

1 **Microhabitat conditions rather than landscape patterns affect post-dispersal seed removal**
2 **in burned and unburned lodgepole pine (*Pinus contorta* var. *latifolia*) forests**

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24 **ABSTRACT**

25 **Context.** In many landscapes, disturbances create spatial variation at multiple scales and alter
26 wildlife habitat in ways that may influence animal behavior. Small mammals may respond to
27 disturbance patterns, and because many are seed predators, their foraging behavior can influence
28 seed supply and thus plant establishment. Although well studied in other systems, effects of
29 disturbance on spatial patterns of seed removal by small mammals in western North American
30 conifer forests are generally unknown.

31 **Objectives.** We conducted a seed removal study in lodgepole pine (*Pinus contorta* var. *latifolia*)
32 forests of Greater Yellowstone (Wyoming, USA) to answer two questions: (1) How do seed
33 removal and small mammal abundance vary between recently burned and adjacent unburned
34 forests and with distance from fire perimeter? (2) Within burned and unburned forests, which
35 environmental variables explain variability in seed removal and small mammal abundance?

36 **Methods.** We established 80-m transects ($n = 23$) centered on and perpendicular to the edge of
37 recent (2012 and 2013) stand-replacing wildfires during summer 2014. Each transect included
38 four stations, with one station established near (10 m) and far (40 m) from the fire's edge in both
39 burned and unburned forest. Lodgepole pine seeds (1.0 g, ~259 seeds) were supplied in a tray at
40 each station and left in the field for 28 days. Habitat structure and seed abundance were
41 quantified at each station; wildlife cameras were deployed at a subset ($n = 33$) of stations. Upon
42 retrieval, cameras and remaining seeds were returned to the laboratory for processing.

43 **Results.** Seed removal averaged 85% across all stations (15% of supplied seeds remained in
44 trays as intact seeds), and evidence of *in situ* seed consumption (seed hulls) was found in 99% of
45 trays. Small mammals (mice or voles, chipmunks, and squirrels) were the most abundant animals

46 captured by cameras. Seed removal and small mammal abundance did not differ between burned
47 and unburned forests or with edge distance, but both varied with local coarse woody habitat.

48 **Conclusions.** Seed removal was high in burned and unburned forests at both distances from fire
49 edge, and small mammals were not deterred from using forests one to two years after stand-
50 replacing fire. If observed seed removal rates represent natural conditions and removed seeds are
51 either consumed or relocated to unsuitable germination sites, animal foraging could influence
52 post-fire recruitment of a widespread foundation tree species.

53

54 **KEYWORDS:** motion-triggered wildlife cameras, seed predation, subalpine forest, American
55 red squirrel (*Tamiasciurus hudsonicus*), rodents, granivores, Yellowstone National Park,
56 Bridger-Teton National Forest, fire ecology, behavioral landscape ecology

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71 **INTRODUCTION**

72 Disturbances create spatial patterns that can structure landscapes for years to centuries,
73 leading to important biological consequences for ecosystems and the organisms living within
74 them (Turner 2010). Disturbance-generated patterns occur over multiple scales, including
75 patches of disturbed versus undisturbed areas across landscapes and varied conditions within the
76 perimeters of disturbed and undisturbed patches. Disturbance mosaics affect vegetation
77 succession (e.g., Johnstone et al. 2011) and habitat-use patterns by many wildlife species (e.g.,
78 Boyce et al. 2003), and responses of herbivores to changing patterns of habitat structure and
79 quality are well-studied (e.g., Mao et al. 2005, Forester et al. 2007). Perhaps less well-studied are
80 potential effects of granivores (i.e., seed predators) that may influence post-disturbance
81 succession by affecting seed supplies (but see Tallmon et al. 2003, Zwolak et al. 2010).
82 Understanding how granivores respond behaviorally to disturbances and the scale(s) at which
83 they respond could inform predictions of animal community dynamics in disturbance-prone
84 landscapes and identify potential effects of seed-eating animals on succession.

85 Seed-eating animals can have important effects on plants (Hulme 1998; Crawley 2000;
86 Hulme and Kollmann 2005), and small mammals are often the dominant granivore in a variety of
87 ecosystems. Small mammal seed predation can limit plant abundance in early successional
88 systems (Orrock et al. 2006) and can affect vegetation patterns (e.g., Brown and Heske 1990;
89 Ostfeld et al. 1997; Siepielski and Benkman 2008). Variation in small mammal seed predation
90 may be an outcome of landscape heterogeneity (Orrock and Danielson 2005; Orrock and
91 Damschen 2005; Craig et al. 2011), as small mammals are known to respond to both landscape
92 patterns and microhabitat conditions. However, the responses of small mammal seed predators to

93 both disturbance-created landscape patterns and microhabitat conditions are not widely studied
94 in single studies.

95 Wildfire, which modifies landscape patterns and microhabitat conditions important to
96 small mammals, is an ideal disturbance for examining granivore behavioral responses. Fires
97 affect multiple habitat characteristics to which small mammals respond, including food
98 resources, canopy cover, ground cover, and vegetation cover (Brown 1988; Manson and Stiles
99 1998; Orrock et al. 2004). Demographic responses of small mammals to forest fires have been
100 extensively studied (e.g., Fisher and Wilkinson 2005, Fontaine and Kennedy 2012, Griffiths and
101 Brook 2014), but behavioral responses such as foraging activity are less understood. Further,
102 aspects of forest structure important to small mammals need to be quantified, especially at
103 multiple spatial scales (Fisher et al. 2005; Fisher and Wilkinson 2005). Effects of granivory on
104 post-fire plant regeneration can be substantial (e.g., Auld and Denham 2001; Denham 2008). In
105 Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forests affected by
106 stand-replacing wildfire, the effects of small-mammal foraging behavior on plant recruitment can
107 be stronger than those of wildfire (Zwolak et al. 2010). However, millions of hectares of western
108 North America are occupied by lodgepole pine (*Pinus contorta* var. *latifolia*) forests, in which
109 the potential effects of wildfire on small mammal seed predators have not yet been tested.

110 Lodgepole pine, a fire-dependent foundational tree species (Critchfield 1980), is a conifer
111 that produces serotinous cones that open and release their seeds when heated, assuring rapid
112 post-fire tree regeneration. Lodgepole pine often dominates subalpine conifer forests in the
113 northern Rocky Mountains including those in the Greater Yellowstone Ecosystem (GYE;
114 Wyoming, USA). The 80,000 km² GYE, one of the world's last and largest near-intact north-
115 temperate ecosystems, experiences a stand-replacing fire regime that drives vegetation patterns.

116 The broad-scale variation in post-fire lodgepole pine regeneration across the GYE has been
117 extensively studied and depends largely on pre-fire serotiny levels and local burn severity
118 (Anderson and Romme 1991; Turner et al. 1997; Turner et al. 1999; Turner et al. 2003). Across
119 the landscape, levels of serotiny vary with fire-return interval and stand age (Schoennagel et al.
120 2003), and serotiny levels may also respond to selective pressure of American red squirrels
121 (Benkman and Siepielski 2004; Talluto and Benkman 2013), the dominant pre-dispersal seed
122 predators of lodgepole pine (Smith 1970). Despite considerable research into landscape patterns
123 of serotiny and post-fire regeneration, fine-scale variability in post-fire lodgepole pine
124 recruitment is still poorly understood. The potential role of seed predation in post-fire lodgepole
125 pine forests has not previously been studied, although researchers have suggested that post-
126 dispersal seed predation by small mammals could limit lodgepole pine recruitment (e.g., Lobo
127 2014).

