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Context-dependent disturbance synergies: Subcortical competitors may constrain bark beetle outbreaks following wildfires

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Abstract

Wildfires and bark beetles have historically interacted to create complex and resilient forests. However, recent record-breaking wildfires in western North America raise concerns that the large areas of injured and dead trees could facilitate increases in insect populations that respond to resource pulses. Populations of Douglas-fir beetle (*Dendroctonus pseudotsugae*), the primary mortality agent of Douglas-fir (*Pseudotsuga menziesii*), often irrupt following fires due to the resultant ephemeral pulses of defensively compromised hosts. Other subcortical phloeophagous insects are also attracted to fire (e.g., woodboring Coleoptera: Buprestidae, Cerambycidae) and similarly colonize damaged trees. Although Douglas-fir beetle and woodboring beetle species are known to colonize the phloem of injured trees, the potential for interactions among them following fire is relatively unknown. Rapid colonization by woodborers of the bark beetle niche following fires could constrain bark beetle population growth, potentially suppressing population irruptions through subcortical competition. To evaluate this hypothesis, we studied three wildfire complexes in mature Douglas-fir forests that burned in British Columbia in 2017. We found that Douglas-fir beetle preferentially colonized mature stands containing large-diameter trees with moderate fire injury and that these trees were frequently co-colonized by woodborers. In the absence of woodborers, we found that potential rates of increase in Douglas-fir beetle populations (i.e., offspring per female) were sufficient to lead to a local population irruption. Conversely, when woodborers were common (>50% of trees infested per stand), potential rates of increase in Douglas-fir beetle populations fell below replacement. These findings suggest that competition by woodboring beetles may suppress irruptions of Douglas-fir beetle in fire-injured forests. Our results reveal complex, context-dependent interactions among disturbance agents and indicate that population irruptions by resource pulse-driven bark beetles following fire may depend upon the response of local subcortical competitors. Forest management practices that enhance the diversity and abundance of non-irruptive phloeophagous insects such as many woodboring beetle species may limit the potential for wildfires to contribute to subsequent bark beetle outbreaks.

KEYWORDS
bark beetles, Buprestidae, Cerambycidae, disturbance, disturbance synergy, Douglas-fir beetle, interspecific competition, population irruptions, Scolytinae, wildfire

INTRODUCTION

Disturbances that alter the structure and function of forest ecosystems, communities, or populations are critical processes that enable regeneration and succession, aid in nutrient cycling, and increase biodiversity and resilience (Parker et al., 2006; Seidl et al., 2011). Natural disturbance events, whether biotic (e.g., insect outbreaks, disease) or abiotic (e.g., fires, drought), can be extensive, affecting millions of hectares of forests every year (Doerr & Santín, 2016; Kautz et al., 2017). Over large spatial scales and long time spans, disturbances tend to recur within a historical range of variability (Keane et al., 2009; Landres & Swanson, 1999), comprising a disturbance regime (Pickett & White, 1985; Turner, 2010). Recent climate-change-related increases in disturbance frequency and severity in many forest types, however, have raised concerns that historical ranges of variability have been surpassed, disturbance regimes have been altered, and that these changes could push forests past their capacity for resilience by crossing key ecological tipping points (Hessburg et al., 2019; Seidl et al., 2017).

Changes in disturbance frequency and severity have been very apparent among fires and insect outbreaks in dry conifer forests. For example, in western North America, fire seasons have become longer and more severe (Hanes et al., 2018; Jain et al., 2017), and in recent decades, annual area burned has increased dramatically (Barbero et al., 2015; Parisien et al., 2023). At the same time, vast outbreaks by bark beetles (i.e., the mountain pine beetle [*Dendroctonus ponderosae* Hopkins] and spruce beetle [*D. rufipennis* Kirby]) have killed trees across millions of hectares of historic and novel habitats, altering forest landscapes (Raffa et al., 2008) and even affecting global carbon dynamics (Kurz et al., 2008). While there has been considerable research investigating the causes and consequences of individual disturbances, disturbance regimes comprise multiple events that interact through space and time (Pickett & White, 1985; Turner, 2010). These interactions range from synergistic to antagonistic, amplifying or dampening overall impacts to forests. Despite the potential for complex outcomes arising from interacting disturbances, these interactions have been largely understudied (reviewed by Seidl et al., 2017), thus compromising our capacity to determine whether contemporary impacts are exceeding historical ranges of variability.

Disturbances by bark beetles and fire potentially synergize in two ways. First, during an outbreak, irruptive bark beetles often kill many mature trees within stands and across landscapes (Raffa et al., 2008). Resultant dead trees modify fuel conditions (i.e., "fuel loading") that may affect subsequent fire behavior (e.g., Harvey et al., 2014; Waymon & Safford, 2021), although there remains a general lack of consensus regarding the potential for fuels to exacerbate fires (Fettig et al., 2022; Hicke et al., 2012; Romualdi et al., 2023). Second, although fires are typically associated with tree mortality, many trees are injured but not directly killed by fire (Bär et al., 2019). Pulses of injured, defensively compromised trees (i.e., "food loading") have been associated with rapid increases in bark beetle populations after many different types of disturbance events (Boulanger & Sirois, 2007; Furniss & Carolin, 1977; Hood & Bentz, 2007; McHugh & Kolb, 2003); however, it is unclear whether post-fire food loading always leads to bark beetle outbreaks (Davis et al., 2012; Powell et al., 2012; Tabacaru et al., 2016). Indeed, several recent studies have demonstrated reduced bark beetle activity after fires, positing that this could be due to intraspecific competition driven by a lack of host availability (Powell et al., 2012; Tabacaru et al., 2016) or interspecific competition by other subcortical insect species (Davis et al., 2012; Powell et al., 2012; Tabacaru et al., 2016). A general lack of predictability regarding fire and bark beetle interactions suggests that there are other undescribed, critical factors that affect these outcomes.

Fires have been linked to food loading for many insect taxa that feed on injured, defensively impaired trees. In seasonally dry forests, woodboring insects (Coleoptera: Buprestidae, Cerambycidae, and Curculionidae; Hymenoptera: Siricidae) commonly colonize injured trees immediately following fires (Costello et al., 2011; McHugh & Kolb, 2003; Ryan & Amman, 1996). Recent evidence suggests that members of the woodboring guild preferentially attack trees with moderate levels of fire injury that may have otherwise lived, thereby exacerbating post-fire tree mortality (Kitchens et al., 2022). Rapid colonization by woodborers of the same niche as bark beetles could lead to high levels of interspecific competition and potentially lower the likelihood of bark beetle outbreaks after fire. To evaluate this hypothesis, we tested the prediction that interspecific competition associated with feeding by woodboring cerambycids and buprestids within the phloem of fire-injured trees limits the reproductive potential and outbreak likelihood of an irruptive bark beetle, the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins; hereafter DFB).

MATERIALS AND METHODS

The potential for phloeophagous woodborers to constrain population increases by irruptive bark beetles will manifest through exploitation and/or interference competition (e.g., Hassell & Varley, 1969). To assess the former, we quantified the likelihood of DFB colonization (i.e., preference) of trees and stands following fires in relation to the presence of woodboring beetles. To assess the latter, we quantified the performance (i.e., offspring production) of DFB that co-occurred in trees and stands along with woodboring beetles after fire.

