Environmental Entomology, 54(2), 2025, 274–286
https://doi.org/10.1093/ee/nvaf014
Advance Access Publication Date: 27 February 2025
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Ecosystem Ecology

Woodborers and wood-decay related beetle responses to a major forest disturbance event in the central and southern Sierra Nevada, California

Jackson P. Audley[1,*], Christopher J. Fettig[1], Leif A. Mortenson[2], and Shakeeb M. Hamud[1]

[1]Pacific Southwest Research Station, USDA Forest Service, Vallejo, CA, USA
[2]Pacific Southwest Research Station, USDA Forest Service, Placerville, CA, USA

[*]Corresponding author. Pacific Southwest Research Station, USDA Forest Service, 1323 Club Drive, Vallejo, CA 94592, USA (Email: jackson.audley@usda.gov).

Subject Editor: Matthew Ginzel

Received on 4 October 2024; revised on 11 December 2024; accepted on 22 January 2025

Disturbance plays a critical role in the ecology of forests including influencing the abundance and diversity of fauna. Although numerous studies have focused on forest responses to various disturbance events, less attention has been given to arthropod community responses. California experienced an extreme, multi-year drought from 2012 to 2015 which severely stressed trees and incited epidemics of several bark beetle species (Coleoptera: Curculionidae: Scolytinae). Water stress and bark beetles contributed to a significant mortality event of hundreds of millions of trees in the central and southern Sierra Nevada, causing significant structural and compositional changes in forests. Our study sought to characterize woodborer and wood-decay-related beetle responses to various levels of tree mortality and snag (dead standing tree) retention resulting from this tree mortality event. Of particular interest were responses to differences in the orientation of dead wood, standing snags versus fallen snags. Ethanol-baited panel flight intercept traps were deployed for multiple weeks in 2022 and 2023 on plots representative of 3 disturbance classes: (i) low tree mortality (<30%), (ii) high tree mortality (>50%) with low snag fall (≤50%), and (iii) high tree mortality (>50%) with high snag fall (>60%). Woodborers and wood-decay-related beetle assemblages were compared at the family and species level. Our analyses revealed several significant differences in community assemblages among disturbance classes. Despite these differences, our results failed to reveal clear, qualitatively distinctive assemblages among disturbance classes. Rather, we could only conclude general patterns from the observed dissimilarities in richness and abundance. In general, we observed a greater diversity of woodborers on high-mortality plots than on low-mortality plots. Similarly, the diversity of wood-decay-related beetles generally increased with greater amounts (basal area) of snag fall. The amount of tree mortality and snag fall were positively related to several woodborer and wood-decay-related beetles. Observed beetle assemblages, their corresponding life histories, and the influences of altered habitat availability are discussed.

Keywords: Buprestidae, Cerambycidae, Curculionidae, disturbance ecology, Elateridae

Introduction

Forests experience numerous abiotic and biotic disturbances, including wildfire, wind, drought, and insect and disease outbreaks. Numerous studies have characterized responses of forest vegetation to disturbance; however, fewer studies have focused on insect community responses, particularly in North America (Supp and Ernest 2014). Woodborers and wood-decay-related beetles inhabit dead woody materials (Dodds et al. 2023) and are significant contributors to decay processes and nutrient cycling in forests (Ulyshen 2016). We define "wood-decay related beetles" as those forest-dwelling beetles that are associated with decaying (typically by fungi) wood and forest detritus (eg Cyptophagidae, Dermestidae, Elateridae, etc.) as opposed to "woodborers" (eg Buprestidae, Cerambycidae, etc.) that consume xylem tissues more directly (Evans 2021). Woodborers and wood-decay-related beetles are important components of forest food webs. Some woodborers are capable of colonizing and killing

relatively healthy trees while others transmit fungi and nematodes that are deleterious to tree health. Lumber recovery values from trees salvaged after disturbance can be adversely affected by the colonization of woodborers and wood-decay-related beetles (Dodds et al. 2023). Populations are affected by abiotic and biotic factors and their interactions that influence host availability at various spatial and temporal scales (Gandhi et al. 2007). The relative effects of these factors vary among woodborer and wood-decay-related beetle species according to their life histories, which in some cases are not well known (Evans 2021, Hébert 2023).

California experienced an extreme, multi-year drought from 2012 to 2015 that was characterized by significant precipitation deficits and abnormally high temperatures (Williams et al. 2015). Drought conditions in some areas were reported to be the most severe in 1,200 years (Griffin and Anchukaits 2014). Drought can have significant effects on ecosystem structure, function, and composition. In forests, droughts result in reductions in tree growth, tree vigor, tree defensive capabilities, and often incite bark beetle (Coleoptera: Curculionidae: Scolytinae) epidemics (Hart et al. 2017, Fettig et al. 2019a, Reed and Hood 2021, Robbins et al. 2022). In the Sierra Nevada, drought may incite epidemics of several endemic, irruptive species including engraver beetles, *Ips* spp., fir engraver, *Scolytus ventralis* LeConte, Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopkins, mountain pine beetle, *D. ponderosae* Hopkins, and western pine beetle, *D. brevicomis* LeConte (Fettig 2016).

The 2012–2015 drought resulted in tens of millions of dead trees in California forests, contributing significantly to a reported 237 million dead trees since 2010. In response to this unprecedented level of tree mortality (Stephens et al. 2018), the California Tree Mortality Network (CTMN) was established by the USDA Forest Service to determine and better understand the biophysical drivers, effects, and long-term consequences of tree mortality (Fettig et al. 2019b). Initial assessments of the CTMN showed that from 2014 to 2017 ~49% of trees, including almost 90% of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. died. Mortality of *P. ponderosa* was highest at the lowest elevations, concentrated in larger-diameter trees, and attributed primarily to *D. brevicomis*. Sugar pine, *P. lambertiana* Dougl., exhibited the second highest levels of tree mortality (48.1%). Mortality of *P. lambertiana* was concentrated in the mid-diameter classes and attributed primarily to *D. ponderosae*. White fir, *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebrand, and incense cedar, *Calocedrus decurrens* (Torr.) Florin, exhibited 26.3% and 23.2% mortality, respectively. This tree mortality event significantly altered forest structure and composition (Fettig et al. 2019b). The number of snags (standing dead trees) and amount of downed wood significantly increased (Fettig et al. 2019b, Villanova et al. 2023).

Our objective was to characterize woodborer and wood-decay-related beetle responses to various levels of tree mortality and snag retention based on captures in ethanol-baited, panel flight intercept traps on CTMN plots. Of particular interest were responses to differences in the orientation of dead wood, standing snags versus fallen snags. We hypothesized there would be (i) distinct beetle communities associated with low levels versus high levels of tree mortality (snags) and (ii) distinct beetle communities associated with low versus high levels of snag retention (snags, fallen snags).

Materials and Methods

Our study was conducted on the CTMN. In brief, the CTMN is a network of 180 11.3-m fixed-radius plots (0.041-ha) established on the Eldorado, Stanislaus, Sierra, and Sequoia National Forests, California in 2016 to 2017 (Fettig et al. 2019b). Fifteen plots (3 groups of 5 plots) are distributed in each of 3 elevation bands on each national forest: 914 to 1,219 m, 1,219 to 1,524 m, and 1,524 to 1,829 m on the Eldorado, Stanislaus, and Sierra, and 1,219 to 1,524 m, 1,524 to 1,829 m, and 1,829 to 2,134 m on the Sequoia. At establishment, plots were required to be ≥35% *P. ponderosa* by basal area (a measure of density based on the cross-sectional area of trees at 1.37 m in height), to contain ≥10% *P. ponderosa* mortality in the last 2 yr, and unburned in the last decade. These criteria were selected as the primary objective of the CTMN was to monitor changes in forest conditions resulting from tree mortality attributed to drought and bark beetle epidemics, which were most severe in *P. ponderosa*. Plots meeting these criteria were randomly selected within groups but separated by ≥100 m. Groups within elevation bands were separated by >1.6 km. Tree mortality and snag fall occurrences have been recorded each year on CTMN plots since establishment.

We sampled woodborer and wood-decay-related beetle communities on a subsample of CTMN plots on the Eldorado, Stanislaus, and Sierra National Forests in 2022 and on the Eldorado and Stanislaus National Forests in 2023. Plot selection was based on assessments of tree mortality and snag fall in the spring and summer of the prior year (eg in 2022 plot selections were based on stand data collected in 2021). As such, there may have been instances where additional trees died and/or snags fell prior to the deployment of traps. However, annual rates of tree mortality and snag fall were low (<5%) during this period (C.J.F. et al., unpublished data). Initial plot selections were based on percent tree mortality and percent snag fall while optimizing for the greatest numbers of trees, snags, and fallen snags possible based on 3 disturbance classes. In 2022, disturbance classes were (i) low mortality (<30% tree mortality with no restrictions on snag fall; Low); (ii) high mortality, low snag fall (>50% tree mortality with ≤50% snag fall; High/Low); and (iii) high mortality, high snag fall (>50% tree mortality with >60% snag fall; High/High). In 2023, to better represent less-disturbed forest conditions, we established additional 11.3-m fixed-radius plots ≥100 m from CTMN plots in adjacent stands. Similar selection protocols and measurements were used as described by Fettig et al. (2019b) for the CTMN but excluded the ≥10% *P. ponderosa* mortality selection criterion. In 2023, disturbance classes were (i) Low (<20% tree mortality with no restrictions on snag fall); (ii) High/Low (>50% tree mortality with ≤50% snag fall); and (iii) High/High (>60% tree mortality with ≥70% snag fall). Examples of the 4 disturbance classes are depicted in Fig. 1.

