

1 Demographic processes underpinning post-fire resilience in California closed-cone pine forests:
2 the importance of fire interval, stand structure, and climate

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15 Submitted to *Plant Ecology*

16

17 ABSTRACT

18 The resilience of serotinous obligate-seeding plants to fire may be compromised if increasing fire
19 frequency curtails time available for canopy seed bank accumulation (i.e., immaturity risk), but
20 how various drivers affect seed availability at the time of fire is poorly understood. Using field
21 data from California closed-cone pine (*Pinus attenuata* and *P. muricata*) stands, we assess two
22 critical demographic processes during the inter-fire period—reproductive capacity and mortality.
23 At tree- and stand-levels, we test how these processes are affected by stand age and are mediated

24 by biotic and abiotic factors. We found that stand age was the key driver of reproductive
25 capacity; older stands had a greater proportion of reproductively mature individuals and greater
26 closed cone density. Stand density mediated the effect of age; greater stand density resulted in
27 greater closed cone density and a lower proportion of reproductively mature individuals, but
28 reproductive capacity in low- and high-density stands converged over time. Increased moisture
29 stress reduced the stand-level proportion reproductively mature but had no effect on closed cone
30 density. Mortality was strongly associated with density-dependent thinning and increased in
31 stands with high moisture stress. Reproductive capacity began to increase sharply 10 years after
32 fire and by 20 years immaturity risk is low. However, prior to 20 years, low-density stands with
33 high moisture stress may be more susceptible to immaturity risk. Understanding these
34 relationships is critical to predicting serotinous population persistence under changing climate
35 and disturbance conditions.

36 KEYWORDS

37 Canopy seed bank, cone production, demographic shift, *Pinus attenuata*, *Pinus muricata*,
38 serotiny

39 DECLARATIONS

40 **Funding**

41 This research was funded by the Australian Research Council award DP170101288 to NJE and
42 JBF and a Murdoch University Strategic PhD Scholarship to MCA, a U.S. Geological Survey
43 Northwest Climate Adaptation Science Center award G17AC000218 to BJH and MCA, the
44 Achievement Rewards for College Scientists (ARCS) Foundation to MCA, the Graduate

45 Research Innovation Award from the Joint Fire Science Program (award #19-1-01-16) to BJH
46 and MCA, and the University of Washington.

47 **Conflicts of interest**

48 None.

49 **Availability of data and material**

50 All data presented in this study are available from the first author upon reasonable request.

51 **Code availability**

52 The code used for analysis is available upon reasonable request.

53 **Authors' contributions**

54 All authors contributed to the study conception and design. Data collection and analysis were
55 performed by Michelle C. Agne. The first draft of the manuscript was written by Michelle C.
56 Agne and all authors commented on previous versions of the manuscript. All authors read and
57 approved the final manuscript.

58 **ACKNOWLEDGEMENTS**

59 We thank J. Gibson, E. Engber, S. Kren, and K. Kephart for supporting this research. We
60 received analytical advice from M. Buonanduci and K. Rodman. Field and logistical support
61 were provided by D. Canestro, D. Chapman, J. Hulbert, A. Link, F. Nelson, T. Sternberg, K.
62 Stork, A. Ubaka-Sampson, and W. Veber. This research was funded by the Australian Research
63 Council award DP170101288, a Murdoch University Strategic PhD Scholarship, a U.S.
64 Geological Survey Northwest Climate Adaptation Science Center award G17AC000218, the
65 Achievement Rewards for College Scientists (ARCS) Foundation, the Graduate Research

66 Innovation Award from the Joint Fire Science Program (award #19-1-01-16), and the University
67 of Washington.

68

69 INTRODUCTION

70 Widespread changes to climate and disturbance regimes are altering plant populations in
71 terrestrial ecosystems globally (Johnstone et al. 2016). Changes in size, frequency, seasonality,
72 or severity of a disturbance regime can have strong effects on ecosystem structure and function
73 (Turner 2010). Such changes can combine with direct effects of climate warming to erode
74 population resilience – the capacity to experience disturbance without transitioning to an
75 alternative state (Holling 1973). Fire activity has increased in many temperate forest and
76 woodland ecosystems during the period from 2000 to the early 2020s (Jolly et al. 2015; Parks
77 and Abatzoglou 2020; Boer et al. 2020), challenging resilience mechanisms that promote post-
78 fire recovery and driving ecosystem type conversion (e.g., conversion from forest to non-forest;
79 Coop et al. 2020). Such transitions are most likely where plant adaptations to fire are misaligned
80 with fire characteristics (Pausas and Keeley 2014; Johnstone et al. 2016).

