

24 **Abstract**

25 **1.** Drought events occurring under warmer temperatures (i.e., “hotter droughts”) have resulted in
26 widespread tree mortality across the globe, and may result in biome-level vegetation shifts to
27 alternate vegetation types if there is a failure of trees to regenerate. We investigated how
28 overstorey trees, understorey vegetation, and local climatic and edaphic conditions interact to
29 influence tree regeneration, a key prerequisite for resilience, in a region that has experienced
30 severe overstorey tree mortality due to hotter droughts and beetle infestations.

31 **2.** We used detailed field observations from 142 sites that spanned a broad range of
32 environmental conditions to evaluate the effects of climate and recent tree mortality on tree
33 regeneration dynamics in the spatially extensive piñon (*Pinus edulis*)-juniper (*Juniperus*
34 *osteosperma*, *J. monosperma*) woodland vegetation type of the southwestern USA. We used a
35 structural equation modeling framework to identify how tree mortality and local climatic and
36 edaphic conditions affect piñon and juniper regeneration and electivity analyses to quantify the
37 species-specific associations of tree juveniles with overstorey trees and understorey shrubs.

38 **3.** Piñon regeneration appears to be strongly dependent upon advanced regeneration, (i.e., the
39 survival of juvenile trees that established prior to the mortality event), the survival of adult seed-
40 bearing trees (inferred from basal area of surviving trees), and the facilitative effects of
41 overstorey trees for providing favourable microsites for seedling establishment. Model results
42 suggest that local edaphoclimatic conditions directly affected piñon and juniper regeneration,
43 such that stands with hotter, drier local climatic conditions and lower soil available water
44 capacity had limited tree regeneration following large-scale dieback.

45 **4. Synthesis.** We identify four indicators of resilience to hotter drought conditions: (1) abundant
46 advance regeneration of tree seedlings; (2) sufficient canopy cover for survival of emergent

47 seedlings and existing regeneration; (3) sufficient seed source from surviving trees with high
48 reproductive output; (4) areas with cooler and wetter local climates and greater soil available
49 water capacity. In the absence of these conditions, there is greater likelihood of woodlands
50 transitioning to more xeric vegetation types following die-back.

51

52 **Introduction**

53

54 Droughts occurring under warmer temperatures associated with global climate change
55 have resulted in widespread tree mortality in forests and woodlands globally (Allen *et al.* 2010;
56 Carnicer *et al.* 2011). These large-scale forest die-off events can strongly affect water and energy
57 fluxes (Royer *et al.* 2011; Guardiola-Claramonte *et al.* 2011), and carbon cycling (Kurz *et al.*
58 2008; Brown *et al.* 2010), and lead to cascading effects on ecosystems globally (Bonan 2008;
59 Stark *et al.* 2016). As a result, there is concern that these forests and woodlands lack resilience to
60 climate change, where resilience is defined as the capacity of an ecosystem to absorb disturbance
61 without shifting to a qualitatively different state with altered function, or that is controlled by a
62 different set of ecological processes (Holling 1973; Standish *et al.* 2014). This concern is
63 predicated on the assumption that mortality of overstorey trees due to drought will result in
64 biome-level vegetation shifts to alternate vegetation types that are better adapted to the hotter and
65 drier climate conditions (Gonzalez *et al.* 2010; Allen, Breshears & McDowell 2015).

66 Forest resilience to climate change depends not only on overstorey mortality processes
67 (i.e. resistance component of resilience; Hodgson, McDonald & Hosken 2015), but also on the
68 ability of dominant tree species to regenerate following drought-related mortality of the canopy
69 vegetation (i.e. recovery component of resilience). Yet despite the intense level of scientific

70 focus on forest mortality, relatively little is known concerning the response of tree regeneration
71 to the co-occurrence of drought and associated overstorey mortality events (Martínez-Vilalta &
72 Lloret 2016). This disparity in research interest may be due to the dramatic, visual nature of
73 forest mortality, which is more readily observed than forest regeneration and can be detected
74 across large areas using remote sensing approaches (e.g., Huang *et al.* 2010; Van Gunst *et al.*
75 2016). As a result, fundamental population-level processes such as tree seedling establishment
76 and juvenile survivorship are not well understood and yet necessary to determine vegetation
77 shifts following drought-related dieoff (Lloret *et al.* 2012).

78 The climatic extremes that result in overstorey tree mortality may also strongly affect tree
79 regeneration dynamics. In arid and semi-arid forests and woodlands, regionally synchronous tree
80 recruitment events have been associated with cooler and wetter climatic conditions (League &
81 Veblen 2006; Barger *et al.* 2009). Experimental water manipulations also show negative effects
82 of drought on tree establishment and survival (McCallum 2011; Dulamsuren, Hauck &
83 Leuschner 2013). However, it is unclear that the same drought conditions that result in large-
84 scale overstorey tree mortality will consistently lead to negative effects on tree regeneration.

85 The microclimate conditions a juvenile tree experiences are strongly controlled by
86 availability of 'safe sites' that have the potential to ameliorate water stress during hot and dry
87 periods, decoupling regeneration from regional climate (Bertness & Callaway 1994; von Arx *et*
88 *al.* 2013). For instance, the shading provided by overstorey vegetation can result in over two-
89 fold reductions in summer potential soil evaporation in arid and semi-arid ecosystems (Franco &
90 Nobel 1988; Breshears *et al.* 1997), which may explain why juvenile tree establishment and
91 survival during drought is generally higher beneath the canopy of overstorey trees and shrubs
92 (Kitzberger, Steinaker & Veblen 2000; Gómez-Aparicio *et al.* 2004; Redmond *et al.* 2015). The

93 loss in overstorey tree microsites due to recent mortality events may therefore adversely affect
94 new recruitment and juvenile survival. Alternatively, dead logs and snags generated by
95 overstorey mortality may provide sufficient microclimatic conditions to facilitate tree
96 recruitment and thus forest and woodland resilience (Flake 2016). Tree recruitment may also be
97 strongly limited by competition for water and nutrients from perennial grasses (Scholes &
98 Archer 1997; Chambers, Vander Wall & Schupp 1999), and overstorey tree mortality may
99 indirectly affect tree recruitment by affecting understorey vegetation (Kane *et al.* 2010).

100 Forest and woodland resilience to drought may strongly vary among populations due to
101 physiographic and edaphic characteristics that affect the local climatic conditions experienced by
102 juvenile trees. Populations experiencing hotter, drier local climates, such as those at lower
103 elevations or in soil with poor water holding capacity, have generally been more vulnerable to
104 increasing temperatures and drought (Carnicer *et al.* 2011; Peterman *et al.* 2012). Yet because
105 vegetation strongly controls the microclimate conditions a juvenile tree experiences, the effects
106 of these local climatic conditions and soil properties on juvenile tree recruitment may be largely
107 due to the indirect effects on tree cover and composition and the understorey plant community.

108 There are two different pathways to obtain tree regeneration following drought that may
109 be differentially affected by overstorey tree mortality: advanced regeneration (i.e. the survival of
110 juvenile trees that established prior to the drought) and new recruitment (i.e. seedling
111 establishment and survival after the drought). New recruitment may be more strongly affected by
112 recent overstorey mortality compared to advanced regeneration due to limited seed availability.
113 Overstorey vegetation that facilitates seedling establishment and survival can shift to becoming
114 competitive as seedlings age (Miriti 2006; Soliveres *et al.* 2010), suggesting that older, advanced
115 regeneration juveniles may not be as strongly affected by microsite changes following dieoff.

116 The surviving advanced regeneration juveniles had to survive the multi-year drought, however,
117 and thus may be more strongly affected by local climatic conditions and soil properties.

118 We focused our study on the widely distributed piñon (*Pinus edulis*) -juniper (*Juniperus*
119 *monosperma*, *J. osteosperma*) woodlands of the southwestern USA, which have been particularly
120 susceptible to large-scale tree mortality events associated with hotter drought conditions
121 resulting from climate change processes (Breshears *et al.* 2005; Gaylord *et al.* 2013). Extreme
122 drought in combination with warmer temperatures and bark beetle infestations resulted in
123 woodland decline over at least 12,000 km² in the southwestern USA, with upwards of 90% piñon
124 mortality in some stands between 2002-2004 (Breshears *et al.* 2005; Shaw, Steed & DeBlander
125 2005). Most dead piñon trees were infested by the pinyon ips (*Ips confusus*) bark beetle, which
126 specifically targets adult piñon trees, leading to particularly high levels of adult piñon mortality
127 at regional scales (Floyd *et al.* 2009). Juniper, the other co-dominant species, had low mortality
128 rates and no evidence of insect infestations (Floyd *et al.*, 2009), and, as a result, woodland
129 composition shifted to becoming much more juniper-dominated (Mueller *et al.*, 2005). However,
130 piñon-juniper woodlands experiencing widespread drought mortality could still be considered
131 resilient to climate change if woodland cover was ultimately maintained through tree seedling
132 regeneration and subsequent stand development.

