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 2 **Bark beetle effects on fuel profiles across a range of stand structures in**
 3 **Douglas-fir forests of Greater Yellowstone**

4
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 12

13 **Abstract**

14 Consequences of bark beetle outbreaks for forest wildfire potential are receiving
 15 heightened attention, but little research has considered ecosystems with mixed-severity fire
 16 regimes. Such forests are widespread, variable in stand structure, and often fuel-limited,
 17 suggesting that beetle outbreaks could substantially alter fire potentials. We studied canopy and
 18 surface fuels in interior Douglas-fir [*Pseudotsuga menziesii* v. *glauca*] forests in Greater
 19 Yellowstone, Wyoming, USA, to determine how fuel characteristics varied with time since
 20 outbreak of the Douglas-fir beetle (*Dendroctonus pseudotsugae*). We sampled five stands in
 21 each of four outbreak stages, validated for pre-outbreak similarity: green (undisturbed), red (1-3
 22 yr), gray (4-14 yr), and silver (25-30 yr). General linear models were used to compare variation
 23 in fuel profiles associated with outbreak to variation associated with the range of stand structures
 24 (dense mesic forest to open xeric parkland) characteristic of interior Douglas-fir.

25 Beetle outbreak killed 38-83% of basal area within stands, generating a mix of live trees
 26 and snags over several years. Canopy fuel load and bulk density began declining in the red stage
 27 via needle drop and decreased by ~50% by the silver stage. The dead portion of available
 28 canopy fuels peaked in the red stage at 41%. After accounting for background variation, there

29 was little effect of beetle outbreak on surface fuels, with differences mainly in herbaceous
 30 biomass (50% greater in red stands) and coarse woody fuels (doubled in silver stands). Within-
 31 stand spatial heterogeneity of fuels increased with time since outbreak, and surface-to-crown
 32 continuity decreased and remained low because of slow/sparse regeneration. Collectively, results
 33 suggest reduced fire potentials in post-outbreak stands, particularly for crown fire after the red
 34 stage, although abundant coarse fuels in silver stands may increase burn residence time and heat
 35 release. Outbreak effects on fuels were comparable to background variation in stand structure.
 36 The net effect of beetle outbreak was to shift the structure of mesic closed-canopy stands toward
 37 that of parklands, and to shift xeric parklands toward very sparse woodlands. This study
 38 highlights the importance of evaluating outbreak effects in the context of the wide structural
 39 variation inherent to many forest types in the absence of beetle disturbance.

40
 41 **Keywords** disturbance interaction, mixed-severity fire regime, lower montane forest, fuel
 42 complex, fuel loads, fuel heterogeneity, Douglas-fir beetle, *Dendroctonus pseudotsugae*,
 43 *Pseudotsuga menziesii*, Rocky Mountain Douglas-fir

44

45 **Introduction**

46 Outbreaks of native bark beetles (*Dendroctonus* spp.) have recently resulted in
 47 widespread tree mortality across tens of millions of hectares of forest in western North America
 48 (Raffa et al. 2008). The resulting areas of abundant dead trees have led to key management
 49 concerns regarding the potential for altered fire behavior and related effects on forest resources
 50 (Jenkins et al. 2008, Jenkins et al. 2012). Emerging research shows that beetle outbreaks can
 51 substantially change the arrangement, quantity, and composition of forest fuels (i.e., fuel
 52 profiles), but significant knowledge gaps remain with respect to this disturbance interaction
 53 (Hicke et al. 2012). Reciprocal interactions between insect outbreaks and wildfires are
 54 increasingly important to understand, as warming climate is implicated in both recent and
 55 projected increases in both disturbances (Bentz et al. 2010, Westerling et al. 2011).

56 Although research has begun to address the effects of bark beetle outbreaks on fuels and
 57 fire behavior/effects (Bebi et al. 2003, Kulakowski and Veblen 2007, Page and Jenkins 2007a,b,
 58 DeRose and Long 2009, Klutsch et al. 2011, Simard et al. 2011, Hoffman et al. 2012a,b,
 59 Schoennagel et al. 2012), studies to date have focused almost exclusively on forests with
 60 climate-driven, stand-replacing fire regimes. For example, bark beetle-induced mortality has
 61 been found to significantly alter fuel profiles in *Pinus contorta* and *Picea engelmannii* forests,
 62 but it is acknowledged that such forests generally burn at high-severity with or without prior
 63 beetle outbreaks (Klutsch et al. 2011, Schoennagel et al. 2012). In contrast, drier, lower montane
 64 forests with mixed-severity fire regimes have received almost no study in this regard, despite
 65 being among the most widespread fire regimes in the temperate zone (Halofsky et al. 2011).
 66 Highly variable in structure and typified by sensitive thresholds between surface and crown fire
 67 behavior, these systems can be comparatively fuel-limited, such that changes in stand structure

68 may have important influences on fire potentials (Perry et al. 2011). Drier forests are speculated
 69 to respond differently to bark beetle outbreaks due to more open conditions, greater herbaceous
 70 cover, lower biomass, or lower tree crown base heights (Parker et al. 2006, Jenkins et al. 2008,
 71 Hicke et al. 2012); however this hypothesis has received little empirical study.

72 Interior Douglas-fir (*Pseudotsuga menziesii* v. *glauca*) forests provide a key example of
 73 lower montane, mixed-severity fire ecosystems affected by bark beetle outbreaks (*Dendroctonus*
 74 *pseudotsugae*). Characterized by both surface and crown fires over time and space (Baker 2009),
 75 interior Douglas-fir forests often possess fuel structures more similar to dry *Pinus ponderosa*
 76 forests than to *Pinus contorta* or mixed-conifer types (Cruz et al. 2003). Additionally, Douglas-
 77 fir comprises an exceptionally broad range of stand structure and composition, from dense
 78 closed-canopy forests on mesic sites to open parklands on xeric sites — the latter often ecotonal
 79 with low-elevation grasslands (Fig. 1; Despain 1990, Barrett 1994, Heyerdahl et al. 2006).
 80 Because bark beetle impacts on fuel profiles vary strongly depending on the state of the system
 81 prior to outbreak (DeRose and Long 2009, Klutsch et al. 2011, Hicke et al. 2012), variable
 82 forests such as Douglas-fir likely respond differently not only from other forest types but also
 83 among stands within the forest type.

84 We conducted a field study to examine the effects of Douglas-fir beetle outbreaks on fuel
 85 profiles of Douglas-fir forests in the Greater Yellowstone Ecosystem (GYE). Epidemic
 86 outbreaks (large-scale “mass attacks” of healthy live trees) in the 1980s, 1990s, and 2000s
 87 afforded an opportunity to quantify fuel profiles in stands of differing time since outbreak, across
 88 a wide range of pre-outbreak stand structures. Stands with ongoing/recent (1-3 yr), intermediate-
 89 term (4-14 yr), and old (25-30 yr) outbreaks were compared to each other and to undisturbed
 90 forests in terms of stand structure and fuel characteristics. We addressed the following

91 questions: 1) How do fuel profiles that affect fire potentials vary among stands of differing time
 92 since bark beetle outbreak?, and 2) How do variations in fuel profiles associated with outbreak
 93 compare to variations associated with the wide range of stand structures for which Douglas-fir
 94 forests are known (dense mesic forests to open xeric parklands; Baker 2009)?

95 Bark beetle outbreaks are expected to initially reduce stand-level foliar moisture via tree-
 96 crown deaths (briefly increasing crown fire initiation and spread potential), then thin canopies
 97 via needle/branch drop (reducing crown fire spread and energy release potential), increase
 98 surface loading of both live and dead fuels via increased light availability and needle/branch drop
 99 (increasing potential surface fire intensity and torching into tree crowns), and, in later stages,
 100 increase ladder fuels via growth of regenerating trees (increasing torching potential) (Page and
 101 Jenkins 2007a,b, Jenkins et al. 2008, DeRose and Long 2009, Klutsch et al. 2011, Simard et al.
 102 2011, Hicke et al. 2012, Hoffman et al. 2012b, Schoennagel et al. 2012). We hypothesized that,
 103 compared to other studied systems, lower montane forests would exhibit greater increases in live
 104 herbaceous fuels, lesser increases in coarse woody fuels, and higher importance of canopy fuel
 105 reductions because of already abundant herbaceous understories and relatively sparse trees. We
 106 further hypothesized increased within-stand spatial heterogeneity in fuels after beetle outbreak,
 107 and that outbreak effects on fuels would be larger than the variability in background conditions.

108 To our knowledge this study represents one of the most detailed field assessments of
 109 post-disturbance fuels conducted to date, and the first to specifically compare disturbance effects
 110 to background variation in stand structure. We build on the methods of Simard et al. (2011) and
 111 Schoennagel et al. (2012) — comprehensively sampling fuels in a replicated series of stands
 112 validated for pre-outbreak similarity via dendrochronology. We expand on prior work by
 113 refining canopy fuel estimates in post-outbreak stands and by evaluating changes in within-stand

114 heterogeneity in fuels, as the spatial arrangement (not just mean loading) of live and dead fuels
 115 could influence fire propagation. Our focus is on fuel profiles rather than modeled fire behavior
 116 because currently available models have known shortcomings in post-disturbance environments
 117 that are yet to be resolved, and thus only account for a portion of beetle effects on fuels (Jenkins
 118 et al. 2008, Cruz et al. 2010, Klutsch et al. 2011, Hicke et al. 2012); as such, fuel profiles
 119 effectively contain more comprehensive and reliable information than fire models for this
 120 application. We report the key variables that drive fire models plus several for which available
 121 models cannot currently account (e.g., dead-tree foliar moisture, changes in spatial
 122 heterogeneity).

123

124 **Methods**

125 *Study area*

126 The Greater Yellowstone Ecosystem is centered in northwest Wyoming, USA,
 127 comprising ~80,000 km² of mountains and plateaus associated with the Yellowstone super-
 128 volcano. The area is representative of the Middle Rocky Mountains ecoregion which extends
 129 over 200,000 km² of interior, largely coniferous montane forests (Omernik 1987). Our study
 130 occurred in the Lamar River drainage in northern Yellowstone National Park (“north zone;”
 131 latitude/longitude 44° 55’ N, 110° 15’ E), and the upper Snake River drainage in and around
 132 Grand Teton National Park (“south zone;” 43° 52’ N, 110° 26’ E). Both zones are characterized
 133 by mean July high temperature of 25 °C and mean January low of -15 °C, while mean annual
 134 precipitation is 34 and 64 cm in the north and south zone, respectively
 135 (www.prism.oregonstate.edu). Slopes of study sites range from 10-30° (mean 22°) on all

136 aspects, at elevations between 2000 and 2350 m. Soils are well-drained and non-rhyolitic,
 137 derived from both sedimentary and volcanic/metamorphic parent materials.