81 Serotinous obligate seeders – non-sprouting species that accumulate and store a canopy
82 seed bank over multiple years – depend upon relatively predictable fire return intervals that
83 exceed the time needed to develop a canopy seed bank sufficient for self-replacement (Lamont
84 and Enright 2000). Although typically adapted to high-severity, stand-replacing fires, serotinous
85 plant populations may be threatened through three important mechanisms that collectively make
86 up the interval squeeze framework of Enright et al. (2015). First, shortened fire-free intervals can
87 lead to immaturity risk if populations burn prior to accumulating a sufficient canopy seed bank

88 (Keeley et al. 1999). Second, stressful climate conditions during the first year post-fire—a
89 crucial window for serotinous populations in which most recruitment occurs following *en masse*
90 seed release (Turner et al. 1999; Harvey and Holzman 2014) – can result in recruitment failure
91 even if sufficient seed is available (Enright et al. 2014; Hansen and Turner 2019). Third,
92 warming and drying climate can directly affect demographic processes by delaying or decreasing
93 reproductive capacity and increasing plant mortality (Enright et al. 2015). Shifts in demographic
94 processes can combine with changing disturbance regimes to produce compound disturbance
95 effects (*sensu* Paine et al. 1998), where two or more drivers combine to cause a synergistic effect
96 on resilience. Shortened fire intervals and post-fire recruitment failure associated with climate
97 change have been increasingly documented in recent years (Fairman et al. 2017; Stevens-
98 Rumann et al. 2018; Davis et al. 2019; Turner et al. 2019). However, the effects of warming
99 climate on demographic processes and the implications for availability of seed at the time of fire
100 are poorly understood and represent a key gap in understanding serotinous plant population
101 persistence under future climate (Davis et al. 2018).

102 Demographic processes in plants are controlled by many drivers occurring at multiple levels
103 of organization. The probability of producing seeds (i.e. reproductive maturity) strongly
104 increases with plant age in perennial, obligate seeder species (Harper 1977; Viglas et al. 2013),
105 as does individual seed production (Andrus et al. 2020). Seed production similarly increases with
106 plant size (Harper 1977; Davi et al. 2016), as greater access to resources generally results in
107 greater seed production (Greene et al. 2002). However, trade-offs between vegetative growth and
108 seed production can occur during early successional stages and when intraspecific competition is
109 high (Climent et al. 2008). High initial population density can delay age to reproductive maturity
110 by years to decades (Borchert 1985), resulting in low individual seed production as compared

111 with individuals in low-density stands (Esler and Cowling 1990; Alfaro-Sánchez et al. 2015).
112 However, despite lower tree-level production, high-density stands may have greater stand-level
113 seed production when compared with low-density stands (Esler and Cowling 1990; Moya et al.
114 2007; Turner et al. 2007). Moisture stress also affects plants via delayed maturity and chronic or
115 acute reductions in seed production (Redmond et al. 2012; Alfaro-Sánchez et al. 2015) and by
116 increasing mature tree mortality, thereby decreasing the population of reproductive individuals
117 (Williams et al. 2013), especially where competition for resources is strong (Andrus et al. 2021).
118 Warm and dry conditions can also trigger cone opening for some serotinous species, further
119 depleting the canopy seed bank available at time of next fire (Borchert 1985; Verkaik and
120 Espelta 2006). Compounding these climatic stressors, damage caused by biotic agents (e.g.,
121 insect pests, diseases) may further decrease seed production and seed availability for some tree
122 species (Schooley 1978; Schaffer et al. 1983; Singh and Carew 1990). Understanding how these
123 factors interact to influence demographic processes is critical to predicting how serotinous plant
124 populations may respond following increasing fire frequency in a warming, drying world.

125 The closed-cone pine forests of California, USA, are a model system for understanding
126 demographic mechanisms of serotinous forest resilience with climate warming and concomitant
127 altered disturbance regimes. Typically, these forests are dominated by a single cohort of closed-
128 cone pines established following stand-replacing fire—similar to other serotinous forests in
129 North America (e.g., lodgepole pine [*Pinus contorta*], jack pine [*P. banksiana*])—but stand
130 development occurs more rapidly (Vogl 1973; Harvey et al. 2011). California closed-cone pines
131 reach reproductive maturity at a relatively young age and proceed through the stages of stand
132 dynamics quickly compared with other serotinous forests in North America (Keeley et al. 1999,
133 Harvey and Holzman 2014). Stands are also short-lived with relatively short inter-fire periods,

134 with mean fire return intervals varying from 30 to 90 years (Vogl 1973; Sugnet 1985; van de
135 Water and Safford 2011). Because of the rapid pace of stand development, empirical
136 measurement of demographic processes across the inter-fire period is more logistically feasible
137 than in other obligate seeding serotinous forests in North America with much longer fire return
138 intervals (Romme 1982; Gauthier et al. 1996). Insights from California closed-cone pine forests
139 may illuminate the demographic mechanisms that control species persistence in forests in which
140 these processes unfold across longer temporal scales.

