted for at least 80 % of the morphological variation among species.

We excluded *Sericoda bembidioides* Kirby from trait-based analyses due to broken antennae on the single specimen in our dataset. We also excluded *Clinidium calcaratum* LeConte (Carabidae: Rhysodinae), which is phylogenetically, ecologically, and morphologically distinct from the other species in our sample (Bell, 1994), and would have had an outsized influence on composite trait metrics (Figure C.2).

2.5.2. Comparisons of community composition and species traits

We aggregated ground beetle samples from all traps, plots, and collection periods to the stand level for analysis (12 traps per stand, 6 weeks of sampling in total). To test for differences in species composition among disturbance × stand age categories, we used species-specific generalized linear models (GLMs) with negative binomial link functions, implemented in the mvabund R package (Wang et al., 2012). We used these GLMs to test overall differences in composition between groups by summing likelihood ratio test statistics across species. This

Table 1
Loadings of individual traits on rotated principal components (RCs) used as composite trait variables for analyzing ground beetle community patterns in early seral forest stands of southwest Oregon, USA. Values in parentheses are the amount of variance in trait space explained by each component after varimax rotation. Bold numbers indicate loadings used to interpret each component. Refer to Table B.3 for individual species scores on each RC.

Interpretation	Trait	RC1 (22.4 %)	RC2 (21.5 %)	RC3 (20.5 %)	RC4 (17.8 %)	References
Size	Body length	–	–	–	–	Ribera et al. (2001)
Wedge-pushing	Femur width	**0.92**	-0.01	0.31	0.00	Forsythe (1983); (1991)
	Trochanter length	**0.91**	-0.27	0.00	0.04	
Walking speed	Elytra width	0.08	**0.84**	0.24	0.31	Forsythe (1983); (1991); Ribera et al. (1999b)
	Leg length	-0.43	**0.81**	-0.06	-0.05	
	Antenna length	-0.22	**0.72**	-0.49	-0.19	
Robustness	Pronotum width	0.47	-0.12	**0.73**	0.38	Barton et al. (2011); Forsythe (1987)
	Prothorax depth	0.00	0.34	**0.80**	0.12	
	Head width	0.11	-0.25	**0.75**	-0.19	
Flight ability	Elytra length	-0.35	0.32	0.24	**0.77**	Forsythe (1987)
	Metasternum length	0.17	-0.03	-0.08	**0.83**	
N/A	Mandible shape	-0.49	0.47	-0.10	-0.55	Sultaire et al. (2021)

sum-of-likelihood-ratio approach detects between-group differences in species composition as powerfully as distance-based methods (e.g., PERMANOVA analysis), but correctly models the mean-variance relationship common in species abundance data, unlike distance-based methods (Anderson and Walsh, 2013; Warton et al., 2012). We included categorical predictors for the seven combinations of disturbance × stand age that comprised our study design, with an offset to account for differences in sampling intensity (i.e., due to destruction of pitfall traps by wildlife). For the offset, we calculated total sampling days by summing the length of sampling time across all traps in a stand that were intact upon collection. We included an additional covariate for UTM easting after inspecting spatial correlograms of Moran's I from model residuals with the R package ncf (Bjornstad, 2022), which effectively resolved spatial autocorrelation.

To infer differences in species composition between disturbance types (i.e., fire, clearcut, salvage), we tested pairwise contrasts in sum-of-likelihood-ratio test statistics between disturbance × stand age categories, adjusting for multiple comparisons using a free step-down resampling approach (Westfall and Young, 1993). We assessed significance for this and all other mvabund models using PIT-trap (probability integral transform residual bootstrap) resampling with 999 iterations, which preserves and accounts for any among-species correlations by resampling rows of data (Warton et al., 2017). We also calculated model estimates of species-specific abundances for each disturbance × stand age category. We visualized species composition using model-based ordination of latent variables with the R package ecoCopula (Popovic et al., 2019) after accounting for UTM easting.

We evaluated the degree to which traits explained variation in multispecies abundances among disturbance × stand age categories using fourth-corner analysis, also in the R package mvabund (Wang et al., 2012). Fourth-corner analysis refers to testing for trait-environment relationships with information contained in site-species, site-environment, and species-trait matrices (Brown et al., 2014). We formulated the fourth-corner models similarly to multivariate GLMs used to compare species composition, but with the addition of interaction terms between traits (body length and each composite trait) and disturbance × stand age categories (Warton et al., 2015). We evaluated the importance of each trait using likelihood ratio tests and assessed significance with PIT-trap resampling. We also made pairwise comparisons of fourth-corner coefficient estimates to evaluate how traits characterized potential differences in composition between disturbance × stand age categories. As an index of overall ground beetle abundance, we also compared estimated abundances of species with average trait values. Traits like body length and flight ability can influence capture rates (Lang, 2000), so baseline coefficients for disturbance × stand age categories from this model can serve as an index of abundance that accounts for trait differences. Prior to model fitting, we centered all trait values at their mean and scaled them to unit variance.

2.5.3. *Comparisons of taxonomic and functional diversity*

We estimated both taxonomic and functional diversity of the ground beetle assemblage in each stand using Hill numbers. Hill numbers are a mathematically unified approach to quantifying diversity from abundance data, with each Hill number differing only by a single parameter q controlling the degree to which species relative abundances are weighted (Chao et al., 2014). For ground beetle assemblages in each stand, we calculated Hill numbers with $q = 0$, 1, and 2—equivalent to species richness (no weight to relative abundance), Shannon diversity (each species weighted in proportion to abundance), and Simpson diversity (common species given more weight than rare species). Hill numbers express diversity as the effective number of species, i.e., the number of equally abundant species that would produce the same diversity value as the observed community. Functional Hill numbers additionally incorporate species traits and represent the effective number of equally abundant *and equally distinct* species in the assemblage.

To generate a trait dissimilarity matrix for estimating functional Hill numbers, we calculated Gower's distance among each species (Pavoine et al., 2009) using the same allometrically scaled traits that were used as inputs to principal components analysis, and untransformed body length. When calculating Gower's distance, we weighted each trait by its mean correlation with other input traits, as including multiple correlated traits would otherwise artificially inflate distances between species.