138 Douglas-fir covers ~30% of the forested area of the GYE, typically occupying steep
 139 terrain at middle to low elevations. Common associates in mesic sites include lodgepole pine
 140 (*Pinus contorta* v. *latifolia*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies*
 141 *lasiocarpa*); and in xeric sites include limber pine (*Pinus flexilis*) and Rocky Mountain juniper
 142 (*Juniperus scopulorum*). Abundant understories of tree regeneration, woody shrubs, and herbs
 143 are common in mesic sites, while open understories dominated by grasses and herbs are typical
 144 of xeric sites (Fig. 1). The fire ecology of interior Douglas-fir forests is poorly understood
 145 compared to other Rocky Mountain forest types, but the few published studies indicate a mixed-
 146 severity fire regime with small, low- to moderate-severity fires occurring at ~20-80 year intervals
 147 (prior to effective fire exclusion) and large or stand-replacing fire events occurring at longer
 148 intervals of perhaps 100-200 years (Houston 1973, Loope and Gruell 1973, Barrett 1994, Littell
 149 2002, Korb 2005, Huerta et al. 2006, Baker 2009). The balance of these fire types almost
 150 certainly varies across the xeric-mesic gradient that Douglas-fir occupies, but such variation
 151 remains largely unstudied.

152 The Douglas-fir beetle is an important native disturbance agent in Douglas-fir forests,
 153 usually killing small groups of stressed or dying trees, but occasionally reaching epidemic
 154 population levels that mass attack healthy live trees in outbreaks across large tracts of forest
 155 (Schmitz and Gibson 1996). Trees are attacked in early summer as adults bore under the bark
 156 and excavate galleries along which females oviposit. Tree mortality occurs via girdling of the
 157 phloem layer by larvae and effects of associated fungi (Schmitz and Gibson 1996). After
 158 successful attack, a tree's foliage turns red within a year, then drops from the canopy over the

159 course of ~1-4 years. Stands are typically infested over the course of 4-6 years and only a
 160 portion of trees within a stand are killed (Negron 1998, McMillin and Allen 2003), generating a
 161 fine-scale mix of live trees and dead trees in varying stages of post-attack condition.

162

163 *Sampling design*

164 We measured forest fuels in 20 Douglas-fir stands that included undisturbed and up to
 165 30-year post-outbreak conditions. Sampling was conducted in 2010 and included five stands in
 166 each of the following time-since-outbreak (TSO) classes commonly described in the literature
 167 (e.g., Simard et al. 2011): green (undisturbed); red stage (1-3 yr post-outbreak, with >50% of
 168 beetle-killed basal area retaining red needles and/or trees still being attacked); gray stage (4-14 yr
 169 post-outbreak, all beetle-killed trees with <<50% needle retention, most fine branches still intact,
 170 no new attack occurring); and silver stage (25-30 yr post-outbreak, beetle-killed trees
 171 deteriorating structurally, a.k.a. ‘old-attack’). Each class was sampled to span the continuum of
 172 Douglas-fir stand structures present in the GYE, from open xeric parklands to closed-canopy
 173 mesic forests (Fig. 1). Sample stands were multi-aged but had dominant trees ~150-200 years
 174 old; thus our data may be most relevant to forest of similar age, which are among the most
 175 commonly affected by *Dendroctonus* outbreaks. No signs of other recent disturbances were
 176 evident in the field or in agency fire history records. All stands within a class were separated by
 177 at least 1.7 km (mean 53 km apart), were interspersed with the other classes geographically, and
 178 were sampled in both the north and south zones. Abiotic characteristics of slope, aspect,
 179 elevation, and soil origin were all similar among the TSO classes (Table 1).

180 We used dendrochronological analysis (Appendix A) on 250 live-tree cores and 75 dead-
 181 tree samples to a) reconstruct initial stand conditions and verify that all classes were similar prior

182 to outbreak, and b) verify the outbreak severity and timing of each TSO class (Johnson and
 183 Miyanishi 2008, Simard et al. 2011). In brief, stand reconstruction entailed subtracting post-
 184 outbreak growth and recruitment from the basal area of currently living trees, and adding in
 185 beetle-killed basal area after adjusting for falling, bark loss, and desiccation shrinkage (Appendix
 186 A). To establish outbreak timing, we cross-dated samples from beetle-killed trees against master
 187 chronologies constructed for each of the north and south sampling zones (Appendix A; Donato
 188 and Timme 2012). This analysis confirmed that all classes had similar pre-outbreak basal area
 189 (mean $46.3 \text{ m}^2 \text{ ha}^{-1}$), stem density (mean 378 ha^{-1}), quadratic mean tree diameter (mean 29.5 cm),
 190 and Douglas-fir dominance (mean 93%) (Table 1). Outbreak timing was confirmed to be 1-3
 191 years prior to sampling for red stands, 4-14 years for gray stands, and 25-30 years for silver
 192 stands. Outbreak severity in beetle-affected stands was verified to be highly similar among TSO
 193 classes in both absolute and relative terms (Table 1).

194
 195 *Field measurements*

196 We measured stand structure and fuels in a 0.25-hectare (50x50 m) plot within each of
 197 the 20 stands. To assess canopy fuels, trees $>1.4 \text{ m}$ height were surveyed in three parallel 6x50
 198 m transects (300 m^2 each), spaced at 25-m intervals. For each live tree rooted in the transects, we
 199 recorded species, diameter at breast height (dbh; 1.4 m above ground), and total height and
 200 crown base height using a laser rangefinder/clinometer. Crown base height was considered the
 201 lowest vertically contiguous green/red needles, usually the first full whorl. Dead trees were also
 202 recorded for standing/down status, broken top presence and height, decay class (1-5, adapted
 203 from Harmon et al. (2011) to emphasize branch and bark loss), evidence of bark beetle attack
 204 (adult and larval galleries, exit holes, boring frass), and red needle retention level (100%

205 retention/fading, >50% retention, <50% but >5% retention, or <5% retention). For needle-less
 206 dead trees that retained fine branches, which could still support transition to crown fire, we
 207 estimated crown base height using stand-specific outputs from a general linear model relating
 208 crown base height to dbh and stand for 1171 trees having both measurements ($R^2 = 0.60$)
 209 (Simard et al. 2011, Schoennagel et al. 2012). Trees <1.4 m height were measured for species,
 210 live/dead status, height, and crown base height. Canopy cover was measured at 12 systematic
 211 points within each stand using a spherical densiometer with one user.

212 Surface fuels were measured along ten 20-m long planar intercept transects (Brown 1974)
 213 originating at regular intervals along the outer tree transects. Five surface fuel transects were
 214 oriented in the SW-NE direction, and five in the NW-SE direction. Down wood particles <0.64
 215 cm (1-h fuels) and 0.64-2.54 cm (10-h fuels) were tallied along a 2-m subsection of each
 216 sampling plane, particles 2.54-7.62 cm (100-h fuels) were tallied along a 5-m subsection, and
 217 particles >7.62 cm (1000-h fuels) were recorded for diameter, species, and decay class along the
 218 entire 20-m sampling plane. Depths of the litter (recognizable organic matter) and duff
 219 (decayed, unrecognizable organic matter) layers were recorded at 2 systematic points along each
 220 transect, and dead fuel depth (distance from bottom of litter layer to highest particle in plane)
 221 was recorded in three systematic 0.5-m intervals along each transect. Surface vegetation and
 222 ground cover characteristics were recorded in twenty 0.25-m² microplots, one at the start and end
 223 of each of the 10 planar intercept transects. We recorded percent cover and height of tall woody
 224 shrubs (>20 cm height), low shrubs, herbs, and graminoids; and percent cover of litter, wood,
 225 bryophytes, bare soil, and rock.

226 To assess effects of beetle outbreak on surface temperatures and relative humidities
 227 during summer (i.e., fire season), we deployed micrometeorological probes in three stands in

228 each TSO class (iButton, Maxim Integrated Products, Dallas Semiconductor, Sunnyvale,
 229 California, USA). Measured stands spanned the range from cool to warm aspects in each class
 230 (Kruskal-Wallis test on cosine-transformed aspect versus TSO class, $P=0.87$, mean 1.0 out of
 231 possible range 0-2). In each stand an air temperature and relative humidity (RH) probe in a
 232 ventilated white PVC tube was installed on a tree at 1.5 m above ground level. Temperature
 233 probes were also installed at the litter-duff interface at three systematic locations in each stand.
 234 Temperature and RH were recorded every 2 hours with a resolution of 0.5 °C and 0.6%,
 235 respectively, between 10 July and 15 August 2010. For analysis we summarized temperature
 236 and RH data into daily mean and daytime-hours (1000-1800 hours) mean values.

237

238 *Fuel computations*

239 We used field data to generate a comprehensive fuel profile for each stand. These data
 240 provide very similar inference as common fire models, as they include the main variables which
 241 drive model outputs, plus others for which models cannot currently account. Chief among the
 242 model-driving responses are canopy bulk density (amount of fuel per unit volume of canopy, a
 243 determinant of mass flow rate and spread potential of crown fire), available canopy fuel load
 244 (potential energy available for release from crown fuels), canopy base height (vertical gap
 245 beneath the base of tree crowns, which affects the ability of fire to move vertically from the
 246 surface to the canopy), and surface fuel loads by size class and live/dead category (which affect
 247 fireline intensity, spread, and transition to crowns) (see Van Wagner 1977, Rothermel 1983,
 248 Cruz et al. 2003, Reinhardt and Crookston 2003, Reinhardt et al. 2006).

249 Crown fuel masses of foliage and 1-h, 10-h, and 100-h woody fuels were estimated for
 250 each tree using species-specific equations for Rocky Mountain conifers based on dbh, height,

251 and/or crown length (Brown 1978). Following convention, we use the term ‘crown’ for tree-
 252 level metrics and ‘canopy’ for stand-level metrics (Cruz et al. 2003). For dead trees, each
 253 individual was corrected for loss of needle biomass based on a multiplier representing the
 254 midpoint of its red-needle retention level: 1.0, 0.75, 0.25, and 0.0, respectively, for the
 255 fading/100%, 50-100%, 5-50%, and <5% red-needle ratings. This approach allows for all red
 256 trees to retain all their needles if the outbreak is recent and synchronous. We similarly corrected
 257 for branch loss using the decay class rating of each dead tree (adapted from Harmon et al. 2011):
 258 1-h fuels were designated as 0% loss for decay class 1 and 100% loss for all other decay classes;
 259 10-h and 100-h fuels were designated across decay classes 1-5 as 0%, 20%, 50%, 80%, and
 260 100% loss, respectively. Broken-top trees had a fraction of their crown fuel deducted based on
 261 the ratio of remaining crown length to original crown length derived from a crown length : dbh
 262 regression for 1018 unbroken trees in our dataset ($R^2 = 0.78$).

263 Available canopy fuel load (ACFL) was computed as the sum of live and dead foliage,
 264 plus 50% of the live 1-h fuels and 100% of dead 1-h fuels, across all trees (Reinhardt et al.
 265 2006). Vertical profiles of canopy fuels were generated by distributing available crown fuel for
 266 each tree along its crown length in 0.25-m vertical bins, and summing by bin across all trees in a
 267 stand. This approach is employed by the Fire and Fuels Extension of the Forest Vegetation
 268 Simulator (Reinhardt and Crookston 2003) and in several studies of canopy fuels (Reinhardt et
 269 al. 2006, Simard et al. 2011, Schoennagel et al. 2012). Although the method assumes a vertically
 270 uniform distribution of fuels along individual tree crowns, other crown-shape equations are not
 271 available for species in our study area and, most importantly, this method has been validated via
 272 independent field data to produce unbiased canopy bulk density estimates and to accurately
 273 reflect actual canopy profiles in this region (Reinhardt et al. 2006). Effective canopy bulk

274 density (CBD) was computed as the maximum of a 3-m running mean of the profile within each
 275 stand (Reinhardt et al. 2006); however we also graphically present 1-m bins to better evaluate
 276 vertical heterogeneity in canopy fuels.