Sampling of woodborer and wood-decay-related beetles were conducted using panel flight intercept traps (Product #4019, Synergy Semiochemical Corp., Delta, BC, Canada) baited with high-release ethanol lures (Product #3366, Synergy Semiochemical Corp.; release rate of 0.7 g/d at 25 to 28 °C). Beetle responses were evaluated to a single generic attractant (ethanol, Klimetzek et al. 1986), instead of multiple attractants, to avoid potential biases among families or species. Traps were hung from metal conduit poles placed over rebar inserted in the ground. Each panel trap was placed in each plot 1 m north of the plot center. In 2022, traps were hung from 1.5-m tall, curved conduit poles. In 2023, we used 2.4-m tall, straight conduit poles in an attempt to reduce disturbances by wildlife (*see* below). In 2022, 40 traps (13 Low, 14 High/Low, and 13 High/High) were deployed 14 June to 6 July. In 2023, 30 panel traps (10 Low, 10 High/Low, and 10 High/High) were deployed 23 May to 30 August of which 9 traps (3 per disturbance class) were not deployed until 21 June 2023 on the Eldorado National Forest due to snowpack levels restricting plot access. Lures were only replaced following wildlife disturbances that resulted in punctures to the lure, otherwise, the

Fig. 1. Plots representative of each of the 4 disturbance classes in which woodborer and wood-decay related beetles were sampled on the California Tree Mortality Network: (A) high mortality, high snag fall (>50% tree mortality, >60% snag fall); (B) high mortality, low snag fall (>50% tree mortality, ≤50% snag fall); (C) low mortality (2022; <30% tree mortality, no snag fall restriction); and (D) low mortality (2023; <20% tree mortality, no snag fall restrictions).

amount of ethanol contained in lures was sufficient to last the entire trapping interval. A 6.5 cm^2 Hot Shot No-Pest strip (18.6% 2,2 dichlorovinyl dimethyl phosphate, Spectrum Brands Inc., Middelton, Wisconsin, USA) was placed in the bottom of each collection cup. Traps were checked and samples were collected every 2 wk. All beetles were identified as family and specimens from 4 key families, Buprestidae, Cerambycidae, Curculionidae, and Elateridae, were identified to species (based on Triplehorn and Johnson 2005, Evans 2021).

Statistical Analyses

We compared woodborer and wood-decay-related beetle assemblages among 3 disturbance classes at multiple taxonomic levels in each of 2 yr using multiple approaches. First, we calculated Shannon-Wiener indexes (H') to compare beetle family-level richness (alpha diversity) and Sorenson's Similarity indexes (SSI) to compare changes in family-level diversity (beta diversity) among disturbance classes (Li et al. 2007, Chima et al. 2013, Kapinska et al. 2024). Alpha and beta diversities were compared among all beetle families and then for 2 subsets of beetle families based on broadly defined niches—woodborers (Bostrichidae, Buprestidae, Cerambycidae, Curculionidae, and Ptinidae) and wood-decay-related beetles (eg Cryptophagidae, Dermestidae, Elateridae, etc.) based on family-level descriptions (Evans 2021).

To elucidate influential families and species (from select families) that drove observed differences in beetle assemblages we used non-metric multidimensional scaling (NMDS) ordination with pairwise Bray-Curtis dissimilarity distance matrices (*metaMDS()* function; Rubia 2022, Kaprinska et al. 2024). A dissimilarity matrix was fit for each comparison run and fit was assessed by NMDS stress value and non-metric R^2 value from stress plots (Rubia 2022). Next, ordination plots with disturbance class ellipses (*ordiellipse()* function)

Table 1. Conditions on California Tree Mortality Network plots in which woodborer and wood-decay-related beetles were sampled, 2022 and 2023.

	Low	High/Low	High/High
2022			
% Tree mortality	23.5 ± 1.8 B	65.4 ± 3.7 A	71.1 ± 4.1 A
% Snag fall	57.6 ± 6.4 B	28.6 ± 4.2 C	87.3 ± 2.7 A
Number of live trees	11.1 ± 2.5 A	7.4 ± 1.7 AB	4.2 ± 1.0 B
Live tree basal area (m^2/ha)	36.4 ± 5.9 A	15.4 ± 3.9 B	5.7 ± 1.4 C
Number of snags	2.7 ± 0.5 B	8.9 ± 1.6 A	1.2 ± 0.3 B
Snag basal area (m^2/ha)	19.7 ± 3.9 A	27.8 ± 4.4 A	5.6 ± 2.2 B
Number of years since tree death	5.6 ± 0.4 B	6.5 ± 0.1 A	5.8 ± 0.5 AB
Number of fallen snags	5.2 ± 0.7 B	5.9 ± 1.5 B	10.6 ± 1.0 A
Fallen snag basal area (m^2/ha)	19.7 ± 3.2 B	25.5 ± 5.7 AB	36.9 ± 4.8 A
Number of years since snag fall	2.0 ± 0.2 B	1.9 ± 0.2 B	2.7 ± 0.2 A
2023			
% Tree mortality	5.2 ± 2.0 B	63.3 ± 3.8 A	78.5 ± 4.0 A
% Snag fall	0.0 ± 0.0 C	38.6 ± 4.4 B	84.1 ± 3.8 A
Number of live trees	13.9 ± 1.6 A	10.2 ± 2.8 AB	5.6 ± 1.8 B
Live tree basal area (m^2/ha)	79.2 ± 12.5 A	21.7 ± 5.0 B	8.3 ± 2.3 C
Number of snags	1.0 ± 0.5 B	7.4 ± 1.8 A	1.5 ± 0.6 B
Snag basal area (m^2/ha)	3.4 ± 2.2 B	22.4 ± 5.3 A	9.2 ± 3.8 B
Number of years since tree death	NA	7.2 ± 0.1 A	7.6 ± 0.1 A
Number of fallen snags	0.0 ± 0.0 B	8.3 ± 2.1 A	10.2 ± 1.6 A
Fallen snag basal area (m^2/ha)	0.0 ± 0.0 B	32.5 ± 9.0 A	42.9 ± 6.3 A
Number of years since snag fall	NA	2.2 ± 0.4 A	3.0 ± 0.2 A

Values are mean ± SEM. Means ± SEM followed by the same letter within rows are not significantly different ($P > 0.05$) based on Kruskal–Wallis test followed by post hoc Dunn's test.

NA = data not available.

Low = <30% tree mortality (2022) and <20% tree mortality (2023), no snag fall restrictions; High/Low = >50% tree mortality, ≤50% snag fall; High/High = >50% tree mortality, >60% snag fall.

were visually inspected for overlap (more overlap equates to more similarity among groups).

Following matrix ordination, a permutation test for homogeneity of multivariate dispersions (PERMANOVA) was run using the *adonis2()* function with method = "bray" and 999 permutations. Next, we conducted a test for homogeneity of dispersion among the disturbance classes (*betadisper()* function). Post hoc Tukey's HSD was used to discern what pair(s) had differences in dispersions. When PERMANOVA tests revealed significant results, a similarity percentage (SIMPER) test (*simper()* function) was conducted to reveal the most influential families or species that explain observed dissimilarity between disturbance classes in pairwise comparisons. Results of SIMPER tests provide an ordered list of influential families or species and the cumulative percentage of the dissimilarity each species contributes for 70% of the observed dissimilarity between groups. We presented these results using figures of mean trap captures with total numbers caught per family/genus by disturbance class to assist with interpretation. Finally, we investigated the relationship of live tree, snag, and fallen snag basal area (m^2/ha) on the observed count data for response variables highlighted by the previous analyses utilizing generalized linear modeling (GLM). Given the strong positive relationship between basal area and volume of aboveground biomass (Chiba 1998) we chose to use basal area instead of measuring volume given the number of snags and logs in the study. Based on the overdispersed nature of these data (*DHARMa:dispersionTest()* function) we fitted GLMs with a negative binomial (*glm.nb()* function) distribution. The model selection followed a backward stepwise approach where each initial model included live tree basal area, snag basal area, and fallen snag basal area, and the variable with the greatest *P*-value was removed at each step. Final model selections were made based on Akaike information criterion (AIC) values and likelihood ratio tests (Zuur et al. 2009).

Comparisons of disturbance class stand characteristics were made using Kruskal–Wallis non-parametric tests with post hoc Dunn's tests. Shannon–Weiner and Sorenson's Similarity analyses were conducted using Microsoft Excel. All other analyses were conducted using R Statistical Software (version 3.6.3) via RStudio (version 1.2.5033) with vegan, FSA, DHARMa, and base packages (R Core Team 2020).

Results

Table 1 provides a comprehensive description of stand characteristics among disturbance classes. Overall, our use of percent tree mortality and percent snag fall to distinguish among disturbance classes translated well with absolute measures with a few notable exceptions. For example, the basal area of fallen snags did not differ between High/Low and High/High in 2022 and 2023 (Table 1). Another significant component of habitat availability in dead wood is decay. While we did not measure decay directly, we compared snag ages (ie years since mortality) and the length of time that fallen snags were on the forest floor. These variables were similar among

disturbance classes with the exception of snags being ~1 yr younger on Low than High/Low and fallen snags being ~1 yr older on High/High than Low and High/Low in 2022 (Table 1).