We estimated all Hill numbers using coverage-based rarefaction in the R package iNEXT.3D (Chao et al., 2021), which allowed us to account for differences in sample coverage among stands. Sample coverage is an estimate of the proportion of individuals at a sampling location represented by species observed in the sample. Variability in sample coverage can confound diversity comparisons and can arise from variation in sampling intensity and/or from true variation in sample diversity. As a target sample coverage, we used the minimum estimated sample coverage for double the number of sampled individuals in any one stand, which results in minimal bias for undersampled (low coverage) stands while maximizing the use of species data in more complete samples (Chao et al., 2020). Each estimation was completed with 999 bootstrap replicates, providing a measure of variability around each estimate.

To compare taxonomic and functional diversity among disturbance × stand age categories, we used estimated dependent variable (EDV) regression. Ordinary Least Squares Regression assumes constant sampling variance, which is violated by different degrees of uncertainty around diversity estimates with different levels of sample completeness. To account for this issue, we used an approach for EDV regression that weights observations by their sampling variance and the model error variance (Lewis and Linzer, 2005). We fit EDV regression models with taxonomic and functional Hill numbers of orders 0, 1, and 2 estimated at a fixed sample coverage as response variables. Comparative EDV regression models included categorical predictors for the seven disturbance × stand age categories, and we evaluated the magnitude and uncertainty of pairwise contrasts between categories using the R package multcomp (Hothorn et al., 2008). We found no evidence of spatial autocorrelation in model residuals after inspecting spatial correlograms of Moran's I with the R package ncf (Bjornstad, 2022).

2.5.4. *Ground beetle relationships to habitat characteristics*

To evaluate associations between ground beetle community composition, traits, and habitat characteristics, we used the same multispecies GLM and fourth-corner approaches described above but with environmental variables that we expected to help explain contrasts among disturbance types and age classes as predictor variables. Predictor variables in these models included: percent cover of bare ground, percent cover of herbaceous plants, shrub-layer cover, volume of downed dead wood, and heat load index.

To calculate herbaceous cover, we summed cover estimates of all forb and graminoid species below 0.5 m height. We calculated shrub-layer cover as the sum of cover estimates for all shrub and tree species across 0.5–2-m and 2–5-m strata to represent a gradient in overhead cover for ground-dwelling arthropods in early seral stands containing limited overstory canopy. For downed dead wood, we calculated total volume (m^3ha^{-1}) as $\pi^2 * \sum(d^2 \div 8L)$, where d is the piece diameter (m) and L is transect length (m) (Harmon et al., 1986). For model inputs, we then calculated stand-level averages for each explanatory variable. We also compared these environmental variables among disturbance × stand age categories by fitting linear models and calculating confidence intervals for between-category comparisons using the R package emmeans (Lenth, 2024).

2.5.5. *Relationships between diversity and habitat characteristics*

To evaluate associations between ground beetle diversity and habitat characteristics, we fit EDV regression models with percent cover of herbaceous plants, ground-layer plant diversity, shrub-layer cover, heterogeneity in shrub-layer cover, and volume of downed dead wood as predictors of taxonomic or functional diversity. We calculated ground-layer plant diversity using Shannon's index, with cover values aggregated across subplots within a stand. To calculate heterogeneity in shrub-layer cover, we used an alternative to the coefficient of variation that is robust to skewed distributions (RCV_M: Arachchige et al., 2022), calculated using cover values from 12 subplots in each stand. We centered all continuous predictors and scaled them to unit variance prior to model fitting and conducted all analyses using R statistical software, version 4.2.3 (R Core Team, 2023).

3. Results

We sampled 5834 individual ground beetles representing 40 species from 22 genera (Table B.1). Due to widespread animal disturbance to pitfall traps, sampling intensity at each stand ranged from 297 to 540 trap nights, with a median of 492 trap nights. Five species made up 78.5 % of the individuals in our sample: *Omus audouini* Reiche / *O. cazieri* van den Berghe, *Pterostichus algidus* LeConte, *P. herculaneus* Mannerheim, *P. lama* Ménétries, and *Scaphinotus rugiceps* Horn. We extracted four sets of species scores from principal components analysis of ground beetle morphology after accounting for the effect of body size on each trait measurement. These four axes captured 82.1 % of the variation in species morphology (Table 1) and we interpreted them as wedge-pushing ability, walking speed, robustness, and flight ability (Appendix C).

3.1. Comparisons of community composition and traits

We found evidence for differences in ground beetle community composition among nearly all pairs of disturbance × stand age categories, but community composition of young fire-origin stands was particularly distinct from that of other categories (Fig. 1, Table 2). Contrasts in community composition between fire-origin and clearcut stands were strongest in the young age class (LR = 119.8, p = 0.005) and progressively weaker for older age classes (Fig. 1, Table 2). We did not find evidence of compositional differences between disturbance types for the advanced age class (LR = 26.2, p = 0.143). This pattern of convergence in composition between disturbance types was disproportionately driven by compositional changes in fire-origin stands: the magnitude of differences between young and advanced age classes was nearly twice as high for fire-origin (LR = 104.3) as for clearcut stands (LR = 57.0). The composition of salvage-logged stands, sampled in the intermediate age class, was also distinct from both intermediate fire-origin (LR = 59.7, p = 0.037) and clearcut stands (LR = 73.7, p = 0.019).