133 Through an observational field survey across a gradient of environmental conditions in
134 Colorado, Arizona, and New Mexico, this study assesses the effects of recent drought- and
135 concomitant beetle-induced tree mortality, local climate, soil properties and vegetation structure
136 on piñon and juniper recruitment dynamics. Using a structural equation modeling approach, we
137 explore the following hypotheses: 1.) Overstorey trees affect piñon and juniper recruitment by
138 providing favourable microsites (*Hypothesis 1A*; Fig. 1) or indirectly by altering understorey

139 vegetation cover (*Hypothesis 1B*; Fig. 1); 2.) Overstorey piñon mortality indirectly affects new
140 piñon recruitment by reducing seed availability (*Hypothesis 2A*; Fig. 1) or by reducing
141 overstorey microsites (*Hypothesis 2B*; Fig. 1); 3.) Variability in local climate and soil properties
142 affects piñon and juniper recruitment directly (*Hypothesis 3A*; Fig. 1) or indirectly through
143 changes in overstorey and understorey vegetation (*Hypothesis 3B*; Fig. 1). To more directly
144 explore the relationship between tree regeneration and tree versus shrub microsites, we
145 performed electivity analyses to quantify the species-specific associations of piñon and juniper
146 juveniles with overstorey trees and understorey shrubs.

147

148 **Materials and Methods**

149

150 *Study Areas*

151

152 We focused our study on three areas within the Colorado Plateau ecoregion: southwestern
153 Colorado, northern Arizona, and central New Mexico (Fig. 2). Data collected from the three
154 study areas were sampled between 2012 and 2014 using comparable methods. The three study
155 areas differed slightly in the sampling design and the placement of sample plots, with the New
156 Mexico and Colorado study areas spanning a much larger area (7,500 and 22,000 km²,
157 respectively) than the Arizona study area (1,100 km²). In all study areas, the sampling methods
158 followed the same protocol except for differences in the plot layout and the sampling area,
159 outlined below.

160

161 *Colorado Study Area*- Fifty two study sites were established and sampled between 2012 (28
162 sites) and 2013 (24 sites) across southwestern Colorado that spanned an elevational (1827 – 2317
163 m), soil available water capacity (7 – 18%), and latitudinal gradient (Fig. 2). Sites were selected
164 using Geographic Information Systems (ArcMap 10.1, Redlands, California, USA), digital
165 elevation models (USGS 2013), and NRCS soils maps (NRCS 2004) to ensure sites varied in
166 elevation, soil type, and were within 1 km of a road (Fig. 2; and see Redmond & Barger 2013;
167 Redmond *et al.* 2017a for site selection details). In the 2013 field survey only, sites also had to
168 have live adult piñon trees present, and thus, mortality could not reach 100% (maximum piñon
169 mortality was 99.6%). Mean annual precipitation was 368 mm across the Colorado study area
170 from 1900 to 2012, with 25% of annual precipitation occurring during the summer months. Mean
171 monthly temperatures averaged 8.8°C, with July having the warmest temperatures (21.5°C) and
172 January having the coolest temperatures (−3.1°C) on average (PRISM Climate Group 2014). The
173 dominant tree species in the Colorado study area were piñon pine and Utah juniper (*J.*
174 *osteosperma*), with ponderosa pine (*Pinus ponderosa*) present at a small subset of the higher
175 elevation sites. The common shrub species were antelope bitterbrush (*Purshia tridentata*),
176 mountain mahogany (*Cercocarpus montanus*) and sagebrush (*Artemisia*
177 spp.).

178 At each site, we established three 50 m long transects, spaced 25 m apart, to quantify
179 vegetation cover using the line intercept methods (see *Field Methods* for sampling protocol).
180 Tree juveniles (< 5 cm in basal trunk diameter) were sampled within a 10 m belt of each transect
181 whereas adult trees (≥ 5 cm in basal trunk diameter) were sampled within five circular plots of 7
182 m in radius (see *Field Methods* for juvenile and adult tree sampling protocol). One soil core was

183 taken from 0 to 10 cm soil depth at each transect end (six per site) to estimate soil available
184 water capacity in surface soils.

185
186 *Arizona Study Area*- Forty two study sites were sampled in 2014 in the northern Arizona study
187 area, approximately 27 km north of Flagstaff, Arizona, USA on the north side of the San
188 Francisco Peaks mountain range (Fig. 2). Sites were selected in a stratified random approach to
189 ensure the sites spanned an elevational (1680 - 2300 m) and soil available water capacity (4 –
190 16%) gradient, with the one requirement that they need to be < 1 km from a road for accessibility
191 (see Redmond *et al.* 2015 for site selection details). This study area averages 9°C in mean annual
192 temperature and 380 mm in total annual precipitation, with approximately 65% falling as rain
193 and snow over winter and the rest as rain over summer (PRISM Climate Group, 2014). The
194 dominant tree species in the Arizona study area are piñon pine and oneseed juniper (*Juniperus*
195 *monosperma*), although ponderosa pine and alligator juniper (*J. deppeana*) are also present at
196 some of the sites. Dominant shrub species include apache plume (*Fallugia paradoxa*), rubber
197 rabbitbrush (*Ericameria nauseosa*), and Fremont's mahonia (*Mahonia fremontii*).

198 At each site, we established a 10 m x 200 m transect and divided that transect into twenty
199 10 m x 10 m plots. We then sampled alternating plots along each transect (i.e., 10 plots total per
200 transect). At a subset of sites (n = 7) with lower tree densities, longer transects were established
201 (up to 300 m) resulting in a larger number of plots sampled at those sites (up to 15 plots per
202 transect). We established a 14-m transect diagonally across each plot to quantify vegetation
203 cover using the line intercept methods (see *Field Methods* for sampling protocol). Within each
204 plot, all trees (including both adult and juvenile trees) were sampled (see *Field Methods* for

205 sampling protocol). One soil core was taken from 0 to 10 cm soil depth at the center of each plot
206 (ten per site) to estimate soil available water capacity in surface soils.

207

208 *New Mexico Study Area-*

209 Forty five study sites were surveyed in the central New Mexico study area in 2014 (Fig.
210 2). Site locations were selected following a stratified random protocol (see Clifford et al., 2013
211 for details), such that locations were chosen by the proximity to a road (> 50 m and < 1 km), and
212 the proximity to other sites (c. 5 km from another site). The sites ranged in elevation from 1670
213 m to 2300 m, and extended approximately 150 km latitudinally. Available soil moisture was
214 between 4% and 15% on the sites. This study area averages 414 mm in mean annual
215 precipitation, with approximately 42% of annual precipitation occurring during the summer
216 months, although sites varied considerably in the amount of annual precipitation (mean annual
217 precipitation ranged from 294 mm to 538 mm across the 45 study sites). Mean monthly
218 temperatures averaged 10.4°C, although there was also considerable variability in mean annual
219 temperature across the study area, ranging from 8.6 to 12.7°C across the 45 study sites (PRISM
220 Climate Group 2014). Sites were generally co-dominated by piñon pine and oneseed juniper,
221 however alligator juniper and ponderosa pine were also present on sites at higher elevations. The
222 common shrub species included broom snakeweed (*Gutierrezia sarothrae*), sagebrush, and
223 Apache plume.

224 Sites were comprised of three, 100 m² square plots aligned in a triangular shape 75 m
225 apart (Clifford *et al.* 2013). A 14 m long transect was established diagonally across each plot to
226 measure understorey plant cover using line point intercept. All trees found within each plot were

227 sampled, and a soil core was taken from 0 to 10 cm depth in each plot (3 cores per site) to
228 estimate soil available water capacity in surface soils.