128 Because the first few years following fire represent a critical window for tree
129 regeneration (Turner et al. 1997), we evaluated effects of recent stand-replacing wildfire on
130 animal foraging on lodgepole pine seeds to determine whether granivores have the potential to
131 drive local variation in post-fire lodgepole pine regeneration by asking two questions: (1) How
132 do seed removal and small mammal abundance vary between recently burned and adjacent
133 unburned forests and with distance from fire perimeter? and (2) Within burned and unburned
134 forests, which environmental variables explain variability in seed removal and small mammal
135 abundance? Because small mammal abundance, in general, tends to be equal or lower in forests
136 after fire (Bendell 1974), we hypothesized that small mammal abundance and seed removal
137 would be lower in recently burned compared to adjacent unburned forests. In burned forests, we
138 further hypothesized that overall small mammal abundance and seed removal would decrease

139 with increasing distance from the fire perimeter and increase with increasing habitat structure
140 (which may provide better cover from predators) and food resources (which may affect the
141 response of small mammal behavior to risk-reward tradeoffs (Holbrook and Schmitt 1988)). We
142 also expected the relative frequency of small mammal species to differ between burned and
143 unburned forests, e.g., with American red squirrels (*Tamiasciurus hudsonicus*) being more
144 abundant in unburned forests (e.g., Podruzny et al. 1999), mice being more abundant in burned
145 forests (e.g., Zwolak 2008), and chipmunks being equally abundant between burned and
146 unburned forests (e.g., Zwolak and Foresman 2007).

147

148 **METHODS**

149 ***Study area and design***

150 Our study was conducted in lodgepole pine-mixed conifer forests in Yellowstone
151 National Park (YNP) and Bridger-Teton National Forest (BTNF), located in the northwest corner
152 of Wyoming (USA) within the GYE. The climate of the GYE is characterized by cold, snowy
153 winters and cool, dry summers, and elevations in our study sites range from 2,474 to 2,667 m.
154 Lodgepole pine dominates the subalpine forests of YNP, although subalpine fir (*Abies*
155 *lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) may
156 be locally abundant at the higher elevations. Douglas-fir (*P. menziesii*) and aspen (*Populus*
157 *tremuloides*) are more abundant in low- to mid-elevation forests, which also include limber pine
158 (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*). Fire has long been a part of
159 Yellowstone's forested landscape, with natural, stand-replacing fires occurring at 100 to 300 year
160 intervals throughout the Holocene (e.g., Whitlock et al. 2008). A variety of granivorous small
161 mammals occur within GYE forests, including American red squirrels, golden-mantled ground

162 squirrels (*Spermophilus lateralis*), northern flying squirrels (*Glaucomys sabrinus*), least
163 chipmunks (*Tamias minimus*), yellow pine chipmunks (*Tamias amoenus*), deer mice
164 (*Peromyscus maniculatus*), and southern red-backed voles (*Myodes gapperi*).

165 Field sampling occurred in and adjacent to wildfires that burned lodgepole pine forests in
166 2012 (Cygnet and Fontenelle Fires) or 2013 (Alum Fire) within YNP and BTNF (**Table 1**). At
167 each fire, we established four to ten 80-m transects separated by at least 100 m, except for one
168 pair of transects that were separated by ~92 m. The 100-m separation was selected to maximize
169 the likelihood of detecting multiple American red squirrels, whose territories average less than 1
170 hectare (Gurnell 1984). Transects were perpendicular to distinct, straight boundaries between
171 forests affected by stand-replacing (hereafter, “burned”) and non-stand-replacing fire (hereafter,
172 “unburned”; defined as the end of live green trees) and centered on the fire’s edge, extending 40
173 m into both burned and unburned forest. The number of transects per fire (**Table 1**) was largely
174 determined by fire size and shape, burn severity pattern, and site access. Each transect traversed
175 forests of the same pre-fire successional stage class and was buffered in all directions by at least
176 40 m of similar forest. Due to tortuosity of fire perimeters and variation in burn severity, 40 m
177 was the average maximum distance at which a sufficient buffer of similar habitat could be
178 achieved. Geographic coordinates and elevation of the center of each transect, as well as each
179 station (see next section), were obtained by using a handheld global positioning system (Garmin
180 GPSmap 60CSx), and the compass bearing toward the burned forest was recorded. Burned and
181 unburned forests were photographed from the fire perimeter for each transect (example in
182 **Figure 1**).

183

184 *Seed removal experiment and wildlife cameras*

185 To quantify seed removal, four stations were established along each transect ($n = 23$): one
186 each at 10 and 40 m from the fire's edge in both burned and unburned forests ($n = 92$ stations
187 total). Seed removal trays were positioned at each station within 0.5 m of the transect based on
188 the presence of logs or snags. For the subset of stations ($n = 33$) with wildlife cameras (see
189 below), seed removal trays were positioned up to 3 m from the transect to obtain clear sight lines
190 for each camera. Trays were installed by carefully excavating and placing soil into a plastic
191 container (12.5 by 18.5 cm wide and 3.5 cm deep) with a base of mesh window screen to allow
192 water drainage. Each tray was supplied with 1.0g (259 ± 2.34 SE seeds, $n = 5$) of lodgepole pine
193 seeds (Sheffield's Seed Co, Inc., collected in Wyoming, 98% germination) that were sterilized
194 by microwaving to limit germination. Lodgepole pine seed weights average about 4.1-5.5 mg per
195 seed in Wyoming and Colorado (Siggins 1933; Elliott 1988; McGinley et al. 1990), although
196 others have documented averages of 3.0 and 3.2 mg per seed for the species (Wheeler 1981 and
197 Birot 1978, respectively).

198 All seed removal trays were deployed for 28 days (study dates provided in **Table 1**) to
199 include a full lunar cycle because moonlight has been shown to be an indirect cue of predation
200 risk to small mammals (e.g., Orrock and Danielson 2004). Seed data from 16 of the 92 stations
201 were excluded from analysis because the trays were disturbed (likely by large animals) while
202 deployed in the field or soil samples were lost because of a drying oven malfunction, leaving 76
203 stations for analyses. After retrieval of trays, soils were air-dried and/or dried in an oven to
204 prevent fungal decomposition of seeds. All material > 0.7 mm from the trays was searched for
205 remaining seeds and seed hulls, and remaining seeds were categorized as "intact" or "damaged"
206 and tallied. Seeds were considered intact and, thus, potentially viable (i.e., containing a
207 endosperm) if no visible part of the seed was missing and/or damaged and the seed was not

208 found to be empty upon a gentle squeeze or press between two fingers, similar to the apparent
209 viability method used by Ball and Miller (1990). Any seeds not categorized as intact were
210 considered to be non-viable and therefore included in seed removal counts, although damaged
211 seeds could have been non-viable before use in the field or killed by invertebrate seed predators.
212 As is common in seed removal studies (e.g., Moles et al. 2003), we assumed that seed removal
213 represented seed predation rather than seed dispersal. Seed hulls tallied from the trays' soils (i.e.,
214 *in situ* seed consumption) supported this assumption (see *Results*).