Study system

Douglas-fir (*Pseudotsuga menziesii*) forests cover much of western North America and are both economically and culturally important. In seasonally dry montane ecosystems dominated by Douglas-fir, historical disturbance regimes include a variety of disturbances, including drought, fire, defoliator, and bark beetle outbreaks (Leclerc et al., 2021; McCullough et al., 1998). Fire is the dominant abiotic disturbance in Douglas-fir forests, with historic regimes comprising frequent (i.e., <30-year interval) low- to mixed-severity surface fires and less frequent moderate- to high-severity fires that caused stand-level tree mortality (Brookes et al., 2021; Hessburg et al., 2019; Heyerdahl et al., 2012). The most significant biotic disturbance agent within dry Douglas-fir forests is Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins; hereafter DFB), a univoltine bark beetle that colonizes trees in spring and early summer and overwinters in natal galleries as late-larval instars and adults. Like many bark beetles, DFB is a resource pulse-driven irruptive species (Howe et al., 2022), meaning outbreaks will only occur after a large pulse of defensively compromised host trees arises due to a primary disturbance agent, such as windthrow, drought, or fire (Furniss, 1962; Schmitz & Gibson, 1996). DFB outbreaks typically last 2–5 years following a resource pulse and cause tree mortality within and adjacent to the primary disturbance before populations collapse (Aukema et al., 2016; Dodds et al., 2006; Negron, 1998).

The woodboring insect guild in dry-interior forests comprises primarily species of Buprestidae and Cerambycidae that feed as larvae within phloem; however, most complete their life cycles within the sapwood of their hosts (Sreedevi et al., 2022). Recent research (Kitchens et al., 2022; Ray et al., 2019) suggests that these woodborers are more aggressive and ubiquitous after fire than previously thought and may significantly contribute to fire-related mortality, particularly in Douglas-fir ecosystems. Given concerns that increases in fire frequency and extent may increase the vulnerability of widespread areas to subsequent disturbances by the Douglas-fir beetle, this system was chosen to test our prediction that competition from the coleopteran woodboring guild may limit the outbreak potential of irruptive pulse-driven bark beetles.

Data collection

Three mixed- to high-severity wildfires that burned across large areas of Douglas-fir forests in British Columbia, Canada, from early July to mid-September in 2017 (Cariboo Regional District, 2018) were chosen for study: Hanceville-Riske Creek (hereafter HRC), Elephant Hill (hereafter EH), and Prouton Lakes (hereafter PL; fire numbers C50647, K20637, and C30870 in B.C. Wildfire Service, 2022). Field sampling to determine the abundance and diversity of subcortical insect populations was conducted between May and August 2019, which allowed a full generation of DFB to develop after the 2017 fire season. Following methods by Kitchens et al. (2022), 37 sample plots (400 m^2, radius = 11.28 m; 14 at HRC, 11 at EH, and 12 at PL) were placed across a range of fire-severity classes (unburned, low, moderate, high) in each fire complex (Figure 1). Stands were dominated by mature (defined as ≥13.5 cm dbh [1.3 m]) Douglas-fir (>50% species composition by plot) trees, with replicates within each fire complex selected to approximate the full range of forest conditions. Latitude, longitude, and elevation were recorded at plot centers. In total, 693 trees were sampled across the 37 plots (Figure 1).

Within sample plots, standing trees with dbh ≥ 13.5 cm were assessed and attributes were recorded as follows: tree species, tree height (in meters), dbh (in centimeters), fire injury (in meters), woodborer infestation status, and DFB infestation status. To measure the extent of fire injury on trees, the highest and lowest visible bole char was recorded for each tree. dbh was measured using a diameter tape, while tree height and visible bole char were measured using a Vertex IV laser. Evidence of buprestid

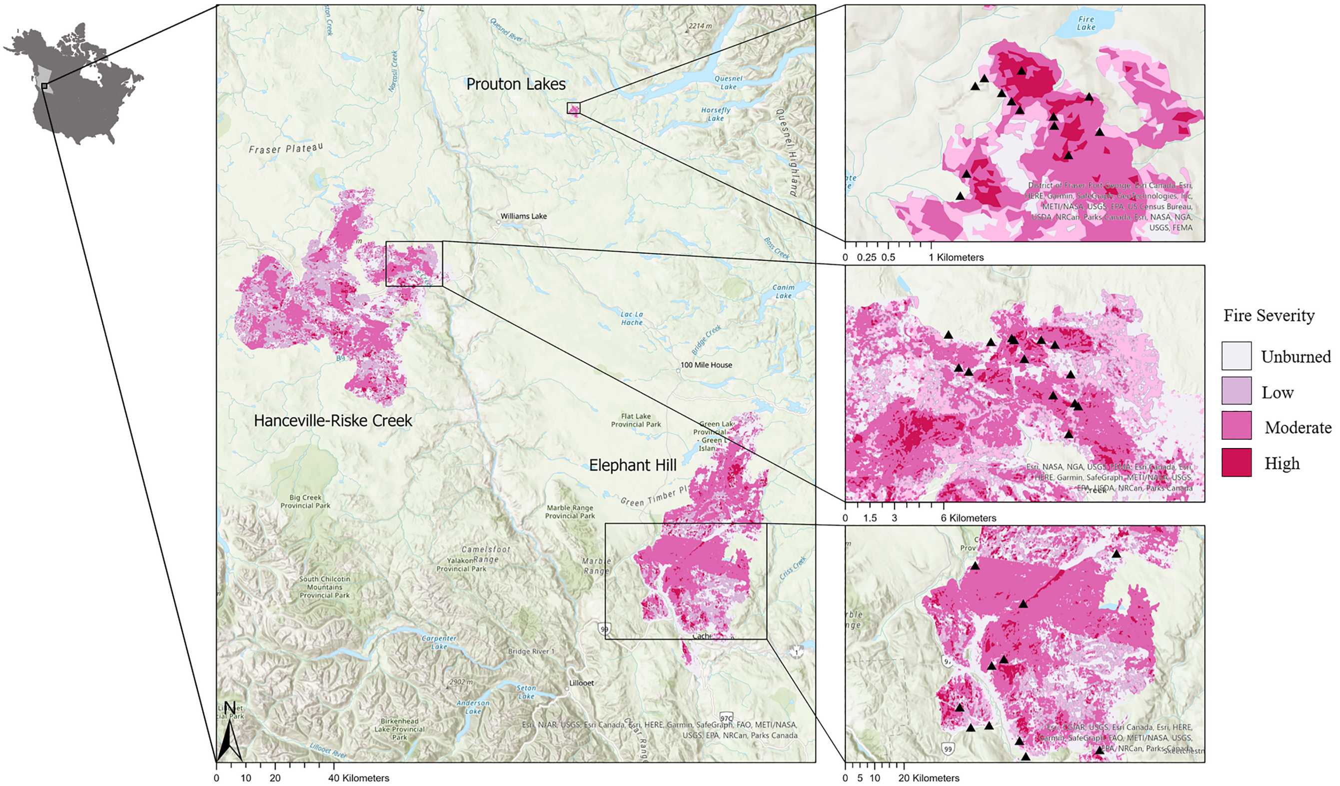


FIGURE 1 Location of field sites sampled in 2019 across three fire complexes that burned in south-central British Columbia, Canada. Fire severity is denoted from light to dark pink across four fire severity classes: unburned, low, moderate, and high (B.C. Ministry of Forests, 2024). Sample plots ($N = 37$) are denoted in black triangles within each fire complex: Elephant Hill (EL; $n = 11$), Hanceville-Riske Creek (HRC; $n = 14$), and Prouton Lakes (PL; $n = 12$).

and cerambycid infestation (hereafter woodborers) was identified by removing a 10 cm × 10 cm bark sample at breast height from each conifer tree and checking for evidence of frass, sapwood scoring, and/or woodchips characteristic of larval activity (Kitchens et al., 2022). Evidence of DFB infestation was identified by an initial examination of Douglas-fir boles for red-orange boring dust indicative of beetle emergence and/or circular entrance and/or exit holes in the bark ~2 mm in diameter. Trees displaying evidence of DFB infestation were subsequently destructively sampled to determine the number of offspring produced per attacking female based on standardized bark beetle sampling methods (i.e., *r*-value surveys [Ministry of Forests, 1995; Safranyik, 1968]). Briefly, two 15-cm-wide × 30-cm-tall rectangular areas (900 cm^2 per tree), centered at breast height, were delineated on the north- and south-facing aspects of each tree with evidence of infestation. Within these areas, visible exit holes in the bark indicative of emerging DFB offspring were counted, after which the bark section was removed with a hammer and chisel and the number of galleries in the phloem initiated by DFB females was recorded. If evidence of woodborer activity such as frass, galleries, or holes in the phloem or into the sapwood of the tree was detected within DFB *r*-survey areas, these bark samples were photographed for subsequent assessment of total area colonized by woodborers using ImageJ. Photographs were processed, and woodborer occupation was calculated using standardized ImageJ measurement tools (Rasband, 1997).