277 Effective canopy base height (CBH) was defined as the lowest height at which CBD
 278 (including both live and dead fuels) exceeded 0.04 kg m^{-3} , a commonly used value that the few
 279 empirical validations have supported in terms of the ability to support crown fire initiation
 280 (Sando and Wick 1972, Cruz 2004, see Mitsopoulos and Dimitrakopoulos 2007). Because no
 281 universal solution exists for assessing canopy base height (Cruz and Alexander 2010), we also
 282 compare CBH results using a threshold CBD of 0.011 kg m^{-3} (Scott and Reinhardt 2001) and by
 283 using the mean of tree crown base heights within a stand (Cruz et al. 2003).

284 Evaluating canopy-level foliar moisture in outbreak stands is challenging due to the
 285 spatial mix of live and dead tree crowns, with high and low moisture content, respectively. Most
 286 fire prediction frameworks require stand-level canopy moisture, but there are limitations to such
 287 spatial averaging which may obscure patchy influences on fire behavior. We therefore took two
 288 complementary approaches. First, we estimated stand-level canopy foliar moisture by applying a
 289 standard assumption for live-needle moisture of 100%, and a reduced moisture for dead needles,
 290 then computing an abundance-weighted average within each stand. Estimates of dead-needle
 291 moisture are available for *P. contorta* (~10-20%; Jolly et al. 2012) but not *P. menziesii*; we
 292 therefore applied a conservative estimate of 5%. Second, we summarized the separate
 293 abundances of live trees, dead trees with needles and fine branches, and dead trees with no
 294 needles and fine branches.

295 We computed the mass of surface woody fuels by size class using standard geometric
 296 scaling and species- and decay-class-specific wood density values (Brown 1974, Harmon and

297 Sexton 1996). For coarse (1000-h) fuels, biomass was summarized separately for sound (decay
 298 class 1-3) and rotten (decay class 4-5) particles. Dry biomass of live understory fuels was
 299 estimated using percent cover data and previously published allometric equations for the GYE
 300 (Turner et al. 2004, Simard et al. 2011). Biomass of shrubs was summed to obtain live woody
 301 fuel load; biomass of forbs, grasses, and sedges was summed to obtain herbaceous fuel load. All
 302 surface and canopy fuel data were slope-corrected to obtain per-hectare estimates.

303

304 *Data analysis*

305 To evaluate beetle outbreak effects while accounting for the inherent variation in
 306 Douglas-fir stand structure (Fig. 1), we analyzed fuel responses within a general linear model
 307 (GLM) that included predictors of TSO class (categorical) and pre-outbreak basal area
 308 (continuous). Basal area was chosen as the integrative metric of pre-existing structure because
 309 of its well-established use as an indicator of forest stature and biomass density (Husch et al.
 310 2003), its known strong correlations with canopy fuel characteristics including ACFL and CBD
 311 (Cruz et al. 2003), and its observed correspondence with the xeric-mesic gradient of Douglas-fir
 312 forests in the GYE (basal area increases from xeric to mesic stands; Fig. 1). In essence, our
 313 approach was to regress a given fuel metric against pre-outbreak basal area, then test for
 314 statistically significant shifts in the regression line among TSO classes. We did not formally
 315 evaluate interaction terms in the GLMs owing to insufficient available degrees of freedom
 316 (however, exploratory analyses with them included did not suggest important interactions;
 317 $P > 0.10$ for virtually all possible interaction terms). Pre-outbreak basal area was retained in all
 318 the GLMs for consistency and because, even when not significant (minority of cases), the sign of
 319 the basal area effect (+/-) was ecologically sensible for both canopy and surface fuels (Appendix

320 B). Residuals and model fits were checked using diagnostics described by Ramsey and Schafer
 321 (2002). Percent data were logit-transformed prior to analysis (Ramsey and Schafer 2002).

322 For fuel and cover data, basal-area-corrected means and standard errors for each class
 323 were obtained by centering the regression on the grand mean basal area and extracting the
 324 intercept terms from the GLM (Ramsey and Schafer 2002). Bar graphs therefore represent the
 325 responses at the grand mean pre-outbreak basal area. To aid interpretation, we present family-
 326 wise Tukey-Kramer comparisons among TSO classes after accounting for pre-outbreak basal
 327 area. Because our field observations suggested wide natural variability in this system, we
 328 interpreted P below an α -level of 0.05 as strong evidence of differences, and $P < 0.10$ as
 329 suggestive/moderate evidence. This approach guards against missing ecologically meaningful
 330 effects because of modest sample size (i.e., Type II error).

331 We also used the GLM framework to compare the influence of beetle outbreaks to
 332 background variation associated with the xeric-mesic gradient. The background effect
 333 represented the range in a given fuel metric in undisturbed stands, obtained by extracting the
 334 slope term from the model (relationship between fuel metric and pre-outbreak basal area) and
 335 multiplying it by a representative range of basal area in undisturbed stands. The basal area range
 336 was obtained using reconstructed pre-outbreak basal area in all 20 stands. To be conservative,
 337 we used the 10th and 90th percentiles of basal area rather than the raw range in order to avoid
 338 influence of extremes; the resulting range was 31-61 m² ha⁻¹. For the beetle outbreak effect, we
 339 considered the largest effect size possible, by computing the maximum difference in means
 340 between the undisturbed condition and any post-outbreak class.

341 The above GLM framework was only employed for fuels and cover data that are likely
 342 associated with pre-outbreak stand structure; for other responses such as estimated foliar

343 moisture content and pre-outbreak validations, a one-way ANOVA among TSO classes was
 344 used. For microclimate data, we applied non-parametric Kruskal-Wallis tests due to smaller
 345 sample size. All analyses were conducted using the program R, version 2.12.0 ([http://www.R-](http://www.R-project.org)
 346 [project.org](http://www.R-project.org)).

347 To assess changes in fine-scale heterogeneity of fuels within stands, we computed the
 348 coefficient of variation (CV) in fuels among transects within each plot (Fraterrigo and Rusak
 349 2008). This approach still treats the stand as the experimental unit, with one value for each
 350 stand; however the response becomes the variation among subsamples within the plot, rather
 351 than their mean. We computed this within-stand CV for broad classes of surface fuels as well as
 352 canopy fuels in different strata. We computed heterogeneity in ACFL separately for the lower
 353 (<10 m height), middle (10-20 m), and top (>20 m) canopy strata. We additionally computed
 354 ACFL heterogeneity along the vertical dimension, using the CV among 1-m canopy layers.

356 **Results**

357 *Post-outbreak stand structure*

358 Stand structure in each of the TSO classes reflected the partial and gradual nature of
 359 Douglas-fir beetle outbreaks (Table 2, Fig. 2). Outbreak severity ranged from 38-83% of pre-
 360 outbreak basal area and did not differ among red, gray, and silver classes (mean 59%, compared
 361 to the endemic level of 4% in green stands) (Tables 1-2, Fig. 2). Live basal area declined with
 362 time since outbreak, but remained at 14-16 m² ha⁻¹ in gray and silver stands (Table 2, Fig. 2).
 363 Live stems were as numerous as dead stems in all TSO classes, even in the overstory (Table 2).

364 The gradual nature of the outbreak is apparent in the structure of red stands (Fig. 2),
 365 which included a mix of fading trees (current attack), those of both high and low needle

366 retention, and some trees with complete needle-loss. Dendrochronological analysis also showed
 367 peak outbreak periods lasting 4-7 years (Appendix A). Minor amounts of stem breakage began
 368 in the gray stage, and by the silver stage 25-30 years after peak mortality, most beetle-killed
 369 stems were broken-topped, with a lesser portion having fallen completely (Fig. 2).

370
 371 *Canopy fuels*

372 After accounting for pre-outbreak basal area, there were significant reductions in
 373 available canopy fuel load and canopy bulk density with increasing time since outbreak (Figs. 3,
 374 4A-B). Total ACFL declined monotonically and was approximately halved by the silver stage
 375 (8.0 vs. 17.0 Mg ha⁻¹ in green stands); however, the proportion dead was elevated in both the red
 376 and gray stages (Fig. 4A). Foliage biomass began declining in the red stage (8.0 Mg ha⁻¹ versus
 377 12.1 Mg ha⁻¹ in green stands) (Fig. 4G). Canopy bulk density declined by ~30% in post-
 378 outbreak stands compared to green stands (0.10 kg m⁻³) (Fig. 4B); the initial decline in the red
 379 stage is significant at the $\alpha=0.10$ level. Effective canopy base height increased in post-outbreak
 380 stands and became significantly higher by the silver stage (3.4 m) compared to green stands (0.6
 381 m) (Fig. 4C). Estimated stand-level foliar moisture content, the weighted average for all live and
 382 dead needle biomass, decreased significantly to 75% in red stands, from effectively 100% in
 383 green stands and other post-outbreak stages (Fig. 4H). See Appendix B for full statistical outputs
 384 from GLMs of all canopy fuel variables, including their live and dead subcomponents.

385 Pre-outbreak basal area was an important correlate with post-outbreak canopy fuel
 386 properties, confirming its use in representing the effect of pre-existing stand structure. As a
 387 predictor within the GLMs, pre-outbreak basal area was significant for 14 of 18 canopy fuel

388 metrics (see Appendix B). Ranges in canopy fuels in undisturbed stands, associated with the
 389 xeric-mesic gradient, were on par with beetle outbreak effects (Fig. 6).

390 The use of alternative methods for canopy fuel calculations only made a difference for
 391 canopy base height. Computing CBH using a threshold of 0.011 kg m^{-3} (Reinhardt et al. 2006)
 392 resulted in much lower CBH values (mean 0.5 m), while the simple-means method of Cruz et al.
 393 (2003) yielded similar absolute values as ours (mean 2.6 m); both alternate approaches resulted
 394 in no significant differences in canopy base height among TSO classes. Computing CBD via the
 395 method of Cruz et al. (2003) (dividing ACFL by canopy depth) yielded the same qualitative
 396 results as shown in Fig. 4B, with higher absolute values (mean 0.16 kg m^{-3}).

397

398 *Surface fuels*

399 There were few significant changes in surface fuels associated with beetle outbreak, after
 400 accounting for pre-existing variation in stand basal area (Fig. 5). Most size classes of surface
 401 woody fuels showed no trend with time since outbreak (Fig. 5A-E), except that silver stands had
 402 comparatively low levels of 1-h fuels and high levels of 1000-h sound fuels (see Appendix B for
 403 comparisons with $\alpha=0.10$). The only other significant response was herbaceous biomass, which
 404 showed an increase in the red stage that was moderately significant (Fig. 5J, Appendix B). Full
 405 statistical outputs from GLMs for all surface fuel variables are in Appendix B.

406 Pre-outbreak basal area was an important correlate with post-outbreak surface fuel
 407 properties, with significant effects for 8 of 13 surface fuel metrics within the GLMs (Appendix
 408 B). Ranges in surface fuel loads in undisturbed stands, associated with the xeric-mesic gradient,
 409 were greater than the beetle outbreak effect for woody fuels and of similar or less magnitude for
 410 live herbaceous fuels and forest floor depth (Fig. 6).