215 At 33 stations, motion-triggered wildlife cameras (22 Bushnell Trophy Cam Trophy
216 XLTs, seven Reconyx Silent Image RM30s, three Reconyx HyperFire PC900s, and one Reconyx
217 HyperFire PC900 Professional Covert IR) were secured to trees < 2 m away from and aimed at
218 trays to record activity by potential seed predators. The number of stations with cameras was
219 determined by equipment availability. Cameras were deployed in each fire at stations at both
220 distances from the edge with equal coverage in burned and unburned forests. Cameras were
221 deployed and collected at the same time as seed removal trays. Data from 2 of the 33 wildlife
222 cameras were excluded from analysis due to setup errors. The remaining 31 cameras were
223 deployed for a total of 863.9 days, or an average of 27.9 days per camera. However, photos were
224 captured only for a total of 719.8 days (382.0 days in burned forests vs. 337.8 days in unburned
225 forests), or a mean of 23.2 days per camera (23.9 days per camera in burned forests vs. 22.5 days
226 per camera in unburned forests) because five cameras malfunctioned within the first three days
227 of deployment. After the field season, each photograph was viewed and scored for the presence
228 of animals, which were counted and identified to the lowest taxon possible (species, genus, etc.).
229 At minimum, identifiable animals were categorized into one of the following categories: bird,
230 ungulate, lagomorph, carnivore, small mammal, possible small mammal or carnivore, unknown

231 flying animal, or unknown terrestrial animal. Categories other than known small mammals were
232 not analyzed. We also recorded the location of the animal (“on” or “off” the seed removal tray)
233 and the animal’s behavior in one of five categories: standing or resting, moving, eating,
234 interacting with other animals, or other. We were interested in relative abundance of different
235 small mammals instead of precise estimates of population size. Thus, we used a simple detection
236 rate, defined as the total number of detection events of a taxon per total survey effort time for
237 each camera (Kays et al. 2009) as a general index of small mammal abundance.

238

239 *Habitat covariates*

240 *Habitat structure.* Tree diameter at breast height (DBH) was recorded by species for all
241 live and dead canopy trees within the 3-m radius plot centered on each station. Canopy cover
242 was measured in each direction parallel and perpendicular to transect (four measurements per
243 station) using a spherical densiometer. Ground cover was recorded visually to the nearest 5% in
244 four 1-m x 1-m quadrats positioned 3 m from each station (again, in each direction parallel and
245 perpendicular to the transect). Cover categories included standing trees (not analyzed); coarse
246 wood (> 8 cm in diameter); litter and downed wood < 8 cm in diameter; shrubs and tree
247 seedlings; herbaceous plants; and bare soil, moss, etc. Coarse wood abundance was estimated
248 using a planar intercept method (Brown 1974), with diameters measured to the nearest 0.1 cm
249 along four 3-m transects in each direction parallel and perpendicular to the main transect
250 centered on the station. At the 1-, 2-, and 3-m marks along these four 3-m transects, the height of
251 coarse wood (if coarse wood was present within a 10-cm radius) was also recorded.

252 *Potential seed abundance.* As an index of potential food resources for small mammals,
253 cone abundance was tallied for the three nearest canopy trees rooted in each quadrant of the 9-m

254 radius circular plot surrounding each station, for a total of up to 12 trees per station. Only trees
255 that were alive before the fire (and therefore could be a seed source) were sampled. We recorded
256 the tree species and, based on visual inspection with binoculars, scored cone abundance in one of
257 five categories: no cones, 1-10 cones, 11-100 cones, 101-1,000 cones, or >1,000 cones. For
258 analyses of potential lodgepole pine seed supply, we used the midpoint cone abundance for each
259 category (e.g., 5 cones for the “1-10 cones” category) or 1,000 cones for the “>1,000 cones”
260 category. For lodgepole pine, we also noted whether trees were serotinous or non-serotinous (as
261 in Tinker et al. 1994, Turner et al. 1997, 1999). However, because only 7 of the 758 trees we
262 counted were serotinous lodgepole pines, we did not calculate potential indices for pre-dispersal
263 seed supply (i.e., seeds held within serotinous lodgepole pine cones, only available to pre-
264 dispersal specialist seed predators such as American red squirrels). We did calculate indices to
265 represent the annual mean post-dispersal lodgepole pine seed supply (i.e., seeds released from
266 cones, available to any ground-foraging animals) both before and after fire. For the before-fire
267 indices, all lodgepole pine trees we measured in 2014 would have been alive before the fire, so
268 we estimated the post-dispersal seed supply as the sum of (i) seeds released annually from
269 canopy cones of all (live or dead) non-serotinous lodgepole pines, assuming a mean of 25% of
270 cones per tree open (Mason 1915), and (ii) seeds from cones that dropped from all (live or dead)
271 non-serotinous and serotinous lodgepole pines and later opened on the ground, assuming a mean
272 of 3% of cones per tree are dropped (Hellum 1983) and 48% of dropped cones open due to soil-
273 surface heating (Teste et al. 2011). For the after-fire indices, all the trees recorded as dead in
274 2014 were assumed to have been killed by fire, so we estimated the post-dispersal seed supply as
275 described above except that (i) seeds released annually from canopy cones were counted for live,
276 non-serotinous lodgepole pines only and (ii) seeds from cones that dropped were counted for

277 live, non-serotinous and serotinous lodgepole pine only, and we also included (iii) seeds released
278 from serotinous cones of dead serotinous lodgepole pines (of which we recorded none) due to
279 fire. We assumed all cones contained 10 seeds each (Koch 1996), all of which were released
280 upon cone opening.

281

282 ***Statistical analyses***

283 To characterize habitat in burned and unburned forests, we calculated descriptive
284 statistics for all environmental covariates and analyzed differences used paired *t*-tests.

285 *(1) How do seed removal and small mammal abundance vary between recently burned*
286 *and adjacent unburned forests and with distance from fire perimeter?* We used a linear mixed
287 model (LMM) to test for differences in the proportion of intact seeds remaining in stations (i.e.,
288 differences in seed removal). We fitted a model with three fixed effects (*Burned*, with two levels:
289 burned or unburned forest; *Distance*, with two levels: 10 or 40 m; and the interaction of
290 *Burned*Distance*) and one random effect with a split-plot error structure (*Burned|Transect*) to
291 account for our split-plot study design (*Distance* nested within *Burned*) of each transect.
292 Levene's test was used to confirm equal variance among all the fixed effects levels before model
293 fitting. For the proportion of intact seeds, a Box-Cox transformation best improved normality of
294 the data over more common transformations but still failed the Shapiro-Wilk normality test.
295 After fitting the LMM with maximum likelihood, we used the Kenward-Rogers approximation
296 for degrees of freedom in analyses of variance (ANOVAs) of type 3 for hypotheses testing of our
297 split-plot design (Littell et al. 2006) and performed model diagnostics to check residuals for
298 normality, linearity, and constant variance. For small mammal abundance, we used the number
299 of animal detections in photos from wildlife cameras per survey effort time (reported as

300 detections per day) as a detection rate for each station with a camera. To test for differences in
301 detection rates among stations, we also used a LMM as described above, with one additional
302 random effect term to account for potential differences in camera types. We again used a Box-
303 Cox transformation because it best improved normality of the data compared to more common
304 transformations and did not fail Levene's and Shapiro-Wilk tests.