141 In this study, we used field data collected in California closed-cone pine stands dominated by
142 either knobcone pine (*P. attenuata*) or bishop pine (*P. muricata*) across the early stages of the
143 inter-fire period to address these knowledge gaps about the demographic mechanisms
144 underpinning post-fire resilience. Specifically, to assess the relative effects of multiple drivers on
145 reproductive capacity and tree mortality—two demographic processes that are important for
146 post-fire resilience—we asked: 1) How does reproductive capacity develop over time since the
147 last stand-replacing fire? 2) How do biotic (e.g., population density) and abiotic (e.g., local
148 climate) factors drive variability in reproductive capacity at two levels of organization:
149 individual trees and forest stands? 3) How does stand-level density-dependent tree mortality vary
150 across abiotic and biotic drivers, and what are the implications for the canopy seed bank? We
151 expected that: 1) Time to a high proportion of individuals within a stand reaching reproductive
152 maturity is short and canopy seed bank production increases rapidly over time. 2) Tree size and
153 stand age have the strongest effects on both measures of reproductive capacity at the tree- and
154 stand-levels, respectively. Increased stand density has negative effects on tree-level reproductive
155 capacity and stand-level reproductive maturity, and positive effects on canopy seed bank
156 production. Conversely, warmer, drier climate, disease incidence, shrub cover and less fertile soil

157 have negative effects on both measures of reproductive capacity at both levels of organization. 3)
158 Stand-level density-dependent mortality increases with warmer, drier climate, greater disease
159 incidence, greater shrub cover and stand density, resulting in decreased reproductive capacity.
160 Understanding the relative magnitudes of multiple drivers of demographic processes is key to
161 anticipating serotinous population persistence with implications for conifer-dominated forests
162 across North America.

163 METHODS

164 *Study area and site selection*

165 This study was conducted in closed-cone pine stands in California, USA within the
166 Klamath Mountains and Northern and Southern Coast Ranges where stand-replacing fire has
167 occurred since 1985 (Appendix S1 in the Electronic supplementary material). The region has a
168 Mediterranean climate and covers a wide range of average winter (January) temperatures (3.3–
169 12.2 °C), average summer (July) temperatures (14.9–26.9 °C), and annual average precipitation
170 (467–1996 mm; 800-m gridded 30 year climate normals from 1981–2010 [PRISM Climate
171 Group 2019]). There is a strong seasonality in precipitation, with >90% falling between October
172 and May (PRISM Climate Group 2019), and summer fog produces a moderating effect across
173 the study area (Vogl et al. 1977; Torregrosa et al. 2016). Bishop pine occupies areas that receive
174 less annual precipitation (467–1034 mm), and lower seasonal variation (due in part to coastal
175 proximity) in average temperature (8.8–12.2 °C in January and 14.9–18.7 °C in July) than
176 knobcone pine (average annual precipitation of 785–1996 mm, mean temperatures of 3.3–9.9 °C
177 in January and 20.7–26.9 °C in July).

178 The study area encompasses low elevation to lower montane zones (84–1344 m above
179 sea level [asl]), with bishop pine occupying a narrower elevational zone (84–413 m asl) than

180 knobcone pine (334–1344 asl). Stands are often characterized by steep slopes and soils are
181 typically shallow and rocky, with serpentine substrate common for knobcone pine (Vogl et al.
182 1977). Closed-cone pine communities often occur as dense forest stands for several decades
183 following establishment but can also be characterized by low-density stands interspersed with
184 chaparral. Understory plant communities are composed of a high diversity of shrub and
185 herbaceous species that vary across the study area. Common co-occurring shrub species include
186 *Adenostoma fasciculatum*, *Arctostaphylos* spp., *Ceanothus* spp., *Heteromeles arbutifolia*,
187 *Vaccinium ovatum*. *Quercus* spp. are also common on the landscape, existing both in shrub and
188 tree form. Herbaceous vegetation, where it is present, commonly includes *Acmispon glaber*,
189 *Lupinus* spp., and *Mimulus* spp.