A total of 4,077 beetles were captured, 1,881 in 2022 and 2,196 in 2023. All but 175 (95 in 2022, 60 in 2023) were identified to family. The 175 were primarily unidentifiable due to damage. Individuals spanned 29 families in 2022 with Latridiidae (506), Curculionidae (284), and Cryptophagidae (223) most common, and 34 families in 2023 with Elateridae (534), Dermestidae (410), and Curculionidae (308) most common. Individuals spanned 36 woodboring and wood-decay-related species in 2022 with *Xyleborinus saxesenii* (Ratzeburg) (Curculionidae; 216), *Athous* spp. (Elateridae; 48), and *Hemicrepidius obscurus* (LeConte) (Elateridae; 37) most common, and 44 woodboring and wood-decay related species in 2023 with *X. saxesenii* (Curculionidae; 222), *Athous* spp. (Elateridae; 146), and *Cardiophorus edwardsi* Horn (Elateridae; 95) most common. Trap disturbance from wildlife, primarily black bears, *Ursus americanus* Pallas, was problematic. In 2022, 10 traps (25%) were disturbed during the first collection date and 9 traps (22%) were disturbed during the second collection date. Despite using taller conduit in 2023, trap disturbance remained an issue with 4–10 traps disturbed per collection date in 2023. Efforts were made to collect beetles from disturbed traps. One trap (High/Low, 2023) was repeatedly disturbed and the corresponding data were omitted from analyses.

Shannon–Weiner and Sorenson's Similarity

In 2022, family-level alpha diversity for all beetle families and for woodborers was highest on High/High (Table 2). Interestingly, diversity among wood-decay-related beetle families was highest on Low (Table 2). Pairwise beta diversity comparisons indicated that beetle assemblages on Low and High/Low were least similar (66.7% similarity; Table 2). Among woodborers, Low was less diverse than High/Low and High/High. This difference was driven by a lack of cerambycid captures on Low. Wood-decay-related beetle family-level diversity was least similar between Low and High/Low (64%; Table 2). In 2023, alpha diversity was highest on High/Low for all families, woodborers, and wood-decay-related beetle families (Table 2). Beta diversity was least similar between Low and High/High for all families (63%) and wood-decay-related beetle families (50%). Woodborer beta diversity was similar among disturbance classes (Table 2).

NMDS Ordinations 2022

To better understand the families and species (of the 4 key families: Buprestidae, Cerambycidae, Curculionidae, and Elateridae) that drove differences in assemblages among disturbance classes we used NMDS ordination combined with PERMANOVA tests. Ordination of all beetle families captured in 2022 fit well (NMDS stress = 0.16, non-metric R^2 = 0.97), and the PERMANOVA test revealed family assemblages were similar among disturbance classes (pseudo-F = 0.952, df = 37, P = 0.518). Ellipses from the ordination plot (Fig. 2) showed significant overlap. More overlap represents less dissimilarity among disturbance classes. Because the PERMANOVA was not significant, a SIMPER test was not run.

NMDS ordination fit well for the species data from 2022 (NMDS stress = 0.16, non-metric R^2 = 0.98) and the PERMANOVA test revealed there were differences among beetle assemblages among disturbance classes (pseudo-F = 1.627, df = 36, P = 0.044). The ordination plot showed divergence between Low and High/High while High/Low intersected both similarly (Fig. 3). Permutation test of homogeneity of dispersion was not significant (pseudo-F = 0.284, df = 36, Permutations = 999, P = 0.756) indicating detected differences among disturbance classes were based on generic assemblage and not from variance within disturbance classes. Pairwise, SIMPER

Table 2. Assessment of alpha (within disturbance class), beta (between disturbance classes), and gamma (overall) diversity among 3 disturbance classes in which woodborer and wood-decay related beetles were sampled on the California Tree Mortality Network in 2022 and 2023.

			Alpha diversity	Beta diversity (SSI comparisons)			Gamma diversity
Year	Niche	Plot disturbance class	H'	High/Low	High/High	# Families	Total # Families
2022	All families	Low mortality	2.33	**66.7**	71.4	23	29
		High/Low	2.10	-	-	22	
		High/High	**2.50**	75	-	**26**	
	Woodborers	Low mortality	1.01	**80**	**80**	4	5
		High/Low	0.91	-	-	**5**	
		High/High	**1.13**	100	-	**5**	
	Wood-decay related	Low mortality	**1.77**	**63.6**	65.2	17	22
		High/Low	1.42	-	-	15	
		High/High	1.75	72.7	-	**19**	
2023	All families	Low mortality	2.32	66.7	**63.3**	**28**	34
		High/Low	**2.40**	-	-	27	
		High/High	2.26	79.3	-	24	
	Woodborers	Low mortality	1.37	100	100	5	5
		High/Low	**1.38**	-	-	5	
		High/High	1.33	100	-	5	
	Wood-decay related	Low mortality	1.71	57.7	**50**	**21**	27
		High/Low	**1.76**	-	-	20	
		High/High	1.65	72.7	-	17	

Alpha diversity (richness within a defined area) was assessed based on Shannon-Weiner indices (H'); bold values indicate the condition class with the greatest amount of diversity. Beta diversity (change in richness among defined areas) was assessed using Simpson's Similarity indices (SSI); bold values represent the pairwise comparison with the greatest amount of difference. Gamma diversity (geographic-level richness) was assessed as the total number of families. High/Low = high mortality, low snag fall and High/High = high mortality, high snag fall. "-" = already compared or self-comparison.

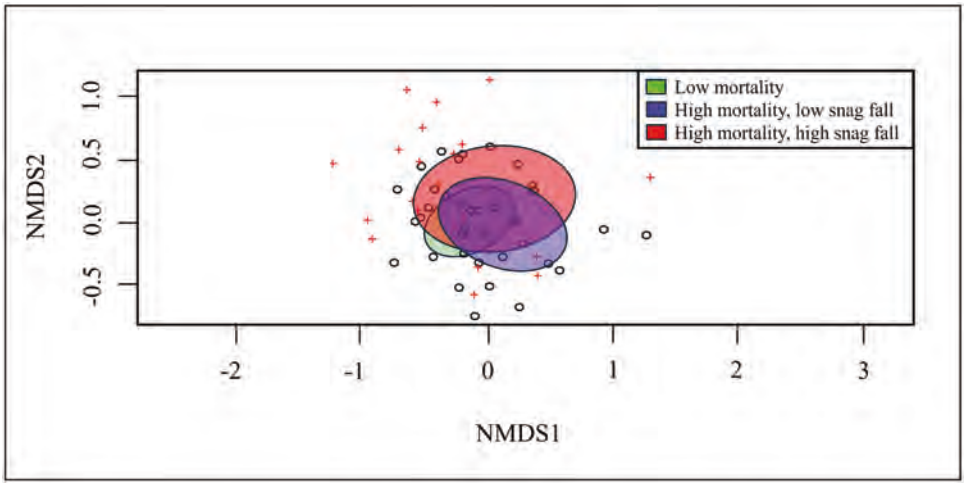

Fig. 2. Results of Non-Metric Multidimensional Scaling (NMDS) ordination (metaMDS() function in vegan package) of woodborer and wood-decay related beetle families captured in panel traps baited with high-release ethanol from plots representative of 3 disturbances classes: (1) low mortality (<30% tree mortality, no snag fall restrictions); (2) high mortality, low snag fall (>50% tree mortality, ≤50% snag fall); and (3) high mortality, high snag fall (>50% tree mortality, >60% snag fall). NMDS stress = 0.16 non-metric fit R^2 = 0.97; permutation test for homogeneity of multivariate dispersions test (PERMANOVA) was not significant (F = 0.952, df = 37, P = 0.518). Traps were deployed 14 June–6 July 2022.

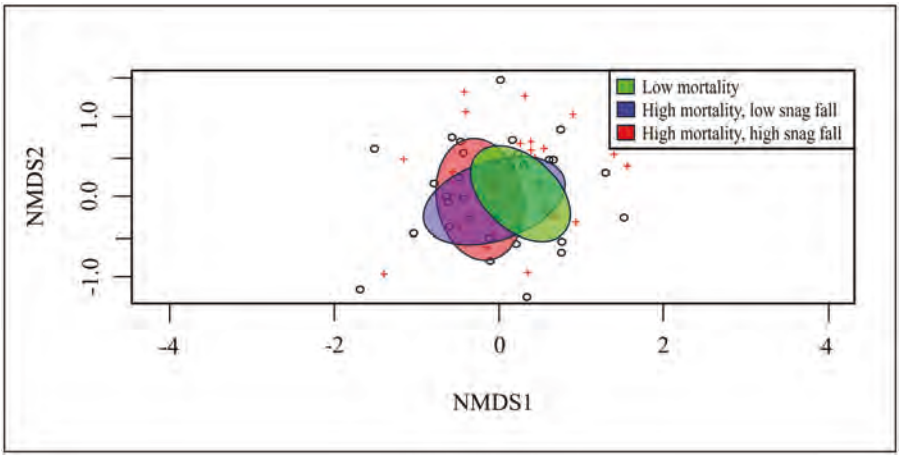

Fig. 3. Results of Non-Metric Multidimensional Scaling (NMDS) ordination (metaMDS() function in vegan package) of woodborer and wood-decay related beetle species from 4 families (Buprestidae, Cerambycidae, Curculionidae, and Elateridae) captured in panel traps baited with high-release ethanol from plots representative of 3 disturbances classes: (1) low mortality (<30% tree mortality, no snag fall restrictions); (2) high mortality, low snag fall (>50% tree mortality, ≤50% snag fall); and (3) high mortality, high snag fall (>50% tree mortality, >60% snag fall). NMDS stress = 0.16 non-metric fit R^2 = 0.98; permutation test for homogeneity of multivariate dispersions test (PERMANOVA) was significant (F = 1.627, df = 36, P = 0.044. Traps were deployed 14 June to 6 July 2022.