305 (2) *Which environmental variables explain variability in seed removal and small*
306 *mammal abundance?* We used LMMs to test for differences in the response variables
307 (proportion of intact seeds and small mammal detection rates) due to fixed effects, but ran
308 separate models in burned and unburned forests because these environments differ substantially
309 (**Table 2**). Based on univariate relationships between response variables and each potential
310 environmental covariate (explored by Kendall rank correlation tests), we selected eight
311 explanatory variables for use in the models: mean percent canopy cover, mean percent ground
312 cover by coarse wood, mean diameter of coarse wood, mean height of coarse wood, mean DBH
313 of dead trees, mean DBH of live trees, mean DBH of all trees (live and dead combined), and
314 before-fire post-dispersal seed abundance index (hereafter, "seed abundance index" or "SAI").
315 Univariate relationships between pairs of the selected environmental covariates (again using
316 Kendall rank correlation tests) found one covariate pair that was highly correlated (i.e., > 0.60)
317 and consequently never included together in the same model: mean height of coarse wood and
318 mean diameter of coarse wood ($z = 8.57$, $p < 0.0001$, $\tau\text{-}b = 0.71$). Explanatory variables were
319 standardized by subtracting the mean and dividing by the standard deviation for comparison of
320 parameters, and the same response variables were used as in previous LMMs. For each of the
321 data subsets (burned or unburned forests), we developed 63 candidate models that all included a
322 random effect term for *Transect* but varied in the number and identity of explanatory variables:

323 an intercept-only model (1 model); models for each explanatory variable (8 models); and models
324 with two (12 models), three (23), four (13), five (4), or six variables (2). After fitting all LMMs,
325 we used Akaike's information criterion corrected for small sample size (AICc) for model
326 selection. We again used the Kenward-Rogers approximation for hypotheses testing and
327 performed model diagnostics to check residuals for normality, linearity, and constant variance
328 for the top models ($\Delta \text{AICc} < 2$) of each data subset.

329 Because animal abundance is commonly assumed to be correlated with seed removal, we
330 also used Kendall rank correlation tests to examine whether seed removal in burned and
331 unburned forests was positively associated with abundance of all small mammals, squirrels, mice
332 or voles, and chipmunks. Data from an additional three wildlife cameras were excluded due to
333 loss of the soil sample from the camera's station, resulting in 28 cameras for these analyses.

334 All analyses were performed in R (R version 3.2.1, R Core Team, Vienna, Austria, 2015).
335 We used the *lmer* function in the lme4 package to fit LMMs, and the *AICc* and *r.squaredGLMM*
336 functions in the MuMIn package to calculate AICc and pseudo- r^2 values, respectively. Because
337 our sample size was small and we did not want to miss a biologically meaningful relationship,
338 we used $\alpha = 0.10$ for hypotheses testing.

339

340 **RESULTS**

341 ***Site and environmental data***

342 Lodgepole pine was the most abundant tree species on our transects, but its relative
343 abundance differed among fires. The Alum and Cygnet Fires in YNP were > 99% lodgepole
344 pine, whereas the Fontenelle Fire in the BTNF burned a mixed conifer forest: lodgepole pine
345 (36%), *A. lasiocarpa* (33%), *P. menziesii* (13%), *P. engelmannii* (10%), *P. flexilis* (5%), and *P.*

346 *tremuloides* (3%). As expected, burned forests were characterized by more and larger dead trees
347 (17.69 cm DBH in burned forests vs. 7.23 cm in unburned forests) and less and smaller live trees
348 (3.91 vs. 13.86 cm DBH) compared to unburned forests (**Table 2**). Both overall tree size and SAI
349 did not differ between burned and unburned forests (**Table 2**). Canopy cover, which averaged
350 69% in unburned forests, was lower but still considerable in burned forests, averaging 49%
351 (**Table 2**). Percent cover by litter, although significantly lower in burned forests, was relatively
352 similar in burned and unburned forests (48% vs. 57%) (**Table 2**). Shrub cover was 10x less in
353 burned forests (1% vs. 11%), and bare ground was nearly 3x greater in burned forests (31% vs.
354 11%) compared to unburned forests (**Table 2**). However, percent cover by coarse wood and
355 herbs averaged 7-9 and 11-12%, respectively, and did not differ in burned and unburned forests
356 (**Table 2**). Notably, coarse wood height did not differ, although the mean diameter of coarse
357 wood was slightly greater in burned forests (9.5 cm vs. 7.6 cm) (**Table 2**).

358

359 ***(1) Seed removal and small mammal abundance between recently burned and adjacent***
360 ***unburned forests and with distance from fire perimeter***

361 *Seed removal.* A total of 3,016 out of approximately 19,684 supplied seeds remained in
362 76 trays as intact seeds (i.e., overall 85% seed removal, which includes *in situ* granivory of 2,407
363 seeds remaining as hulls (i.e., 12% of supplied seeds)). Among all 76 stations, seed removal
364 ranged from 11 to 100% (mean = 85% \pm 2.7% SE) (**Table 3a**). For ease of interpretation, intact
365 seeds are reported here as percentages instead of proportions and discussed in terms of seed
366 removal as previously described (see *Methods*). We detected no difference in the proportion of
367 intact seeds remaining between trays in burned and unburned forests (86% vs. 83% seed
368 removal, respectively; $F_{1,21} = 0.007$, $p = 0.934$), at 40 and 10 m from the fire's edge (distance)

369 (83% vs. 86% seed removal, respectively; $F_{1,38} = 0.010, p = 0.919$), and there was no significant
370 interaction between burn status and distance ($F_{1,38} = 0.529, p = 0.472$) (**Table 4a**).

371 *Small mammal abundance.* During the total 719.8 days of survey time, the 31 cameras
372 altogether recorded a total of 2,201 detection events of animals. All cameras recorded at least
373 two animal detections. Of the total detections, 227 detections (10%) of either terrestrial or flying
374 animals were unidentifiable (i.e., unknown). Of the 1,974 identifiable detections, 1,662
375 detections were identifiable to family, order, or class and 312 detections were identifiable to
376 genus or species.

377 Overall, small mammals and unknown terrestrial animals were the species groups
378 detected on the highest percentage of cameras at 90% (for both, on 28 of 31 cameras), followed
379 by unknown flying animals on 23% of cameras (7 of 31 cameras) and possible small mammals
380 or carnivores on 6% (2 of 31). A higher percentage of cameras in unburned forests compared to
381 burned forests detected small mammals (93% of cameras in unburned forests vs. 88% in burned
382 forests, respectively), unknown terrestrial animals (87% vs. 56%, respectively), unknown flying
383 animals (27% vs. 19%, respectively), and possible small mammal or carnivores (13% vs. 0%,
384 respectively).