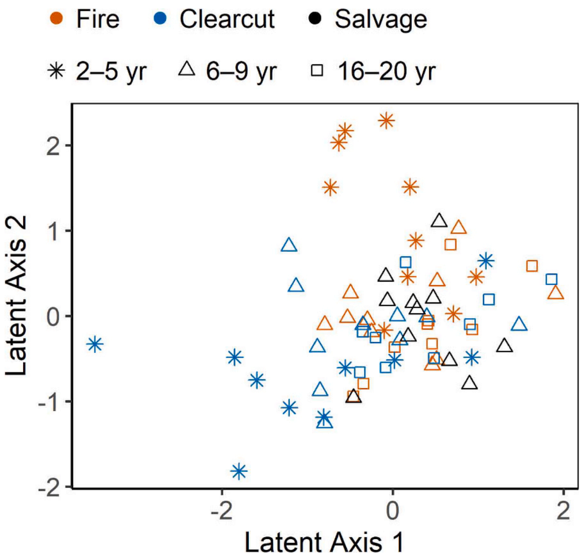

Fig. 1. Ground beetle species composition in early seral forest stands was initially distinct between disturbance types but converged with stand development. Points represent site scores from model-based ordination, with stand age categories indicated by point shapes and disturbance types indicated by colors.

Table 2
Pairwise comparisons of ground beetle species composition between disturbance × stand age categories. Likelihood ratios were summed across models for each species, and p-values were calculated using 999 iterations and are adjusted for multiple comparisons using a free step-down resampling approach. Refer to Table E.1 for additional pairwise comparisons.

Comparison			Likelihood Ratio	p
Disturbance comparisons within age-classes				
Fire (2–5 yr)	vs.	Clearcut (2–5 yr)	119.8	0.005
Fire (6–9 yr)	vs.	Clearcut (6–9 yr)	69.5	0.020
Fire (16–20 yr)	vs.	Clearcut (16–20 yr)	26.2	0.143
Salvage (6–9 yr)	vs.	Fire (6–9 yr)	62.5	0.029
Salvage (6–9 yr)	vs.	Clearcut (6–9 yr)	73.7	0.019
Age-class comparisons within disturbance types				
Fire (2–5 yr)	vs.	Fire (6–9 yr)	93.2	0.006
Fire (2–5 yr)	vs.	Fire (16–20 yr)	104.6	0.005
Fire (6–9 yr)	vs.	Fire (16–20 yr)	56.1	0.030
Clearcut (2–5 yr)	vs.	Clearcut (6–9 yr)	38.8	0.143
Clearcut (2–5 yr)	vs.	Clearcut (16–20 yr)	57.0	0.030
Clearcut (6–9 yr)	vs.	Clearcut (16–20 yr)	61.2	0.029

Species traits provided a functional perspective on contrasts in community composition and an index of ground beetle abundance independent of traits. For species with average trait values, abundance was highest in young fire-origin stands, 2.6 × that of young clearcut stands (90 % CI: 1.9, 3.7 ×) and 6.1 × that of advanced fire-origin stands (90 % CI: 4.1, 9.1 ×). Advanced fire-origin stands had the lowest estimate of any category but it was comparable to that of advanced clearcut stands (90 % CI: 0.6, 1.3 ×; Fig. 2). Incorporating "fourth-corner" trait-environment relationships explained significantly more variation in species abundance (i.e., capture rates) among disturbance × stand age categories than species identities alone (LR = 122.4, df = 30, p = 0.001). Specifically, body length (LR = 20.7, p = 0.001), flight ability (LR = 23.2, p = 0.001), and body shape (i.e., robustness; LR = 19.1, p = 0.003) were the most important traits, both overall and for characterizing the strong contrast in composition we observed between young fire-origin and clearcut stands.

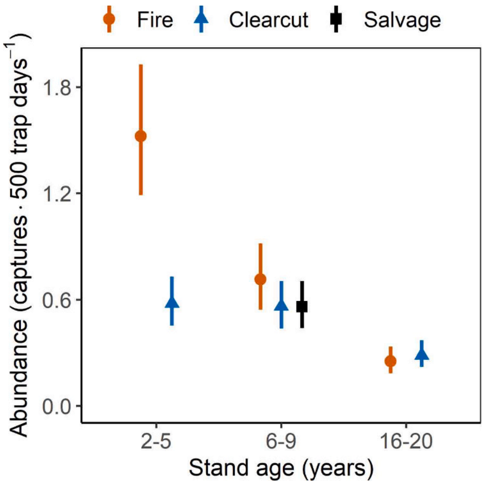

Fig. 2. Abundance estimates (i.e., mean capture rates and 90 % CI) for a hypothetical ground beetle species with average trait values, for each disturbance × stand age category. These values serve as an index of abundance after accounting for traits, as pitfall capture rates vary with beetle size and other characteristics.

For body length, larger size was generally associated with higher capture rates, but captures of small species were relatively high in young fire-origin stands compared to other categories (Fig. 3). Young clearcut stands were characterized instead by larger species; for a 1 standard deviation (SD) increase in body length, predicted abundance increased 3.3 × more (90 % CI: 1.9, 5.6 ×) in young clearcut than young fire-origin stands. Conversely, inferred flight ability was associated with lower capture rates overall (Fig. 3), but this relationship was 2.5 × more negative (per 1 SD increase; 90 % CI: 1.5, 4.4 ×) for young clearcut stands than young fire-origin stands. Species with robust body shape further distinguished the ground beetle communities of young fire-origin stands from young clearcut stands, as robustness was a 2.4 × more positive predictor of abundance (per 1 SD increase; 90 % CI: 1.4, 4.2 ×) in young fire-origin stands than clearcut stands. As in the young age class, advanced clearcut stands were characterized by large, flightless species, with little change in these coefficients across clearcut stand age classes (Fig. 3). However, fire-origin stands in the advanced age class were characterized by large, flightless species to an even greater degree than advanced clearcut stands; 1 SD increases in size or flight ability were associated with 2.4 × more positive (90 % CI: 1.5, 4.1 ×) or 1.5 × more negative (90 % CI: 0.94, 2.3 ×) abundance responses, respectively, for fire-origin stands than clearcut stands.