Data calculations

To determine the likelihood of a bark beetle irruption, the rate of increase in local populations (offspring per female) must be quantified (Ministry of Forests, 1995; Safranyik, 1968; Safranyik & Carroll, 2006). Local bark beetle populations are normally confined to individual stands (Safranyik & Carroll, 2006), thus interactions between DFB and woodborers were considered both within individual trees, to quantify the form of the interaction, and scaled up to the stand-level to determine the impact of those interactions on DFB populations. Table 1 details the variables measured or calculated for both the tree- and stand-level analyses. Details of data calculations for all relevant variables are further outlined below.

TABLE 1 Tree- and stand-level attributes collected to determine the impact of woodborer (WB) species on Douglas-fir beetle (DFB) infestations following wildfires in the dry-interior forests of British Columbia, Canada.

Variable	Unit
Tree-level model attributes	
dbh[a]	cm[b]
Tree height	m[b]
Fire injury	Percent[b]
WB infestation	Presence/absence[b]
WB occupation	Percent[c]
DFB infestation	Presence/absence[b]
DFB offspring total	Offspring count[b]
Douglas-fir proportion	Percent[d]
Stand density	Stems/ha[d]
Host availability	m^2[d]
DFB distance	km[d]
Stand-level model attributes	
Average dbh[a]	cm[d]
Average tree height	m[d]
Average fire injury	Percent[d]
WB proportion	Percent[d]
DFB *r*	Offspring per female[e]
DFB proportion	Percent[d]
Douglas-fir proportion	Percent[d]
Stand density	Stems/ha[d]
Host availability	m^2[d]
DFB distance	km[d]

Note: Variables and their units of measurement are split between the spatial scales at which they were analyzed, either at the tree level or at the stand level.

[a] Diameter at breast height.

[b] Per tree.

[c] Per tree total r-survey sample (900 cm^2, see *Materials and methods*).

[d] Per measured plot (stand-level).

[e] Total number of offspring per plot divided by the total number of maternal galleries (= females) for all r-surveys within a measured plot (see *Materials and methods*).

Tree-level attributes

Tree-level fire injury (in percent) was specified as the percentage of total tree height affected by visible bole charring, calculated using a model developed by Kitchens et al. (2022). WB infestation (0/1) was defined as the presence or absence of woodborers detected in individual trees. WB occupation (in percent) was determined as the percent of an *r*-survey sample that was affected by woodboring larval feeding per tree, as outlined above. DFB infestation (0/1) was defined as the presence or absence of DFB colonization in Douglas-fir trees within plots, and DFB offspring total was calculated as the total number of offspring per r-survey sample (in square meters) per tree.

To determine whether interactions among DFB, woodborers, and fire in individual trees were affected by conditions in the surrounding forest, several forest-level variables were also considered in our tree-level analyses. First, we defined Douglas-fir proportion (in percent) as the total number of Douglas-fir trees (alive and dead) divided by the total number of conifers within plots. Second, stand density (stems per hectare) was calculated as the number of measured trees per plot, regardless of species and status (alive or dead), and transformed into stems per hectare. Third, host availability (in square meters) was used to determine the influence of host prevalence on DFB irruptive potential, which was calculated from an annually updated provincial vegetation resource inventory (VRI; Forest Analysis and Inventory Branch, 2021). VRI data for 2017 were loaded into ArcGIS Pro (ESRI, 2023) along with plot center coordinates; 250-m buffers were placed surrounding each sample plot, and host availability relative to each sample plot was determined as the area (in square meters) in each buffer with ≥80% Douglas-fir that was >80 years old. Finally, DFB distance (in kilometers), the distance to the nearest detectable infestation prior to fire, was calculated to determine whether the proximity of source beetles affected colonization of individual trees following fire. Data from annual aerial overview surveys (AOS; B.C. Ministry of Forests, 2024) of forest health conditions for the province of British Columbia were loaded in ArcGIS Pro, and DFB distance was calculated as the distance from the center of each sample plot to the nearest infestation, regardless of severity. Due to extensive wildfire smoke, surveys were curtailed in 2017, and so the nearest infestations were derived from data from 2016.

Stand-level attributes

Average dbh (in centimeters), tree height (in meters), and fire injury (in percent) were each calculated as the mean of the tree-level attributes described above. WB proportion (in percent) was calculated as the total number of WB-colonized conifer trees divided by the total number of conifer trees within plots. To determine whether DFB populations were increasing, static, or declining in fire-injured stands, DFB *r* (offspring/female) was calculated for each plot as the total number of offspring divided by the total number of initiating maternal galleries counted for all DFB-surveyed trees in a plot, rounded to the nearest whole number. DFB proportion (in percent) was calculated as the percentage of Douglas-fir trees colonized in each plot. Douglas-fir proportion (in percent), stem density (stems per hectare), host availability (in square meters), and DFB distance (in kilometers) were calculated as detailed above and did not require further manipulation for stand-level analysis.

Model development

To evaluate our hypothesis that interspecific competition from the phloeophagous woodboring beetle guild lowers the likelihood of bark beetle irruptions after fire, we determined whether the preference of DFB (likelihood of colonization) was reduced in the presence of woodborers (exploitation competition) and whether the performance of DFB (offspring production) was negatively affected by the area of phloem occupied by woodborers (interference competition). Our models included the tree, stand, fire, and spatial variables described above. To accommodate potential non-linear relationships among DFB preference/performance, the competitive effects of woodborers, and the additional covariates, we used generalized additive models (GAMs), where variables were tested initially without smoothed terms (i.e., linear relationships) and then with smoothed terms if required, as described below. Modeling was conducted in R (R Core Team, 2023), and GAMs were generated using the *mgcv* package (Wood, 2022). Four models were evaluated (described below) to address differing aspects of potential DFB and woodborer interactions within and among trees and stands. Variable retention within models was based on stepwise selection.

GAM variable selection and model fitness

Each of the four models was tested independently, with unique dependent variables ([I] likelihood of colonization of individual fire-injured trees [tree-level preference], [II] proportion of fire-injured trees in a stand that were colonized [stand-level preference], [III] total offspring per sample for each colonized tree [tree-level performance], [IV] offspring per female for each infested stand [stand-level performance]) to describe the prediction addressed by each analysis. Given that models I and II were derived from presence/absence data, we considered the models within a binomial error distribution (logistic regression). Since models III and IV were constructed from count data, we used a Poisson distribution. Independent variables and their selection process followed the same criteria across model creation, with relevant tree- and stand-level variables placed in corresponding models (Table 2).