385 Among the small mammals, unknown small mammals were the species group detected
386 on the highest percentage of cameras at 61% (19 of 31 cameras; 73% of cameras in unburned
387 forests vs. 50% in burned forests), followed by possible mice or voles on 52% (16 of 31 cameras;
388 67% in unburned vs. 38% in burned), squirrels on 39% (12 of 31 cameras; 60% in unburned vs.
389 19% in burned), chipmunks on 26% (8 of 31 cameras; 33% in unburned vs. 19% in burned), and
390 porcupines on 3% (1 of 31 cameras; in burned forest). Only two small mammals were reliably
391 identifiable to species: American red squirrels (*T. hudsonicus*) were detected on 16% of cameras

392 (5 of 31 cameras; 27% in unburned forests vs. 6% in burned forests) and northern flying squirrels
393 (*G. sabrinus*) were detected on 10% of cameras (3 of 31; 20% in unburned vs. 6% in burned).

394 The mean detection rate, calculated as the means of overall detections per day from each
395 camera, was 6.64 ± 2.29 SE detections per day (8.76 ± 4.42 SE in burned forests; 4.64 ± 8.76 SE
396 in unburned forests; **Table 3b**). Similar to the relative frequency of occurrence of different
397 species groups on cameras described above, small mammals had the overall highest mean
398 detection rate of any species group at 3.64 ± 1.94 SE detections per day, followed by unknown
399 terrestrial animals (0.72 ± 0.29 SE), unknown flying animals (0.60 ± 0.42 SE), and possible
400 small mammal or carnivores (0.01 ± 0.009 SE). However, we detected no difference in detection
401 rates of small mammals between burned and unburned forests (2.25 vs. 5.12 detections per day,
402 respectively; $F_{1,7} = 0.314$, $p = 0.593$), at 40 and 10 m from the fire's edge (1.65 vs. 6.05
403 detections per day, respectively; $F_{1,13} = 0.086$, $p = 0.774$), and there was no significant
404 interaction between burn status and distance ($F_{1,13} = 0.077$, $p = 0.786$) (**Table 4b**).

405 Among the small mammals, possible mice or voles had the overall highest detection rates
406 (1.89 ± 1.34), followed by unknown small mammals (0.88 ± 0.58), chipmunks (0.67 ± 0.63),
407 squirrels (0.19 ± 0.09), and porcupines (0.003 ± 0.003). All groups had higher detection rates in
408 unburned compared to burned forests (**Table 3b**). American red squirrels (*T. hudsonicus*) had an
409 overall higher detection rate (0.11 ± 0.07 SE) than *G. sabrinus* (0.02 ± 0.01 SE), and both had
410 higher detection rates in unburned compared to burned forests (**Table 3b**).

411

412 ***(2) Environmental variables associated with seed removal and small mammal abundance***

413 *Seed removal.* For seed removal in burned forests, the best-fit model found that seed
414 removal increased with larger mean DBH of all trees ($F_{1,24} = 12.255$, $p = 0.002$) and more coarse

415 wood cover ($F_{1,30} = 3.513, p = 0.071$), explaining 24% of the variation in the data (pseudo- $r^2 =$
416 0.24) (**Table 5a**). Two other top models were also supported and found that seed removal
417 increased with larger mean DBH of all trees ($F_{1,24} = 9.290, p = 0.006$) or with larger mean DBH
418 of all trees ($F_{1,23} = 11.709, p = 0.002$), more coarse wood cover ($F_{1,29} = 3.436, p = 0.074$), and
419 higher seed abundance index ($F_{1,31} = 1.057, p = 0.312$) (**Table 5a**). For seed removal in
420 unburned forests, the best-fit model was the intercept-only model, but two other models were
421 supported and found that seed removal increased with smaller mean diameters of coarse wood
422 ($F_{1,30} = 3.233, p = 0.082$) and smaller mean DBH of dead trees ($F_{1,34} = 2.261, p = 0.142$) or with
423 smaller mean diameter of coarse wood ($F_{1,28} = 1.904, p = 0.179$), explaining 5-12% of the
424 variation in the data (**Table 5a**).

425 *Small mammal abundance.* For small mammal abundance in burned forests, the best-fit
426 model was the intercept-only model, but one other top model was also supported and found that
427 small mammal abundance increased with more coarse wood cover, explaining 24% of the
428 variation in the data (pseudo- $r^2 = 0.24$) (**Table 5b**). For small mammal abundance in unburned
429 forests, the best-fit model found that small mammal abundance increased with lower mean height
430 of coarse wood ($F_{1,5} = 5.602, p = 0.067$) explaining 37% of the variation in the data (pseudo- $r^2 =$
431 0.37) (**Table 5b**). Four other top models including the intercept-only model were also supported
432 and found that small mammal abundance increased with larger DBH of all trees, smaller
433 diameters of coarse wood, or lower seed abundance index (**Table 5b**).

434

435 We found no significant correlations between seed removal in burned forests and
436 abundance of all small mammals ($z = -0.10, p = 0.92, \text{tau-b} = -0.02$), squirrels ($z = -0.07, p =$
437 0.94, $\text{tau-b} = -0.02$), mice or voles ($z = 0.17, p = 0.86, \text{tau-b} = 0.04$), or chipmunks ($z = -1.16, p =$

438 0.25, τ -b = -0.26). In unburned forests, we also found no significant correlations between seed
439 removal and abundance of all small mammals ($z = 0.73$, $p = 0.46$, τ -b = 0.16), squirrels ($z =$
440 0.13 , $p = 0.90$, τ -b = 0.03), mice or voles ($z = -1.58$, $p = 0.11$, τ -b = -0.35), or chipmunks ($z =$
441 0.23 , $p = 0.82$, τ -b = 0.05). However, we did record probable *in situ* seed consumption by
442 small mammals from the wildlife camera detections: animals “eating” and located “on” the seed
443 removal trays of a few stations (unknown squirrels and *T. hudsonicus* at a 40-m station in burned
444 forest, chipmunks at 10-m station in burned forest, and mice or voles at a 10-m station in
445 unburned forest).

446

447 **DISCUSSION**

448 Seed removal was surprisingly high, but equal, in recently burned and adjacent unburned
449 subalpine forests of the GYE. Counter to our expectations, seed removal and small mammal
450 abundance did not vary between unburned and burned forests or with distance from fire
451 perimeter, but they were correlated with microhabitat conditions. Environmental covariates
452 seemed to be more important in burned forests than in unburned forests, as we could better
453 explain both seed removal and small mammal abundance in burned forests with the variables
454 measured in this study. Seed removal and small mammal abundance, although correlated with
455 multiple environmental variables, were commonly associated with two environmental variables
456 related to coarse wood size and abundance (percent cover by coarse wood in burned forests and
457 coarse wood diameter in unburned forests); however, we detected no direct correlations between
458 seed removal and small mammal abundance.

459 The high, yet similar, levels of seed removal and small mammal abundance in burned and
460 unburned subalpine forests suggest that small mammals are not deterred from foraging in areas

461 of recent stand-replacing fire up to 40 m from the edge. Other studies have revealed high
462 resilience of vegetation to stand-replacing fire in GYE (e.g., Turner et al. 2007, Romme et al.
463 2011); this study suggests that small mammals may also exhibit behavioral resilience to such
464 fires as quickly as one to two years after fire. Stand-replacing fires kill nearly all trees, consume
465 a considerable amount of the fine canopy fuels and litter layer, and expose mineral soil.
466 However, the standing-dead trees and branches may continue to provide substantial canopy
467 cover, and little coarse wood (16%) is consumed even in high-severity fires (Tinker and Knight
468 2000). Thus, substantial habitat structure and complexity remain in recently burned forests, and
469 this likely provides cover for small mammals that may reduce predation risk. These results
470 provide additional support for the ecological importance of post-disturbance biotic legacies in
471 forest landscapes (Swanson et al. 2011).