411

412 *Within-stand heterogeneity in fuels*

413 Within-stand coefficients of variation (CV) showed increasing spatial heterogeneity with
 414 time since outbreak for several fuel components (Fig. 7). For canopy fuels, horizontal
 415 heterogeneity showed an increasing trend with time since outbreak in all of the top, middle, and
 416 lower canopy strata (Fig. 7A-C), with the effect most significant in the middle stratum. Absolute
 417 magnitudes of the CV tended to decrease from the heterogeneous top layer (Fig. 7A) to the more
 418 homogeneous bottom layer (Fig. 7C). Vertical heterogeneity in canopy fuels also increased
 419 significantly with time since outbreak (Fig. 7D). No significant trend was apparent for crown
 420 base heights, which had very low CVs in general (Fig. 7H). For surface fuels, spatial
 421 heterogeneity in forest floor depth (litter+duff) increased significantly with time since outbreak,
 422 mainly in silver stands compared to other classes (Fig. 7E). Trends were less clear and were not
 423 significant for heterogeneity of surface fine or coarse woody fuels (Fig. 7F-G).

424

425 *Microclimate*

426 We found few ecologically significant trends in microclimate. There were no significant
 427 associations with TSO class for RH daily mean (Kruskal-Wallis $P=0.82$, mean 55%) or RH
 428 daytime-hours mean ($P=0.40$, mean 48%), nor for ground temperature mean ($P=0.91$, mean 13
 429 °C) or daytime-hours mean ($P=0.87$, mean 16 °C). Air temperature daily mean was also not
 430 significant ($P=0.16$, mean 15 °C), while daytime-hours air temperature was marginally
 431 significant ($P=0.09$) but with a small effect size (gray stands 21 °C versus 20 °C in other stands).

432

433 **Discussion**

434 Douglas-fir beetle outbreak was associated with altered fuel profiles in Douglas-fir
 435 forests of Greater Yellowstone; however the magnitude and importance of these changes (and
 436 resulting stand structures) were comparable to the range of pre-outbreak stand conditions. The
 437 strongest effects of beetles were canopy thinning and increased spatial heterogeneity of fuels
 438 over post-outbreak time, whereas effects on surface fuels were generally minor after accounting
 439 for background variation. These results highlight how bark beetle impacts on fuel profiles may
 440 differ between lower montane forests and other systems, as well as the importance of the gradual
 441 and partial nature of beetle disturbance in determining post-outbreak fuel dynamics.

442

443 *Beetle impacts in lower montane, mixed-severity fire forests*

444 *Canopy fuels*— Consistent with findings in *Pinus contorta* and *Picea engelmannii* forests
 445 (Page and Jenkins 2007a, DeRose and Long 2009, Klutsch et al. 2011, Simard et al. 2011,
 446 Schoennagel et al. 2012), a primary effect of beetles was to thin canopy biomass, culminating in
 447 50% loss in silver stands (Fig 4B, Appendix B). However, initial canopy bulk density in green
 448 Douglas-fir stands (0.10 kg m^{-3}) was much lower than in more mesic forests ($0.14\text{-}0.20 \text{ kg m}^{-3}$;
 449 Page and Jenkins 2007a,b, Simard et al. 2011, Schoennagel et al. 2012, see also Cruz et al.
 450 2003). Post-outbreak Douglas-fir stands ($0.06\text{-}0.08 \text{ kg m}^{-3}$) thus had lower absolute values than
 451 in other forest types ($0.07\text{-}0.13 \text{ kg m}^{-3}$). This finding is consistent with expectations in sparsely
 452 treed systems and suggests that outbreaks lead to especially low crown fire spread potential in
 453 these forests once needles and fine branches fall.

454 Significant foliage loss and reduction of canopy bulk density began even in the red stage
 455 (Fig. 4G, Appendix B), consistent with the few other empirical studies (Simard et al. 2011,
 456 Schoennagel et al. 2012). This trend is not incorporated in most conceptualizations of the red

457 stage, which generally emphasize a reduction in canopy foliar moisture without significant
 458 needle drop. The difference between predicted and observed patterns may be ascribed to the
 459 gradual nature of most *Dendroctonus* outbreaks, which usually occur over a period of 3-7 years
 460 (Appendix A; Negron 1998, McMillin and Allen 2003, Klutsch et al. 2009, Simard et al. 2011,
 461 Meigs and Kennedy 2011, DeRose and Long 2012). Initially, foliar moisture would be reduced
 462 for some trees before any needles drop, a 1-2 year window that has not yet been reported
 463 quantitatively; however by the classic peak ‘red stage’ (i.e., peak mortality and red-needle tree
 464 abundance), many trees have already begun losing needles (Figs. 2, 4G; Simard et al, 2011,
 465 Schoennagel et al. 2012). Reduced CBD in red stands occurred in our data despite the
 466 conservative assumption that 100% of fine twigs become available fuel upon death (versus 50%
 467 when live), which could theoretically increase available fuel substantially as crowns die. This
 468 dynamic highlights the importance of clearly defining post-outbreak stages (Hicke et al. 2012);
 469 our red stands were ‘mid-stage,’ a few years after outbreak initiation and thus including a range
 470 of post-mortality needle loss within stands (Fig. 2).

471 Gradual and partial disturbance also affected dynamics of estimated canopy foliar
 472 moisture. As expected, estimated canopy foliar moisture declined during the red stage, to 71-
 473 85% (weighted average of live and dead foliage within stands) (Fig. 4H). This dip was less than
 474 expected, but similar to other studies (e.g., 63-78%; Simard et al. 2011). The stand-level average
 475 does not approach the pure dead-needle moisture for two reasons: mortality is partial within
 476 stands so significant live foliage remains present (Fig. 2), and needle drop reduces the
 477 contribution of dead needles to canopy metrics (Figs. 2, 4G). Similarly, Page and Jenkins
 478 (2007a) reported that dead needles composed 17-29% of stand foliage during epidemic stage
 479 outbreak in *Pinus contorta*. Nevertheless, spatial intermixing of live and dead crowns could be

480 important for localized fire behavior such as individual tree torching. This effect is not captured
 481 in currently available fire models, which assume homogeneous fuels, and has not been studied
 482 empirically.

483 Our expectation regarding increased ladder fuels in later post-outbreak stages was not
 484 supported, due to slow regeneration. Effective canopy base height, a measure of resistance to
 485 fire transition into crowns (torching), increased from 0.6 m in green stands to 3.4 m in silver
 486 stands (Fig. 4C). This trend was due to canopy biomass loss, such that the threshold CBD of
 487 0.04 kg m^{-3} occurred higher, where more trees became part of the canopy profile (Fig. 3). In
 488 contrast, studies in more mesic forests have found that, by ~25 years post-outbreak, the base of
 489 the canopy effectively decreases as growth and recruitment of sapling regeneration fills in the
 490 lower canopy with foliage – thereby increasing torching potential (Simard et al. 2011). In the
 491 drier system we studied, regeneration after disturbance often takes many decades (Baker 2009),
 492 and post-outbreak tree regeneration remains sparse even in silver stands (Table 2). Thus, beetle-
 493 triggered acceleration of succession (release and recruitment of advanced regeneration) and its
 494 effects on torching appear to be less of a factor in drier, lower montane systems.

495 *Surface fuels*— There were surprisingly few significant effects of bark beetle outbreak on
 496 surface fuel loads, and some unique patterns relative to higher-elevation forests. As we
 497 hypothesized, herbaceous biomass increased in the red stage, and the increase of ~50% (0.5 Mg
 498 ha^{-1}) above green stands was at the high end of that reported for higher-elevation forests such as
 499 *Pinus contorta* (Page and Jenkins 2007a, Simard et al. 2011). The pattern of increase followed
 500 by a decline in later TSO classes may be due to an initial flush of light, soil moisture, and
 501 available nitrogen associated with red needle-fall, with nitrogen subsequently becoming
 502 immobilized within the system (Griffin et al. 2011, Griffin and Turner 2012).

503 Patterns of dead surface fuels suggested key differences from other ecosystems. The only
 504 significant effects that emerged over background variation (see below) were reduced 1-h fuels
 505 and increased 1000-h fuels in silver stands (Fig. 5A-H). Coarse fuel (1000-h) accumulation in
 506 silver stands is consistent with expectations of post-disturbance snag-fall and fragmentation (Fig.
 507 2). As we hypothesized, coarse fuel accumulation was much lower in Douglas-fir forests (2x
 508 higher than in green stands) than that reported for higher-elevation forest types (3-8x higher;
 509 Page and Jenkins 2007a, Simard et al. 2011, Schoennagel et al. 2012). The difference may be
 510 due to lower standing biomass in drier systems. Decreased 1-h fuels in silver stands has not been
 511 reported for other systems, and may be due to decreased inputs from a reduced and increasingly
 512 patchy overstory, an effect which is likely pronounced in sparsely treed lower montane systems.

513
 514 *Role of background variability*

515 Our hypothesis that beetle effects would be much larger than background variation was
 516 generally not supported. For most categories of both canopy and surface fuels, effect sizes of the
 517 beetle outbreak were similar or even less than the range associated with background variability
 518 (Fig. 6). Partial R^2 values from the GLMs also showed similar explanatory power between pre-
 519 outbreak basal area and beetle outbreak for most variables. This comparison to an ecologically
 520 meaningful range of pre-outbreak stand structure has important implications for interpreting
 521 beetle outbreak effects, in both ecological and management contexts.

522 Several studies have reported no detectable beetle outbreak effects for many (especially
 523 surface) fuel components (Page and Jenkins 2007a,b, Simard et al. 2011, Jorgensen and Jenkins
 524 2011, Klutsch et al. 2011, Schoennagel et al. 2012)—leading to understandable speculations that
 525 Type II error may be preventing detection of trends over background variation (Hicke et al.

2012). While sampling error likely does play a role in some studies, our analysis shows that weak or undetectable trends can be an ecological phenomenon and not simply a statistical one. First, in our study we validated pre-outbreak comparability of stands via extensive dendrochronological reconstructions, minimizing this common source of sampling error and helping compensate for modest sample size (Johnson and Miyanishi 2008, Simard et al. 2011). Perhaps more importantly, the general linear model approach we used allowed us to explicitly account for background variation in fuel loads, a stronger analysis which aided in detecting several beetle effects. It also showed quantitatively that, while beetles may alter the fuel profile within a given stand, when viewed across stands these effects tend to be of similar magnitude to variation among stands in the absence of beetle disturbance. A similar pattern has also been suggested for *P. contorta* pine forests (Hicke et al. 2012). Although beetle outbreaks necessarily have an impact on fuel profiles (e.g., dead canopy biomass must fall to the surface and decay over time), the relative difficulty in detecting these effects across many studies suggests that the context of background variability is ecologically meaningful when interpreting the overall role of beetles.

Fuel-driven variations in fire behavior can be influenced by other processes as much or more than beetle outbreaks, which may underlie common findings of weak or equivocal outbreak effects in empirical studies of fires burning through recently beetle-affected landscapes (Bebi et al. 2003, Lynch et al. 2006, Kulakowski and Veblen 2007, Bond et al. 2009, Kulakowski and Jarvis 2011). Background variation may be especially important for lower montane systems which vary widely in structure, productivity, and fire regime (Baker 2009). By comparison, in higher-elevation systems with lower structural variation, fires are often climate-driven, rendering bottom-up controls via fuels less important overall (Turner et al. 1994), whether from beetle

549 outbreaks or other factors. For the management of wildland fuels in lower montane forests, the
 550 context of wide background variation suggests recognizing outbreaks as one of many factors
 551 influencing fuel profiles and fire potentials. Prioritization of treatments will benefit by
 552 considering which fuel components are uniquely affected by beetles (e.g., window of reduced
 553 canopy foliar moisture in initial outbreak stage), which components vary with similar magnitude
 554 in response to beetles and other drivers (e.g., canopy fuel load and bulk density), and which
 555 components seem to vary less with beetles than other drivers (e.g., most surface woody fuels)
 556 (Figs 4-6).