To thoroughly investigate the contribution of each tree-, stand-, and landscape-level variable to the preference and performance of DFB following a wildfire-caused resource pulse, we developed our models in three steps. First, we used a stepwise approach, beginning with all possible independent variables. Analysis of deviance tests were performed to assess variable significance (X^2 test, $p \leq 0.05$) and model contribution via residual deviance. Non-significant terms were successively removed until the model contained only significant predictors. Where relevant, hypothesized interaction terms were also tested during this process and retained if: (1) interactions were significant ($p \leq 0.05$), and (2) they increased overall explanatory power compared to models without them (higher adjusted R^2). Variables were assessed for multicollinearity and independence during this process, and where variables were correlated ($r \geq 0.80$) and/or were known to lack independence (i.e., tree height and dbh), they were considered in turn in "parallel models" to determine which of the variables best explained the data (see below).

Second, given that GAMs were used to capture nonlinearities in our system, significant variables were tested with and without smoothed terms. After variable selection, predictors were fit with a cubic regression spline at the minimum number of possible knots (k), indicating the flexibility of the spline fit. The model containing the spline variable was then tested against the model that contained the term without a smoothing regression (i.e., no spline, $k = 0$). Smoothed variables were retained only if they increased the overall explanatory power of the model through (1) decreasing residual deviance, (2) decreasing Akaike information criterion (AIC), and (3) increasing adjusted R^2 (R Core Team, 2023). If retained, the flexibility of smoothed variables followed strict protocols to prevent overfitting of the model by splines, a common issue for GAMs (Larsen, 2015). Increasing k values were tested until k reached the minimum number that increased explanatory power while passing the following tests for robustness using the *gam.check* function, where: (1) $p > 0.05$ for the smoothed term (indicating no significant trends of the residuals), (2) the effective degrees of freedom (edf) >1 (indicating a non-linear relationship), and (3) edf $< k$, indicating the flexibility of the cubic regression spline (k) appropriately fit the indicated non-linearity of the relationship via edf (*mgcv* package, Wood, 2022).

Finally, the best performing of the parallel models that included either tree height or dbh within groups I–IV was determined based on: (1) χ^2 test ($p \leq 0.05$) determining potential significant differences between models and their residual deviance, (2) adjusted R^2 values

TABLE 2 Generalized additive models created to assess the influence of fire injury, tree/stand characteristics, woodborer occupation, host availability and proximity to prior infestation on the colonization preference (model I, DFB infestation; model II, DFB proportion), and subsequent performance (model III, DFB offspring total; model IV, DFB *r*) of Douglas-fir beetle (DFB) among trees and stands following wildfires in south-central British Columbia, Canada.

Model	Dependent variables	Distribution	Independent variables
DFB preference and performance: Tree level			
I	DFB infestation	Binomial, Link = logit	dbh (cm)
III	DFB offspring total	Poisson	Tree height (m)
			Fire injury (% bole char)
			WB infestation (0/1); WB Occupation (%)
			Douglas-fir proportion (%)
			Stand density (stems/ha)
			Host availability (m^2); DFB distance (km)
			Plot[a]; fire complex[a]
DFB preference and performance: Stand level			
II	DFB proportion	Binomial, Link = logit	Average dbh (cm)
IV	DFB r (offspring/female)	Poisson	Average tree height (m); average fire injury (%)
			WB proportion (%)
			Douglas-fir proportion (%)
			Stand density (stems/ha)
			Host availability (m^2)
			DFB distance (km)
			Plot[a]; fire complex[a]

Note: Dependent terms and family distributions (based on data collection) are shown as all are potential independent terms which were tested using a stepwise approach during variable selection.

[a] Plot and fire complex structured as factors for model analysis.

indicating variance explained by each model, and (3) Bayesian information criterion (BIC; R Core Team, 2023). BIC was selected as our information-theoretic criterion to judge parallel model performance given our need to select among the fully parameterized models (Aho et al., 2014). Models that performed better (i.e., lower residual deviance, lower BIC, and higher adjusted R^2) were retained. All models passed applicable assumptions and were visualized using the *ggplot2* and *ggeffects* packages (Lüdecke, 2018; Wickham, 2016). Data and R-code used for all analyses are available in Dryad (Mitchell et al., 2025).

RESULTS

Model I: Tree-level preference

The probability of DFB colonization of individual trees (i.e., presence/absence) was influenced by the presence of woodborers (WB infestation), density of trees within stands (stand density), and degree of fire injury; however, the influence of fire injury was dependent upon tree size (fire injury × dbh) (Table 3; Figure 2).

DFB host preference in relation to fire injury was curvilinear, especially among larger trees, although the response by DFB to large, fire-injured trees was more variable than that to smaller trees (Figure 2a). Smaller trees (15 cm dbh) were unlikely to be attacked by DFB at any level of injury, whereas medium-sized trees (40 cm dbh) were attacked at low levels, with the highest likelihood of attack occurring when fire injury reached ~25% bole char. For the largest trees in a stand (>65 cm dbh), DFB also preferred moderate levels of injury, but the likelihood of attacks was approximately six times greater than that of medium-sized trees at the same level of injury. Beyond 20–30% fire injury, attacks became less likely (Figure 2a). DFB was increasingly likely to attack trees that were also colonized in the same season by woodborers (Figure 2b), although the within-season sequence of colonization is unknown. DFB also preferred trees in denser stands, with attack likelihood strongly increasing within stands with

TABLE 3 Generalized additive model fit statistics and variable parameters for models I: Tree-level preference, II: Stand-level preference, III: Tree-level performance, and IV: Stand-level performance by Douglas-fir beetle (DFB).

		Non-smoothed terms[a]				Smoothed terms[a]			
Model	**Dependent**	**Parameter**	**Estimate**	**SE**	**Z**	**Parameter**	**edf[b]**	**knots[b]**	**χ^2**
I: Tree-level preference	DFB infestation	WB infestation	2.582	0.380	6.79	Fire injury × dbh	1.06	3	4.69
		Stand density	0.004	0.001	5.33				
II: Stand-level preference	DFB infestation	WB proportion	5.049	0.923	5.47	Fire injury × dbh	3.58	4	32.3
		Stand density	0.003	0.001	4.77				
III: Tree-level performance	Offspring total					WB occupation × dbh	3.46	4	74.2
						Fire injury	2.46	4	23.9
						WB occupation × df proportion	4.42	5	40.7
IV: Stand-level performance	*r* (offspring/♀)	DFB distance	−0.190	0.048	−3.98	Fire injury × dbh	2.95	3	36.5
						WB proportion	1.96	3	30.3

Note: Independent parameters are described by their relevant model estimates and significance based on term smoothness.

[a] All parameters significant in models, $p < 0.001$.

[b] Numbers >1 indicate increasing non-linearity.