190 To establish a chronosequence of stand age in bishop pine and knobcone pine forests, we
191 selected 15 fires that overlapped the target species' ranges using Monitoring Trends in Burn
192 Severity data (Eidenshink et al. 2007), species distribution maps, and local land management
193 information. The sample fires occurred between 1985 and 2013 and contained patches of high-
194 severity, stand-replacing fire. Plots were established in monodominant, even-aged stands of the
195 target species that established following the previous fire, with stand ages ranging from 4–32
196 years, and we assumed that all trees had established within the first post-fire growing season.
197 Although there is some evidence of seedling establishment 2–3 years post-fire (Vogl et al. 1977),
198 the vast majority (>95%) of establishment following stand-replacing fire occurs in the first post-
199 fire growing season for both bishop pine (Holzman and Folger 2005; Harvey and Holzman 2014)
200 and knobcone pine (M.C. Agne, unpublished data). The historical fire regime is characterized by
201 mean return intervals ranging from 30–90 years (Sugnet 1985; van de Water and Safford 2011),
202 suggesting that the chronosequence covers the period during which immaturity risk is greatest

203 (i.e., within the first several decades post-fire). Plots were established at least 50 m from roads
204 and had no evidence of management following the most recent fire. Plots covered the range of
205 topographic features and stand densities within each fire perimeter and were separated by at least
206 100 m, except when on opposing aspects. During the summers of 2016–2020, we established 31
207 and 38 plots in bishop pine and knobcone pine stands, respectively. Two to ten plots were
208 sampled in each past fire (each fire represented a single stand age), varying by accessible area
209 that met our sampling criteria.

210 *Field data collection*

211 We measured standing live and dead trees within a central subplot at each plot. Central
212 subplot radii were chosen to capture approximately 50 trees within the subplot and thus varied
213 with stand density, ranging from 2–18 m (total sampling area range: 12.6–1017.9 m²). All trees
214 were categorized as live or dead, assessed for disease presence (western gall rust and pitch
215 canker), and measured for diameter at breast height (DBH; 1.37 m above ground). All cones
216 were tallied by status: closed (majority of cone scales sealed), open (majority of cone scales
217 open), damaged (evidence of seed predation or substantial mechanical damage), or immature
218 (green color, seeds not yet viable). Full visibility of tree crowns allowed counting of all
219 individual cones on each tree. Further, our field work occurred in warm and dry weather, so it is
220 unlikely that scale contraction due to high relative humidity (Vogl 1973) caused us to tally open
221 cones as closed cones. We did not directly assess seed density within cones in this study, but
222 previous estimates of seed density within closed cones range from 61–95 mean seeds cone⁻¹ for
223 knobcone pine (Fry and Stephens 2013) and 62–78 mean seeds cone⁻¹ for bishop pine (S.
224 Bisbing, unpublished data), with evidence of seed viability >60% upon reproductive maturity for
225 both species. Tallies of trees and cones by status were scaled to the plot to obtain per hectare

226 (trees ha⁻¹ and cones ha⁻¹) estimates. We additionally measured understory and shrub cover along
227 two 18-m transects at each plot using a point-intercept method (Fontaine et al. 2012). We tallied
228 shrubs intercepting the transect at 1-m intervals (n = 36) and divided shrub interceptions by the
229 number of points measured at each plot to obtain an estimate of shrub cover.

230 *Climate and site condition variables*

231 We obtained climate data at a monthly resolution for our sites from ClimateNA, a
232 software package that locally downscales historical climate data to scale-free point estimates
233 (Wang et al. 2016). Given that our analysis seeks to understand climate effects on aggregate
234 measures of demographic trends over the inter-fire period (e.g., canopy seed bank accumulation
235 over multiple growing seasons), we aggregated climate variables for the entire growing period
236 for each plot (defined as one year following the most recent fire to the year of measurement). We
237 considered mean annual precipitation and cumulative moisture deficit during the growing season
238 (March to October) as candidate predictor variables given the importance of water availability to
239 reproductive capacity and demographic performance in seasonally dry forests (Redmond et al.
240 2012). The two predictors were strongly collinear, so we assessed parallel model forms with each
241 climate variable included during the model evaluation process (detailed below under *Statistical*
242 *analysis*).

243 In addition to regional climate, we characterized site-level topo-climate using three
244 topographic predictors: heat load index (HLI), topographic position index (TPI), and topographic
245 wetness index (TWI). HLI represents the amount of direct incident radiation to a site (McCune
246 and Keon 2002), TPI represents its relative topographic position (i.e., ridge or valley position)
247 (Weiss 2001; De Reu et al. 2013), and TWI reflects a site's potential moisture balance (Gessler
248 et al. 1995). We calculated all three indices from 30-m digital elevation models (U.S. Geological

249 Survey [USGS] 1999) using the Geomorphometry and Gradient Metric Toolbox (Evans et al.
250 2014) in ArcMap version 10.6.1 (Environmental Systems Research Institute [ESRI] 2018). Of
251 the three variables, only HLI was ultimately retained as a candidate predictor for model fitting
252 due to collinearity among topographic variables and poor interspersions of TPI and TWI across
253 the gradient of stand age.