472 The lack of a detectable edge effect on seed removal and small mammal abundance was
473 also unexpected, but this may reflect the substantial spatial heterogeneity that is present in
474 natural disturbances (Foster et al. 1998). As noted in our methods, 40-m was the maximum
475 buffer distance we could consistently achieve when running transects into areas of stand-
476 replacing fire because the shapes of burned patches were complex. Even in the very large and
477 severe 1988 wildfires in YNP, more than 75% of the area in severe-surface burn was within ~40
478 m of a green forest edge and 50% of the area burned as crown fire was within 50 m of unburned,
479 green forest (Turner et al. 1994). We found that burned forests still provide considerable canopy
480 cover that reduces light penetration, which is an indirect cue of predation risk to small mammals.
481 Complex spatial patterns of burn severity have been quantified for many large fires throughout
482 the intermountain west (e.g., Collins et al. 2007), and our study suggests this spatial

483 heterogeneity may provide adequate cover and opportunities for small mammals to escape
484 predation.

485 The significance of multiple environmental covariates in explaining seed removal and
486 small mammal abundance again underscores the role of habitat structure and biotic legacies for
487 wildlife. The size and abundance of coarse wood was important for explaining both seed removal
488 and small mammal abundance. In burned forests, higher percent cover by coarse wood was
489 associated with higher seed removal and small mammal abundances. However, because mean
490 percent cover by coarse wood did not differ in burned versus unburned forests, our results
491 suggest that coarse wood may have greater importance for small mammals in burned compared
492 to unburned forests. Past studies similarly have found both downed woody material and standing
493 dead wood in burned forests to be important to small mammals (Fisher and Wilkinson 2005). In
494 unburned forests, smaller diameters of coarse wood were associated with both higher seed
495 removal and small mammal abundances. Because mice or voles were the most abundant small
496 mammal species group detected on our wildlife cameras, the significance of coarse wood
497 diameter may reflect microhabitat use by small mammals with small body size, who may be able
498 to better utilize the cover provided by smaller coarse wood compared to larger small mammals
499 such as American red squirrels. Although our seed abundance index was not significant in any
500 models, seed removal in burned forests was positively correlated with tree size, which may be a
501 surrogate for cone abundance, suggesting that animals could potentially be attracted to areas of
502 high seed abundance in burned forests. In unburned forests, small mammal abundance also
503 increased with tree size, but interestingly decreased with increasing coarse wood height, which
504 again may reflect higher microhabitat use of coarse wood by small mammals with smaller body
505 sizes. Our results support an established body of literature documenting the importance of

506 various microhabitat conditions to small mammals (e.g., Yahner 1986; Whelan et al. 1991;
507 Bowers and Dooley 1993; Manson and Stiles 1998).

508 We observed no differences in seed removal or small mammal abundance between
509 burned and unburned forests, but past studies have shown supporting and contrary evidence for
510 small mammals in similar ecosystems. Abundances of many small mammal taxa, especially
511 those with larger body sizes, are often equal or higher in unburned than in burned forests
512 (Griffiths and Brook 2014), but habitat use of burned areas is species-specific (Zwolak 2009). In
513 western Montana, for example, chipmunks were found in similar abundances between burned
514 and unburned conifer forests, whereas deer mice were more abundant and southern red-backed
515 voles were less abundant in burned forests (Zwolak and Foresman 2007). American red squirrels,
516 the primary pre-dispersal seed predators of lodgepole pine, tend to avoid open habitats and may
517 only occasionally forage along the edges of burned forests (e.g., Roppe and Hein 1978, Fisher
518 1999). Because fire can destroy food resources and protective cover, it is likely to have negative
519 short-term impacts on American red squirrels (Fisher and Wilkinson 2005). Two years after fire
520 in mixed conifer forests of Arizona, Mount Graham squirrels occupied increasingly lower
521 proportions of middens in areas of increasing burn severities, with 0% of middens occupied in
522 areas of severe burn (Blount and Koprowski 2012). In our study region, American red squirrels
523 were not found in burned forests immediately after the 1988 fires in YNP (Roy Renkin, personal
524 communication). Deer mice, which are common throughout the United States, also consume
525 lodgepole pine seeds (Lobo et al. 2009). In contrast to red squirrels, deer mice are often found in
526 elevated abundances in burned forests (Zwolak 2008), likely due to increased foraging efficiency
527 (Zwolak et al. 2011), and can contribute to high seed removal in burned forests (Zwolak et al.
528 2010). In other ecosystems, seed predation by small mammals can also vary with distance from

529 habitat edges (e.g., Bowers and Dooley 1993, Ostfeld et al. 1997) and food resources (e.g.,
530 Hulme 1998).

531 Although seed removal and small mammal abundance were correlated with two of the
532 same environmental variables, small mammal abundance was not directly correlated with seed
533 removal. These results are consistent with the hypothesis that animal behavior, not only animal
534 abundance, is important to explaining seed removal patterns. Differences in foraging behaviors
535 and predation risks perceived by different small mammal species (e.g., diurnal versus nocturnal
536 seed predators) and/or individuals could result in variation in *in situ* consumption versus removal
537 of seeds from trays. Also, because 10% of animals in photos were unidentifiable and our small
538 mammal abundance was a simple index, using a more robust abundance metric to estimate true
539 population sizes may lead to different conclusions. We did not account for other granivores such
540 as birds and invertebrates because small mammals are considered the dominant granivore in this
541 system, but both the *in situ* seed consumption counts and camera data including photo evidence
542 of probable *in situ* seed consumption by small mammals at seed removal trays supported this
543 assumption. However, the relative importance of granivore guilds can shift between open and
544 closed habitats (John Stuhler, unpublished data), so future research that rigorously quantifies
545 animal abundances and seed predation by invertebrates and other species in lodgepole pine
546 forests may further assist in explaining patterns of seed removal.

547 Regardless of which animals were responsible for seed removal, we have strong evidence
548 to suggest that seed removal is indicative of seed predation or death instead of seed dispersal
549 (Vander Wall et al. 2005) that might lead to lodgepole pine germination. Ninety-nine percent of
550 stations had evidence of *in situ* seed consumption, and on average, 12% of supplied seeds
551 remained as hulls. Seeds that are removed may be cached by animals instead of immediately

552 eaten, but seed-caching is more likely to occur for large-seeded pine species than for lodgepole
553 pine (Wall 2003). Lodgepole pine seeds, at approximately 3-4 mm long and 2 mm wide
554 excluding seed wings (Koch 1996), are the smallest seed of any pine except for jack pine (*P.*
555 *banksiana*); thus, we expect lodgepole pines are unlikely to benefit from dispersal by animals
556 (Wall 2003). When seeds are cached as cones by larderhoarding animals such as red squirrels
557 (Steele et al. 2005), they are commonly assumed to not contribute to plant recruitment. Also,
558 because lodgepole pine best germinates in specific microsite conditions that are created by fire,
559 seeds would likely die unless moved within burned forests or moved from unburned into burned
560 forests by animals. If we can assume that removed seeds are consumed or relocated to unsuitable
561 germination sites and the seed removal we observed represents natural conditions, then, at
562 maximum, an average of 15% of supplied seeds were potentially viable. The high rates of seed
563 removal quantified in this study suggest that seed predation could influence post-fire recruitment
564 of a widespread foundation tree species, especially where seed supply is limiting for tree
565 recruitment. In areas where levels of pre-fire serotiny are high, seed predators would be less
566 likely to have a strong effect. However, in areas such as our study sites where levels of pre-fire
567 serotiny were low or non-serotinous conifers were abundant, our results suggest that seed
568 predators could depress seed regeneration.