Traits related to locomotion strategy were also important in explaining overall variability in species abundances among disturbance × stand age categories, including walking speed (LR = 14.7, p = 0.010) and wedge-pushing ability (LR = 18.2, p = 0.003). As with size and flight ability, walking speed and wedge-pushing were relatively consistent predictors of abundance across clearcut stand age classes but were much more positive predictors for advanced fire-origin stands than young fire-origin stands (Fig. 3). In advanced fire-origin stands, species with 1 SD higher values for each trait were predicted to be 3.0 × (for walking speed; 90 % CI: 2.2, 4.1 ×) and 7.0 × (for wedge-pushing; 90 % CI: 4.8, 10.1 ×) more abundant than the average species, for which abundance was generally low (Fig. 2). Compared to advanced clearcut stands, these relationships were 2.2 × and 1.9 × more positive in advanced fire-origin stands, for walking speed (90 % CI: 1.4, 3.5 ×) and wedge-pushing (90 % CI: 1.1, 3.2 ×), respectively.

Species traits also characterized compositional differences between salvage-logged and unlogged fire-origin stands in the intermediate age class. Specifically, flight ability (90 % CI: 1.1, 2.8 ×) and wedge-pushing (90 % CI: 1.4, 4.0 ×) were more positive predictors of ground beetle abundance in salvage-logged stands.

Abundance patterns for individual species were more variable than those of community-level traits, but reinforced key findings from the trait-based analysis. For example, *Pterostichus herculaneus* abundance was 6.3 × higher (90 % CI: 8.6, 45.0 more captures per 500 trap days) and *Promecognathus crassus* LeConte abundance was 5.0 × higher (90 % CI: 0.13, 3.1 more captures per 500 trap days) in young clearcut stands than young fire-origin stands, both relatively large, flightless species. Conversely, *A. littoralis* Mannerheim, a smaller flight-capable species, and *Calosoma tepidum* LeConte, a large wing-dimorphic species, were more abundant in young fire-origin stands than young clearcut stands (*A. littoralis* 90 % CI: 2.0, 5.5 more captures per 500 trap days; *C. tepidum* 90 % CI: −0.7, 3.7 more captures per 500 trap days). Other large, flightless species, like *Omus dejeani* Reiche, were just as abundant in young fire-origin stands as young clearcut stands. Refer to Appendix B for additional individual species results.

3.2. Diversity comparisons

Young fire-origin stands had the highest mean species richness of any disturbance × stand age category (Fig. 4a), 29.9 % greater than the estimate for young clearcut stands (90 % CI: 0.0, 59.6 %). Richness estimates were successively lower in each fire-origin age class, such that the modeled mean for advanced fire-origin stands was 38.8 % lower than that for young fire-origin stands (90 % CI: 16.9, 60.7 %) and the lowest of any category. In intermediate and advanced age classes, species richness estimates were similar among disturbance types ($p > 0.95$ for each comparison). For higher order Hill numbers (order $q = 1$ and 2), taxonomic diversity comparisons were similar in direction to richness comparisons but considerably weaker (Appendix D), with no evidence for differences among disturbance × stand age categories ($q = 1$: $F_{6,\,62} = 1.34$, $p = 0.25$; $q = 2$: $F_{6,\,62} = 0.71$, $p = 0.64$). Functional diversity comparisons also had qualitatively similar patterns to taxonomic

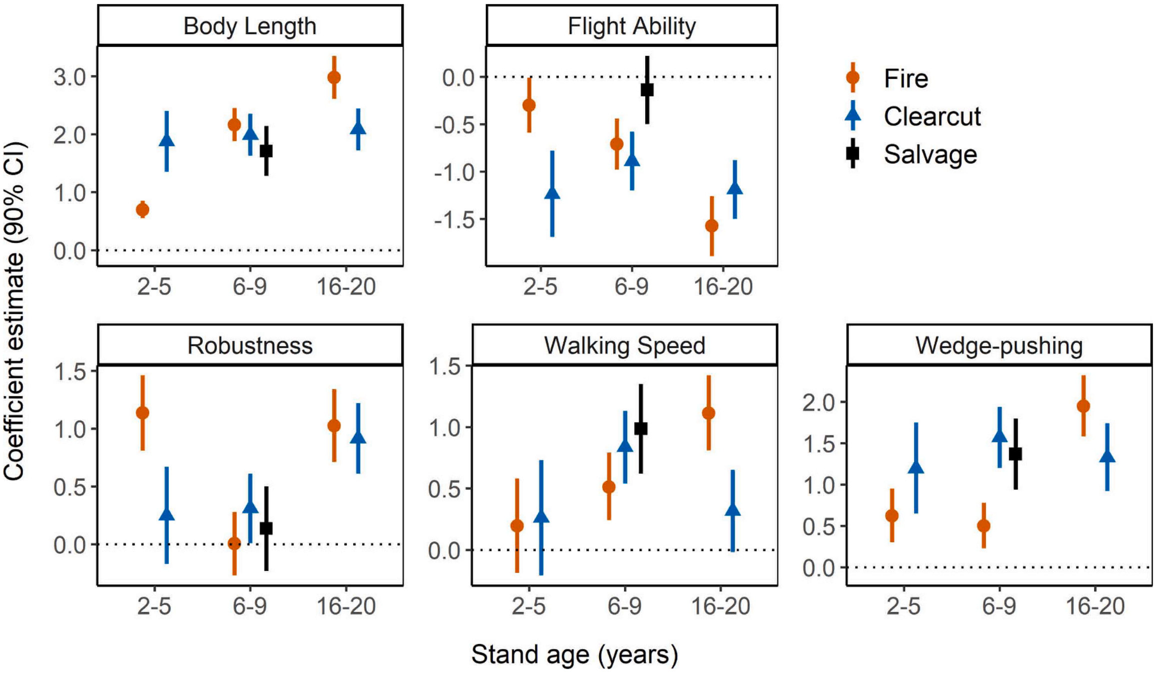

Fig. 3. Fourth-corner coefficient estimates for each disturbance × stand age category of early seral forest stands for five traits representing > 80 % of the morphological variation among ground beetle species sampled in this study. Coefficients reflect the influence of a given trait on ground beetle species abundances from a negative binomial GLM with a log link function.