254 We also obtained spatial data that reflected soil characteristics from the Probabilistic
255 Remapping of SSURGO (POLARIS) database, a spatially contiguous soils dataset that provides
256 a suite of ecologically relevant soil variables (Chaney et al. 2016). We extracted depth to
257 bedrock and percent soil clay as two candidate predictors as they represent a proxy for soil
258 fertility and can influence forest productivity (Romanyà and Vallejo 2004; Wall and Westman
259 2006). However, depth to bedrock was strongly collinear with mean growing season CMD, so
260 only percent soil clay was retained as a candidate predictor for model fitting.

261 *Statistical analysis*

262 To address questions 1 and 2, we fit generalized linear mixed models for each of the
263 following response variables: tree-level probability of reproductive maturity (cone
264 presence/absence on individual live trees), tree-level cone production (total cones [of all classes]
265 individual⁻¹ on live trees with ≥ 1 cone), stand-level proportion reproductively mature individuals
266 (proportion of standing live and dead trees within a stand with ≥ 1 cone; hereafter, stand-level
267 proportion mature), and stand-level closed cone density (closed cones on standing live and dead
268 trees ha⁻¹). To address question 3, we fit a generalized linear mixed model for the response
269 variable stand-level tree mortality (standing dead trees ha⁻¹). Tree-level probability of
270 reproductive maturity was fit with a binomial error structure while tree-level cone production
271 was fit with a negative binomial error structure. Stand-level proportion mature was fit with a

272 zero-inflated beta error structure as appropriate for proportion data (Zuur et al. 2009). Stand-
273 level closed cone density and tree mortality were fit with zero-inflated negative binomial error
274 structures and an offset term ($\log[\text{plot area}]$) to account for variable sampling area (Zuur et al.
275 2009). All models fit with a negative binomial error structure were also fit with a Poisson error
276 structure, but Poisson-distributed models were removed from further consideration due to
277 overdispersion. Stand-level models included a random effect of fire (site), and candidate models
278 included the following suite of potential fixed predictor variables: stand age (years since last
279 stand-replacing fire), species, stand density (\log transformed trees ha^{-1}), shrub percent cover, heat
280 load index, percent soil clay, mean growing period precipitation or CMD, and stand age – stand
281 density interaction. Tree-level models included nested random effects of plot within sample fire,
282 and candidate models included the stand-level fixed predictor variables included for the stand-
283 level models and the following tree-level predictor variables: tree DBH, disease
284 presence/absence (western gall rust or pitch canker), DBH – stand age interaction, DBH –
285 species interaction, DBH – stand density interaction. Predictor variables were assessed for
286 collinearity prior to model fitting.

287 Models were fit using standardized predictor variables (mean-centered per two standard
288 deviations) for ease of discerning relative effects of each predictor. The full model with all terms
289 included was fit for each response variable, and model diagnostic tests were conducted. When
290 the full model did not meet model assumptions, a suite of new models was fit, each with a single
291 predictor term (all except stand age) removed. Model diagnostics were conducted on each model.
292 If all models failed to meet model assumptions, this process was repeated until a model was
293 fitted that met assumptions. If two models with the same number of predictors met assumptions,
294 the model with the lowest AICc was selected for inference. We interpreted $P \leq 0.01$ as strong

295 evidence, $P \leq 0.05$ as moderate evidence and $P \leq 0.10$ as suggestive evidence of an effect
296 (Ramsey and Schafer 2012). Models were fit with the *glmmTMB* package (Brooks et al. 2017)
297 and model diagnostics were conducted using *DHARMA* (Hartig 2021). Model effects were
298 visualized using *broom* (Robinson et al. 2021), *ggeffects* (Lüdtke 2018), *ggplot* (Wickham
299 2016), *ggpubr* (Kassambara 2020), and *jtools* (Long 2020). All analyses were conducted in R
300 version 4.0.5 (R Core Team 2021).