229

230 *Field and Laboratory Methods*

231

232 *Vegetation Sampling-* For each juvenile (basal trunk diameter < 5 cm.) and adult (basal trunk
233 diameter \geq 5 cm) tree encountered within each sampling area, we recorded the species, status
234 (live or dead), and basal trunk diameter. For all juveniles, we also recorded whether the base of
235 the juvenile stem was located beneath the canopy of a tree or shrub (hereafter referred to as a
236 ‘nursed’ juvenile) or in the interspace (i.e. not directly beneath the canopy of a tree or shrub). If
237 the juvenile was nursed, we also recorded the nurse tree or shrub species. For dead adult trees
238 encountered, we noted whether the tree mortality was recent (\leq 10 yr) by following the
239 guidelines in Kearns et al. (2005), which were established for piñon pine in southwestern
240 Colorado. Trees were considered recently dead if 33% or less of the branches were broken, some
241 small limbs were present, and at least 50% of the bark was attached and not > 2 mm from the
242 tree. We used these same guidelines consistently across our study areas. There is the potential for
243 snag decay to differ across our study sites due to different abiotic conditions, although these
244 guidelines accurately worked for the sites sampled by Kearns et al. (2005) in southwestern
245 Colorado that spanned a range of climatic conditions, suggesting that snag decay after 10 years
246 would be similar across our study sites in these semi-arid ecosystems. We quantified tree, shrub,
247 and perennial grass cover using the line point intercept method every 50 cm along the transect in
248 each site (Herrick *et al.* 2005).

249

250 *Soil Laboratory Methods*- We quantified surface soil available water capacity by using estimates
251 of percent sand, silt, and clay from the soil samples collected from each site. To do this, soils
252 were first sieved through a 2-mm sieve and the 2 mm fraction was weighed as gravel and the < 2
253 mm fraction was used to estimate percent sand, silt, and clay using the hydrometer method (Gee
254 & Or 2002) at the Colorado State University Soil Laboratory. We then used the estimates of
255 percentage sand, silt, clay, and gravel from each site to calculate surface soil available water
256 capacity by subtracting the wilting point from field capacity, which we calculated following the
257 equations in Table 1 of Saxton & Rawls (2006).

258

259 *Analyses of Regional Patterns of Tree Regeneration*

260

261 We assessed the effects of abiotic conditions, understorey vegetation, overstorey
262 vegetation, and recent adult piñon mortality on piñon and juniper recruitment across our study
263 area using piecewise structural equation modeling (SEM; see Table 1 for a list of all predictor
264 variables). This approach allowed us to assess whether overstorey tree cover directly affects tree
265 recruitment by providing facilitative microsites or whether overstorey tree cover indirectly
266 affects tree recruitment by altering understorey vegetation cover (H1; Fig. 1). This approach also
267 allowed us to assess more mechanistically how overstorey piñon mortality affects tree
268 recruitment through changes in microsites and/or seed availability (H2; Fig. 1). Using this
269 approach, we were also able to assess the direct and indirect effects of abiotic conditions on
270 juvenile recruitment (H3; Fig. 1).

271 We examined the effects of three abiotic variables that we hypothesised would influence
272 environmental stress: surface soil available water capacity, mean 30 year cumulative climatic

273 water deficit, and mean 30 year cumulative actual evapotranspiration (Table 1; see Appendix S1
274 for details on how these were calculated). Both actual evapotranspiration and climatic water
275 deficit are biologically meaningful measures of plant water balance and collectively are strongly
276 correlated with vegetation distribution (Stephenson 1990), and surface soil available water
277 capacity provides an estimate of water stress and is also highly correlated with nutrient
278 availability in the northern Arizona study area (Cobb *et al.* 1997).

279 In order to assess whether overstorey piñon mortality more strongly affects tree
280 recruitment through changes in microsite or seed availability, we used live piñon basal area as an
281 estimate of current seed availability and total live tree cover as an estimate of current microsite
282 availability in our structural equation model. Previous research in our study area found live piñon
283 basal area to be strongly correlated with surface piñon cone density (Pearson's $r = 0.88$;
284 Redmond *et al.* 2015), suggesting that piñon basal area is a good proxy for seed availability.
285 Further, live piñon basal area was only moderately correlated with live tree cover (Pearson's $r =$
286 0.56), and the variance inflation factors of all models were always less than 2.5.

287 We performed separate SEMs for piñon (*P. edulis*) and juniper (*J. monosperma* and *J.*
288 *osteosperma* combined) as we were interested in how recruitment patterns of piñon and juniper
289 may be differentially affected by abiotic and biotic conditions. We also performed separate
290 analyses for piñon juveniles that likely established after the recent (2002-2004) piñon mortality
291 event (defined as juveniles with a basal diameter ≤ 0.5 cm; hereafter referred to as new piñon
292 juveniles) and for piñon juveniles that likely established before the mortality event (defined as
293 juveniles with a basal diameter > 0.5 and < 5 cm; advanced piñon juveniles). These size classes
294 were chosen using size-age relationships established by Redmond and Barger (2013) in our
295 southwestern Colorado study area, who found that piñon juveniles with a basal diameter ≤ 0.5

296 cm were 3.4 times as likely to have established after the mortality event (i.e. were ≤ 10 years old)
297 whereas piñon juveniles with a basal diameter > 0.5 cm were more likely to have established
298 before the mortality event.

299 The piecewise structural equation modeling used here combines information from
300 multiple separate linear models into a single causal network and allows for non-normal
301 distributions, random effects, and correlated error structures (Shipley, 2009). For the three
302 SEMs, juvenile density response was modeled using generalized linear mixed effect models with
303 a negative binomial distribution (*glmer.nb* function in R package lme4; Bates et al., 2015)
304 whereas all other model components were modeled with a normal distribution using the *lmer*
305 function in the R package lme4 (Bates *et al.* 2015). All models included a random intercept for
306 study area. Prior to SEM modelling, we performed model selection for each model component
307 by fitting all possible model subsets of our overall model (dredge function in the R package
308 MuMIn; Barton 2016) and selecting the model that minimized Akaike Information Criterion
309 modified for small sample sizes (AICc; see Tables S1-S3 for piñon and juniper recruitment
310 model selection results). We also assessed whether the environmental drivers of tree recruitment
311 differed within each of the three study areas by comparing AICc values of models that also
312 included a random slope for study area for each predictor variable to the full model (prior to
313 model selection) used to predict new and advanced pinon recruitment (see Table S4 for a
314 description of each model). We did not perform this analysis for juniper recruitment due to a lack
315 of model convergence once a random slope for study area was added to the model. In all
316 instances, the models that included a random slope had higher AICc values than the full model
317 that only included the random intercept for study area (Table S4). All full models (prior to model
318 selection) had variance inflation factors < 2.5 and all final models had variance inflation factors

319 < 2 (Graham 2003). The SEMs were fit using the R package *piecewiseSEM* following Lefcheck
320 (2016). Following the method described by Shipley (2009), we assessed overall model fit using
321 direct separation tests (d-sep) of conditional independence based on Fisher's C statistic that
322 follows a χ^2 distribution. If the model was considered to have inadequate fit to the data ($P <$
323 0.05), then we revised our model to include the additional pathways until the resulting model had
324 a Fisher's C statistic with $P > 0.05$.

325 To quantify the facilitative and competitive effects of overstorey trees and shrubs on
326 juvenile tree recruitment and how these effects vary by species and juvenile life stage, we used
327 relative interaction indices, also referred to as electivity indices, proposed by Armas *et al.*
328 (2004). The interaction index represents the relative difference in seedling density occurring
329 beneath tree and shrub canopies and the interspace, and is calculated as:

330

331

$$I = \frac{(\text{Density}_{\text{Beneath Canopy}} - \text{Density}_{\text{Interspace}})}{(\text{Density}_{\text{Beneath Canopy}} + \text{Density}_{\text{Interspace}})}$$

332

333 The interaction index thus ranges from -1 to 1, with positive values indicating a facilitative effect
334 (i.e. juvenile trees are more likely to be found beneath tree and shrub canopies than in the
335 adjacent interspaces) and negative values indicating a competitive effect. At each site, we
336 calculated the interaction index for each species (piñon and juniper), juvenile life stage (new
337 seedling [BTD < 0.5], advanced seedling [BTD > 0.5 and < 2.5], sapling [BTD \geq 2.5 and < 5
338 cm]), and nurse type (overstorey trees and shrubs). For calculating the interaction index between
339 overstorey trees and tree juveniles, we excluded trees of the same species to reduce inflated
340 interaction indices due to higher abundances of seeds beneath conspecific tree species. As such,
341 this analytical approach takes into account the relative proportion of overstorey tree cover

342 compared to shrub cover and omitted conspecific trees to reduce the potential confounding effect
343 of differences in seed abundance. However, the higher interaction indices between overstorey
344 trees compared to shrubs may still be partly due to confounding effects of differences in seed
345 abundance due to the caching of seeds underneath heterospecific trees by birds and small
346 mammals (Vander Wall & Balda 1977; Vander Wall 1997). We only calculated the interaction
347 index for each combination of life stage, nurse type, and species, for which there was the
348 statistical expectation of at least one individual assuming a uniform distribution (i.e. total # of
349 individuals_{species X, life stage Y} × proportion canopy cover_{nurse type} ≥ 1).