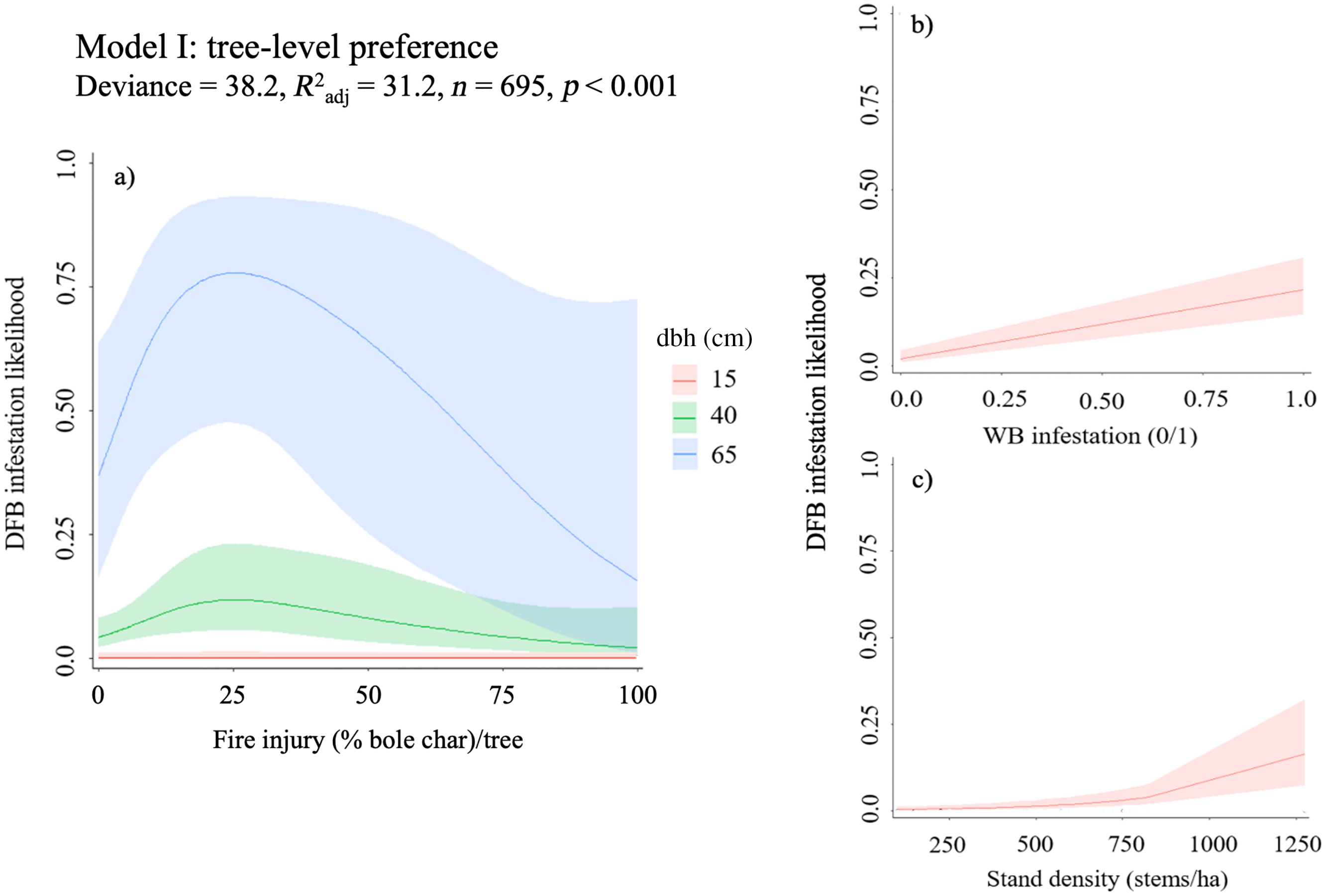


FIGURE 2 (a) Predicted likelihood of Douglas-fir beetle (DFB) infestation of individual trees in relation to the degree of fire injury (% bole charred) and tree size (dbh [1.3 m]). The influence of tree size (dbh) is shown in three size groups to visualize the interaction, with small trees (15 cm dbh) in red, medium-sized trees (40 cm dbh) in green, and large trees (60 cm dbh) in blue. (b) The likelihood of DFB infestation in relation to the presence/absence of cerambycid and buprestid woodborers. (c) The likelihood of DFB infestation in relation to stand density (stems per hectare). Solid lines are model fits, and shaded areas denote 95% CIs around the model prediction.

densities between 750 and 1250 stems per hectare (Figure 2c).

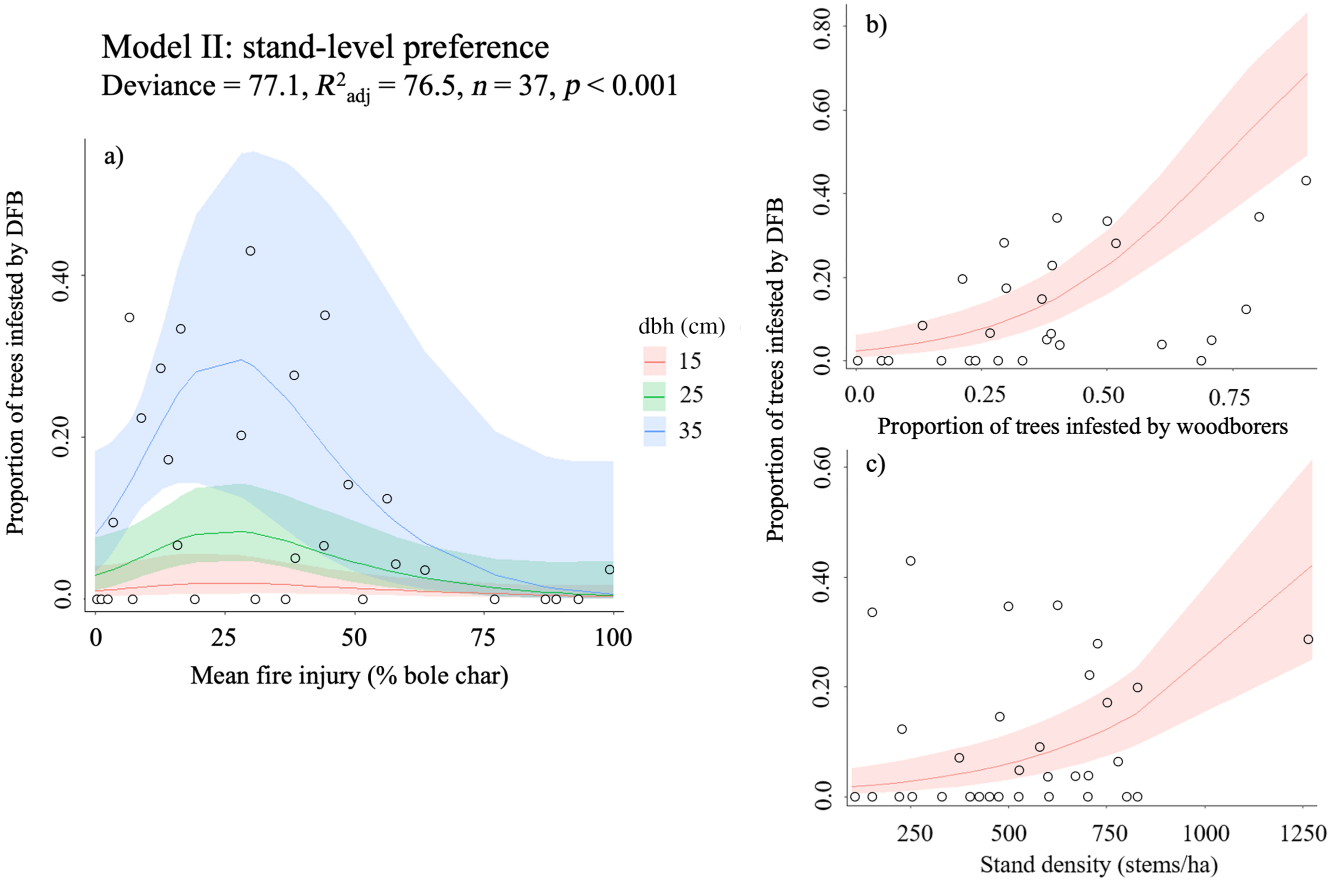
Model II: Stand-level preference

The proportion of trees infested by DFB within stands was dependent upon the proportion of trees occupied by woodborers within stands (WB proportion), the density of stands (stand density), and average fire injury of trees, but like tree-level preferences, the influence of fire injury was dependent upon average tree size (fire injury × dbh) (Table 3; Figure 3).