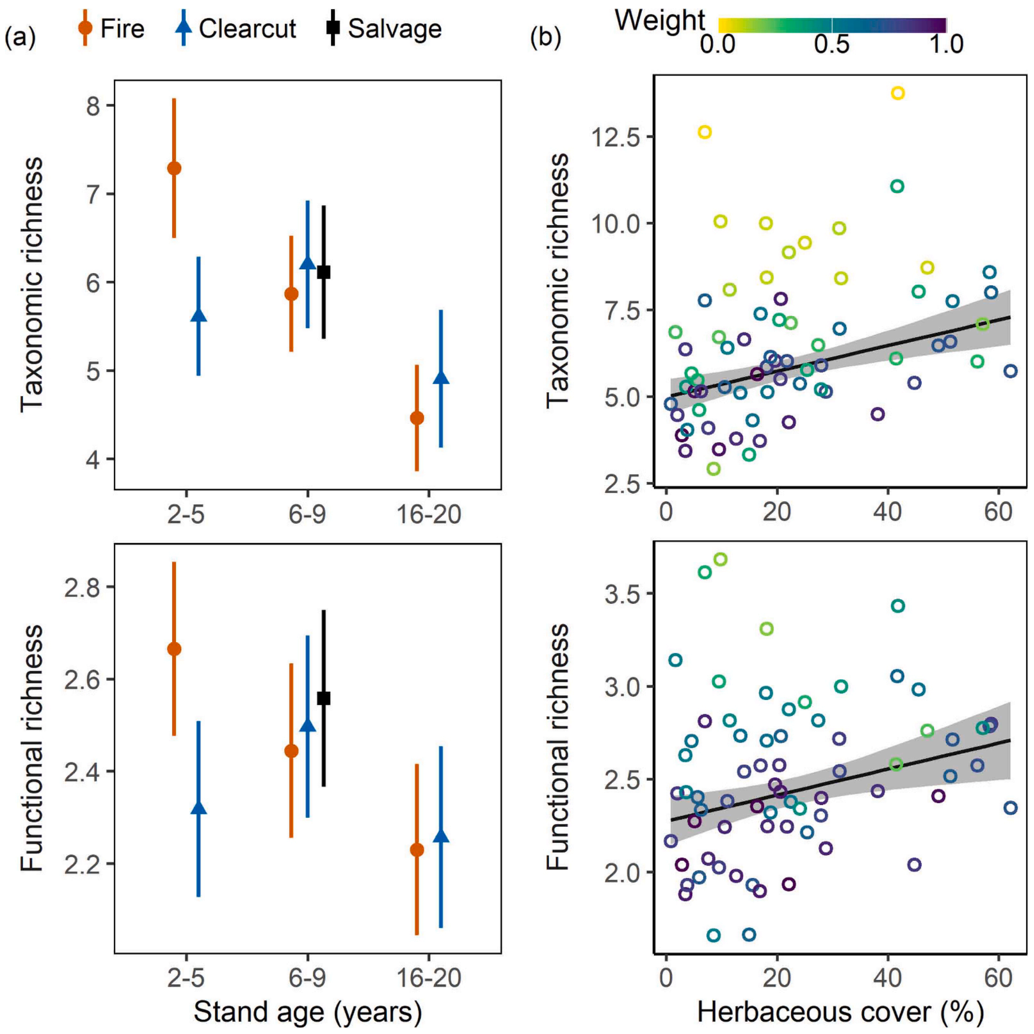

Fig. 4. Patterns in taxonomic and function richness (Hill numbers of order $q = 0$) of ground beetles in early seral forest stands of southwest Oregon, calculated at a fixed sample coverage of 0.918. (a) Mean (90 % CI) richness estimates for disturbance × stand age categories. (b) Partial regressions between richness and herbaceous cover, including 90 % confidence intervals, from models with richness data weighted by estimation uncertainty. Results for higher order Hill numbers and additional explanatory variables are presented in Appendix D.

diversity but with smaller contrasts and more uncertainty (Appendix D). For example, functional richness estimates for young fire-origin stands were only 15.0 % greater than the estimate for young clearcut stands (90 % CI: −3.6, 33.5 %) and the estimated reduction in functional richness between young and advanced fire-origin stands was only 16.3 % (90 % CI: 0.4, 32.2 %).

Samples with low coverage tended to have high estimated species richness but a high degree of uncertainty and were down-weighted in models accordingly; this resulted in more conservative comparisons but did not affect our general conclusions (Appendix D).

3.3. *Comparisons of habitat characteristics*

Of the habitat characteristics included as explanatory variables in multispecies GLMs, herbaceous cover, downed deadwood volume, and shrub-layer vegetation cover varied among disturbance × stand age

Table 3

Mean values (± standard deviation) of stand characteristics included as input variables in explanatory models of ground beetle community composition and/or diversity.

	Stand age	n	Bare ground (%)	Herb cover (%)	Shrub-layer cover (%, two strata)	Down wood vol. (m^3 ha^{-1})	Heat Load Index	Ground-layer Plant Diversity (H')	Woody cover het. (RCV_m)
Fire	2–5	10	17 ± 17	35 ± 21	18 ± 16	101 ± 87	0.75 ± 0.17	2.39 ± 0.25	1.01 ± 0.46
	6–9	10	11 ± 10	19 ± 10	68 ± 40	195 ± 79	0.69 ± 0.20	2.53 ± 0.25	0.44 ± 0.19
	16–20	9	14 ± 7	7 ± 6	94 ± 55	180 ± 55	0.74 ± 0.15	2.16 ± 0.42	0.48 ± 0.21
Clearcut	2–5	10	10 ± 4	20 ± 9	6 ± 8	139 ± 79	0.77 ± 0.17	2.33 ± 0.55	1.28 ± 0.27
	6–9	10	7 ± 6	37 ± 20	14 ± 11	121 ± 80	0.72 ± 0.15	2.39 ± 0.47	0.97 ± 0.37
	16–20	9	9 ± 8	24 ± 16	83 ± 16	106 ± 48	0.75 ± 0.12	2.33 ± 0.52	0.47 ± 0.19
Salvage	6–9	11	15 ± 8	15 ± 8	39 ± 18	218 ± 51	0.66 ± 0.17	2.26 ± 0.48	0.74 ± 0.34
range			1–54	1–62	0–199	2–365	0.38–0.95	1.33–3.01	0.12–1.48
$F_{6,\ 62}$			2.05	5.68	15.58	4.38	0.53	0.67	10.93
p			0.07	< 0.001	< 0.001	< 0.001	0.78	0.67	< 0.001