350 We used the interaction index as a response variable in a mixed-effect multiple linear
351 regression model to assess how the interaction index varies among the two species (piñon and
352 juniper), juvenile life stage (new seedling, advanced seedling, and sapling), and nurse type
353 (overstorey trees and shrubs). We did not perform any transformations prior to analysis as the
354 data were approximately normal and any transformations increased heteroscedasticity. Study
355 area and site (nested within study area) were included as random effects. Analyses were done in
356 R (R Core Team 2014) using the *lme* function in the R package *nlme* (Pinheiro *et al.* 2015).

357

358 **Results**

359

360 As intended by the sampling design, there was high variability in woodland structural
361 and abiotic conditions across our study sites within each of the three study areas: Arizona,
362 Colorado, and New Mexico (Table 2). Adult piñon mortality following the 2002 drought
363 averaged 53% (interquartile range = 20% to 91%) with the Arizona study area having the highest
364 mortality rates and Colorado having the lowest (Table 2). Tree recruitment also varied

365 considerably across our study sites (Table 2), ranging from no juveniles present to upwards of
366 5000 stems ha⁻¹.

367

368 *Effects of recent piñon mortality on tree recruitment*

369

370 New piñon recruitment (i.e. piñon establishment following the 2002-2004 mortality
371 event) was strongly associated with live piñon basal area (our proxy for seed availability) and
372 live tree canopy cover (Fig. 3a), both of which were negatively associated with piñon mortality
373 (Fig. 3a). These findings suggest that new piñon recruitment was negatively affected by recent
374 piñon mortality through both hypothesised mechanisms: reduced seed availability and reduced
375 overstorey tree cover. However, piñon mortality appears to most strongly affect new piñon
376 recruitment by reducing seed availability: live piñon basal area, rather than live tree cover, was
377 most strongly associated with new piñon recruitment (Fig. 3a). SEM model results also suggest
378 that the reduction in overstorey tree cover following recent piñon mortality had no direct effect
379 on new piñon recruitment but instead negatively affected new recruitment indirectly by
380 increasing grass cover: new recruitment was strongly associated with grass cover ($\beta_{\text{std}} = -0.65$; P
381 < 0.001 ; Fig. 4), but not tree cover (Fig. 3a). Unlike new piñon recruitment, SEM model results
382 suggest juniper juvenile density and advanced piñon juvenile density (i.e. piñon juveniles that
383 established prior to the 2002-2004 mortality event) were only moderately affected by recent
384 adult piñon mortality through reductions in overstorey tree cover (Figs. 3b, 3c). Advanced piñon
385 juvenile density was also strongly associated with live and dead piñon basal area (Fig. 4), which
386 represents seed availability at the time of establishment and is also strongly correlated with piñon
387 canopy cover.

388

389 *Effects of overstorey trees on tree recruitment*

390

391 Our piecewise SEM model results suggest overstorey trees had both direct and indirect
392 effects on tree recruitment. Whereas overstorey tree cover was indirectly and positively
393 associated with new piñon recruitment by reducing perennial grass cover (Figs. 3a, 4, 5),
394 overstorey tree cover was directly and positively associated with advanced piñon juveniles (Figs.
395 3b, 4). Interestingly, our model results suggest overstorey tree cover directly and positively
396 affects juniper juveniles but also has a weak, indirect, negative effect on juniper juveniles by
397 reducing perennial grass cover (Figs. 3c, 4, 5). As a result, juniper juvenile density was only
398 moderately correlated with overstorey tree cover (Pearson's $r = 0.28$) compared to both new and
399 advanced piñon juveniles (Pearson's $r = 0.42$ and 0.43 , respectively). There was both greater
400 variability and higher levels of perennial grass cover on average in the Arizona study area (Table
401 2; Fig. 3), suggesting that perennial grass cover may most strongly influence tree regeneration in
402 the Arizona study area compared to the Colorado and New Mexico study areas.

403 Consistent with the piecewise SEM model results, piñon and juniper juveniles were more
404 likely to be found beneath canopies of heterospecific tree species than in the interspaces, as
405 evidenced by the high positive interaction indices (indicating facilitation) between tree cover and
406 juvenile trees (Fig. 6a). Interaction indices were significantly higher between overstorey trees
407 and piñon and juniper juveniles compared to shrubs ($P < 0.0001$; Fig. 6), suggesting that
408 overstorey trees more strongly facilitate juvenile tree recruitment of heterospecific tree species.
409 Our results suggest that piñon juveniles are much more strongly facilitated by overstorey trees
410 than junipers, as evidenced by the significantly higher interaction indices of piñon compared to

411 juniper ($P < 0.0001$; Fig. 6). Facilitation by overstorey trees and shrubs appeared to decrease
412 with tree size of both piñon and juniper (Fig. 6), with juvenile saplings having lower interaction
413 indices ($P = 0.04$).

414

415 *Effects of abiotic conditions on tree recruitment*

416

417 Surface soil available water capacity (soil AWC) was directly positively associated with
418 tree recruitment across both species and piñon size classes (Fig. 3; Fig. 4), and 30 year normal
419 annual evapotranspiration (AET) was also directly positively associated with new piñon
420 recruitment (Fig. 3a; Fig. 4) and weakly with juniper (Fig. 3c; Fig. 4). Our model results suggest
421 there was no direct association between AET and advanced piñon recruitment (Fig 3b), although
422 there was a significant positive correlation between AET and advanced piñon recruitment when
423 the clustering of sites within a study area is not explicitly incorporated into the analyses
424 (Pearson's $r = 0.22$, $P = 0.01$). This is because both AET and advanced piñon recruitment were
425 generally higher at the sites in the New Mexico study area compared to the Arizona study area
426 (Table 2). There was no strong direct association between 30-year normal climatic water deficit
427 (CWD) and tree recruitment (Fig. 3), but there was an indirect negative association of CWD and
428 tree recruitment through reducing overstorey tree cover and piñon basal area (Fig. 3). Soil AWC
429 and AET were also indirectly positively associated with tree recruitment through increasing grass
430 cover and reducing piñon mortality, respectively (Fig. 3).

431

432 **Discussion**

433

434 Drought-induced tree mortality events are occurring globally and are predicted to continue
435 with global climate change (Carnicer *et al.* 2011; Allen *et al.* 2015). Our study highlights how
436 woodland resilience to these tree mortality events varies across the landscape in relation to
437 physiographic conditions and is partially dependent upon the herbaceous vegetation response to
438 overstorey mortality. Further, we show that woodland resilience is strongly dependent upon
439 advanced regeneration, (i.e., the survival of juvenile trees that established prior to the mortality
440 event), the survival of adult seed-bearing trees, and the facilitative effects of surviving tree
441 crowns and nurse shrubs for providing favourable microsites for seedling establishment.

442 Recent widespread adult piñon mortality was strongly negatively associated with piñon
443 regeneration through both hypothesised mechanisms: reducing seed availability and altering
444 available microsites. New piñon recruitment appears to be most strongly negatively affected by
445 recent adult piñon mortality due to limited seed availability (Fig. 3a), but was also associated
446 with microsite availability. Piñon pine has large animal-dispersed seeds and short seed longevity
447 (Chambers *et al.* 1999), two factors that make seed limitation more likely following a
448 disturbance (Clark *et al.* 2007). These results suggest that areas with low densities of older
449 juveniles, such as areas that recently experienced prescribed burning or wildfire, will transition
450 to other vegetation types following overstorey piñon mortality either permanently (i.e. lack
451 resilience) or for an extended time period due to slow recovery.

452 Our results suggest that the effects of overstorey tree mortality on tree regeneration can
453 be mediated by the loss in overstorey tree microsites and subsequent changes in understorey
454 vegetation. Consistent with previous research (Mueller *et al.* 2005; Kane, Dugi & Kolb 2015),
455 juvenile piñon and juniper trees were much more likely to be located beneath the canopies of live
456 overstorey trees and, to a lesser degree, shrubs, highlighting the importance of trees as nurse

457 plants in facilitating juvenile tree recruitment. Similar to other semi-arid ecosystems (von Arx *et*
458 *al.* 2013), woodland tree canopies reduce soil temperatures and increase soil moisture relative to
459 intercanopy patches by reducing evaporation rates during the summer months (Breshears *et al.*
460 1998), which likely explains why there is a strong facilitative effect of overstorey trees on
461 juvenile tree recruitment. This facilitative effect may be particularly evident because of the
462 general warm and dry conditions that have occurred over the past two decades across the study
463 region (Williams *et al.* 2013), which can increase the facilitative effects of nurse plants in semi-
464 arid ecosystems (e.g. stress gradient hypothesis – Bertness & Callaway 1994). Unlike in light (or
465 energy)-limited forests where overstorey tree mortality creates canopy gaps to allow for the
466 recruitment of new trees (Veblen *et al.*, 1991), our findings suggest that the recent, rapid large-
467 scale tree mortality events in water-limited semi-arid woodlands may actually reduce tree
468 recruitment due to limited microsite availability.