tests indicated *X. saxesenii* (Curculionidae) explained the greatest percentage of differences (34% between Low and High/Low; 31% between Low and High/High; 34% between High/Low and High/High). The most influential (those that explain ~70% to 75% of the permutated dissimilarity) were:

(1) Low versus High/Low—*X. saxesenii* (34%), *Athous* spp. (Elateridae, 48%), *Hylastes macer* LeConte (Curculionidae, 56%), *C. edwardsi* (Elateridae, 63%), *Anthaxia* spp. (Buprestidae, 68%), *Melanotus similis* (Kirby) (Elateridae, 72%)
(2) Low versus High/High—*X. saxesenii* (31%), *Athous* spp. (Elateridae, 50%), *Anthaxia* spp. (Buprestidae, 51%), *Hy. macer* (Curculionidae, 59%), *He. obscurus* (Elateridae, 64%), *Alaus melanops* LeConte (Elateridae, 70%), *Me. similis* (Elateridae, 74%)
(3) High/Low versus High/High—*X. saxesenii* (34%), *Hy. macer.* (Curculionidae, 42%), *Athous* spp. (Elateridae, 50%), *He. obscurus* (Elateridae, 55%), *C. edwardsi* (Elateridae, 61%), *Me. similis* (Elateridae, 67%), *Anthaxia* spp. (Buprestidae, 73%)

Mean and total captures highlighted from the SIMPER tests are displayed in Fig. 4 to visually represent the generic assemblages that best define the dissimilarities revealed from these permutations.

The basal area of live trees and basal area of fallen snags were inversely related to captures of woodborers and wood-decay-related beetle families in 2022 (Table 3). The basal area of snags was not retained in either model. The basal area of live trees had a negative relationship with captures of *Hy. macer* and *X. saxesenii*. Captures of *C. edwardsi* were negatively correlated with the basal area of live trees and positively correlated with the basal area of snags. The basal area of fallen snags was positively correlated with captures of *He. obscurus* while the basal area of live trees was negatively correlated with captures of *He. obscurus* (Table 3).

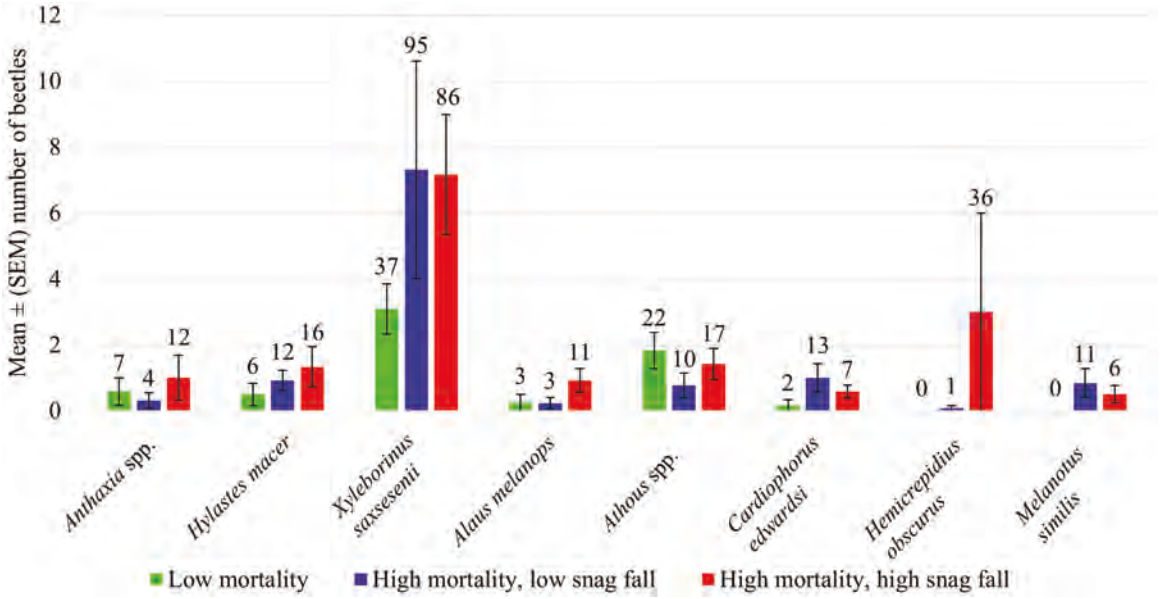

Fig. 4. Mean (± SEM) numbers of woodborer and wood-decay related beetles captured in panel traps baited with high-release ethanol (with total numbers above) from 8 species identified from pairwise similarity percentages (SIMPER) analyses. Species displayed represent the groups that most contributed to dissimilarities between beetle communities observed from the 3 disturbance classes in 2022. Shown are the genera that comprised 70% to 75% (cumulative) of the observed differences from the PERMANOVA permutations. Species analyzed were from 4 influential beetle families: Buprestidae; Cerambycidae; Curculionidae; and Elateridae.

NMDS Ordinations 2023

Ordination of beetle families captured in 2023 fit well (NMDS stress = 0.16, non-metric R^2 = 0.98) and the PERMANOVA test revealed family assemblages were different among disturbance classes (pseudo-F = 2.022, df = 28, P = 0.005). Ellipses from the ordination plot (Fig. 5) showed the high mortality classes (High/Low and High/High) overlapped extensively while the larger, Low ellipse overlapped the high mortality ellipses perpendicularly, covering about half of High/High and most of High/Low. The permutation test of homogeneity of dispersion was significant (pseudo-F = 4.730, df = 28, Permutations = 999, P = 0.023). Post hoc Tukey's HSD indicated dispersion differed between Low and High/Low (P = 0.032) and between High/Low and High/High (P = 0.032). Dispersion was greater in High/Low in both cases. Differences among disturbance classes were likely influenced by both family assemblage and dispersion differences (ie within class variation). Pairwise, SIMPER tests indicated most influential family composition lists with cumulative dissimilarity percentage were:

(1) Low versus High/Low—Elateridae (22%), Curculionidae (35%), Cryptophagidae (47%), Dermestidae (56%), Bostrichidae (62%), Buprestidae (66%), Cerambycidae (70%)
(2) Low versus High/High—Dermestidae (21%), Elateridae (38%), Curculionidae (49%), Cryptophagidae (55%), Bostrichidae (61%), Buprestidae (65%), Cerambycidae (69%), Trogossitidae (73%)
(3) High/Low versus High/High—Dermestidae (23%), Elateridae (37%), Curculionidae (51%), Cryptophagidae (61%), Bostrichidae (68%), Cerambycidae (73%)

Mean and total captures of the 8 families (Bostrichidae, Buprestidae, Cerambycidae, Cryptophagidae, Curculionidae, Dermestidae, Elateridae, and Trogossitidae) highlighted from the SIMPER tests are displayed in Fig. 6 to visually represent the families that best define the dissimilarities revealed from these permutations.

NMDS ordination fit well for the species data from 2023 (NMDS stress = 0.16, non-metric R^2 = 0.98) and the PERMANOVA test revealed there were differences among disturbance classes (pseudo-F = 1.732, df = 28, P = 0.008). The ordination plot showed almost complete divergence between Low and high mortality classes (High/Low and High/High), with High/Low (largest ellipse) overlapping more than half of High/High (Fig. 7). Permutation test of homogeneity of dispersion was not significant (pseudo-F = 2.442, df = 28, Permutations = 999, P = 0.105) indicating the detected differences among disturbance classes are based on generic assemblage and not from dispersion differences within disturbance classes. Pairwise, SIMPER tests indicated the most influential species lists with cumulative dissimilarity percentage were:

(1) Low versus High/Low—*X. saxesenii* (Curculionidae, 17%), *C. edwardsi* (Elateridae, 30%), *Athous* spp. (Elateridae, 42%), *Anthaxia* spp. (Buprestidae, 49%), *Anchastus bicolor* LeConte (Elateridae, 55%), *Dolerosomus silaceus* (Say) (Elateridae, 61%), *Lepturopsis dolorosa* (LeConte) (Cerambycidae, 66%), *Horistonotus simplex* LeConte (Elateridae, 70%), *Monarthrum mali* (Fitch) (Curculionidae, 73%)
(2) Low versus High/High—*X. saxesenii* (Curculionidae 16%), *Athous* spp. (Elateridae, 30%), *C. edwardsi* (Elateridae, 38%), *Anthaxia* spp. (Buprestidae, 45%), *Do. silaceus* (Elateridae, 51%), *Ho. simplex* (Elateridae, 57%), *An. bicolor* (Elateridae, 62%), *Le. dolorosa* (Cerambycidae, 67%), *Megapenthes aterrimus* (Motschulsky) (Elateridae, 70%)
(3) High/Low versus High/High—*X. saxesenii* (Curculionidae, 27%), *C. edwardsi* (Elateridae, 37%), *Le. dolorosa* (Cerambycidae, 45%), *Athous* spp. (Elateridae, 54%), *Ho. simplex* (Elateridae, 59%), *Meg. aterrimus* (Elateridae, 64%), *Anastrangalia laetifica* (LeConte) (Cerambycidae, 68%), *Lepturobosca chrysocoma* (Kirby) (Cerambycidae, 72%)

Mean and total captures highlighted from the SIMPER tests are displayed in Fig. 8.