557

558 *Fuel decay dynamics – closing the loop*

559 At first glance, a significant loss of canopy fuels but relatively few increases in surface
 560 fuels appears incongruent. Biomass clearly must fall from the canopy over time; however two
 561 factors explain why surface fuel accumulations may not be as large as expected: the gradual
 562 nature of beetle outbreaks and the key role of decomposition.

563 The multi-year outbreak produces a gradual input of needle litter to the forest floor,
 564 which allows time for decomposition to influence accumulation concurrently. The decay half-
 565 life of needle litter (3-8 yr; e.g., Keane 2008) is on the same order as the period of beetle
 566 outbreak (3-7 yr), which may explain why post-outbreak litter accumulation in more mesic forest
 567 types have varied from no change to slight increases that do not always mirror canopy loss (Page
 568 and Jenkins 2007a,b, DeRose and Long 2009, Simard et al. 2011, Schoennagel et al. 2012).
 569 Notably, another study of litter dynamics in GYE Douglas-fir forests also reported no significant
 570 change in litter depth or mass following bark beetle outbreak (Griffin and Turner 2012).

571 Gradual inputs and decomposition are also important for woody fuels. Disturbances that
 572 kill trees within a stand over multiple years lead to protracted dead wood inputs, with 20-50%
 573 lower maximum accumulations relative to synchronous disturbance (Cobb et al. 2012). Thus,
 574 dead woody fuels following multi-year beetle outbreaks should be expected to exhibit a more
 575 gradual, flatter accumulation over time rather than a sharp spike consisting of all material at
 576 once.

577 The role of wood decomposition can be explored quantitatively with our data.
 578 Parameterizing standard negative exponential decay models ($Y_t = Y_0 e^{-kt}$; Harmon et al. 1986) with
 579 our field data using all pools (canopy+surface) for each fine fuel size class yields exponential
 580 decay constants of $k=0.037$ for 1-h fuels, 0.014 for 10-h fuels, and 0.016 for 100-h fuels. These
 581 values are within ranges commonly reported for western conifers (Harmon et al. 1986, Keane
 582 2008). In other words, changes in the total amounts of dead fuels over the time period spanned
 583 by our sample (red to silver stage, ~26 yr) are consistent with those predicted by known decay
 584 constants.

585
 586 *Spatial heterogeneity in fuels*

587 Disturbance-driven changes in variability, rather than just means, are increasingly
 588 recognized as fundamental to understanding the effects of both single events and interactions
 589 between multiple disturbances (Fraterrigo and Rusak 2008). We found that within-stand spatial
 590 heterogeneity increased with time since beetle outbreak for several fuel components (Fig. 7),
 591 which may indicate important fine-scale changes in fuel connectivity and fire propagation
 592 potential. Within-stand heterogeneity increased for canopy fuels in both the vertical and
 593 horizontal dimensions (Fig. 7A-D). Greater patchiness in the horizontal dimension was most

594 pronounced in the mid-canopy layer (Fig. 7B), where available fuel loads generally peak and
 595 therefore determine effective canopy bulk density and crown fire spread potential (Fig. 3;
 596 Reinhardt and Crookston 2003, Reinhardt et al. 2006). Combined with increased variation
 597 among vertical canopy layers (Fig. 7D), this pattern suggests reduced potential for both vertical
 598 (torching) and horizontal (spreading) crown fire propagation, all other factors equal. Changes in
 599 variability were less common for surface fuels, although silver stands had patchier litter and duff
 600 depths, which may also influence surface fire spread potential. Overall, increased spatial
 601 heterogeneity in fuels supports the notion that currently available fire models, which assume
 602 homogeneous fuelbeds, are of decreased utility in post-outbreak environments, and that new
 603 models under development may be better suited to this question (see Hoffman et al. 2012b).

604
 605 *Implications for fire potentials*

606 Applying known relationships between fuel profiles and the behavior of both surface
 607 (Rothermel 1983) and crown (Van Wagner 1977) fires, bark beetle outbreaks appear to have a
 608 number of implications for fire potentials in Greater Yellowstone Douglas-fir forests. In red
 609 stands, surface fire potential appears largely unchanged except for a slight increase in frontal
 610 flame length and fireline intensity associated with greater herbaceous biomass (Fig. 5). Coupled
 611 with reduced estimated canopy foliar moisture (Fig. 4), this effect suggests increased potential
 612 for torching into the canopy, while the potential for active crown fire spread appears decreased
 613 due to lowered effective CBD but increased due to lower foliar moisture (Fig. 4). The net
 614 balance of these counteracting influences—especially the effect of dead foliage with <70%
 615 moisture and its patchy spatial distribution—has not been parameterized within most fire
 616 modeling frameworks (Jenkins et al. 2008, 2012, Hicke et al. 2012, but see Hoffman et al.

617 2012b). Reduced foliar moisture may be key in increasing crown fire potential during the red
 618 stage (Jolly et al. 2012; Jenkins et al. 2012); yet so far there is a lack of quantitative empirical
 619 studies on fire behavior in red stands to complement the visual observations reported to date.
 620 Especially needed are studies comparing how otherwise similar red and green stands burn under
 621 a range of weather conditions.

622 In gray stands, surface fire potentials appear no different than in green stands (Fig. 5),
 623 while further thinning of the canopy in terms of mass, bulk density, and connectivity suggests
 624 substantially reduced potential for crown fire initiation and spread (Fig. 4). Most dead 1-h fuels
 625 remain in the canopy at this stage, and we conservatively included these in our calculations of
 626 CBH and CBD, but it is unknown the degree to which these can support crown fire when foliage
 627 is highly discontinuous. Increased spatial heterogeneity in canopy fuel mass becomes important
 628 by this stage, especially in the mid-canopy layer (Fig. 7).

629 By the silver stage, potential fire behavior appears substantially altered from that in
 630 undisturbed stands. Lower 1-h fuel mass and litter+duff continuity suggest diminished surface
 631 fire spread and intensity, while higher coarse fuel loading suggests potentially increased burn
 632 residence time and heat release (Fig. 5). Higher canopy base height (Fig. 4) and vertical
 633 heterogeneity (Fig. 7D) suggest reduced torching potential, and significantly lower canopy bulk
 634 density and connectivity suggest greatly reduced crown fire spread potential (Fig. 4). Potential
 635 mid-flame wind speeds are likely increased due to the open canopy (Reinhardt and Crookston
 636 2003), while microclimatic effects (surface temperature and relative humidity) are within the
 637 range found in undisturbed forests.

638 In the context of the mixed-severity fire regime that characterizes many drier lower
 639 montane forests, even though outbreak effects may be less important relative to background

640 structural variation than in other ecosystems, they may still influence the propensity for surface
 641 versus crown fire. Mixed-severity fire regimes are considered to be more fuel-limited than
 642 comparatively mesic high-elevation forest types (Halofsky et al. 2011), and beetle outbreaks
 643 appear to move the system toward still greater fuel limitation, particularly in older post-outbreak
 644 stages. Reduced vertical fuel continuity suggests a shift away from crown fire behavior, and
 645 toward conditions more likely to support surface fires. Under moderate weather conditions,
 646 therefore, beetle outbreaks may result in lower severity fire in terms of canopy mortality and fire-
 647 created openings, for perhaps several decades. These effects may vary among forest types with
 648 mixed-severity fire regimes, which themselves vary widely in structure and function.

649 The net effect for Greater Yellowstone Douglas-fir forests is that mesic closed-canopy
 650 stands affected by beetles shifted in character toward that of undisturbed xeric parklands
 651 (compare Fig. 1D to Fig. 1A), while xeric parklands affected by beetles shifted toward a very
 652 sparse woodland/savanna condition (Fig. 1C). The latter condition in particular appears very
 653 unlikely to support significant crown fire activity. Thus, any management of fuels in post-
 654 outbreak stands may be better prioritized for denser stands in which crown fuels may still have a
 655 degree of continuity, and coarse woody fuels are more abundant (Fig. 1D).

656

657 **Conclusion**

658 We found evidence that bark beetle outbreak effects on fuel profiles in lower montane
 659 forests differ from those in higher elevation forests with stand-replacing fire regimes. Relatively
 660 low tree density and canopy biomass to begin with, as well as slow regeneration dynamics, were
 661 among the most important differences; canopy thinning associated with beetle-caused tree
 662 mortality thus resulted in very low canopy fuel mass and continuity, with little recovery up to

663 three decades post-outbreak. Changes in surface fuels were comparatively minor. Combined
 664 with increased spatial heterogeneity in fuels, these results suggest overall diminished fire
 665 potentials in post-outbreak stands, particularly for crown fire. A remaining uncertainty is how,
 666 in the red stage, the net effects of reduced foliar moisture, concurrent canopy thinning, and the
 667 patchy spatial distribution of live and dead biomass will influence crown fire potentials. The
 668 gradual and partial nature of outbreak was key in mediating changes to fuel profiles, resulting in
 669 less extreme fluctuations in estimated canopy foliar moisture (red stage) and coarse woody fuel
 670 accumulations (silver stage) than expected. Overall, effects of *Dendroctonus* outbreaks were
 671 generally on par with background variation in stand structure. In essence, formerly dense forests
 672 affected by outbreak became more like open parklands, while open parklands became more like
 673 woodland/savannas (Fig. 1). These results highlight the importance of evaluating outbreak
 674 effects within the context of the structural variation inherent to many forest types in the absence
 675 of beetle disturbance. For management of wildland fuels, this finding suggests that bark beetle
 676 outbreaks can be approached as but one of many influences structuring fuel profiles, and that
 677 treatments in beetle-affected landscapes could continue to address a variety of objectives rather
 678 than focusing singularly on beetle impacts. Although most important in structurally variable
 679 forests such as interior Douglas-fir, such context likely has relevance in other forested
 680 ecosystems affected by bark beetle outbreaks.

681

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691

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859 **Table 1.** Comparison of pre-outbreak stand characteristics and outbreak severity among the
 860 time-since-outbreak classes [mean, (SE)].