469 Drought-induced mortality of overstorey trees can strongly affect the microclimatic
470 conditions that juvenile trees experience and thereby alter recruitment dynamics (Suarez &
471 Kitzberger 2008; Vilà-Cabrera *et al.* 2013), and our results suggest these effects may be partially
472 mediated by understorey vegetation responses. In particular, overstorey trees appeared to affect
473 tree recruitment through changes in understorey vegetation, specifically by reducing the
474 abundance of perennial grasses, which differentially affected piñon and juniper recruitment.
475 Juniper seedlings can better compete with the shallow root system of perennial grasses (Scholes
476 & Archer 1997; Chambers *et al.* 1999), and, unlike piñon, were positively associated with
477 perennial grasses across our study areas. The inability to compete with perennial grasses
478 explains why piñon juveniles are much more likely to establish beneath the canopies of
479 overstorey trees in our study and others (Kane *et al.* 2015). Indeed, piñon juveniles were

480 negatively associated with perennial grass cover across our study areas and survival of juveniles
481 located in the canopy interspaces was much lower in areas with high perennial grass cover in
482 northern Arizona (Redmond *et al.* 2015).

483 The differential effects of perennial grasses on piñon and juniper are likely due to the
484 ecophysiological differences between these two species and have important implications for how
485 these woodlands may respond to overstorey mortality events over longer time-scales. Juniper
486 juveniles have greater water use efficiency and can handle more negative water potentials during
487 drought than piñon (Nowak, Moore & Tausch 1999; West *et al.* 2007). This is likely why juniper
488 is more often found in the tree canopy interspaces, which are both hotter and drier during the
489 summer months (Breshears *et al.* 1997). This is also consistent with previous research that has
490 found juniper to have higher rates of establishment following large canopy disturbances
491 (Redmond *et al.* 2013; Bristow, Weisberg & Tausch 2014). Taken together, this suggests the
492 canopy gaps created by recent drought-induced tree mortality events may favour juniper
493 recruitment over piñon recruitment. In addition, the understorey response to overstorey mortality
494 events (increased establishment of perennial grasses versus shrubs) will likely have a strong
495 influence on tree recruitment dynamics and needs to be further studied.

496 Consistent with studies in other wooded ecosystems (Galiano, Martínez-Vilalta & Lloret
497 2010; Sanger *et al.* 2011), our findings suggest that woodland resilience across the Colorado
498 Plateau region of the southwestern USA to drought will vary spatially due to differences in local
499 physiographic conditions. Surface soil available water capacity and local climatic conditions
500 defining resource availability were directly associated with tree recruitment of both piñon and
501 juniper. Past tree recruitment in piñon-juniper woodlands has generally occurred during cool and
502 wet climate periods (Shinneman & Baker 2009; Barger *et al.* 2009), so it would make sense that

503 recruitment during the warmer and drier conditions over the past decade is more prevalent in
504 areas with more water availability. Similarly, variability in landscape physiography also affects
505 piñon growth responses to climate (Barger & Woodhouse 2015; Redmond *et al.* 2017) and adult
506 piñon mortality rates (Peterman *et al.* 2012). This effect of landscape physiography on tree
507 juvenile densities may explain why there was a limited effect of tree mortality on juvenile tree
508 composition in the generally cooler, wetter sites in southwestern Colorado (Redmond & Barger
509 2013) but a strong effect in northern Arizona (Redmond *et al.* 2015). Overall, these results
510 suggest that under future warmer and drier conditions, recruitment of both piñon and juniper
511 trees may be a bottleneck to woodland recovery in areas with coarse textured soils or dry
512 climatic conditions, and permanent woodland conversion to other more xeric vegetation types
513 may occur.

514

515 *Conclusions*

516

517 The frequency and severity of drought events occurring under warmer temperatures are
518 predicted to increase with global climate change (IPCC 2014). Widespread tree mortality events
519 have already occurred across the globe due to recent hotter droughts (Allen *et al.* 2010; Carnicer
520 *et al.* 2011), which have the potential to result in long-term changes in ecosystem structure and
521 function if there is limited tree regeneration (Lloret *et al.* 2012). Our findings suggest that tree
522 resilience to drought among the widespread piñon-juniper woodlands of the southwestern USA is
523 highly variable and dependent upon several key conditions. In the absence of live seed-producing
524 trees, our results demonstrate that the recovery of piñon pine populations following overstorey
525 piñon mortality is dependent upon advance regeneration. Thus, due to the importance of seed

526 limitation, the timing of drought events (i.e. the drought-free interval) can have a strong impact
527 on woodland resilience to climate change. Overstorey trees often facilitate tree seedling
528 establishment and survival in semi-arid woodlands (Kitzberger, Steinaker & Veblen 2000;
529 Gómez-Aparicio *et al.* 2004), and therefore widespread overstorey mortality caused by droughts
530 could reduce tree regeneration (Vilà-Cabrera *et al.* 2013). Since piñon pine regeneration depends
531 more strongly on facilitation by overstorey trees than juniper, tree mortality caused by droughts
532 could result in a shift to juniper dominance in the semi-arid woodlands of the southwestern USA.
533 Finally, tree regeneration varied among sites due to differences in soil water-holding capacity
534 and site productivity, such that stands with hotter, drier local climatic conditions will have
535 limited piñon and juniper regeneration following large-scale dieback.

536 Based on our results we identify four indicators of resilience to woodland die-back
537 associated with hotter drought conditions: (1) abundant advance regeneration of tree seedlings;
538 (2) sufficient canopy cover for survival of emergent seedlings and existing regeneration; (3)
539 sufficient seed source from surviving trees with high reproductive output; (4) areas with cooler
540 and wetter local climate conditions and high soil available water capacity. In the absence of these
541 conditions, there is greater likelihood of woodlands transitioning to other, more xeric vegetation
542 types following die-back.

543

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551

552 **Authors' Contributions**

553 MDR formulated the idea with critical input from all authors. MDR and MJC conducted the field
554 work and MDR analyzed the data. MDR and PJW wrote the paper with substantial contributions
555 from NSC and MJC.

556

557 **Data Accessibility**

558 All data are available on the Dryad data repository: doi:10.5061/dryad.31887 (Redmond *et al.*
559 2017b).

560

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780 **Supporting Information**

781 **Appendix S1.** Description of the calculations of abiotic variables used in SEM analyses.

782 **Table S1.** A list of parameters and their standardized regression coefficients for all models of
783 new piñon juvenile density with $\Delta AIC_c \leq 2$. Dashes (-) indicate parameters that were not
784 included in a given model. The top model (lowest AICc value) was used in the structural
785 equation modeling. See Table 1 for a detailed description of each parameter.

786

787 **Table S2.** A list of parameters and their standardized regression coefficients for all models of
788 advanced piñon juvenile density with $\Delta AIC_c \leq 2$. Dashes (-) indicate parameters that were not
789 included in a given model. The top model (lowest AICc value) was used in the structural
790 equation modeling. See Table 1 for a detailed description of each parameter.

791

792 **Table S3.** A list of parameters and their standardized regression coefficients for all models of
793 juniper juvenile density with $\Delta AIC_c \leq 2$. Dashes (-) indicate parameters that were not included in

794 a given model. The top model (lowest AICc value) was used in the structural equation modeling.

795 See Table 1 for a detailed description of each parameter.

796

797 **Table S4.** List of models and their AICc values used to assess whether the environmental drivers

798 of new (middle column) and advanced (right column) pinon pine recruitment differed within

799 each of the three study areas. See Table 1 for a list of all parameters used to predict new and

800 advanced pinon pine recruitment. AET = mean 30 year cumulative actual evapotranspiration;

801 CWD = mean 30 year cumulative climatic water deficit; soil AWC = surface soil available water

802 capacity.