categories (Table 3). Herbaceous cover was initially 43 % lower in clearcut stands than fire-origin stands (90 % CI: 0.9, 23.7 percentage-points lower), but stayed relatively consistent across clearcut age classes and declined with age among fire-origin stands (Table 3). Contrasting temporal patterns were also evident for woody vegetation, with shrub-layer cover developing more rapidly in fire-origin stands than clearcut stands but eventually equalizing in the advanced age class (Table 3). Downed dead wood volume was highly variable (Table 3), but mean values for clearcut stands were approximately 40 % lower than fire-origin stands in the intermediate and advanced age classes. Salvage-logged stands, sampled only in the intermediate age class, were characterized by similar herbaceous cover and dead wood volume to fire-origin stands (Table 3) but averaged 43 % less shrub-layer cover (90 % CI: 5.3, 46.0 percentage-points lower). Bare ground and heat load index did not vary systematically among disturbance types or stand age classes (Table 3).

3.4. Community composition and trait relationships to habitat characteristics

Overall, environmental gradients were important in explaining patterns in ground beetle community composition (LR = 503.3, p = 0.001). In the model without species traits, bare ground (LR = 119.9, p = 0.001) and shrub-layer cover (LR = 114.5, p = 0.001) were the most important environmental gradients explaining species composition, and composition also varied with gradients in herbaceous cover (LR = 92.9, p = 0.004), heat load (LR = 100.6, p = 0.002), and downed wood volume (LR = 81.7, p = 0.008).

Ground beetle morphological traits helped explain species abundance relationships to habitat characteristics, as indicated by lower model deviance when including trait-environment interactions (LR = 74.8, p = 0.001). Specifically, relationships with shrub-layer cover, herbaceous cover, and bare ground each varied with body size (Fig. 5), which was the most important trait we examined for explaining species responses to habitat characteristics (LR = 34.9, p = 0.001). A species with average trait values was predicted to decrease in abundance by 7.8 % for every 10-percentage-point increase in shrub cover, whereas a species 5.0 mm larger than average was predicted to increase in abundance by 1.0 %. Conversely, a species with average trait values was predicted to increase in abundance by 15.6 % for every 10-percentage-point increase in herbaceous cover, whereas a species 5.0 mm larger than average was predicted to decrease in abundance by 4.1 %.

Responses also varied with body shape (LR = 12.8.0, p = 0.055), with a negative coefficient for robustness × dead wood (β = −0.32; 90 % CI: −0.45, −0.20) indicating that narrower, flatter species (Table 1) had more positive relationships to dead wood than the average species (Fig. 5). Flight ability was a weaker predictor of species-environment relationships overall (LR = 7.0, p = 0.173) than size or robustness, as were wedge-pushing (LR = 4.1, p = 0.483) and walking speed (LR = 4.1, p = 0.600). However, species with inferred flight ability were more negatively associated with shrub-layer cover than the average species (β = −0.24; 90 % CI −0.39, −0.12).

Individual species were variable in their responses, which were not always represented in trait-based patterns. Notably, *Scaphinotus rugiceps*, the fifth most abundant species in our sample, was predicted to be 82 % more abundant per 100 m^3 ha^{-1} increase in dead wood volume (90 % CI: 44, 119 %). *Clinidium calcaratum*, the wrinkled bark beetle that we excluded from trait-based analyses, also showed strong positive responses to dead wood (73 % increase per 100 m^3 ha^{-1} increase in volume; 90 % CI: 26, 119 %) and to shrub-layer cover (78 % increase per 50-percentage-point increase in shrub cover; 90 % CI: 39, 116 %). For all species-specific coefficient estimates, refer to Table E.3.

3.5. Diversity relationships to habitat characteristics

Taxonomic and functional richness were both positively associated with herbaceous cover (Fig. 4b), with predicted increases of 45 % (90 % CI: 22, 68 %) and 19 % (90 % CI: 6, 32 %), respectively, across an observed 61-percentage-point gradient in herbaceous cover. The other four environmental gradients we examined explained little of the variation in ground beetle diversity across the stands in our sample (Appendix D).

4. Discussion

We found distinct differences in the ground beetle assemblages inhabiting early seral forest stands following stand-replacing wildfire versus intensively managed clearcut stands in the first 2–5 years after disturbance, including community composition, traits, and species richness. These results suggest that forest harvest does not completely emulate fire in terms of its effects on ground beetle community structure. Specifically, ground beetle communities in young (2–5 yr) fire-origin stands were distinguished primarily by smaller species with robust body shape and inferred flight capability, traits that are commonly associated with disturbance and open environments (Barton et al., 2011). The composition of post-fire ground beetle communities changed markedly with stand development, primarily through the loss of these disturbance-adapted species, and these losses drove declines in species richness. Community composition and species richness were more consistent across post-harvest stand ages, but some forest-dwelling species declined in abundance with time since harvest. Ground beetle communities inhabiting salvage-logged stands were distinct in composition from both intermediate-aged fire-origin and clearcut stands, and the importance of flight ability in these stands suggests that salvage