569 Projections for increased fire activity associated with climate change in the GYE
570 (Westerling et al. 2011) and other regions of the world suggest that future landscapes will
571 increasingly be composed of mosaics that include areas of recently burned and adjacent
572 unburned forests, which underscores the need for a more comprehensive understanding of animal
573 community dynamics within these mosaics and the potential drivers of post-fire vegetation and
574 succession. Considerable research has been conducted on pre-dispersal seed predation of

575 lodgepole pine (e.g., Benkman et al. 2012) and our data suggest that post-dispersal seed
576 predation may also affect seed availability for post-fire succession. However, the ecological
577 result of the interrelated dynamics of seed predators, forests, fire, and climate change across
578 changing landscapes in the future is unknown.

579

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598 **LITERATURE CITED**

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773 **TABLES AND FIGURES**

774 **Table 1.** Characteristics of three stand-replacing wildfires in the Greater Yellowstone Ecosystem and study sampling effort and dates.

	Alum Fire [^]	Cygnets Fire	Fontenelle Fire
<u>Characteristics</u>			
Date of fire origin *	August 2013	August 2012	June 2012
Latitude **	44° 35' 31.2"	44° 40' 55.2"	42° 31' 58.8"
Longitude **	-110° 29' 06.0"	-110° 37' 19.2"	-110° 31' 12.0"
Elevation (m)†	2,491 to 2,534	2,474 to 2,554	2,492 to 2,667
Size (ha) **	2,867	1,290	23,523
“High” burn severity area within fire perimeter (%) **	59	26	22
<u>Sampling effort and dates</u>			
Transects: <i>n = 23</i> (22)	4 (4)	10 (9)	9 (9)
Seed removal trays: <i>n = 92</i> (76)	16 (14)	40 (27)	36 (35)
Wildlife cameras: <i>n = 33</i> (31) ‡	6 (6) ‡	6 (6) ‡	21 (19) ‡
Study dates (all in 2014)	July 11-August 8	July 12-August 9	July 19-August 16 (1 transect), July 20-August 17 (2 transect), July 21-August 18 (2 transects), July 22-August 19 (4 transects)

775 [^] One of the Druid Complex fires. * From InciWeb – Incident Information System (<http://inciweb.nwccg.gov>) ** From MTBS

776 database (<http://www.mtbs.gov/>). † Data collected from stations in the field; values are Min. to Max. Sampling effort numbers in **bold**

777 represent sample sizes that were established or deployed; *italicized* numbers following in parentheses represent sample sizes that were

778 analyzed. ‡ For correlation analyses of seed removal and small mammal abundances, $n = 28$ cameras: 5 at Alum, 4 at Cygnet, and 19
779 at Fontenelle.

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792 **Table 2.** Descriptive statistics of explanatory variables used in seed removal and small mammal abundance analyses. All variables
 793 represent mean measurements from $n = 76$ stations (e.g., mean of four canopy cover measurements per station), except for potential
 794 seed abundance (i.e., total seed abundance index; one measurement per station). Values presented as **Means** (SE) [Min-Max].

<i>Environmental covariate</i>	Unburned forests	Burned forests	Results of paired t-tests of unburned and burned forests	
	<i>n</i> = 39 stations: (19 at 40 m, 20 at 10 m)	<i>n</i> = 37 stations: (18 at 40 m, 19 at 10 m)	<i>t</i>	<i>p</i>
Habitat structure				
DBH of live trees (cm)	13.86 (1.85) [0-41.80]	3.91 (2.12) [0-61.60]	-3.647	0.002
DBH of dead trees (cm)	7.23 (1.94) [0-42.70]	17.69 (2.06) [0-39.70]	3.467	0.002
DBH of all trees – live and dead (cm)	11.76 (1.21) [0-23.65]	13.75 (1.36) [0-35.54]	-0.828	0.417
Canopy cover (%)	69.14 (2.99) [12.12-93.50]	49.43 (3.80) [9.52-89.34]	-5.414	<0.0001
Diameter of coarse wood (cm)	7.61 (0.98) [0-21.00]	9.52 (1.18) [0-24.40]	1.992	0.060
Height of coarse wood (cm)	4.10 (0.92) [0-21.00]	3.42 (0.69) [0-21.00]	0.194	0.848
Ground cover by coarse wood (%)	8.62 (1.39) [0-33.75]	7.26 (1.08) [0-28.75]	0.199	0.844
Potential seed abundance				
Before-fire post-dispersal seed abundance index	2,318 (341) [0-7,000]	2,453 (397) [0-8,400]	-0.055	0.957

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798 **Table 3.** Descriptive statistics of response variables for (a) seed removal analyses from $n = 76$ seed removal trays and (b) small
 799 mammal abundance analyses from $n = 31$ cameras. Values presented as **Means** (SE) [Min-Max].

<i>Response variable</i>	Unburned forests	Burned forests
(a) Proportion of intact seeds remaining in trays and seed removal		
	<i>(n = 39 trays: 19 at 40 m, 20 at 10 m)</i>	<i>(n = 37 trays: 18 at 40 m, 19 at 10 m)</i>
Intact seeds remaining in trays (%) ^*	17 (4) [0-78]	14 (4) [0-89]
Seed removal (%)	83 (4) [22-100]	86 (4) [11-100]
(b) Small mammal abundance ‡		
	<i>(n = 15 cameras: 8 at 40 m, 7 at 10 m)</i>	<i>(n = 16 cameras: 9 at 40 m, 7 at 10 m)</i>
Wildlife camera detections per day of: **		
All animals †	4.64 (1.63) [0.07-24.60]	8.76 (4.42) [0.14-68.16]
Unknown terrestrial animals	1.00 (0.49) [0-6.99]	0.46 (0.32) [0-5.18]
Unknown flying animals	1.21 (0.85) [0-12.51]	0.03 (0.01) [0-0.18]
Possible small mammals or carnivores	0.03 (0.02) [0-0.22]	0 (0) [0-0]
Small mammals ^	5.12 (3.78) [0-57.67]	2.25 (1.36) [0-19.42]
Unknown small mammals	1.77 (1.17) [0-17.48]	0.06 (0.02) [0-0.22]
Porcupine	0 (0) [0-0]	0.007 (0.007) [0-0.11]
Chipmunks ^	0.08 (0.06) [0-0.97]	1.23 (1.21) [0-19.42]
Mice or voles ^	3.03 (2.66) [0-40.19]	0.82 (0.75) [0-12.04]
Squirrels ^	0.24 (0.13) [0-1.68]	0.14 (0.13) [0-2.09]
<i>T. hudsonicus</i>	0.13 (0.08) [0-1.14]	0.10 (0.10) [0-1.62]
<i>G. sabrinus</i>	0.05 (0.03) [0-0.32]	0 (0) [0-0]
Unknown squirrels	0.07 (0.02) [0-0.29]	0.04 (0.03) [0-0.47]