803 **Table 1.** Predictor variables included in piecewise structural equation models of juvenile tree
 804 density.
 805

Variable	Description
<i>Abiotic Conditions</i>	
Actual Evapotranspiration (AET)	Mean 30 year cumulative actual evapotranspiration (see Appendix S1 for details). Represents the simultaneous availability of water and energy and ranges from 258 mm (driest sites) to 504 mm (wettest sites) across our study area.
Climatic Water Deficit (CWD)	Mean 30 year cumulative climatic water deficit (see Appendix S1 for details), which represents the amount of water by which potential evapotranspiration exceeds actual evapotranspiration. Ranges from 71 mm (cool, wet sites) to 894 mm (hot, dry sites) across our study area.
Soil Available Water Capacity (soil AWC)	Surface (top 10 cm.) soil available water capacity calculated based off soil texture (see Appendix S1 for details).
<i>Overstorey Vegetation</i>	
Tree Cover	Live tree cover. Represents available tree microsites and was calculated using the line point intercept data. *The majority of dead piñon trees had fallen over across our study area, thus live + dead tree cover was highly correlated with live tree cover ($r = 0.98$).
Piñon/Juniper Basal Area at the time of juvenile establishment	Represents seed availability at the time of juvenile establishment. For the SEM model of juniper juvenile density, total live juniper basal area was used due to low juniper mortality across our study area (8% on average). For the SEM model of new piñon juvenile density, total live piñon basal area was used whereas total live + recently dead piñon basal area was used for the SEM model of advanced piñon juvenile density.
% Piñon Mortality	Percent adult piñon mortality over the past decade, calculated from basal area as: dead piñon basal area / (live + dead piñon basal area) * 100%.
<i>Understorey Vegetation</i>	
Perennial grass cover	Perennial grass cover. Represents available grass microsites and was calculated using the line point intercept data.
Shrub Cover	Live shrub cover. Represents available shrub microsites and was calculated using the line point intercept data.

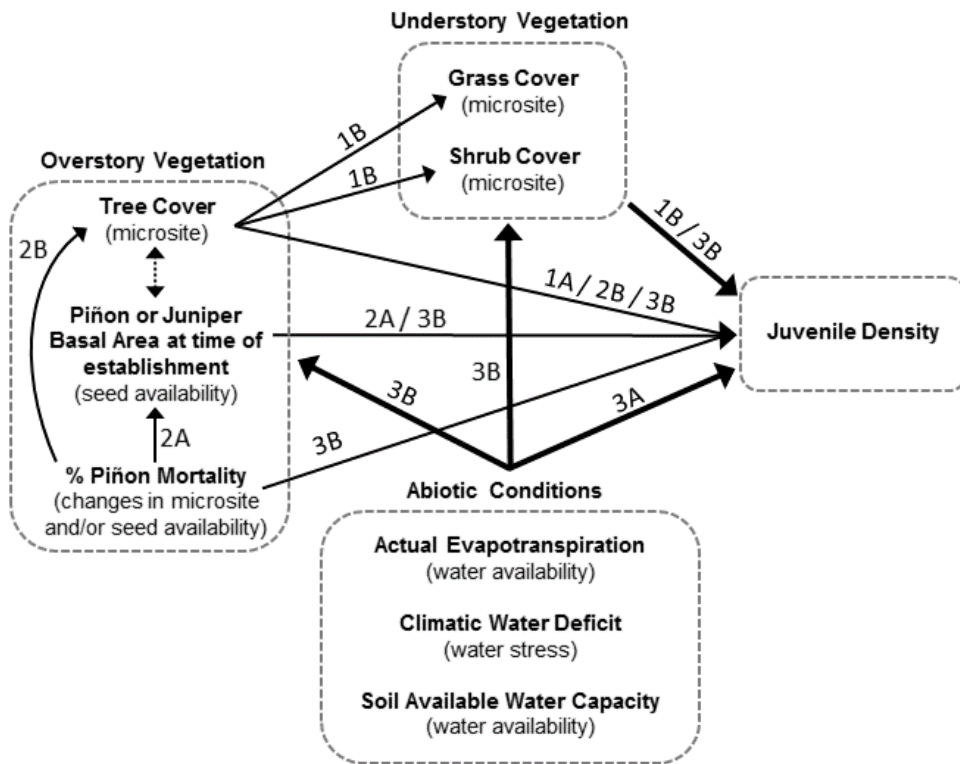
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809 **Table 2.** Mean (range) of abiotic and woodland structural conditions across our study sites in
 810 Arizona, Colorado, and New Mexico.
 811

Variable	Arizona	Colorado	New Mexico
<i>Abiotic Conditions</i>			
Actual Evapotranspiration (mm.)	385 (359 - 419)	373 (340 - 431)	447 (288 - 504)
Climatic Water Deficit (mm.)	338 (71 - 510)	424 (214 - 572)	407 (174 - 769)
Soil Available Water Capacity (%)	10 (4 - 16)	13 (8 - 18)	10 (6 - 15)
<i>Overstorey Vegetation</i>			
Tree Cover (%)	17 (0 - 49)	36 (17 - 64)	26 (0 - 65)
Piñon Mortality (%)	64 (0 - 100)	45 (0 - 100)	51 (0 - 100)
Live + Dead Piñon BA (m ² ha ⁻¹)	3 (0 - 20)	10 (2 - 29)	4 (0 - 14)
Juniper Basal Area (BA; m ² ha ⁻¹)	13 (0 - 44)	27 (2 - 49)	5 (0 - 17)
<i>Understorey Vegetation</i>			
Perennial grass cover (%)	37 (0 - 74)	10 (0 - 44)	16 (0 - 51)
Shrub Cover (%)	5 (0 - 25)	3 (0 - 13)	6 (0 - 40)
<i>Tree Recruitment</i>			
New piñon juvenile density (stems ha ⁻¹)	21 (0 - 220)	180 (0 - 2120)	195 (0 - 2400)
Adv. piñon juvenile density (stems ha ⁻¹)	108 (0 - 960)	435 (20 - 2393)	425 (0 - 2767)
Juniper juvenile density (stems ha ⁻¹)	243 (0 - 3640)	267 (20 - 827)	177 (0 - 1433)