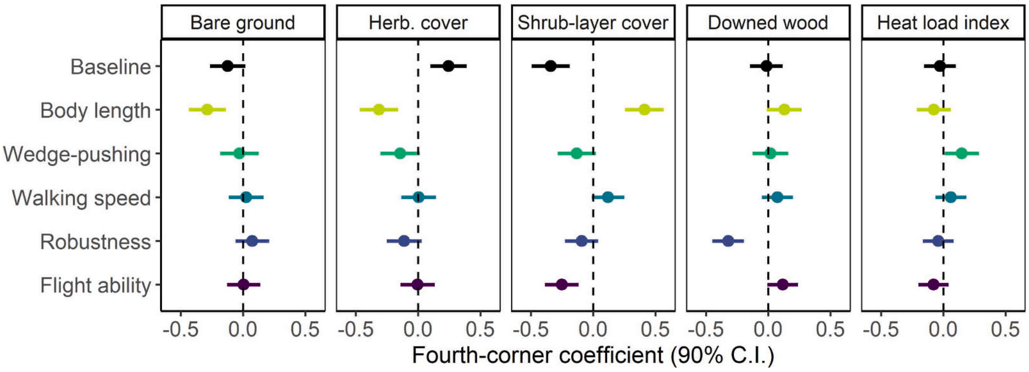

Fig. 5. Fourth-corner coefficient estimates (i.e., trait-environment interactions) from a negative binomial GLM of ground beetle species abundances in early seral forest stands. Fourth-corner coefficients reflect how the associations between multispecies abundance and environmental gradients vary with species traits, and can be interpreted as the difference in species responses for a one standard deviation increase in a given trait value, compared to the "baseline" coefficient estimate for average trait values.

logging functions to increase the severity of fire disturbance effects on ground beetles. Overall, our results suggest a distinctive role for fire as a disturbance agent in generating early seral forest habitat for some ground beetle species, especially in the short-term post-fire.

Our findings are consistent with experimental studies that have shown litter-dwelling arthropods to be highly susceptible to mortality during fires, and that these direct effects are much stronger than those of timber harvest (Paquin and Coderre, 1997; Verble-Pearson and Yanoviak, 2014). The traits and species that distinguished the youngest clearcut stands from fire-origin stands in our study are consistent with this difference in mortality response. For example, an experimental study in southwest Oregon showed *Pterostichus herculaneus* to be negatively affected by prescribed fire (Niwa and Peck, 2002), and this species was much less abundant in young fire-origin stands than young clearcut stands in our results (Figure B.1). Previous work comparing harvest and fire in boreal forests has indicated that old-forest ground beetle communities may recover more quickly after harvest, potentially due to differences in survivorship (Buddle et al., 2006). However, the similarities in ground beetle communities we observed between disturbance types by 16–20 yr after disturbance indicates that differences in recovery rates are unlikely in the geographic and management context of our study.

Legacy effects from higher ground beetle survivorship through harvest than fire may explain why small, robust, flight-capable species that characterized young fire-origin stands were less abundant in clearcut stands. These traits facilitate colonization, as flight ability contributes to dispersal (Venn, 2016) and smaller ground beetles have shorter life cycles (Ribera et al., 1999a). Under the competition-colonization hypothesis of community assembly, species dominating later in succession tend to be stronger competitors that colonize more slowly (Levins and Culver, 1971), which might suggest that populations of ground beetle species that persist through harvest limited the establishment of species adapted to colonizing disturbed sites in our study. However, evidence that competition has a strong influence on ground beetle populations is generally weak (Loreau, 1990; Niemelä, 1993), and niche overlap is probably limited between disturbance-adapted species and those adapted to closed-canopy conditions. Although competition may not be a compelling explanation in our system, intraguild predation can be important in ground beetle communities (Currie et al., 1996) and may be a more likely mechanism for the patterns we observed.

Habitat characteristics also likely influenced ground beetle community composition, but they do not fully explain contrasts between disturbance types in the youngest stands. Herbaceous cover can provide foraging resources that support ground beetle biodiversity (Kašák et al., 2015) and may be related to higher post-fire colonization rates (Holliday, 1992), aligning with our finding that herbaceous cover was positively associated with ground beetle abundance overall and especially smaller species. Higher herbaceous cover in young fire-origin stands might explain contrasts in ground beetle composition with young clearcut stands. However, we found limited evidence for differences in ground beetle composition or traits between young and intermediate age classes of clearcut stands despite herbaceous cover nearly doubling, so the herbaceous cover gradient is an insufficient explanation for the differences between disturbance types we observed. Additional possible explanations for the ground beetle response in young fire-origin stands include the abundant nitrogen-fixing species often observed in post-fire plant communities, which could contribute to a bottom-up trophic stimulus (He et al., 2019). Elevated soil pH in post-fire stands (McRae et al., 2001; Smith et al., 2008), which we did not measure, can also contributed to higher species richness and abundances of disturbance-adapted ground beetle species (Magura et al., 2003; Skłodowski, 2017).

Large, flightless species in the tiger beetle genus *Omus* Eschscholtz (Pearson et al., 2015) were captured frequently in young fire-origin stands, seemingly at odds with overall patterns in species traits. The robust body shapes of these species may confer resistance to higher risks of predation (Fountain-Jones et al., 2015) or desiccation (Le Lagadec et al., 1998) encountered in open environments. *Omus* may also be habitat generalists uniquely capable of surviving fires, as deep burrows (>25–30 cm; Knisley and Haines, 2010) may insulate larvae from even intense surface heating (Smith et al., 2016). Studies on prescribed fire effects in southwest Oregon and the Sierra Nevada of California indicate that *Omus* populations are more resilient to fire than other large, abundant ground beetle taxa (Apigian et al., 2006; Niwa and Peck, 2002).

Species responses 6–9 years after fire with post-fire salvage logging reinforced evidence that salvage logging can have compound effects on ground beetle assemblages and result in distinct assemblages compared to stand-replacing fire (Cobb et al., 2007; Koivula and Spence, 2006; Phillips et al., 2006). Compound disturbances are those in which one disturbance affects the biological legacies of the other in a way that affects subsequent successional trajectories (Paine et al., 1998). All previous work on ground beetle responses to post-fire salvage logging has occurred within one or two years of the initial disturbances and within boreal forests of Canada. In our results, contrasts in fourth-corner coefficients for flight ability indicate that salvage logging favors species with strong dispersal abilities to a greater degree than unlogged fire-origin stands, showing show that the compounding effects of salvage logging extend to the Klamath Mountains and through years 6–9 of stand growth. This pattern may be related to direct mortality effects of post-fire logging operations on ground beetle populations and/or to lower shrub-layer cover in salvage-logged stands. Woody vegetation developed rapidly in fire-origin stands, reflecting a propagule bank of fire-adapted shrubs and broadleaf tree species in the Klamath Mountains (Donato et al., 2009), but may be damaged during post-fire logging operations (Knapp and Ritchie, 2016). Salvage logging may therefore contribute to prolonging habitat for disturbance-adapted species in post-fire landscapes but could also have implications for recovery of mature forest ground beetle communities after disturbance.