301 RESULTS

302 We counted 68,400 cones on a total of 4,573 trees (2,121 knobcone pine and 2,452
303 bishop pine), 3,855 of which were live at the time of sampling (1,960 knobcone pine and 1,895
304 bishop pine). Stand structure varied widely both within and across stand age (Table 1). Stand
305 density ranged from 147–82,800 live trees ha⁻¹. Live basal area and quadratic mean diameter
306 were highly correlated with stand age, with median values of 0.5 m² ha⁻¹ and 2.0 cm at 6 years
307 and 26.2 m² ha⁻¹ and 10.4 cm at 32 years (Table 1).

308 *Reproductive capacity over time since fire*

309 Cones were present in stands by five years for bishop pine and six years for knobcone
310 pine (Table 1), but some stands lacked cones until eight years for both species. Cone density
311 initially increased slowly and remained under an average of 10,000 cones ha⁻¹ for at least 10
312 years post-fire, after which there was a steep and continuous linear increase in cone production
313 (Figure 1). Incidence of cones on dead trees and damaged cones increased with time, but closed
314 cone production represented the greatest proportion of cones at all ages (Figure 1a) and increased
315 most steeply with age (Figure 1b).

316 *Tree-level reproductive capacity*

317 Tree-level reproductive capacity was strongly driven by tree DBH, with an effect size
318 more than two times greater than other predictors (Figure 2, 3). Tree-level probability of
319 reproductive maturity increased from near zero for trees smaller than 2 cm DBH to nearly 100%
320 for trees larger than 9 cm DBH, irrespective of all other drivers (Figure 2A). There was a
321 similarly strong effect of DBH on tree-level cone production, where cone production increased
322 slowly for trees smaller than 10 cm DBH but increased exponentially for trees larger than 15 cm
323 DBH (Figure 3A, 3B). Trees of a similar DBH had a greater probability of reproductive maturity
324 and greater cone production in older stands than trees with the same DBH in younger stands
325 (Figure 2D, 3D). For example, probability of reproductive maturity for a tree of 4 cm DBH
326 increased by over 40% (Figure 2D) and cone production for a tree of 10 cm DBH increased by a
327 factor of four (Figure 3D) between stand ages of 10 and 30 years. The effect of DBH lessened
328 with stand age (Figure 2B, 3B), such that differences in both measures of reproductive capacity
329 that were driven by DBH decreased in older stands (Figure 2D, 3D).

330 Contrary to our expectation, stand density had a positive effect on tree-level probability
331 of reproductive maturity (Figure 2B). Trees in high-density stands were associated with a ~40%
332 greater probability of reproductive maturity than trees in low-density stands at an age of 10
333 years, but this difference decreased to ~10% by 30 years (Figure 2C). The positive effect of stand
334 density was greatest for trees of larger DBH and there was no effect for trees <2 cm DBH
335 (Figure 2E). As expected, trees in low-density stands had greater cone production, although this
336 effect decreased in older stands (Figure 3B, 3G). However, for trees with relatively large DBH,
337 the effect of stand density on cone production was less than for smaller trees, with wide variation
338 around the estimated effect (Figure 3E). Holding all other covariates constant, bishop pine
339 individuals had double the cone production of knobcone pine, but there was no difference in

340 probability of reproductive maturity between species (Figure 2B, Figure 3B, 3C). Similarly, cone
341 production of trees in stands with high soil clay was double that of trees in stands with low soil
342 clay (Figure 3B, 3C). Disease incidence, heat load index, and regional climate (mean growing
343 season CMD or precipitation) had no effect on either measure of reproductive capacity
344 (Appendix S2–S4 in the Electronic supplementary material), while shrub cover (not included in
345 the model for probability of reproductive maturity) had no effect on cone production (Figure 2B,
346 3B).

347 *Stand-level reproductive capacity*

348 Stand-level reproductive capacity increased strongly with stand age. Stand-level
349 proportion mature ranged from 0 to nearly 100%, with all observations of 0% occurring in stands
350 <10 years and all observations >90% occurring in stands ≥ 14 years (Figure 4A). Estimated
351 stand-level closed cone density increased by approximately two orders of magnitude between the
352 initial years of reproductive maturity (5–6 years) and 30 years (Figure 5A). The effect of stand
353 age was mediated by stand density, with contrasting effects on each measure of stand-level
354 reproductive capacity (Figure 4B, 5B). There were strong negative effects of stand density and
355 its interaction with stand age on proportion mature (Figure 4B). For 10-year-old stands,
356 proportion mature was estimated at >50% for low-density stands, compared with <25% for
357 moderate to high-density stands, and the difference increased over time (Figure 4C). Conversely,
358 there was a strong positive effect of stand density on closed cone density, which declined with
359 stand age (Figure 5B). For young stands, estimated closed cone density was more than an order
360 of magnitude greater in high-density stands than in low-density stands, but after ~20 years,
361 closed cone densities were similar across stands of all densities (Figure 5C). Effects of regional
362 climate also varied by response variable. Mean growing season precipitation had a strong

363 positive effect on proportion mature (Figure 4B), while mean growing season CMD had no
364 effect on closed cone density (Figure 5B). Greater soil clay had positive effects on both measures
365 of stand-level reproductive capacity (Figure 4E, 5D), although this effect was lower magnitude
366 than other significant covariates in each model (Figure 4B, 5B). Stand-level reproductive
367 capacity did not differ between species (Figure 4B, 5B; Appendix S5–S7 in the Electronic
368 supplementary material).