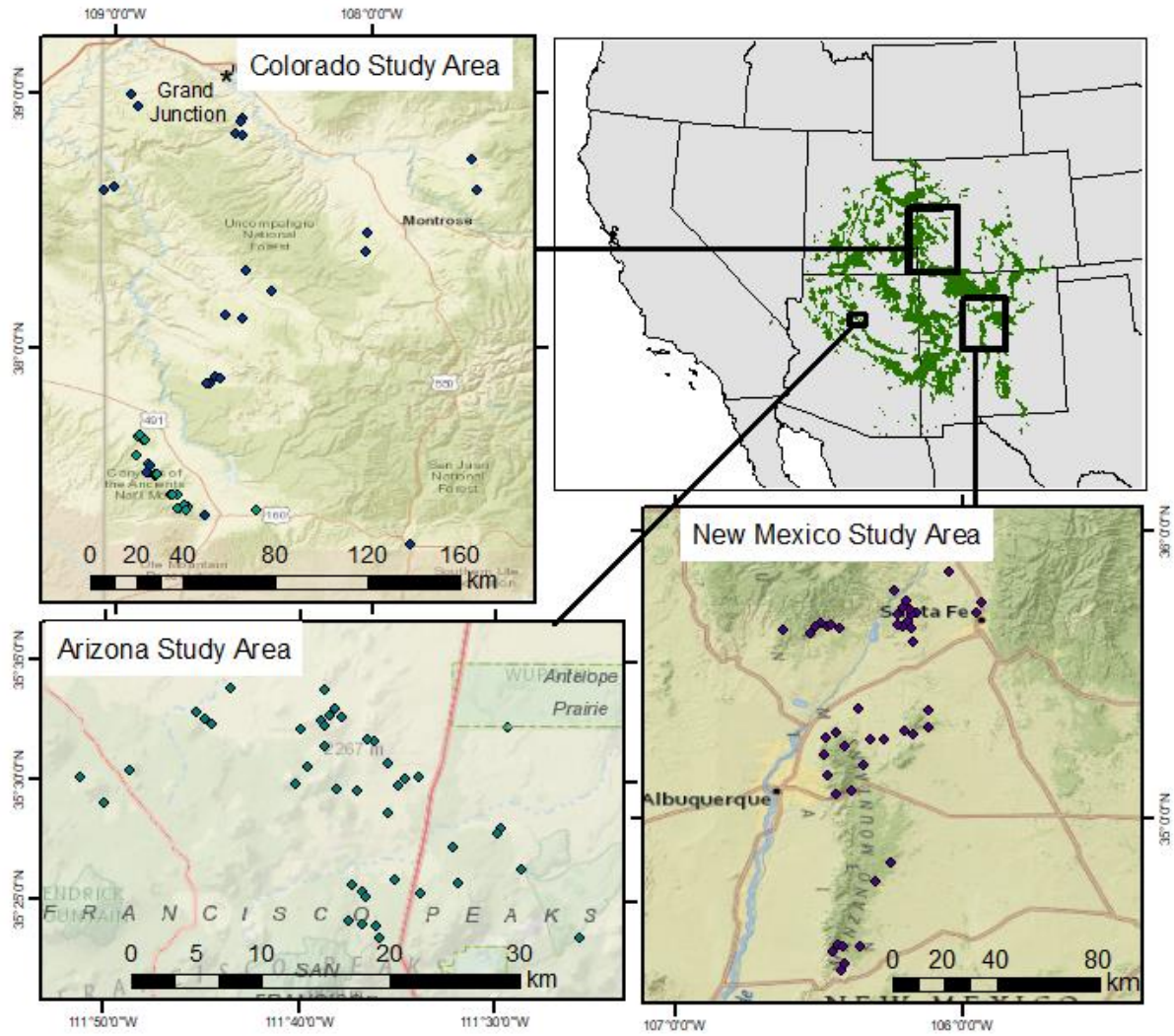
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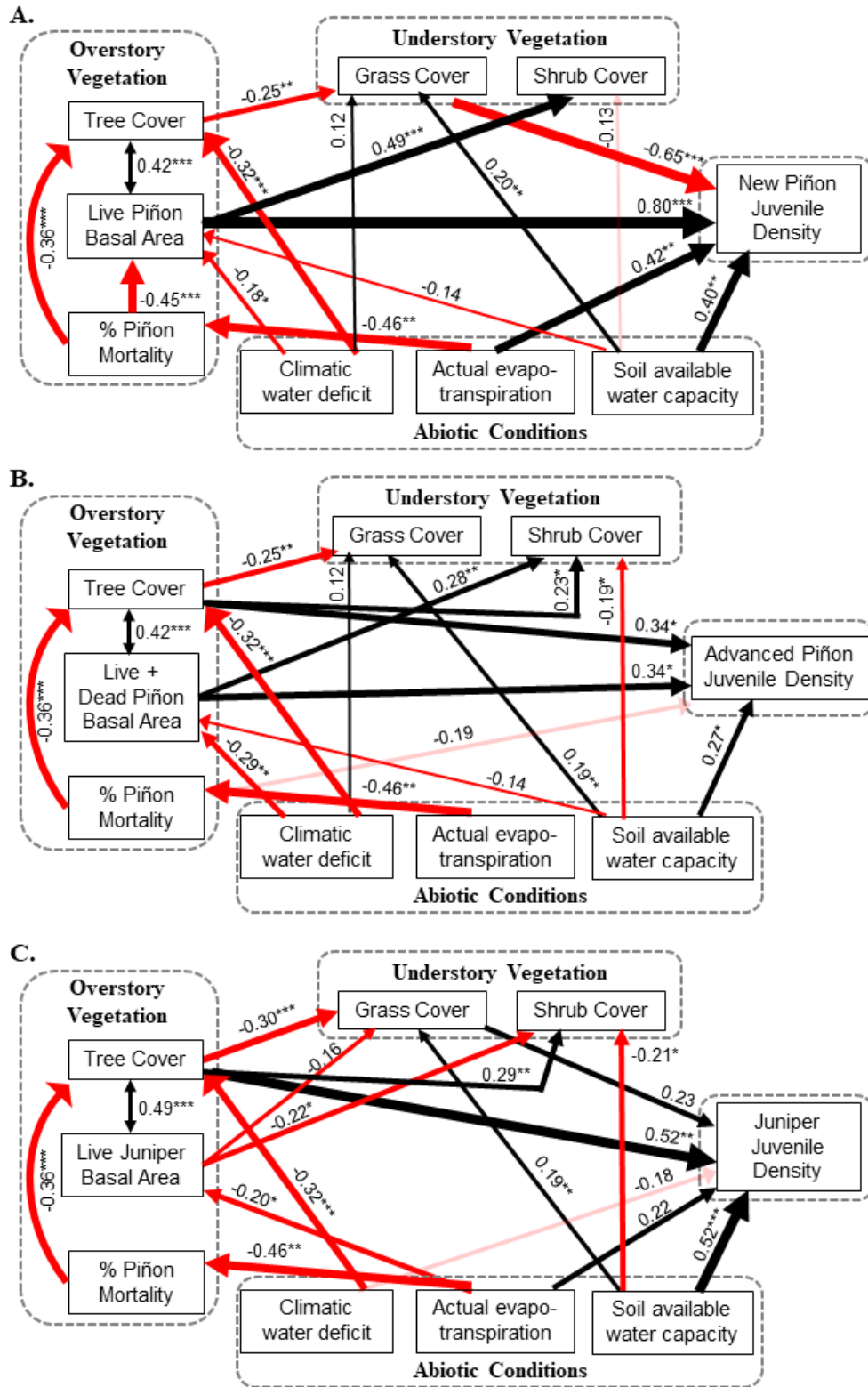


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831 **Figure 1.** Path diagram illustrating the structural equation modeling (SEM) conceptual
832 framework used to understand the effects of abiotic conditions, understorey vegetation, and
833 overstorey vegetation on juvenile tree density. Numbers correspond to each hypothesis described
834 in the introduction. We used three different SEMs to predict new piñon juvenile density,
835 advanced piñon juvenile density, and juniper juvenile density, which differed slightly in their
836 predictor variables (see Table 1). Correlated errors were included between % piñon mortality and
837 piñon or juniper basal area at the time of establishment for the two SEMs predicting juniper
838 juvenile density and advanced piñon juvenile density, whereas a direct causal relationship
839 between % piñon mortality and live piñon basal area were included for the SEM predicting new
840 piñon juvenile density. Thick black lines connecting dashed boxes indicate that all possible
841 pathways were included in the analyses.