The preference of DFB for fire-injured stands was also curvilinear, with the peak proportion of infested trees increasing with increasing average tree size, although the predicted response by DFB to stands with large, fire-injured trees was again more variable than that to stands with smaller trees (Figure 3a). Stands containing smaller trees (15 cm average dbh) were unlikely to be attacked at any level of fire injury, and stands containing medium-sized trees (25 cm average dbh) were predicted to experience low-severity infestation at low to moderate levels of fire injury. Stands with the largest trees (35 cm average dbh) displayed the highest levels of predicted infestation, with the proportion of infestation approximately three times greater than for stands with trees averaging 25 cm diameter. Similar to DFB preference for individual trees (model I), the proportion of trees infested by DFB in a stand decreased at higher levels of average fire injury for all size classes (Figure 3a). The proportion of trees infested by DFB increased in stands that also contained a high proportion of buprestid and cerambycid infestation (Figure 3b), and DFB also preferred stands of increasing density (Figure 3c).

Model III: Tree-level performance

The total number of DFB emerging from bark samples from individual trees (i.e., DFB offspring) was influenced


Model II: stand-level preference

Deviance = 77.1, $R^2_{adj} = 76.5$, $n = 37$, $p < 0.001$

FIGURE 3 (a) Predicted proportion of trees infested by Douglas-fir beetle (DFB) within stands in relation to the degree of average fire injury (% bole charred) and mean tree size (dbh [1.3 m]). The influence of mean dbh is shown for three size groups to visualize the interaction, with small trees (15 cm mean dbh) in red, medium-sized trees (25 cm mean dbh) in green, and large-diameter trees (35 cm average dbh) in blue. (b) Predicted proportion of trees infested by DFB for stands in relation to the proportion of trees colonized by buprestid and cerambycid woodborers. (c) Predicted proportion of trees infested by DFB for stands in relation to stand density (stems per hectare). Solid lines are model fits, shaded areas denote 95% CIs around the model prediction, and points represent raw data.

by fire injury, the presence of woodborers, and size and availability of Douglas-fir trees (Table 3; Figure 4). DFB offspring production was greatest in trees with moderate levels of fire injury, declining both at low and high levels of bole charring (Figure 4c). Interestingly, the influence of woodborers in trees was dependent upon tree size (dbh) (Table 3; Figure 4a). As woodborer occupation increased, small trees (15 cm dbh) produced fewer DFB offspring, whereas medium-sized trees (30 cm dbh) demonstrated limited co-existence until ~10%–15% woodborer occupation, after which woodborers negatively affected DFB offspring totals (Figure 4a). In large trees (45 cm dbh), however, DFB offspring production tended to increase with increasing woodborer occupation up to ~25% of available phloem before declining to almost zero once woodborers reached 80% occupancy of the tree. The productivity of DFB in relation to woodborer occupation of trees was also dependent upon the proportion of Douglas-fir within a stand. In stands of mixed conifers (i.e., 75% Douglas-fir), the productivity of DFB declined significantly faster with increasing woodborer occupation than in stands of pure Douglas-fir (Table 3; Figure 4b).

Model IV: Stand-level performance

The potential rate of increase in DFB infestations within stands (i.e., *r*, offspring/female) was influenced by fire injury, tree size, the proportion of trees in a stand infested by woodborers, and the distance to prior DFB infestations (DFB distance) (Table 3, Figure 5). The number of DFB offspring/female was highest in stands with moderate fire injury, especially in stands with large trees (35 cm mean dbh), although the influence of tree size on offspring production was more variable in larger versus smaller trees (Figure 5a). Stands with small trees (15 cm mean dbh) were unlikely to yield DFB offspring at any fire injury level, but DFB infestations in stands with medium-sized trees (25 cm mean dbh) produced approximately 5 offspring/female at 50% average fire injury (Figure 5a). For stands with large-diameter trees, DFB productivity reached a maximum of 15 offspring/female

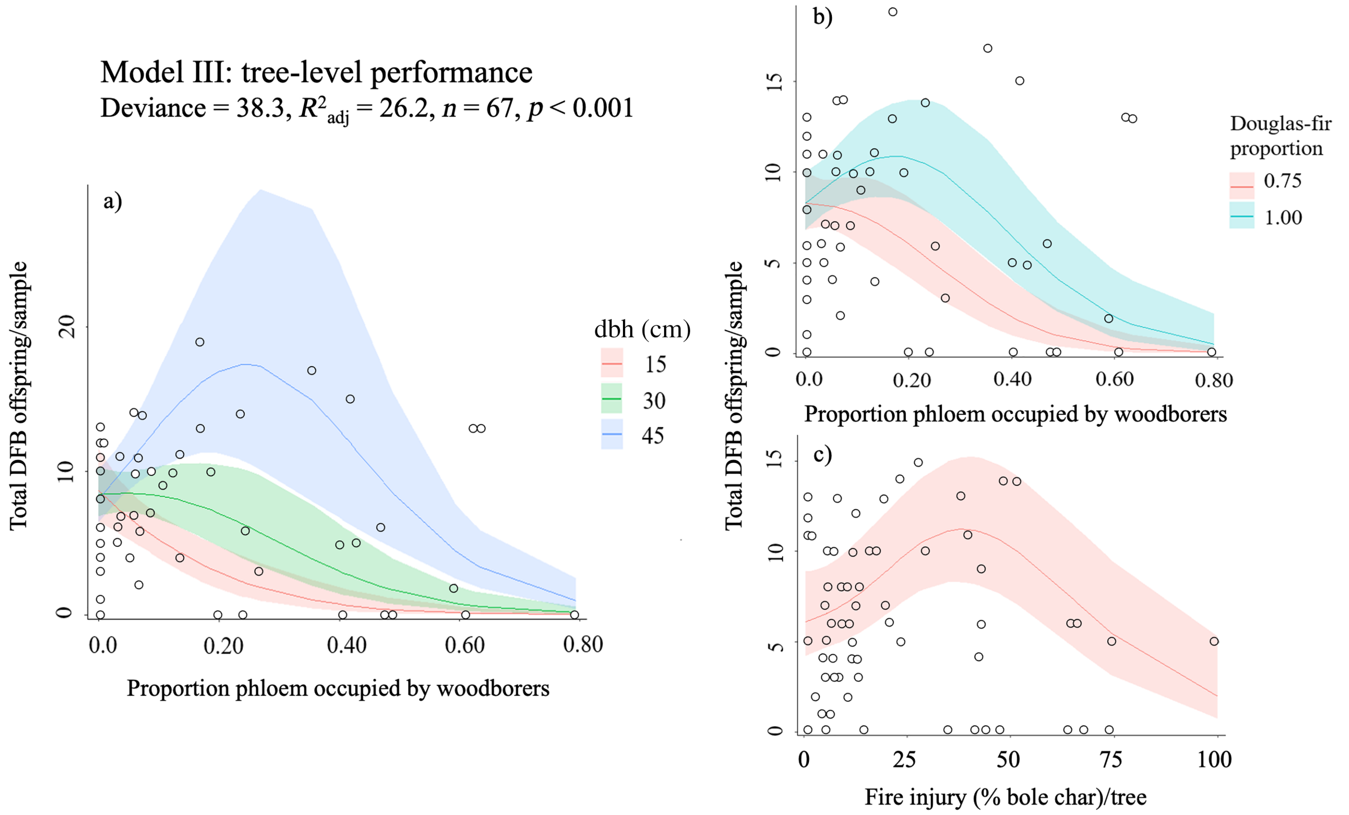


FIGURE 4 (a) Douglas-fir beetle (DFB) performance (total number of offspring per bark sample) for individual trees in relation to the amount of woodborer occupation (proportion of phloem occupied) and tree size (dbh [1.3 m]). The influence of dbh is shown in three groups to visualize the interaction, with red as small trees (15 cm dbh), medium trees in green (40 cm dbh), and large trees in blue (65 cm dbh). (b) DFB performance for individual trees in relation to the amount of woodborer occupation observed (proportion of phloem occupied) and the proportion of hosts in relation to total conifers within a tree's stand (Douglas-fir proportion). (c) DFB performance for individual trees as it relates to fire injury (% bole char) per tree. Solid lines denote the model, shaded areas indicate 95% CIs, and points represent raw data.