800 ^ Response variables used in analyses. * Proportion of intact seeds remaining in trays was used in analyses; percentages presented
801 here for clarity. ‡ For correlation analyses of seed removal and small mammal abundances, $n = 28$ cameras: 13 in unburned forest (7 at
802 10 m, 6 at 40 m), 15 in burned forest (7 at 10 m, 8 at 40 m) due to loss of three soil samples from trays. ** Detections per day (an
803 index of small mammal abundances) represent the total number of detection events of a taxon per total survey effort time for each
804 camera. † Includes animals in all categories: birds, ungulates, lagomorphs, and carnivores (not analyzed); as well as small mammals,
805 possible small mammal or carnivores, unknown flying animals, and unknown terrestrial animals.

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816 **Table 4.** Linear mixed model results of (a) proportion of intact seeds remaining in trays and (b) small mammal abundance between
 817 recently burned versus adjacent unburned forests and with distance from fire perimeter (10 vs. 40 m). Note: As the proportion of intact
 818 seeds remaining in trays decreases, seed removal increases.

<i>Model structure</i>	Intercept	Burned	Distance	Burned*Distance	pseudo-r²
(a) Proportion of intact seeds remaining in trays (n = 76 trays)					
Seeds = Burned*Distance + <i>Burned Transect</i>	3.38(0.30)	-0.19(0.45)	-0.25(0.41)	0.43(0.59)	0.007
(b) Small mammal abundance (n = 31 cameras)					
Smammals = Burned*Distance + <i>Burned Transect + Camera</i>	0.95(0.10)	-0.04(0.15)	-0.0008(0.14)	-0.06(0.19)	0.024

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 820 Coefficients are presented as Estimates (SE). Response variables: Seeds = Box-Cox transformation of proportion of intact seeds
 821 remaining in trays, Smammals = Box-Cox transformation of small mammal detections per day by wildlife cameras at stations. Fixed
 822 effects: Burned (2 levels) = burned or unburned forest, Distance (2 levels) = 10 or 40 m from fire's edge, Burned*Distance =
 823 interaction term. Random effects (*italicized*): *Burned|Transect* = split-plot blocking term (for Distance nested within Burned of each
 824 transect), *Camera* = blocking term for different wildlife camera models. No model coefficients were significant at $\alpha = 0.10$ according
 825 to an ANOVA of type 3 with the Kenward-Rogers approximation for degrees of freedom.

826 **Table 5.** Linear mixed models from top models ($\Delta AICc < 2$) of environmental variables as predictors of (a) proportion of intact seeds
 827 remaining in trays in burned and unburned forests and (b) small mammal abundance in burned and unburned forests. Note: As the
 828 proportion of intact seeds remaining in trays decreases, seed removal increases.

<i>Model structure</i>	Intercept	PercCW	Diam	Height	TotalDBH	DeadDBH	SAI	AICc	pseudo- r²
(a) Proportion of intact seeds remaining in trays									
<u>Burned forests</u> (<i>n</i> = 37 trays: 18 at 40 m, 19 at 10 m)									
Seeds = PercCW + TotalDBH + <i>Transect</i>	6.30(1.09)	-2.92(0.76)	-	-	-2.03(0.99)	-	-	238.39	0.24
Seeds = TotalDBH + <i>Transect</i>	6.28(1.15)	-	-	-	-2.51(0.77)	-	-	239.70	0.16
Seeds = SAI + PercCW + TotalDBH + <i>Transect</i>	6.33(1.06)	-2.01(0.98)	-	-	-2.86(0.75)	-	-1.01(0.88)	239.98	0.27
<u>Unburned forests</u> (<i>n</i> = 39 trays: 19 at 40 m, 20 at 10 m)									
Seeds = 1 + <i>Transect</i>	5.85(0.88)	-	-	-	-	-	-	250.31	0
Seeds = Diam + DeadDBH + <i>Transect</i>	6.72(0.93)	-	1.88(0.96)	-	-	1.60(0.97)	-	250.66	0.12
Seeds = Diam + <i>Transect</i>	6.04(0.87)	-	1.40(0.94)	-	-	-	-	250.67	0.05
(b) Small mammal abundance									

Burned forests ($n = 16$ cameras: 9 at 40 m, 7 at 10 m)

Smammals = 1 + <i>Transect + Camera</i>	0.88(0.06)	-	-	-	-	-	-	10.65	0
Smammals = PercCW + <i>Transect + Camera</i>	0.93(0.06)	0.15(0.07)	-	-	-	-	-	11.50	0.24

Unburned forests ($n = 15$ cameras: 8 at 40 m, 7 at 10 m)

Smammals = Height + <i>Transect + Camera</i>	0.97(0.06)	-	-	-0.14(0.05)	-	-	-	15.84	0.37
Smammals = 1 + <i>Transect + Camera</i>	0.96(0.08)	-	-	-	-	-	-	15.85	0
Smammals = TotalDBH + <i>Transect + Camera</i>	0.91(0.06)	-	-	-	0.22(0.09)	-	-	16.31	0.34
Smammals = Diam + <i>Transect + Camera</i>	0.93(0.06)	-	-0.13(0.06)	-	-	-	-	16.57	0.33
Smammals = SAI + <i>Transect + Camera</i>	0.93(0.06)	-	-	-	-	-	-0.17(0.07)	16.86	0.31

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830 Coefficients are presented: estimates (SE). Response variables: Seeds = Box-Cox transformation of the proportion of intact seeds

831 remaining in trays, Smammals = Box-Cox transformation of the small mammal detections per day by wildlife cameras at stations.

832 Fixed effects: PercCW = percent ground cover by coarse wood; Diam = diameter of coarse wood; Height = height of coarse wood;

833 TotalDBH = DBH of all trees (live and dead combined); DeadDBH = DBH of dead trees; SAI = seed abundance index (i.e., before-
834 fire post-dispersal seed supply index). All environmental variables represent mean measurements from stations (e.g., mean of four
835 canopy cover measurements per station), except for potential seed abundance (i.e., total seed abundance index, one measurement per
836 station). Random effects (*italicized*): *Transect* = blocking term for each transect; *Camera* = blocking term for different wildlife camera
837 models. **Bolded** parameters were significant at $\alpha = 0.10$ according to an ANOVA of type 3 with the Kenward-Rogers approximation
838 for degrees of freedom.

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843 **Figure legends**

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845 **Figure 1.** Example of variation in burn severity along a transect (in the Alum Fire) as viewed
846 from fire's edge: into recently burned forest (left) and adjacent unburned forest (right). Stations
847 at 10 m and 40 m in burned forest were in severe-surface burn and crown fire, respectively;
848 stations at 10 m and 40 m in unburned forest were in light-surface burn and unburned, green
849 forest, respectively.

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864 **Figure 1.**