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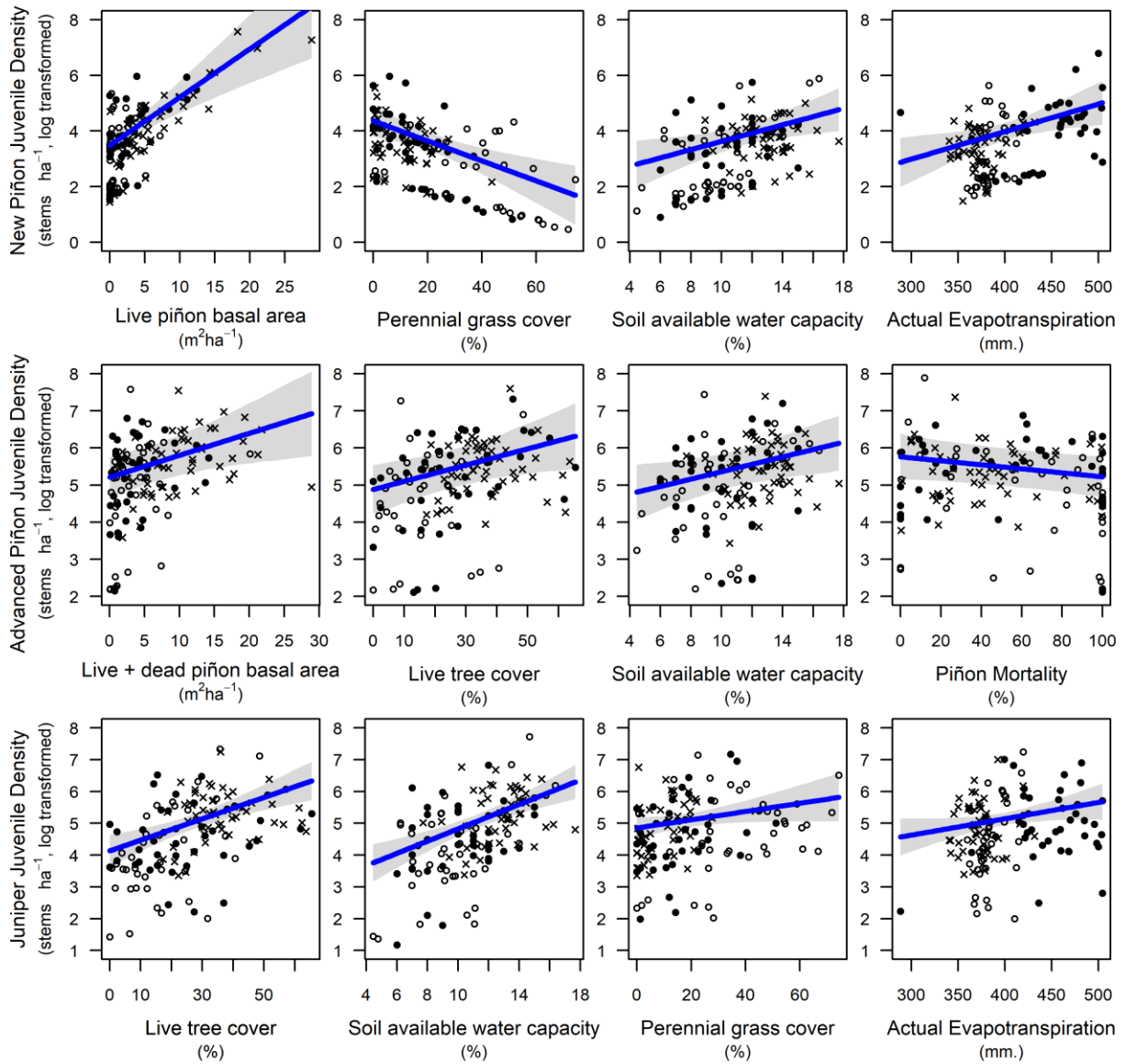
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 845 **Figure 2.** Map of the sites sampled within the three study areas. Shaded green area in the top
 846 right map shows the distribution of piñon pine (Cole et al., 2006). Map was created using ESRI
 847 software (ArcMap version 10.3), and the base maps used is the National Geographic World Map,
 848 which includes data from National Geographic, DeLorme, HERE, UNEP-WCMC, USGS,
 849 NASA, ESA, METI, NRCAN, GEBCO, NOAA, and increment P Corp.
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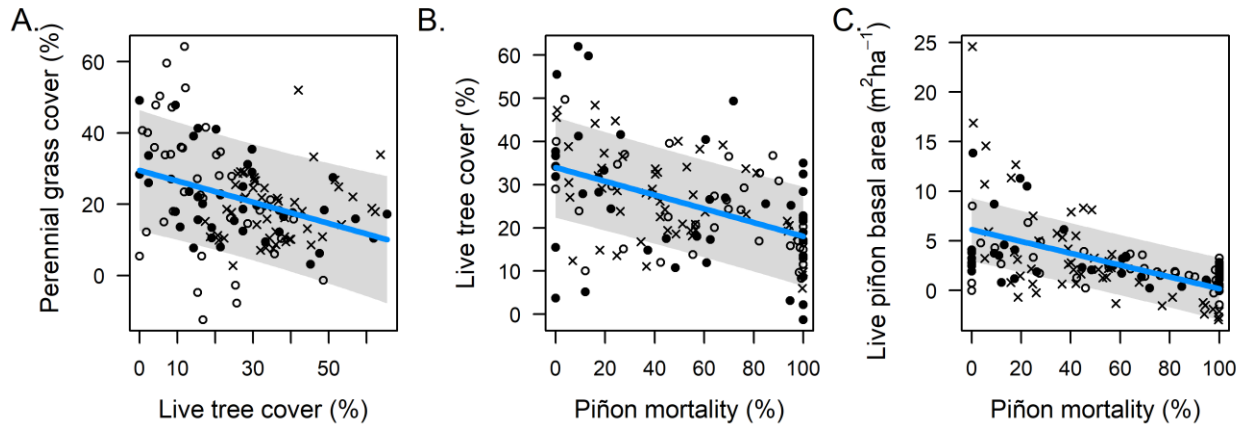
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Figure 3. Final piecewise structural equation models illustrating the factors that affect (A) new piñon juvenile density (i.e. juveniles with a basal diameter ≤ 0.5 cm, which are juveniles that likely established after the 2002-2004 adult piñon mortality event), (B) advanced piñon juvenile

855 density (i.e. juveniles with a basal diameter > 0.5 cm and < 5 cm, which are juveniles that likely
 856 established prior to the 2002-2004 adult piñon mortality event) and (C) juniper juvenile density
 857 (i.e. trees with a basal diameter < 5 cm). Line thickness is proportional to standardised path
 858 coefficients that are shown next to the line and significance is denoted as *** $P < 0.001$, ** $P <$
 859 0.01 , * $P < 0.05$. Lines are colored red for negative associations and black for positive
 860 associations. Paths where $P > 0.10$ are lighter in color.
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 865 **Figure 4.** Partial residual plots showing the relationship between the predictor variables that
 866 were most strongly directly associated with new piñon juvenile density (*top*), advanced piñon
 867 juvenile density (*middle*), and juniper juvenile density (*bottom*) across the Arizona (open
 868 circles), Colorado (cross symbols), and New Mexico (closed circles) study areas.
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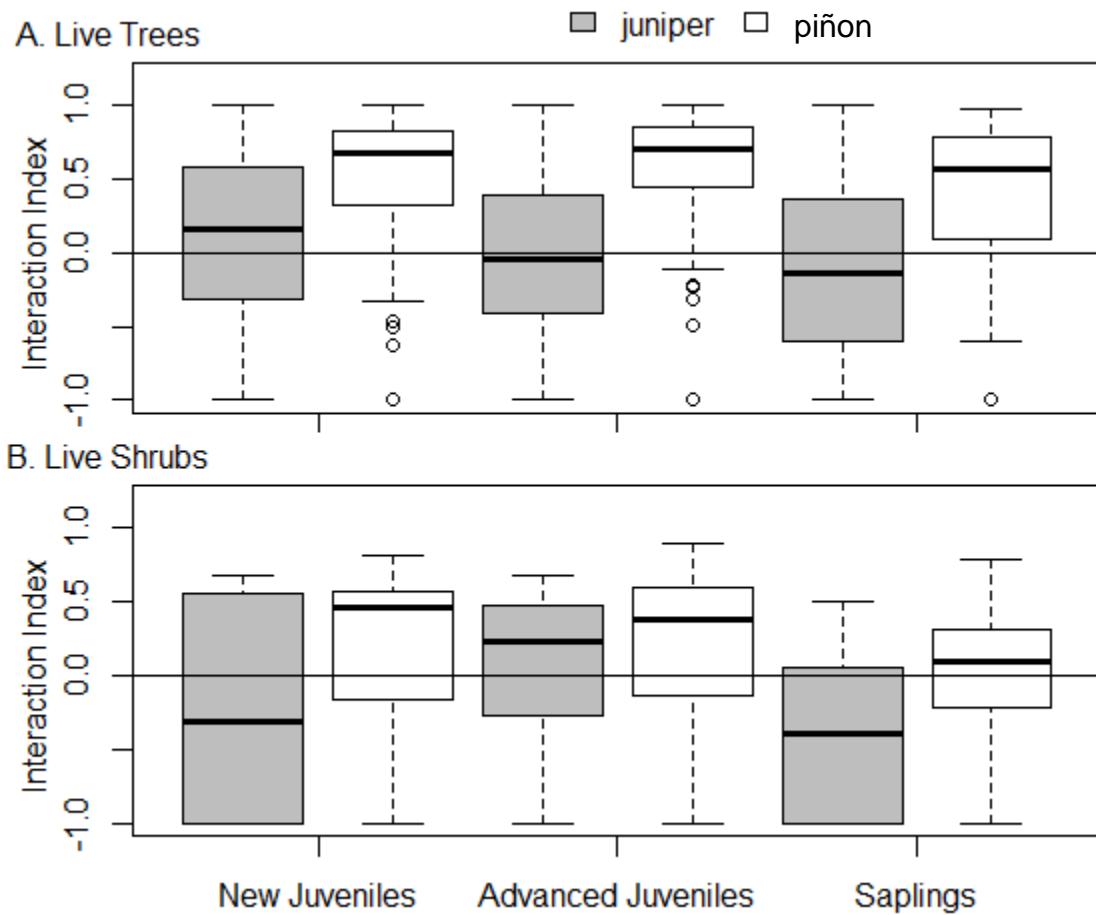
872 **Figure 5.** Partial residual plots showing the relationship between (A.) live tree cover and
 873 perennial grass cover, (B.) percent piñon mortality and live tree cover, and (C.) piñon mortality

874 and live piñon basal area, which were indirectly associated with tree recruitment (Fig. 3) across

875 the Arizona (open circles), Colorado (cross symbols), and New Mexico (closed circles) study

876 areas.

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880 **Figure 6.** Interaction indices between live trees (excluding conspecific species; A.) and shrubs
 881 (B.) and juvenile juniper (grey boxes) and piñon (white boxes) trees. Interaction indices between
 882 0 and 1 represent a facilitative effect of trees and shrubs on piñon and juniper recruitment, with
 883 increasingly positive values representing an increasingly facilitative effect. Interaction indices
 884 were higher for piñon than juniper ($P < 0.0001$), live trees (excluding conspecifics) than shrubs
 885 ($P < 0.0001$), and new juveniles than saplings ($P = 0.04$).