Table 3. Results of generalized linear modeling of the basal area (BA) of live trees, snags, and fallen snags on response variables highlighted from NMDS and similarity analyses.

		Correlation with response variable			Coefficient estimate; *Z* value, *P* value		
Year	Response Variable	LiveBA	SnagBA	FallenBA	LiveBA	SnagBA	FallenBA
2022	Woodborers	**Neg**	na	**Neg**	−0.03; *Z* = −3.1, *P* = 0.002	na	−0.02; *Z* = −2.1, *P* = 0.034
	Wood-decay	**Neg**	na	**Neg**	−0.02; *Z* = −2.6, *P* = 0.008	na	−0.02; *Z* = −3.1, *P* = 0.002
	Anthaxia spp.	Neg	na	na	−0.03; *Z* = −1.3, *P* = 0.208	na	na
	Hylastes macer	**Neg**	na	na	−0.04; *Z* = −2.3, *P* = 0.019	na	na
	Xyleborinus saxesenii	**Neg**	na	na	−0.03; *Z* = −3.3, *P* = 0.001	na	na
	Alaus melanops	Neg	na	na	−0.06; *Z* = −1.9, *P* = 0.054	na	na
	Athous spp.	na	Neg	na	na	-0.004; *Z* = -0.3, *P* = 0.74	na
	Cardiophorus edwardsi	**Neg**	**Pos**	na	−0.05; *Z* = −2.3, *P* = 0.021	0.03; *Z* = 2.5, *P* = 0.012	na
	Hemicrepidius obscurus	**Neg**	**Neg**	**Pos**	−0.02; Z = -2.0, *P* = 0.043	-0.26; Z = -4.9, P < 0.001	0.04; Z = 2.7, P = 0.006
	Melanotus similis	na	Pos	na	na	0.04; *Z* = 1.8, *P* = 0.079	na
2023	Woodborers	na	na	**Pos**	na	na	0.02; *Z* = 3.3, *P* = 0.001
	Wood-decay	na	na	Pos	na	na	0.01; *Z* = 1.5, *P* = 0.133
	Curculionidae	Neg	**Neg**	na	−0.01; *Z* = −1.8, *P* = 0.078	−0.04; *Z* = −2.9, *P* = 0.003	na
	Cryptophagidae	na	Pos	na	na	0.02; *Z* = 1.4, *P* = 0.151	na
	Dermestidae	na	na	**Pos**	na	na	0.03; *Z* = 3.8, *P* < 0.001
	Bostrichidae	na	**Neg**	Pos	na	−0.05; *Z* = −2.4, *P* = 0.015	0.02; *Z* = 1.9, *P* = 0.054
	Buprestidae	**Pos**	na	na	0.01; *Z* = 2.1, *P* = 0.039	na	na
	Cerambycidae	na	na	**Pos**	na	na	0.02; *Z* = 4.0, *P* < 0.001
	Trogossitidae	**Neg**	na	na	−0.01; *Z* = −2.1, *P* = 0.036	na	na
	Elateridae	Pos	na	na	0.002; *Z* = 0.7, *P* = 0.496	na	na
	Anastrangalia laetifica	na	na	**Pos**	na	na	0.02; *Z* = 2.4, *P* = 0.017
	Anthaxia spp.	**Pos**	na	Pos	0.03; *Z* = 2.5, *P* = 0.014	na	0.02; *Z* = 1.3, *P* = 0.200
	Lepturobosca chrysocoma	na	Neg	Pos	na	−0.10; *Z* = −1.9, *P* = 0.062	0.03; *Z* = 1.8, *P* = 0.071
	Lepturopsis dolorosa	na	na	**Pos**	na	na	0.04; *Z* = 3.5, *P* < 0.001
	Dendroctonus spp.*	na	Neg	na	na	−0.04; *Z* = −1.2, *P* = 0.224	na
	Monarthrum mali	na	Neg	na	na	−0.06; *Z* = −1.4, *P* = 0.160	na
	Xyleborinus saxesenii	**Neg**	**Neg**	na	−0.01; *Z* = −2.2, *P* = 0.025	−0.05; *Z* = −3.5, *P* < 0.001	na
	Athous spp.	Pos	Pos	na	0.01; *Z* = 1.1, *P* = 0.268	0.04; *Z* = 1.7, *P* = 0.084	na
	Anchastus bicolor	na	na	Neg	na	na	−0.03; *Z* = −1.9, *P* = 0.056
	Cardiophorus edwardsi	na	Neg	na	na	−0.02; *Z* = −1.2, *P* = 0.227	na
	Dolerosomus silaceus	na	Neg	na	na	−0.04; *Z* = −1.1, *P* = 0.284	na
	Horistonotus simplex	na	**Pos**	Neg	na	0.09; *Z* = 2.7, *P* = 0.007	−0.02; *Z* = −0.8, *P* = 0.401
	Megapenthes aterrimus	na	na	Pos	na	Na	0.01; *Z* = 1.2, *P* = 0.247

Influence on response variables include Pos = positive relationship, Neg = negative relationship, and na = not included in final model. Bold influence categories indicate the influence was statistically significant (α = 0.05). Model selection was made by stepwise subtractions where the explanatory variable with the highest *P* value was removed and informed by AIC value comparisons.

**Dendroctonus brevicomis* and *D. valens* combined.

The basal area of fallen snags was positively correlated with captures of all woodborers and for Dermestidae, Cerambycidae, and *Le. dolorosa* (Cerambycidae) in 2023 (Table 3). Snag basal area was negatively correlated with captures of Curculionidae, Bostrichidae, and *Xyleborinus saxesenii* (Curculionidae), but positively correlated with captures of *Ho. simplex* (Elateridae) (Table 3). The basal area of live trees was positively correlated with captures of Buprestidae and *Anthaxia* spp. (Buprestidae) and negatively correlated with captures of Trogossitidae and *X. saxesenii* (Curculionidae).

Discussion

We found differences in woodborer and wood-decay-related beetle responses to levels of tree mortality and snag retention 6 to 7 yr after peak disturbance in *P. ponderosa* and mixed-conifer forests. In 2022, we observed the highest woodborer family-level richness (alpha diversity) on plots with high mortality and high snag fall. Surprisingly, the highest alpha and beta diversity for wood-decay-related beetle families (which included Dermestidae and Elateridae) occurred on plots with low mortality (Table 2). However, it is important to note that the low mortality class had a relatively high basal area of fallen snags (19.7 ± 3.2 m^2/ha) at the time of our study (Table 1). While we did not measure the decay of snags or fallen snags, the mean ages of snags and fallen snags among disturbance classes differed by <1 yr (Table 1, all cases). Rates of decay vary by tree species and microclimate, among other factors; however, we believe it is reasonable to assume similar levels of decay based on time since death or snag fall. Of note, even the oldest snags and fallen snags in our study were well below reported averages representative of late-stage decay classes (Barth et al. 2015).

It is reasonable to infer that the basal area of fallen snags provided a substantial amount of habitat for wood-decay-related beetles. Interestingly, our best-fit GLM indicated the basal area of fallen snags was inversely related to captures of wood-decay-related beetles (Table 3). In 2023, family-level alpha diversity was highest on High/Low for all families, woodborer families, and wood-decay-related beetle families (Table 2). The High/Low disturbance class likely represents the greatest niche diversity within our study, as

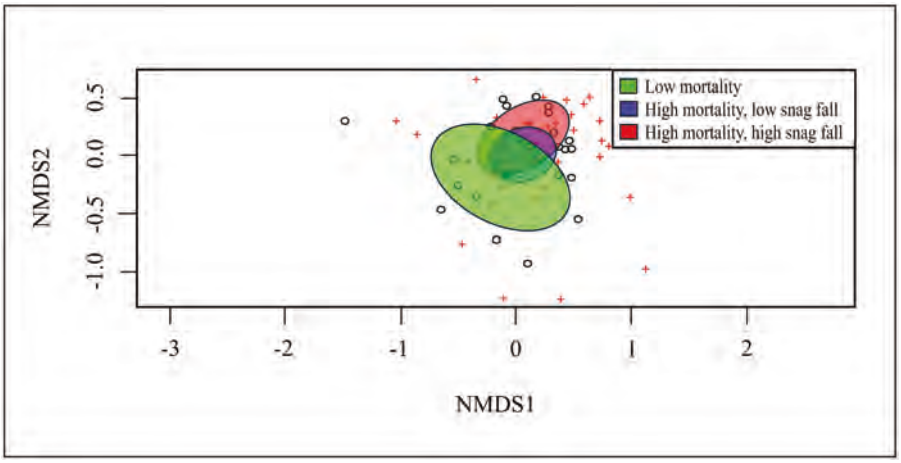

Fig. 5. Results of Non-Metric Multidimensional Scaling (NMDS) ordination (metaMDS() function in vegan package) of woodborer and wood-decay related beetle families captured in panel traps baited with high-release ethanol from plots representative of 3 disturbances classes: (1) low mortality (<20% tree mortality, no snag fall restrictions); (2) high mortality, low snag fall (>50% tree mortality, ≤50% snag fall); and (3) high mortality, high snag fall (>60% tree mortality, ≥70% snag fall). NMDS stress = 0.15 non-metric fit R^2 = 0.98; permutation test for homogeneity of multivariate dispersions test (PERMANOVA) was significant (F = 2.022, df = 28, P = 0.005). Traps were deployed 23 May–30 August 2023.