	Green Undisturbed	Red 1-3 yr post- outbreak	Gray 4-14 yr post- outbreak	Silver 25-30 yr post- outbreak	One-way ANOVA	
					$F_{3,16}$	P
<i>Abiotic</i>						
Slope (degrees)	20.6 ^a (2.6)	24.0 ^a (3.1)	24.2 ^a (3.1)	19.2 ^a (4.3)	0.56	0.65
Aspect (cosine transform)	1.12 ^a (0.29)	1.18 ^a (0.27)	1.01 ^a (0.26)	1.06 ^a (0.38)		
Elevation (m)	2110 ^{ab} (38)	2234 ^a (38)	2246 ^a (43)	2041 ^b (49)	5.51	0.01†
Soil origin	volcanic/ metamorphic, sedimentary	volcanic/ metamorphic, sedimentary	volcanic/ metamorphic, sedimentary	volcanic/ metamorphic, sedimentary		
<i>Biotic (pre-outbreak) ‡</i>						
Basal area (m ² ha ⁻¹)	41.1 ^a (4.4)	56.8 ^a (6.7)	43.5 ^a (6.7)	43.6 ^a (6.8)	1.30	0.31
Overstory stem density ¥ (trees ha ⁻¹)	427 ^a (73)	361 ^a (59)	341 ^a (31)	381 ^a (98)		
Quadratic mean diameter (cm)	23.6 ^a (3.3)	37.5 ^a (5.6)	28.3 ^a (2.9)	28.6 ^a (2.4)	2.37	0.11

Douglas-fir dominance	88.2 ^a	91.0 ^a	96.2 ^a	96.2 ^a	0.59	0.63
(% of basal area)	(7.3)	(6.6)	(2.1)	(2.7)		
<i>Disturbance severity*</i>						
Beetle-killed basal area	2.2 ^a	31.4 ^b	26.6 ^b	26.2 ^b	8.83	0.001
(m ² ha ⁻¹)	(2.0)	(2.7)	(5.2)	(5.4)		
Outbreak severity	4.0 ^a	57.2 ^b	60.2 ^b	59.8 ^b	29.9	<0.001
(% basal area killed)	(3.5)	(6.3)	(7.3)	(5.4)		

861 *Note:* Superscript letters are results of Tukey-Kramer comparisons among TSO classes within a
 862 one-way ANOVA; different letters denote statistical differences.

863 † Statistically but not biologically significant because of narrow elevation range sampled; we
 864 confirmed that elevation was not associated with pre-outbreak basal area ($P=0.35$, $R^2=0.05$),
 865 stem density ($P=0.33$, $R^2=0.04$), quadratic mean diameter ($P=0.35$, $R^2=0.05$), or Douglas-fir
 866 dominance ($P=0.52$, $R^2=0.02$).

867 ‡ Reconstructed via dendroecological analysis.

868 ¥ All trees >15 cm dbh.

869 * In this summary, live-but-fading ‘green attack’ trees in red stands are classified as beetle-killed
 870 to reflect eventual outbreak severity.

871 **Table 2.** Post-outbreak stand structure in each of the time-since-outbreak classes [mean (SE)].

	Green Undisturbed	Red 1-3 yr post- outbreak	Gray 4-14 yr post- outbreak	Silver 25-30 yr post- outbreak	One-way ANOVA	
					$F_{3,16}$	P
<i>Basal Area (m² ha⁻¹)</i>						
Live	35.5 (2.7) ^a	26.4 (5.2) ^{ab}	16.3 (3.9) ^b	14.5 (4.1) ^b	5.74	0.007
Dead	5.6 (3.0) ^a	29.0 (5.8) ^b	28.1 (5.3) ^b	21.1 (4.0) ^{ab}	7.78	0.002
<i>Quadratic mean diameter (cm)</i>						
Live	23.6 (3.3) ^a	32.7 (6.7) ^a	21.9 (4.5) ^a	24.0 (3.0) ^a	1.10	0.38
Dead	17.4 (3.0) ^a	40.0 (4.4) ^b	36.4 (1.9) ^b	31.9 (3.3) ^b	9.18	<0.001
<i>Stem density – Overstory (trees ha⁻¹) †</i>						
Live	364 (61) ^a	198 (24) ^{ab}	181 (36) ^{ab}	164 (63) ^b	3.55	0.038
Dead (fine fuels attached)	19 (14) ^a	104 (10) ^{ab}	121 (38) ^b	36 (12) ^{ab}	5.32	0.010
Dead (fine fuels fallen)	45 (21) ^a	47 (28) ^a	61 (38) ^a	136 (31) ^a	2.06	0.146
<i>Stem density – Understory (trees ha⁻¹)</i>						
Live	654 (271) ^a	289 (165) ^a	369 (128) ^a	183 (70) ^a	1.34	0.300
Dead (fine fuels attached)	45 (19) ^a	37 (14) ^a	23 (21) ^a	62 (36) ^a	0.49	0.693
Dead (fine fuels fallen)	35 (9) ^a	86 (46) ^a	61 (28) ^a	46 (18) ^a	0.59	0.632

872 *Note:* Superscript letters are results of Tukey-Kramer comparisons among TSO classes within a
873 one-way ANOVA; different letters denote statistical differences.

874 † Overstory-understory threshold is 15 cm dbh. Dead trees were classified as having fine fuels
875 attached if they retained components that contribute to available canopy fuel load (foliage or
876 twigs <0.64 cm diameter) (Reinhardt et al. 2006). In this summary, live-but-fading trees in red
877 stands are classified as currently live to reflect actual stand conditions rather than eventual
878 outbreak severity.

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881 **Figure Captions**

882

883 **Figure 1.** Forest structures and bark beetle effects in Douglas-fir forests of Greater Yellowstone.
 884 Undisturbed stands span a range of background conditions, from **(A)** low basal-area parklands
 885 near the grassland (xeric) ecotone, to **(B)** high basal-area forests in mesic sites. Stand structure
 886 after bark beetle outbreak varies widely between low basal area **(C)** and high basal area **(D)**
 887 stands (28 years post-outbreak in these examples). Douglas-fir beetle outbreaks in the GYE are
 888 typically a partial disturbance at both stand and watershed scales **(E)**. Photo credits: D.C.
 889 Donato.

890

891 **Figure 2.** Progression of stand structure with time since outbreak. Each column represents a
 892 sample stand. Basal areas include trees standing at the time of outbreak. All stages contained a
 893 mix of live trees and beetle-killed trees with different levels of post-death fragmentation,
 894 reflecting the partial and gradual nature of the disturbance. Beetles typically killed ~40-80% of
 895 basal area (mean 59%) within stands.

896

897 **Figure 3.** Vertical profiles of available canopy fuel in each of the 5 stands within time-since-
 898 outbreak class, and averaged by class.

899

900 **Figure 4.** Canopy fuels in each time-since-outbreak class. Bars represent basal-area-corrected
 901 mean values (i.e., the response value at the mean basal area) and standard errors from the GLM.
 902 Lower-case letters are results of Tukey-Kramer pairwise comparisons among groups ($\alpha = 0.05$),
 903 after accounting for variation in pre-outbreak conditions (basal area). See Appendix B for full

904 statistical outputs from general linear model for all variables, including live/dead
 905 subcomponents. Fuel size classes are standard timelag classes: 1-h fuels, <0.64 cm diameter; 10-
 906 h fuels, 0.64-2.54 cm; 100-fuels, 2.54-7.62 cm. Note that estimated canopy foliar moisture is a
 907 weighted-average including all live and dead foliage within a stand; for separate abundances of
 908 live and dead tree crowns, see Table 2.

909

910 **Figure 5.** Surface fuels in each time-since-outbreak class. Statistical outputs are results of
 911 general linear models with predictors of pre-outbreak basal area and time since outbreak. Bars
 912 represent basal-area-corrected mean values (i.e., the response value at the mean basal area) and
 913 standard errors from the GLM. Lower-case letters are results of Tukey-Kramer pairwise
 914 comparisons among groups ($\alpha = 0.05$), after accounting for variation in pre-outbreak conditions
 915 (basal area). See Appendix B for full statistical outputs from general linear model for all
 916 variables. Fuel size classes are standard timelag classes: 1-h fuels, <0.64 cm diameter; 10-h
 917 fuels, 0.64-2.54 cm; 100-fuels, 2.54-7.62 cm, 1000-fuels, >7.62 cm.

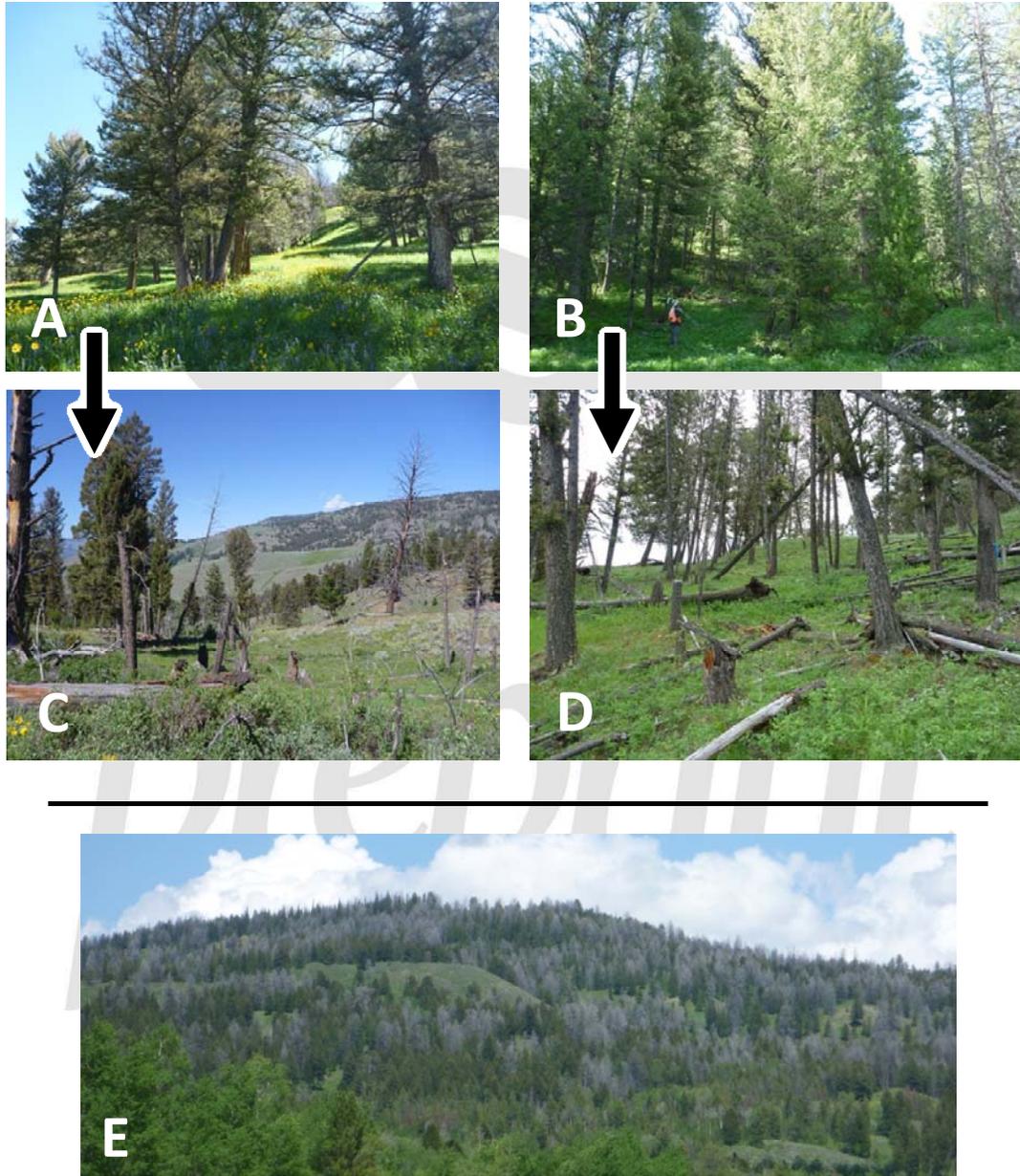
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919 **Figure 6.** Relative effect size on fuels of beetle outbreak versus background variability in pre-
 920 outbreak conditions. Background variation value is the range present in undisturbed green
 921 stands, obtained by multiplying the basal-area effect (regression slope from GLM) times a
 922 representative range of basal area for undisturbed stands (10th and 90th percentiles to avoid
 923 influence of extremes, equating to 31-61 m² ha⁻¹). For the beetle outbreak, effect size is the
 924 maximum difference in means between any post-outbreak class and undisturbed green stands
 925 (Figs. 4-5; see also Appendix B). Fine woody fuels = 1-100-h particles (<7.6 cm); Coarse
 926 woody fuels = all 1000-h particles (>7.6 cm).