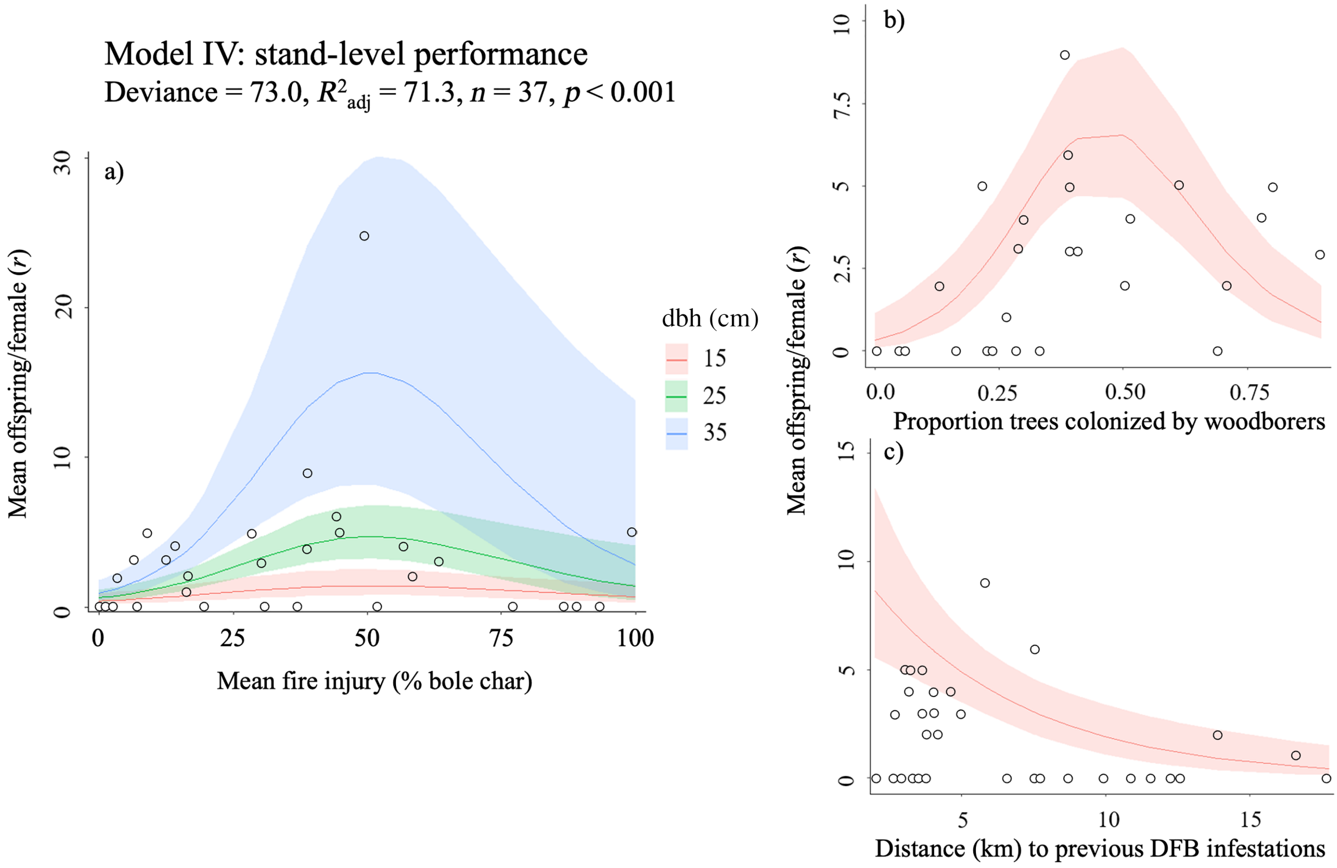


FIGURE 5 (a) Douglas-fir beetle (DFB) performance (mean offspring/female) for stands in relation to the degree of fire injury (average % bole char) and tree size (average dbh [1.3 m]). The influence of dbh is illustrated for three size groups to visualize the interaction: small dbh stands (15 cm average dbh) in red, medium-sized stands in green (25 cm average dbh), and large stands in blue (35 cm average dbh). (b) The performance of DFB for stands in relation to the proportion of trees colonized by buprestid and cerambycid woodborers (WB proportion). (c) DFB performance for stands in relation to their distance to previous DFB infestations (DFB distance). Solid lines denote the model, shaded areas indicate 95% CIs, and raw values are represented by points.

at 50% average fire injury; >3 times higher than stands with medium-sized trees, and >10 times higher than stands with smaller trees (Figure 5a). Beyond 50% average fire injury, the number of DFB offspring/female steeply decreased for all stands. Productivity of DFB infestations was also influenced by the proportion of trees infested by woodborers within stands, with offspring/female increasing with increasing woodborer proportion until a maximum of 50% of trees within a stand were colonized by woodborers, after which offspring/female decreased (Figure 5b). Additionally, DFB productivity within stands was affected by the distance to prior infestations, with the number of offspring/female doubling if they were within 5 km of a stand compared to 10 km (Figure 5c).

DISCUSSION

Douglas-fir beetle populations increased rapidly in response to pulses of high-quality phloem following wildfires that were otherwise unavailable to them. Existing studies indicate that stand conditions and fire injury influence DFB dynamics. Specifically, fire injury (Cunningham et al., 2005; Furniss, 1965), tree size (Hood & Bentz, 2007), and stand density (Negron, 1998) have been suggested as important predictors of DFB preference and productivity that increase the risk of an outbreak. Though the results presented herein concur with existing studies, we demonstrate that the response by DFB to a resource pulse associated with wildfire was contingent upon complex interactions leading to non-linear outcomes such that a localized population increase was not always observed or assured.

Factors influencing DFB preference were consistent across spatial scales, with fire injury and tree/stand characteristics predominantly affecting colonization patterns when subcortical competitors were absent. DFB preferred to colonize larger trees; however, this preference was dependent upon fire severity, with larger trees requiring greater injury than smaller trees. This suggests that beetles preferentially colonize large trees with sufficient injury to impair defensive responses, but with phloem that has not been degraded by heat, a key characteristic of pulse-driven irruptive species (Howe et al., 2022; Raffa et al., 2008) that seek to maximize access to thick phloem while minimizing exposure to tree defenses (Lindgren & Raffa, 2013). Though other studies have suggested that tree size and fire severity may increase the risk of bark beetle irruptions after fire (e.g., Cunningham et al., 2005; Powell et al., 2012), our results indicate that this outcome is nonlinear and varies not only with fire injury levels but also with tree size and density. The likelihood of DFB colonization increased with the density of available hosts, in agreement with other studies of DFB outbreaks (Negron, 1998). While our models indicate a positive relationship with host density across spatial scales, we expect this relationship to become negative at higher densities (>1250 stems/ha) due to decreases in quantity/quality of phloem with higher inter-tree competition (Amman & Baker, 1972).