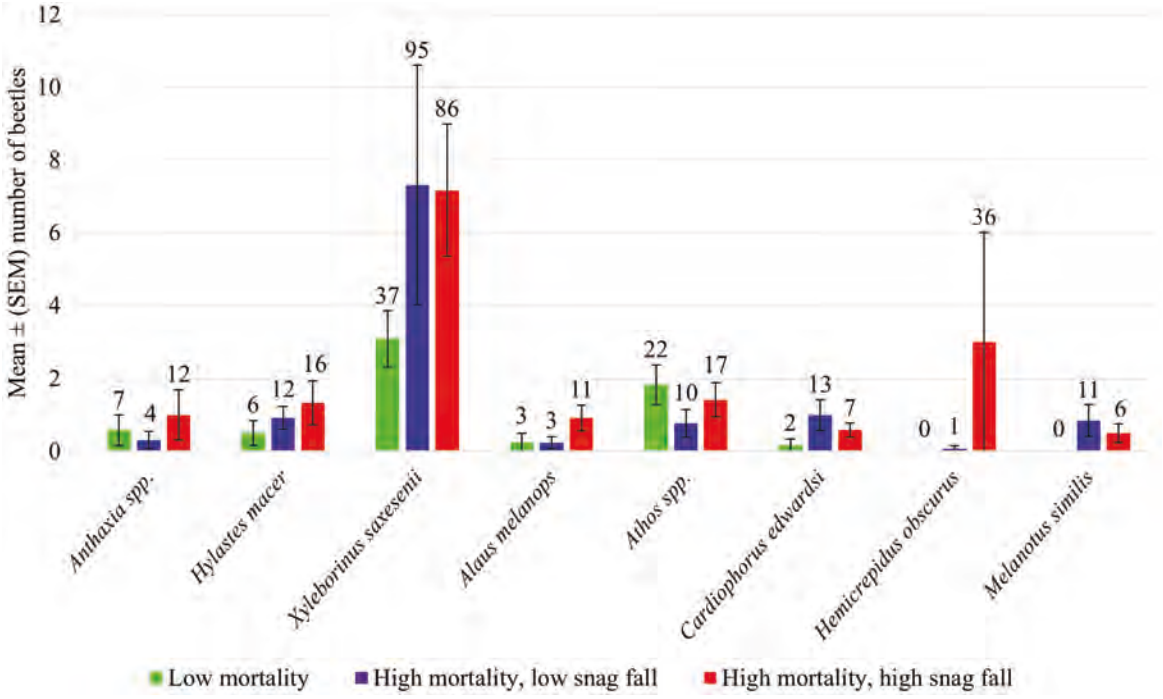

Fig. 6. Mean (± SEM) numbers of woodborer and wood-decay related beetles captured in panel traps baited with high-release ethanol (with total numbers above) from 8 families identified from pairwise similarity percentages (SIMPER) analyses. Families displayed represent the groups that most contributed to dissimilarities between beetle communities observed from the 3 disturbance classes in 2023. Shown are the families that comprised 70% to 75% (cumulative) of the observed differences from the PERMANOVA permutations.

these plots had high levels of tree mortality with a mix of snags and fallen snags (downed wood). Contrary to the 2022 analyses, the basal area of fallen snags was positively correlated with captures of woodborers in 2023 (Table 3). The incongruence in model performance and shift in family richness may be explained by the longer trapping interval in 2023. Our trapping interval in 2022 was largely informed by the peak flight activity of buprestids and cerambycids reported by Ray et al. (2019) for montane forests in California; however, the longer trapping period in 2023 resulted in greater species richness in buprestids (5 species in 2022 versus 6 species in 2023) and cerambycids (4 species in 2022 versus 10 species in 2023).

Influential Families

Family assemblages in 2022 were not significantly different among disturbance classes (Fig. 2), which may be influenced by the relatively high amount (basal area) of fallen snags on Low, High/Low, and High/High plots in 2022 (Table 1). A shorter trapping interval in 2022 likely also influenced this result, as we may have missed some captures of woodborers and wood-decay-related beetles.

Permutated family assemblages were different among disturbance classes in 2023 (Fig. 5). Post hoc, pairwise SIMPER tests revealed 8 influential families that explained most of the dissimilarity among disturbance classes. Elateridae was the most influential

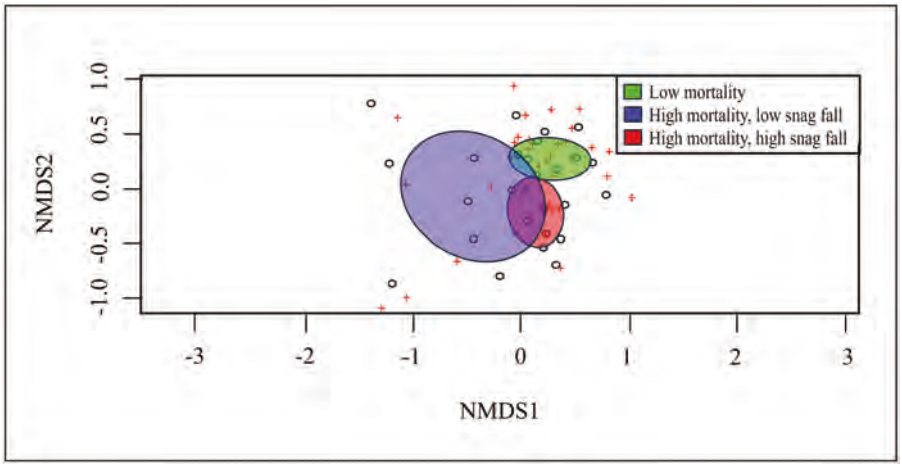

Fig. 7. Results of Non-Metric Multidimensional Scaling (NMDS) ordination (metaMDS() function in vegan package) of woodborer and wood-decay related beetle species from 4 families (Buprestidae, Cerambycidae, Curculionidae, and Elateridae) captured in panel traps baited with high-release ethanol from plots representative of 3 disturbances classes: (1) low mortality (<20% tree mortality, no snag fall restrictions); (2) high mortality, low snag fall (>50% tree mortality, ≤50% snags fallen); and (3) high mortality, high snag fall (>60% tree mortality, ≥70% snags fallen). NMDS stress = 0.16 non-metric fit R^2 = 0.98; permutation test for homogeneity of multivariate dispersions test (PERMANOVA) was significant (F = 1.732, df = 28, P = 0.008). Traps were deployed 23 May to 30 August 2023.

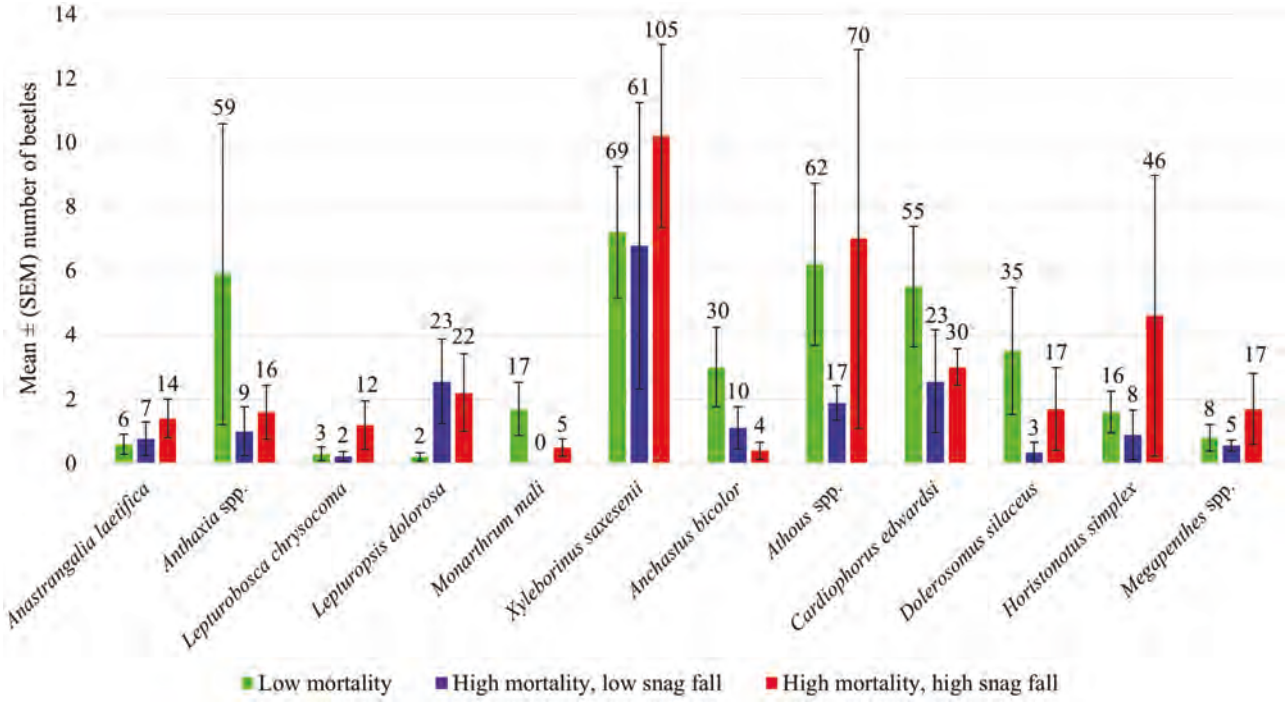

Fig. 8. Mean (± SEM) numbers of woodborer and wood-decay related beetles captured in panel traps baited with high-release ethanol (with total numbers above) from 12 species identified from pairwise similarity percentages (SIMPER) analyses. Species displayed represent the groups that most contributed to dissimilarities between beetle communities observed from the 3 disturbance classes in 2023. Shown are the genera that comprised 70% to 75% (cumulative) of the observed differences from the PERMANOVA permutations. Species analyzed were from 4 influential beetle families: Buprestidae; Cerambycidae; Curculionidae; and Elateridae.

family, explaining 22% of the permuted dissimilarity between Low and High/Low. Elaterids are commonly associated with decaying wood and other plant materials in forests (Triplehorn and Johnson 2005, Evans 2021). Surprisingly, the best-fit GLM did not include the basal area of snags or fallen snags (Table 3). It should be noted that Elateridae is a large, diverse family with a wide variety of life history strategies ranging from detritivores to herbivores to predators (Evans 2021). Our results (Fig. 6) likely reflect some of this diversity.