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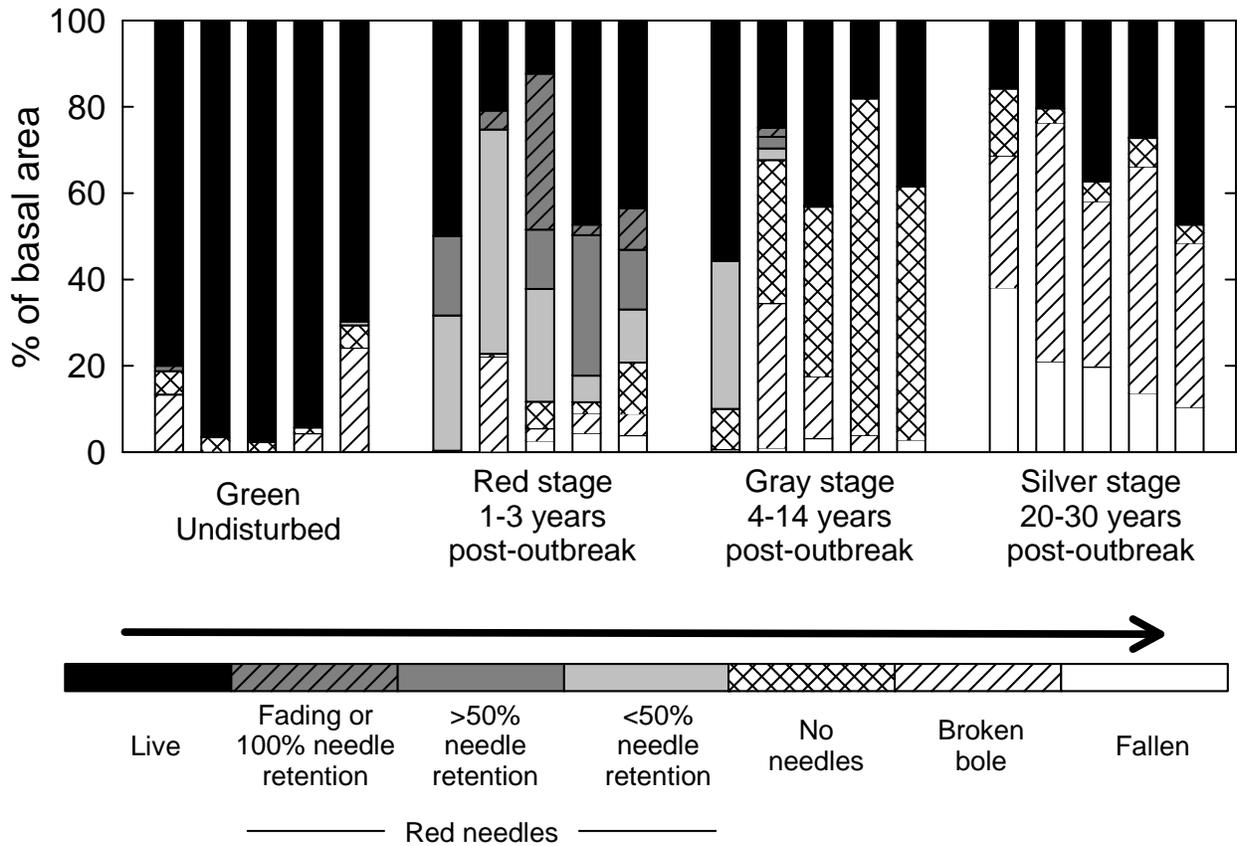
928 **Figure 7.** Fine-scale (within-stand) spatial heterogeneity of fuels in each time-since-outbreak
 929 class (mean, SE). The coefficient of variation within each sample plot is derived by computing
 930 the standard deviation among subsamples (transects) and scaling by the plot mean, generating a
 931 single estimate of fine-scale heterogeneity for each stand (Fraterrigo and Rusak 2008).
 932 Horizontal heterogeneity in canopy fuels is shown for the bottom (**A**; 0-10 m height), middle (**B**;
 933 10-20 m height), and top (**C**; >20 m height) strata, as well as for the vertical dimension (**D**;
 934 variation along z-axis among 1-m canopy layers). Surface fuel variation (**E-G**) is shown by
 935 aggregated size class (fine woody fuels = 1-100-h particles (<7.6 cm); coarse woody fuels = all
 936 1000-h particles (>7.6 cm)), and crown base height (**H**) includes live and dead trees. Statistical
 937 outputs are results of one-way ANOVA among time-since-outbreak classes. Note that these
 938 within-plot CVs differ fundamentally from more traditional class-level (between-plot) CVs,
 939 which were generally <50% for canopy fuels and <70% for surface fuels (Figs 4-5).

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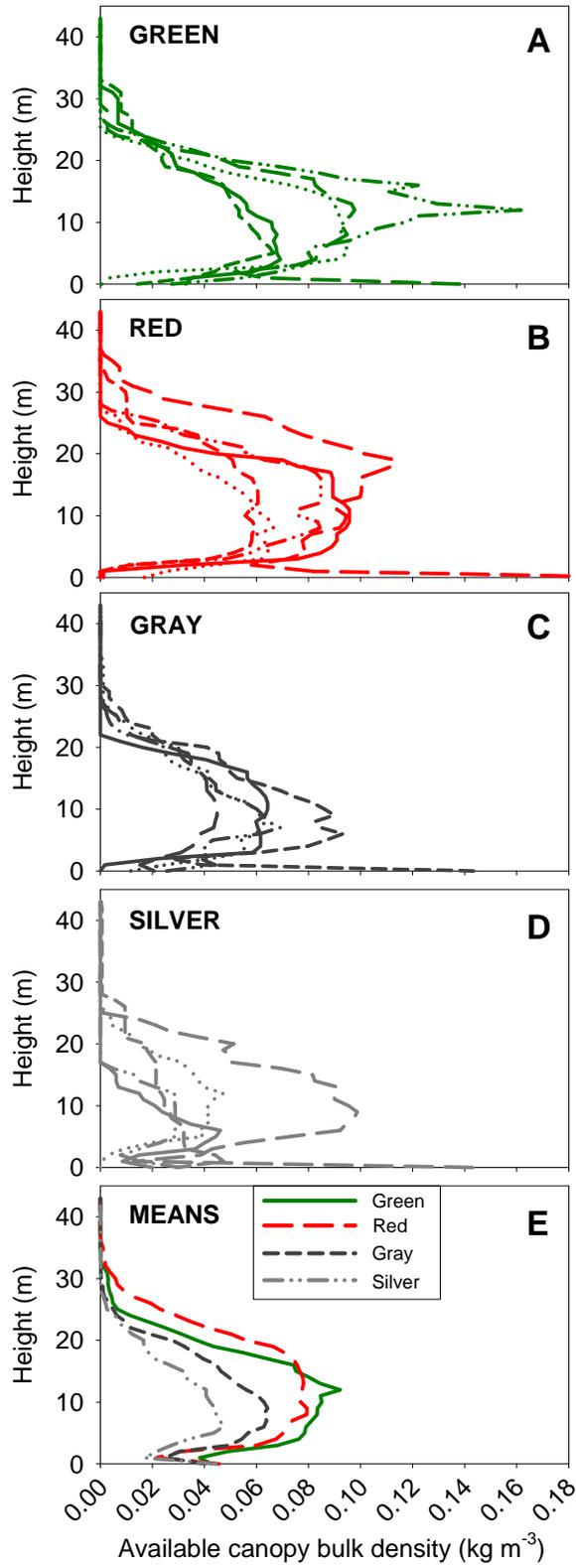
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942 **Figure 1**

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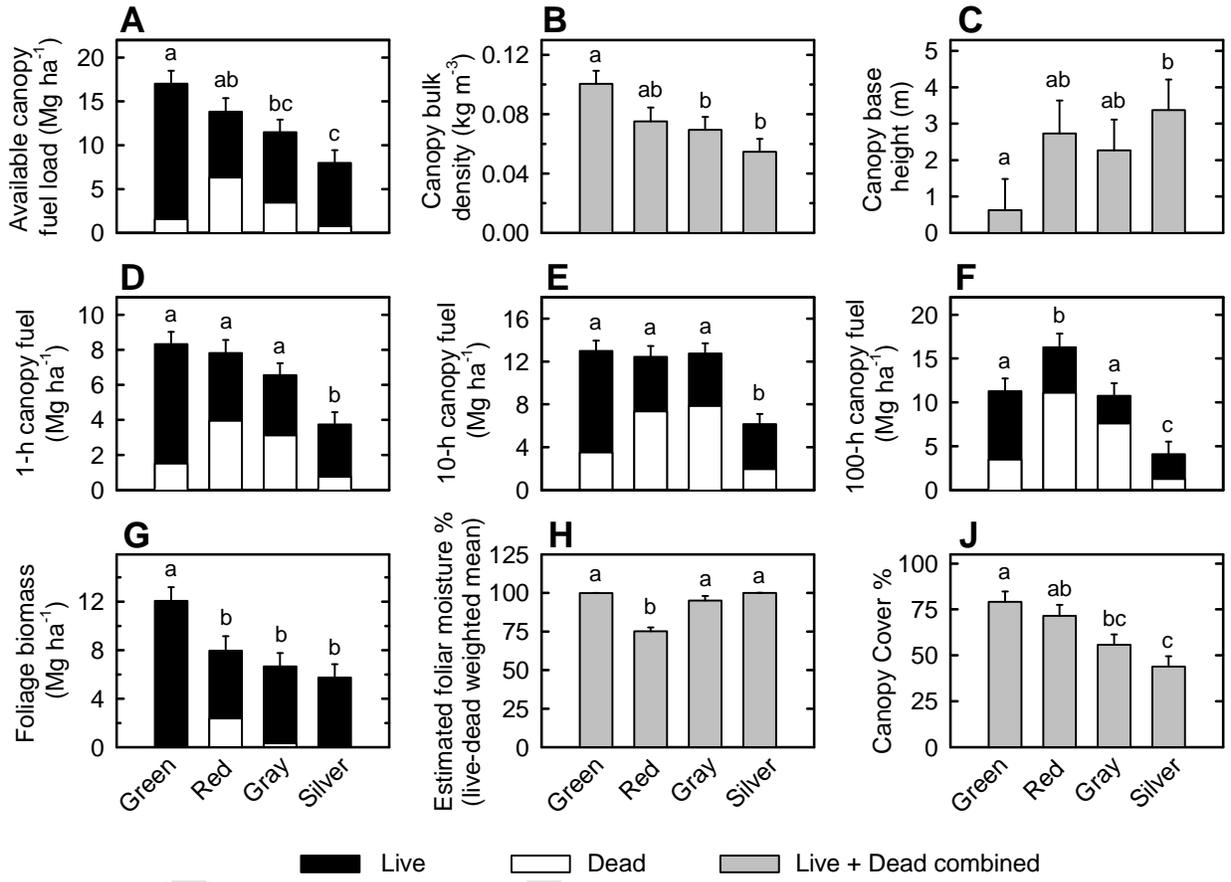
Figure 2