The greater species richness we observed in young fire-origin stands relative to young clearcut stands is consistent with previous comparative studies and may be partially explained by compositional differences. Studies in northern Europe (Martikainen et al., 2006) and in the Sierra Nevada of California (Apigian et al., 2006) have found higher ground beetle species richness in the short-term after fire than forest harvest, and these patterns were driven by rarely captured species in both studies. Similarly, we observed stronger contrasts for species richness than for diversity metrics that place greater weight on species abundances. While the small and/or flight-capable species that distinguished young fire-origin stands may be captured less often in pitfall traps (Engel et al., 2017; Lövei and Sunderland, 1996), we accounted for this potential sampling bias in fourth-corner analyses by including main effects for each trait, but interspecific variability in activity may have masked contrasts in higher-order diversity metrics. High colonization rates during early phases of community assembly (Holliday, 1992) can also contribute to high species richness in samples (Merritt et al., 2010). Our ability to infer process from pattern is limited in a chronosequence study and disentangling how processes of ground beetle community assembly differ between fire-origin and post-harvest early seral forest stands will require investments in long-term repeat sampling across disturbance types (Holliday, 1992) and multiple trapping methods (Butterfield, 1997).

We found little evidence for relationships between ground beetle diversity metrics and elements of structural complexity, including dead wood, heterogeneity in shrub-layer cover, and ground-layer plant diversity. This was especially surprising in light of a recent experimental study of forest structural retention during clearcut harvest in Douglas-fir forests in the Pacific Northwest (Sultaire et al., 2021) which found that retaining patches of trees in larger aggregations, especially near riparian zones, are more effective at supporting a functionally and taxonomically diverse beetle community. Nonetheless, we found positive relationships with dead wood volume for two notable species, *Scaphinotus rugiceps* and

Clinidium calcaratum. Relationships of non-saproxylic beetles with dead wood are often context-dependent and species specific, such that consistent community-level patterns may be rare (Basile et al., 2023; Pearce et al., 2003; Seibold et al., 2016). *Clinidium* live between cell layers in dead wood and are adapted to feeding on slime molds (Bell, 1994). *Scaphinotus* Dejean (tribe Cychrini) have specialized adaptations for foraging on land snails (Thiele, 1977) and large dead wood has been correlated with activity abundance of *S. angusticollis* Mannerheim and abundance of their snail prey in forest harvests of British Columbia (Lavallee, 2006). Abundant dead wood may be necessary to support a full suite of early seral ground beetle species, a hypothesis further supported by findings that experimental dead wood removal in jack-pine (*Pinus banksiana*) forests of western Quebec negatively affected some species that otherwise responded positively to timber harvest (Work et al., 2014).

A potential limitation of our quantitative, morphological approach to functional traits is that body size—the most important ground beetle trait in our analyses—may have also encompassed additional aspects of ground beetle morphology. Although we accounted for allometric scaling effects, larger species in our sample tended to have disproportionately long appendages and long narrow mandibles (Appendix C). Long legs facilitate fast walking speeds for actively searching predators and are often accompanied by longer and narrower mandibles (Forsythe, 1991; Ribera et al., 1999a; Sultaire et al., 2021). Larger species also had disproportionately short metasterna, consistent with the known flightlessness of most of these species (Larochelle and Larivière, 2003). The multiple functional traits reflected by body size likely explain its importance in our results and the poor interpretability of mandible shape after allometric scaling.

Our results highlight an ephemeral phase of early post-fire succession for ground beetle communities that is not apparent following short-rotation clearcuts characteristic of intensive forest management in the Pacific Northwest. A prolonged early seral period after fire promotes biodiversity for some taxa (e.g., bees; Frank et al., 2025a) but the small differences we observed between disturbance types by 16–20 yr suggests that management that shortens the early seral period, such as post-fire tree planting, may have relatively limited effects on ground beetle biodiversity. In production landscapes, a shifting mosaic of young stand ages may support early seral species diversity at broad scales for some taxa. For ground beetles, however, we observed little variability across post-harvest stand ages and none supported the same ground beetle abundance, species richness, or composition of recently burned stands, suggesting limits to the degree to which logging can emulate natural disturbance in the absence of fire's effects on the forest floor. Nonetheless, a complete accounting of the early seral forest biodiversity supported by clearcut stands will require a landscape-scale perspective to complement the stand-scale approach we have taken here. The importance of fire as a disturbance agent is to be expected in fire-adapted landscapes, such as the one studied here (Agee, 1993; Reilly et al., 2021), but the short-term nature of the response we observed may specifically reflect the role of fire frequency for maintaining biodiversity in a system historically shaped by frequent fire (Taylor and Skinner, 1998). Managers attempting to support early seral forest biodiversity on public lands or small private forests should consider how fire, as a potentially irreplaceable component of the natural disturbance regime, might be intentionally incorporated into these efforts.

CRediT authorship contribution statement

Graham S. Frank: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **James R. LaBonte:** Writing – review & editing, Methodology, Investigation. **Matthew G. Betts:** Writing – review & editing, Methodology, Funding acquisition. **Andrew J. Kroll:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **James W. Rivers:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Jake Verschuyl:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Mark E. Swanson:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Meg A. Krawchuk:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

Author AJK was employed by Weyerhaeuser Company, one of the landowners in this study, at the time the research was conducted. Neither the landowners nor the companies that supported this work influenced the study design, data analysis, interpretation, or decision to publish.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123395.

Data availability

Data and code necessary to reproduce results, tables, and figures are available in the Open Science Framework at: https://doi.org/10.17605/OSF.IO/PYWD5.

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