Dermestids were responsible for the most dissimilarity between Low and High/High (21%) and between High/Low and High/High (23%). The basal area of fallen snags was positively correlated with captures of dermestids (Table 3). Dermestidae are typically scavengers of protein and organic debris and are commonly associated with fugus-infested wood (Evans 2021). Our results reflect this ecological association as captures of dermestids increased with levels of tree mortality and downed wood (Fig. 6, Table 3). Wood decay is accelerated in fallen snags compared to standing snags (Lewis and

Thompson 2011, Rhoades et al. 2020), positively influencing habitat availability for dermestids.

Four of the 5 woodborer families (Ptinidae excluded) were influential in each of the pairwise comparisons. Ray et al. (2019) reported significant buprestid and cerambycid responses to bark beetle epidemics and wildfires in a study in the northern Sierra Nevada. Interestingly, we caught large numbers of buprestids (primarily *Anthaxia*) on low mortality plots (Fig. 6), contradicting our expectations. In fact, the best-fit GLM revealed a positive relationship with the basal area of live trees (Table 3). Despite being widely known for feeding in and inhabiting xylem tissues (Dodds et al. 2023), many adult buprestids complete maturation by feeding on foliage pollen and nectar (Evans 2021, Dodds et al. 2023). Captures of Cerambycidae comported with our expectation of a positive relationship with tree mortality as more individuals were captured on high mortality plots (Fig. 6). This is further reinforced by GLM which indicated the basal area of fallen snags was positively correlated with captures of cerambycids (Table 3). Conversely, captures of Curculionidae and Bostrichidae were similar among disturbance classes (Fig. 6). The basal area of snags was negatively correlated with captures of curculionids and bostrichids (Table 3). This is surprising given both families have similar habitat requirements for dead wood (Evans 2021, Gomez et al. 2023). While many snags on our plots were likely too old to provide suitable habitat for some curculionids (Table 1); more surprising is the negative correlation between the basal area of snags and bostrichid captures given that several bostrichids infest older dead wood and even wood products (Liu et al. 2015).

Influential Species

Interestingly, *X. saxesenii* (Curculionidae), an invasive species well-established across North America (Seybold et al. 2016), was most frequently captured in our study (Figs. 4 and 8). *Xyleborinus saxesenii* is not a forest pest but does cause damage and losses in tree nurseries and orchards (Baniszewski et al. 2024). In 2023, the basal area of live trees was negatively correlated with captures of *X. saxesenii* (Table 3), which is not surprising given the species association with dead and dying trees (Seybold et al. 2016, Gomez et al. 2023). However, the negative correlation with the basal area of snags was unexpected. This may result from the ubiquitous presence of *X. saxesenii* on the landscape (Seybold et al. 2016, Baniszewski et al. 2024) and/or its high level of attraction to high-release ethanol lures (Ranger et al. 2011). In fact, Baniszewski et al. (2024) report that non-native ambrosia beetles, including *Xyleborinus* spp., were captured at a 341:1 rate compared to native scolytines in Ohio.

Five species of elaterid were identified as influential from the 2022 data and 6 from the 2023 data. *Athous* spp. were captured in similar numbers among disturbance classes in both years (Figs. 4 and 6). Stand metrics were not correlated with captures of *Athous* spp. *Cardiophorus edwardsi*, *He. obscurus*, and *Me. similis* were almost exclusively trapped on high mortality plots in 2022 (Fig. 4). The basal area of snags was positively correlated with captures of *C. edwardsi* while the basal area of fallen snags was positively correlated with captures of *He. obscurus* (Table 3). *Hemicrepidius obscurus* and *Me. similis* were not highlighted in 2023 and more *C. edwardsi* were captured on low mortality plots than high mortality plots in 2023 (Fig. 8). More *An. bicolor* were also captured on low mortality plots (Fig. 8); however, stand metrics were not correlated with captures of either species (Table 3). Snag basal area was positively correlated with captures of *Ho. simplex* (Table 3) and was the only significant relationship found among elaterids.

Captures of buprestids and cerambycids were lower than expected in both years. *Anthaxia* spp. (Buprestidae) was the only species highlighted in 2022 (Fig. 4) while 4 species, *An. laetifica* (Buprestidae), *Anthaxia* spp., *Lep. chrysocoma* (Cerambycidae) and *Le. dolorosa* (Cerambycidae), were highlighted in 2023 (Fig. 8). While no distinct patterns emerged for *Anthaxia* spp. in the 2022 data, more *Anthaxia* spp. were captured on low mortality plots in 2023 (Fig. 8) and the basal area of live trees was positively correlated with captures of *Anthaxia* spp. (Table 3). While captures of *An. laetifica* in 2023 did not reveal a distinct pattern (Fig. 8), the basal area of fallen snags was positively correlated with captures of *An. laetifica* (Table 3). No discernable patterns were found for *Lep. chrysocoma* while more *Le. dolorosa* were captured on high mortality plots (Fig. 8). Basal area of fallen snags was positively correlated with captures of *Le. dolorosa* (Table 3).

We were particularly interested in elucidating differences in woodborer and wood-decay-related beetle assemblages between low snag fall and high snag fall. While there isn't a distinct pattern, our results show a general trend of increasing abundance with increasing disturbance. The lack of resolution may be, in part, explained by a lack of difference in the basal area of fallen snags on High/Low and High/High plots in 2023 (2023: High/Low, 8.3 ± 2.1 m^2/ha; High/High, 10.2 ± 1.6 m^2/ha), despite differences in the percentage of fallen snags (Table 3). As discussed earlier, the percentage of fallen snags was used to distinguish between High/Low and High/High disturbance classes (2023: High/Low, ≤50% snag fall; High/High, >70% snag fall). Basal area is a measure of the cross-sectional area of trees (snags), which we include as an indicator of the amount of fallen snag (downed wood) habitat. The amount of fallen snags on a plot is also influenced by snags outside the plot failing into the plot, which are not accounted for in our analyses.

Our analyses revealed several significant differences and interesting patterns in the response of woodborers and wood-decay-related beetles among disturbance classes. However, we failed to reveal clear, distinctive assemblages indicative of the 3 levels of disturbance. There are several factors that likely influenced our results: (i) Trap efficacy varies with differences in forest structure and composition (Irvine and Woods 2007, Dodds et al. 2024). Despite this, we consistently observed similar trap captures within families and species among disturbance classes (eg *see* Elateridae and Cryptophagidae (Fig. 6) and *Athous* spp. (Figs. 4 and 8)), which suggests this effect was limited; (ii) We only sampled with ethanol-baited, panel flight intercept traps placed on conduit poles 1.5 to 2.4 m in height. The addition of different sampling methods (eg trap types and attractants, placement of traps, and/or rearing of beetles from logs) would provide for a more comprehensive assessment of woodborer and wood-decay-related beetle responses (Miller et al. 2020, Miller and Crowe 2022, Dodds et al. 2024); (iii) We sampled 7 to 8 yr after peak disturbance (Fettig et al. 2019b). It takes time for woodborers to locate and colonize bark beetle-killed trees and generally 1 to 3 yr for emergence to occur (Costello et al. 2013). Sampling during multiple periods since disturbance (eg 3 to 4 and 7 to 8 yr after peak disturbance) would have provided for a more comprehensive assessment of woodborer and wood-decay related beetle responses; and (iv) As part of the CTMN, sampling was limited to 0.041-ha circular plots indicative of our disturbance classes. The environment in these plots is affected, in part, by conditions external to these plots, which could be particularly important in some cases (eg if there were large differences in tree mortality and/or snag retention between plots and adjacent areas). Sampling larger plots could provide a more comprehensive assessment of woodborer and wood-decay-related beetle responses. Further investigation

is required to better resolve beetle community responses to major forest disturbance events. Additionally, the biology and ecology of several woodborer and wood-decay-related beetle families and genera identified in our study are poorly understood and warrant further study.

Acknowledgments

We thank B. Bulaon (Forest Health Protection, USDA Forest Service) for technical assistance. We also wish to thank the Eldorado, Sierra, and Stanislaus National Forests for facilitating this study.