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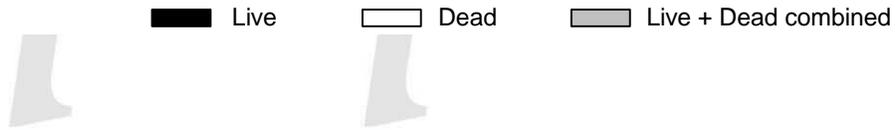
Figure 3

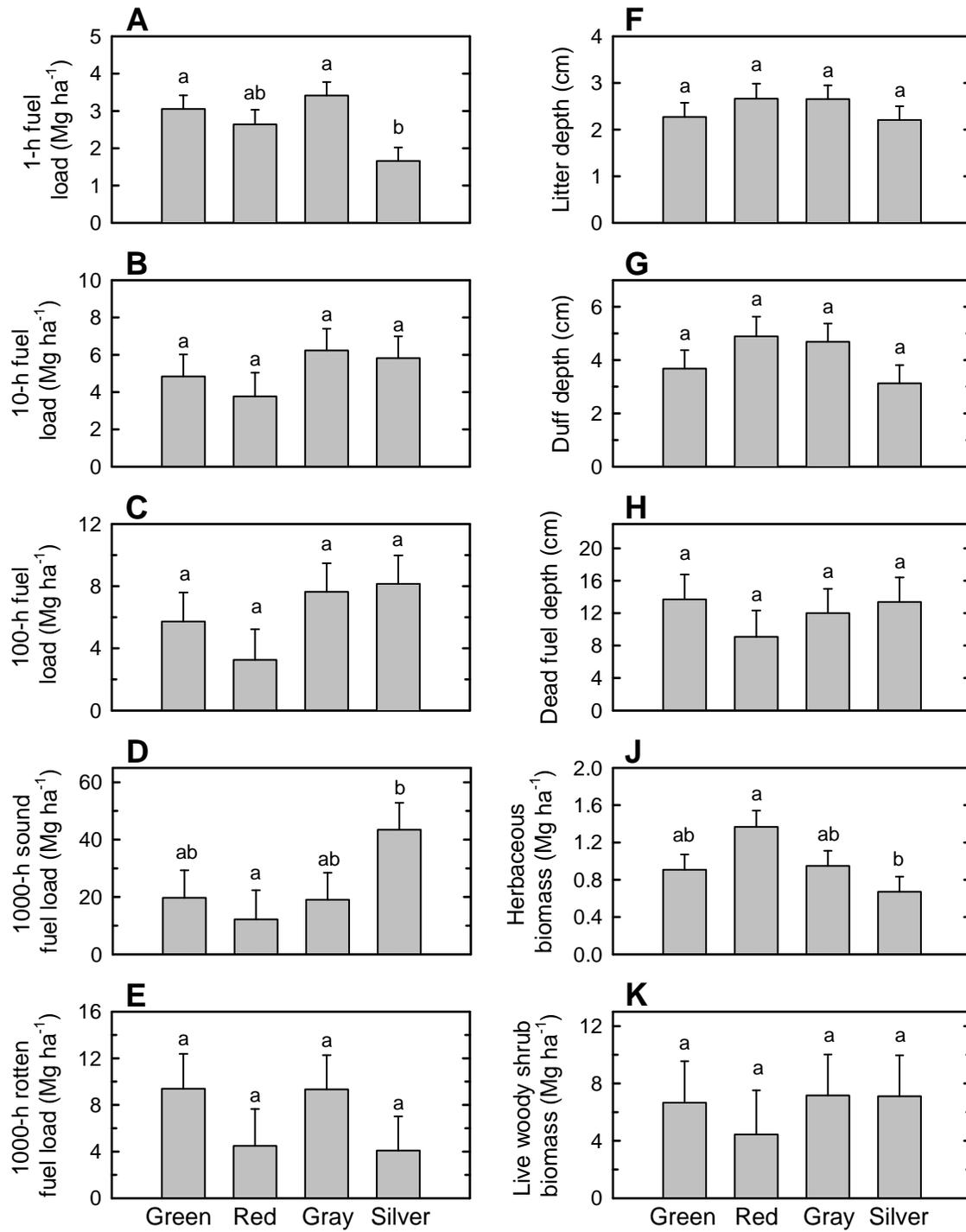
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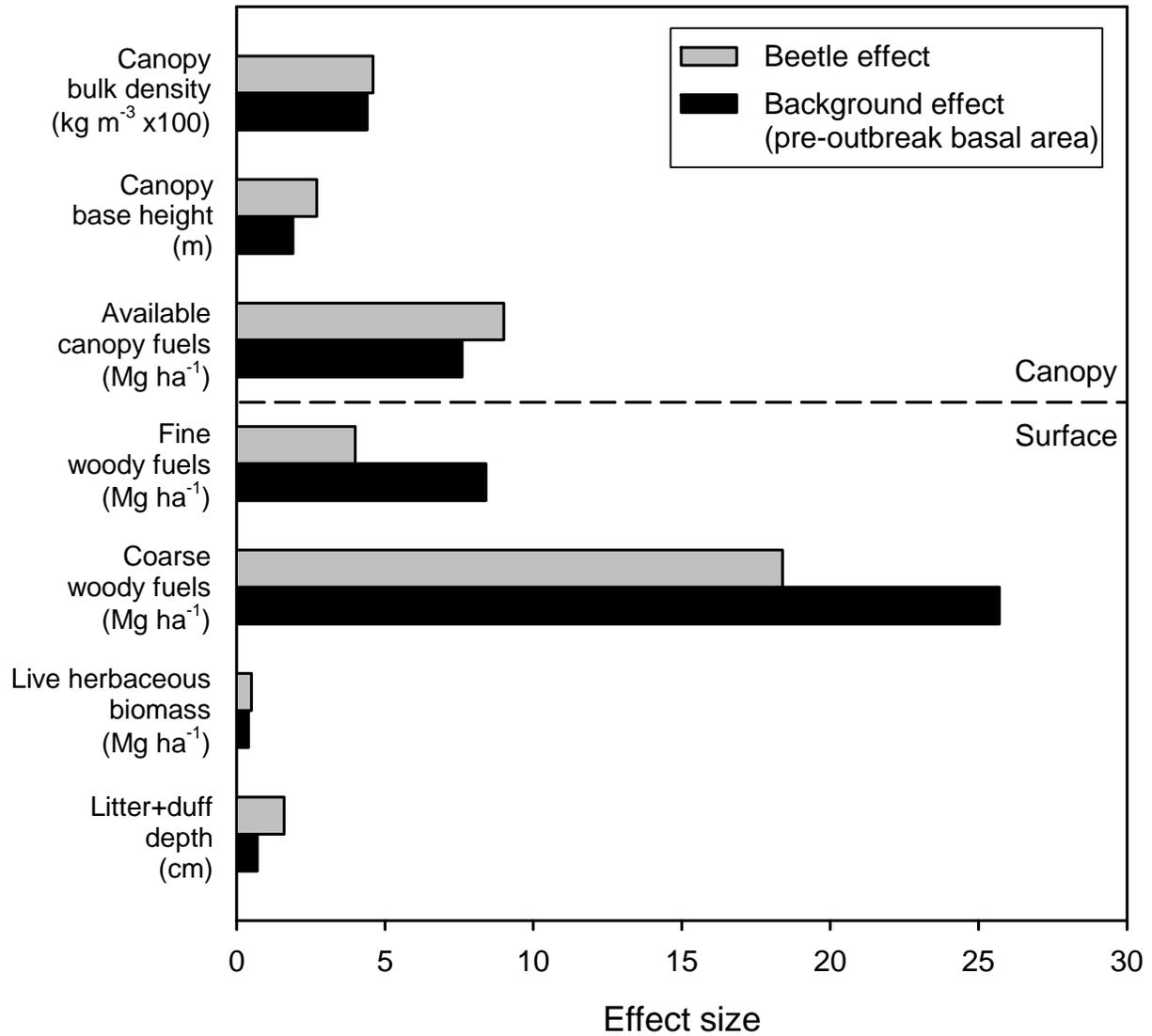
Figure 4





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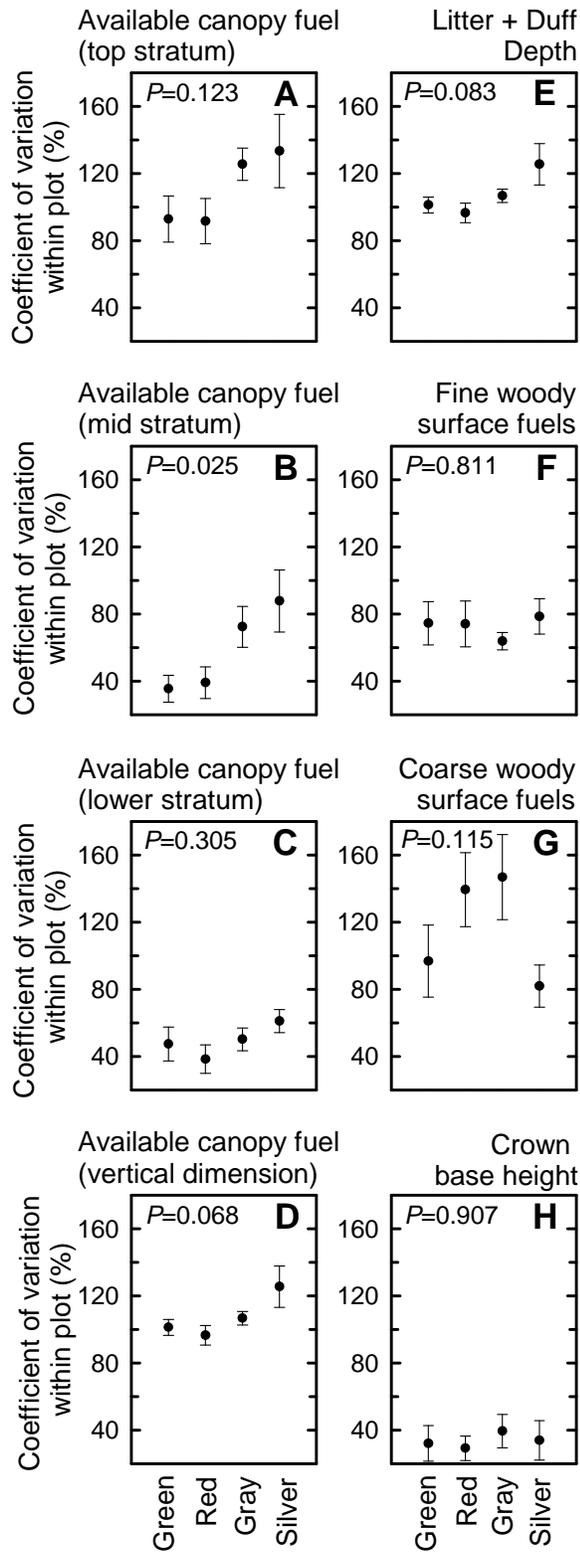
Figure 5



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Figure 6

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Figure 7