369 *Stand-level tree mortality*

370 For stands ten years and older ($n = 47$), observed stand-level tree mortality ranged from 0
371 to 85,100 standing dead trees ha^{-1} , and was strongly positively correlated with stand-level
372 proportion dead trees (Appendix S8 in the Electronic supplementary material). Stand density and
373 stand age drove tree mortality (Figure 6B); tree mortality in high-density stands was two orders
374 of magnitude greater than that of low-density stands of the same age (Figure 6D). Similarly, tree
375 mortality increased by nearly two orders of magnitude between 10- and 30-year-old stands of the
376 same density (Figure 6A, 6D). Moisture stress (high CMD) further exacerbated tree mortality
377 (Figure 6B); high mean growing season CMD was associated with approximately one order of
378 magnitude greater tree mortality compared with stands with low mean growing season CMD
379 (Figure 6E). Bishop pine stands also had significantly greater tree mortality than knobcone pine
380 stands of a similar age and stand density (Figure 6C), while heat load index had no effect (Figure
381 6B; Appendix S5, S9 in the Electronic supplementary material).

382 DISCUSSION

383 Our study identifies three critically important drivers of demographic processes in serotinous
384 forests as they develop following stand-replacing fires. First, stand age is the key driver of

385 reproductive capacity—older stands have greater reproductive capacity regardless of all other
386 drivers. Second, intraspecific competition associated with stand density plays a critical role in
387 mediating tree- and stand-level reproductive capacity at a given stand age. Third, there were
388 modest decreases in reproductive capacity and increases in tree mortality associated with warm
389 and dry regional climate. Collectively, these findings have important implications for serotinous
390 forest resilience in a changing climate. Overriding all other factors is the minimum fire-free
391 period necessary for serotinous population persistence—change in other drivers cannot override
392 the importance of the fire interval. However, once stands exceed the minimum fire-free period,
393 differences in stand structure produce divergent outcomes in reproductive maturity for stands of
394 the same age. Our results are also consistent with the demographic shift described by Enright et
395 al. (2015) suggesting that warming and drying conditions can constrain the reproductive output
396 of serotinous populations during the fire-free period. Although the demographic mechanisms
397 underpinning resilience are aligned to current conditions, continued climate warming and
398 increased fire activity are likely to have profound effects on serotinous forest persistence.

399 Rapid post-fire canopy seed bank accumulation suggests that the window for immaturity risk
400 is brief for California closed-cone pine species. Closed cone development first occurred at five
401 and six years for bishop pine and knobcone pine, respectively, suggesting that complete loss of
402 these species from a site would occur if fire return intervals were shorter than this period. Early
403 onset of cone production is common in strongly serotinous species adapted to relatively frequent
404 stand-replacing fire (Gill and McMahon 1986; Enright et al. 1996; Turner et al. 2007; Climent et
405 al. 2008), serving as an important mechanism of resilience to population loss to short interval fire
406 (Tapias et al. 2001). Population self-replacement, however, is likely to require a considerably
407 longer fire-free interval (Burrows 2008; Gosper et al. 2013). Estimates for knobcone pine

408 suggest the mean cone to seedling conversion ratio is 1:1 (M.C. Agne, unpublished data),
409 equivalent to approximately 60–100 seeds for one established seedling (Fry and Stephens 2013).
410 Therefore, mean canopy seed bank accumulation to regenerate a stand at 1,500 seedlings ha⁻¹ (a
411 low seedling density for closed-cone pine [Keeley et al. 1999]) and at 15,000 seedlings ha⁻¹ (a
412 moderate seedling density for closed-cone pine [Holzman and Folger 2005]) does not occur until
413 10 and 20 years, respectively. Although self-replacement is dependent on a variety of factors, we
414 expect that the seedling density associated with self-replacement is toward the high end of this
415 range. Canopy seed bank accumulation may begin to slow near the end of our chronosequence
416 (~30 years; Figure 1a), providing further evidence that sufficient seed is stored and available to
417 regenerate the stand in advance of three decades post-fire (Lamont et al. 1991). Thus, seed
418 limitation is most likely to occur prior to 10 years and is less likely after 20 years since the last
419 stand-replacing fire. Additional factors can alter seed availability for stands of any age, but their
420 effects are most important during the period between 10 and 20 years.