Author contributions

Jackson Audley (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Investigation [equal], Methodology [equal], Writing—original draft [equal], Writing—review & editing [equal]), Christopher J. Fettig (Conceptualization [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal], Writing—original draft [equal], Writing—review & editing [equal]), Leif Mortenson (Data curation [supporting], Investigation [supporting], Writing—review & editing [equal]), and Shakeeb Hamud (Data curation [supporting], Investigation [supporting], Writing—review & editing [equal])

Funding

None declared.

Conflicts of interest. None declared.

References

Baniszewski JA, Barnett J, Reding ME, et al. 2024. Seasonal dominance of exotic ambrosia beetles compared to native species within deciduous and coniferous woodlots. Biol. Invasions. 26:1651–1668. https://doi.org/10.1007/s10530-024-03255-z

Barth MAF, Larson AJ, Lutz JA. 2015. A forest reconstruction model to asses changes to Sierra Nevada mixed-conifer forest during the fire suppression era. For. Ecol. Manag. 343:104–118. https://doi.org/10.1016/j.foreco.2015.06.030

Chiba Y. 1998. Architectural analysis of relationship between biomass and basal area based on pipe theory. Ecol. Modell. 108:219–225. https://doi.org/10.1016/S0304-3800(98)00030-1

Chima UD, Adekunle AT, Okorie MCF. 2013. Ecological and ethnomedicinal survey of plants within homesteads in Abia State, Nigeria. J Forest Environ. Sci. 29:257–274. https://doi.org/10.7747/jfs.2013.29.4.257

Costello SL, Jacobi WR, Negrón JF. 2013. Emergence of Buprestidae, Cerambycidae, and Scolytinae (Coleoptera) from mountain pine beetle-killed and fire-killed ponderosa pines in the Black Hills, South Dakota, USA. Coleopterists Bull. 67:149–154. https://doi.org/10.1649/0010-065x-67.2.149

Dodds KJ, Sweeney J, Allison JD. 2023. Woodborers in forest stands. In: Allison J, Paine TD, Slippers B, Wingfield MJ eds. Forest entomology and pathology: volume 1: entomology. Springer International Publishing, p. 361–415. https://doi.org/10.1007/978-3-031-11553-0

Dodds KJ, Sweeney J, Francese JA, et al. 2024. Factors affecting catches of bark beetles and woodboring beetles in traps. J. Pest Sci. 97:1767–1793. https://doi.org/10.1007/s10340-024-01774-1

Evans AV. 2021. Beetles of western North America. Kirk R and Johnson A, eds. Princeton University Press, p. 624.

Fettig CJ. 2016. Native bark beetles and wood borers in Mediterranean forests of California. In: Lieutier F, Paine TD eds. Insects and diseases of Mediterranean forest systems. Springer International Publishing, p. 499–528. https://doi.org/10.1007/978-3-319-24744-1_18

Fettig CJ, Wuenschel A, Balachowski J, et al. 2019a. Managing effects of drought in California. In: Vose J, Patel-Weynand T, Peterson DL, Luce CH eds. Gen. Tech Rep. WO-98. Effects of drought on forests and rangelands in the United States: translating science into management responses. U.S. Department of Agriculture, Forest Service, 71–93.

Fettig CJ, Mortenson LA, Bulaon BM, et al. 2019b. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. Forest Ecol. Manag. 432:164–178. https://doi.org/10.1016/j.foreco.2018.09.006

Gandhi KJK, Gilmore DW, Katovich KA, et al. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. Environ. Rev. 15:113–152. https://doi.org/10.1139/A07-003

Gomez DF, Riggins JJ, Cognato AI. 2023. Bark beetles. In: Allison J, Paine TD, Slippers B, Wingfield MJ, eds. Forest entomology and pathology: volume 1: entomology. Springer International Publishing, p. 299–227. https://doi.org/10.1007/978-3-031-11553-0

Griffin D, Anchukaitis KJ. 2014. How unusual is the 2012–2014 California drought? Geophys. Res. Lett. 41:9017–9023. https://doi.org/10.1002/2014gl062433

Hart SJ, Veblen TT, Schneider D, et al. 2017. Summer and winter drought drive the initiation and spread of spruce beetle outbreak. Ecology. 98:2698–2707. https://doi.org/10.1002/ecy.1963

Hébert C. 2023. Forest arthropod diversity. In: Allison J, Paine TD, Slippers B, Wingfield MJ, eds. Forest entomology and pathology: volume 1: entomology. Springer International Publishing, p. 45–89. https://doi.org/10.1007/978-3-031-11553-0

Irvine KM, Woods SA. 2007. Evaluating shading bias in Malaise and window-pane traps. J. Acad. Entomol. Soc. 3:38–48.

Kapinska OK, Kamionka-Kanclerska P, Czortek MK, et al. 2024. Mechanisms shaping the functional diversity of birds' composition in the primeval forest ecosystem of the Bialowieza National Park. Euro. J. For. Res. 143:1015–1033. https://doi.org/10.1007/s10342-024-01675-z

Klimetzek D, Köhler J, Vité JP, et al. 1986. Dosage response to ethanol mediates host selection by 'secondary' bark beetles. Naturwissenschaften. 73:270–272. https://doi.org/10.1007/BF00367783

Lewis K, Thompsons RD. 2011. Degradation of wood in standing lodgepole pine killed by mountain pine beetle. Wood Fiber Sci. 43:130–142.

Li F, Ye G, Wu Q, et al. 2007. Arthropod abundance and diversity in *Bt* and non-*Bt* rice fields. Environ. Entomol. 36:646–654. https://doi.org/10.1603/0046-225x(2007)36[646:aaadib]2.0.co;2

Liu L, Schönitzer K, Yang J. 2015. A review on the literature on the life history of Bostrichidae. Mitt. Münch. Ent. Ges. 98:91–97.

Miller DR, Crowe CM. 2022. Trap type affects catches of bark and woodboring beetles in a southern pine stand. J. Entomol. Sci. 57:145–155. https://doi.org/10.18474/jes21-28

Miller DR, Crowe CM, Sweeney JD. 2020. Trap height affects catches of bark and woodboring beetles (Coleoptera: Curculionidae, Cerambycidae) in baited multiple-funnel traps in Southeastern United States. J. Econ. Entomol. 113:273–280. https://doi.org/10.1093/jee/toz271

R Core Team. 2020. R: a language and environment for statistical computing. R Core Team, Vienna, Austria.. https://R-project.org/

Ranger CM, Reding ME, Gandhi KJK, et al. 2011. Species dependent influence of (−)-α-pinene on attraction of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) to ethanol-baited traps in nursery agroecosystems. J. Econ. Entomol. 104:574–579. https://doi.org/10.1603/ec10243

Ray C, Cluck DR, Wilkerson RL, et al. 2019. Patterns of woodboring beetle activity following fires and bark beetle outbreaks in montane forests of California, USA. Fire Ecol. 15:1–20. https://doi.org/10.1186/s42408-019-0040-1

Reed CC, Hood SM. 2021. Few generalizable patterns of tree-level mortality during extreme drought and concurrent bark beetle outbreaks. Sci. Total Environ. 750:141306. https://doi.org/10.1016/j.scitotenv.2020.141306

Rhoades CC, Hubbard RM, Hood PR, et al. 2020. Snag-fall the first decade after severe bark beetle infestation of high-elevation forests in Colorado, USA. Ecol. Appl. 30:e02059. https://doi.org/10.1002/eap.2059

Robbins ZJ, Xu C, Aukema BH, et al. 2022. Warming increased bark beetle-induced tree mortality by 30% during an extreme drought in California. Global Change Bio. 28:509–523. https://doi.org/10.1111/gcb.15927

Rubia R. 2022. NMDS plotting and analysis using the Vegan package. GitHub. https://eddatascienceees.github.io/tutorial-rayrr13/. Last accessed: 9/26/2024.

Seybold SJ, Penrose RL, Graves AD. 2016. Invasive Bark and Ambrosia Beetles in California Mediterranean Forest Ecosystems. In: Paine T, Lieutier F eds. Insects and Diseases of Mediterranean Forest Systems. Springer, Cham, p. 582–663. https://doi.org/10.1007/978-3-319-24744-1_21

Stephens SL, Collins BM, Fettig CJ, et al. 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. BioScience. 68:77–88. https://doi.org/10.1093/biosci/bix146

Supp SR, Ernest SKM. 2014. Species-level and community-level responses to disturbance: a cross-community analysis. Ecology 95:1717–1723. https://doi.org/10.1890/13-2250.1

Triplehorn CA, Johnson NF. 2005. Borror and DeLong's introduction to the study of insects. Howe E, Feldman E, Michel L eds. Brooks/Cole Publishing, p. 864.

Ulyshen MD. 2016. Wood decomposition as influenced by invertebrates. Biol. Rev. Camb. Philos. Soc. 91:70–85. https://doi.org/10.1111/brv.12158

Vilanova E, Mortenson LA, Cox LE, et al. 2023. Characterizing ground and surface fuels across Sierra Nevada forests shortly after the 2012–2016 drought. Forest Ecol. Manag. 537:120945. https://doi.org/10.1016/j.foreco.2023.120945

Williams AP, Seager R, Abatzoglou JT, et al. 2015. Contribution of anthropogenic warming to California drought during 2012–2014. Geophys. Res. Lett. 42:6819–6828. https://doi.org/10.1002/2015GL064924

Zuur A, Leno E, Walker N, et al. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, p. 574.