In the absence of subcortical competition, the reproductive output of DFB was largely a function of phloem quality and availability. Consistent with known beetle preference, the number of DFB offspring produced within individual trees was greatest in the largest trees with moderate fire injury. Although previous studies have suggested that DFB productivity is greater in larger, fire-injured trees (Cunningham et al., 2005; Hood & Bentz, 2007), our results show that even in the largest trees, the fitness of beetles declines when fire injury exceeds approximately one third of the bole. At the stand scale, the potential for population increase was also dependent upon the interaction of fire injury and tree size, indicating that there is an optimal coincidence of fire severity (moderate injury) and host-tree quality (large size) that facilitates DFB population growth during the first year following fire. In addition, proximity to recent infestations influenced DFB reproductive success within stands, indicating that immigration of beetles from adjacent areas is likely important for recruitment to mass attacks and colonization success. High local population densities of DFB are likely to increase aggregation and mating success. Furthermore, increased flight distances are associated with decreased fat reserves and lower realized fecundity in bark beetles (Elkin & Reid, 2005; Williams & Robertson, 2008). Thus, the size and proximity of populations of an irruptive species like DFB may influence outbreak probabilities after disturbance-related resource pulses. Taken together, these results suggest that in the absence of other constraints, mature Douglas-fir ecosystems with large trees exposed to moderate levels of fire injury, and in close proximity to ongoing epidemic DFB infestations, are most likely to be the source of rapidly growing DFB populations in the year after wildfires.

Although the preference and performance of DFB was consistently highest within large trees with moderate fire injury, the fits of our models at the tree and stand scale were weakest among the trees in the largest size class. It is well known that beetles from high-density populations preferentially colonize large trees, but their preference for tree size may vary with population size (reviewed by Aukema et al., 2016). Furthermore, among aggressive *Dendroctonus* species, their preference for large trees while in the epidemic state has evolved given the propensity of these trees to offer high-quality phloem (Lindgren & Raffa, 2013); however, the relationship between tree size and phloem quantity/quality in Douglas-fir can vary as mature trees are exposed to adverse conditions or begin to senesce (Shore et al., 1999). Thus, the variation in DFB preference among large trees may reflect differences in host preference associated with variation in population densities over the landscape, while variation in their productivity in bigger trees may be the consequence of a weak relationship between tree size and phloem quantity/quality. Future research into the interrelationships among bark beetles, host trees, and wildfire should seek to quantify as much as possible the density of beetles over the landscape and the condition of phloem within their host trees.

Consistent with our prediction, woodboring beetles regularly co-occurred in trees with DFB and appeared to constrain its irruptive potential. The presence of woodborers was a significant predictor of the likelihood of DFB colonization and subsequent performance among trees and stands. The likelihood of infestation by both DFB and buprestid/cerambycid woodborers increased following fire at the tree- and stand-level, indicating that the same trees that were vulnerable to bark beetle attacks were also susceptible to woodborer colonization. Kitchens et al. (2022) demonstrated that woodborers preferentially attack moderately injured trees after fires, suggesting that they are attracted to the same hosts as bark beetles during resource pulses and may act more aggressively under disturbed conditions than previously considered. Additionally, woodborer occupation affected DFB reproductive success. Within trees, the relative effect of woodborer competition on DFB productivity decreased with increasing tree size, indicating that competitive effects relaxed in larger trees putatively due to thicker phloem. However, this effect diminished with increasing woodborer density such that when the percentage of phloem occupied by woodborers exceeded 60%, DFB produced few offspring from co-attacked trees of any size. Within-tree competition was significantly influenced by stand composition; DFB produced more offspring per tree in pure Douglas-fir stands than in mixed-species environments (75% Douglas-fir). Increasing flight and foraging time have been linked to decreased bark beetle fecundity due to energy expenditure trade-offs between dispersal and reproduction (Elkin & Reid, 2005; Wijerathna & Evenden, 2019). Thus, DFB females in pure Douglas-fir stands should expend less energy during host selection than those in mixed-species stands, leading to increased offspring production per tree despite the presence of woodborers. Among stands, the competitive effect of woodborers also constrained the rate of increase in DFB populations. Stands with <50% trees colonized by woodborers were associated with static to increasing DFB populations (offspring/female [r] > 2.5; Ministry of Forests, 1995), indicating successful guild co-existence. Conversely, occupation of >50% of stems by woodborers was associated with declining values of r for DFB such that when the proportion of fire-injured trees with woodborers exceeded 75%, DFB populations were expected to decline (offspring/female [r] < 2.5; Ministry of Forests, 1995), and no DFB emergence was observed in stands approaching 100% woodborer occupancy.

Although prior studies have investigated relationships between bark beetles and other subcortical species (Dodds et al., 2001; Rankin & Borden, 1991), there remains a paucity of work describing the extent of subcortical inter-guild competition and its effects on bark beetle population dynamics. Our observations of bark beetles and phloeophagous woodborer co-occurrence in dry-interior forests after fire suggest a degree of interaction that has not been attributed to this system. Bark beetles and woodborers are generally thought to infest conifers in temporal succession, with bark beetles functioning as "primary" disturbance agents causing tree mortality and woodborers as "secondary" to them, causing phloem and sapwood degradation after bark beetle-induced mortality (Coulson, 1979; Furniss & Carolin, 1977; Raffa et al., 2015). Existing reports of bark beetle and woodborer co-infestation often describe spatially or temporally distinct niche occupation within individual trees (Ray et al., 2019; Ryan & Amman, 1996). We propose this may be the case for undisturbed forests, where the absence of a resource pulse limits subcortical insect populations and maintains niche separation between guilds. In contrast, we suggest that this temporal sequence breaks down under highly disturbed conditions, with events like wildfires allowing for "secondary" agents such as woodborers to invade the niche occupied by "primary" bark beetles (Kitchens et al., 2022). This phenomenon may lead to direct competition within the phloem, with asymmetric outcomes mediated by the larger body size of woodborers, thus limiting the potential for bark beetle irruptions (Pimentel et al., 2023; Schroeder & Weslien, 1994). Additionally, woodborers may act as facultative predators, actively seeking out bark beetle larvae under conditions of co-occurrence (Dodds et al., 2001; Schoeller et al., 2012), though further research is required to fully characterize this interaction after wildfires.

Tools to mitigate potentially negative consequences of disturbance interactions are vital in forested landscapes increasingly prone to disturbance. Although population irruptions by resource pulse-driven bark beetles are common outcomes following abiotic and biotic disturbances (Raffa et al., 2008), they are spatially and temporally difficult to predict after wildfires (reviewed by Fettig et al., 2022). We have shown that when large populations of cerambycid and buprestid woodborers are present, the increase in DFB populations after fire may be constrained. Thus, semiochemical-based monitoring of woodborer abundance (reviewed by Allison & Redak, 2015) may help predict the likelihood of local bark beetle increases after disturbance, though additional research on this aspect is required. More broadly, forest management practices that promote habitat for phloeophagous woodborers could help mitigate population irruptions and potential outbreaks by resource pulse-driven bark beetles, although this tactic may contradict efforts to minimize fuels for wildfires (Fettig et al., 2022).

The dry-interior forests of western North America are increasingly at risk of climate-mediated disturbances. Since 2000, there have been multiple record-breaking fire seasons (Parisien et al., 2023), extreme heat (Zhang et al., 2023), severe droughts (Overpeck & Udall, 2020), and widespread bark beetle outbreaks (Fettig et al., 2022). With the increasing likelihood of these stressors affecting dry conifer forests, the probability of outbreaks by resource pulse-driven species also increases and poses questions regarding their potential to affect forests at novel frequencies, severities, and scales. Our investigation reveals that interactions among disturbance agents are complex and context-dependent, with population irruptions by resource pulse-driven bark beetles following wildfires dependent upon the response of local subcortical competitors.

AUTHOR CONTRIBUTIONS

Katherine A. Mitchell, Lori D. Daniels, and Allan L. Carroll conceived the ideas and designed the methods. Katherine A. Mitchell collected and analyzed the data. Katherine A. Mitchell wrote the manuscript in collaboration with Lori D. Daniels and Allan L. Carroll. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R-code (Mitchell et al., 2025) are available in Dryad at https://doi.org/10.5061/dryad.dv41ns262.

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