421 Although stand age is the key driver of reproductive capacity in California closed-cone pines,
422 strong effects of intraspecific competition suggest buffering against immaturity risk differs by
423 stand structure. The strong negative effect of intraspecific competition on tree-level cone
424 production is common for serotinous species (Borchert 1985; Esler and Cowling 1990; Moya et
425 al. 2008). However, we found that this applied most strongly to the smallest trees (based on
426 DBH). Tree-level reproductive capacity, in terms of probability of reproductive maturity and
427 cone production, was greatest for relatively large trees, regardless of other factors, suggesting a
428 synergy rather than trade-off between vegetative and reproductive growth (Alfaro-Sánchez et al.
429 2015). These tree-level effects scaled up beyond the individual to delay the peak in stand-level
430 reproductive maturity. Similar delays in stand-level reproductive maturity in stands with high

431 levels of intraspecific competition have been described for *P. coulteri* and *P. halepensis*
432 (Borchert 1985; Moya et al. 2008). Despite negative effects on tree-level cone production, high
433 stand densities during the first two decades of stand development increased the canopy seed
434 bank, as has been observed in several other serotinous species (Esler and Cowling 1990; Moya et
435 al. 2007; Turner et al. 2007). This suggests that despite strong intraspecific competition, high
436 post-fire stand densities provide a buffer against immaturity risk should a subsequent fire occur
437 prior to the mean fire return interval, in addition to providing a post-fire environment with
438 relatively low interspecific competition (Harvey and Holzman 2014). Such short interval fire
439 activity has been common within the study area within the past several decades (Reilly et al.
440 2019) and may become increasingly common with continued climate warming. By
441 approximately 20 years, closed cone density converges across levels of stand density, indicating
442 that the range of stand structural development pathways that occur for serotinous species
443 (Harvey and Holzman 2014; Turner et al. 2016) can lead to sufficient canopy seed bank
444 development, given adequate time.

445 Tree mortality associated with regional moisture stress suggests a demographic shift is
446 expected with climate warming and drying in California closed-cone pine forests. Stand-level
447 tree mortality was primarily driven by stand age and density, suggesting the dominant process
448 controlling mortality was density dependent thinning, consistent with expected stand dynamics
449 (Harvey et al. 2011). However, an additional, albeit lower magnitude, effect of high growing
450 season cumulative moisture deficit during the stand growth period suggests that warming climate
451 may exacerbate background mortality, similar to findings in subalpine forests (Andrus et al.
452 2021). Increased tree mortality could decrease the reproductive capacity of stands if live trees are
453 not able to compensate for the loss of reproductively mature trees through increased cone

454 production. Stand-level reproductive maturity was also delayed where growing season
455 precipitation was low, signaling some evidence of direct climate effects on reproductive
456 capacity. However, there was no evidence of depressed canopy seed bank availability (as
457 estimated by closed cone density) due to regional or local climate. Climate can also influence
458 seed density within cones and seed viability (Moya et al. 2007), which were not evaluated in this
459 study. Fluctuations in cone production linked to interannual climate variability can occur for
460 species that produce cones annually (though to a lesser extent than for masting species).
461 Understanding how annual cone and seed production respond to annual variation in climate
462 conditions, drought conditions, and heatwave events is needed to predict future demographic
463 trends in a warming climate.

464 Our findings have broad implications for demographic mechanisms underpinning
465 serotinous forest persistence across North America. We expect that while rates of cone
466 production vary among species, the period prior to reproductive maturity is brief relative to the
467 historical mean fire return interval (Tapias et al. 2001; Turner et al. 2007). However, time to
468 accumulate a canopy seed bank sufficient to regenerate a stand is considerably longer and varies
469 with stand density (Moya et al. 2007). Rapid development of a large canopy seed bank in high-
470 density stands suggests that extremely high establishment densities exhibited by many serotinous
471 conifers (Turner et al. 1999; Verkaik and Espelta 2006; Harvey and Holzman 2014) represent a
472 resilience mechanism to short interval fires. While serotinous populations may be able to persist,
473 albeit at a stand lower density, following a single short interval severe fire (Keeley et al. 1999;
474 Turner et al. 2019), they are unlikely to withstand recurrent short interval fire activity (Espelta et
475 al. 2008; Bassett et al. 2015). Demographic rates must be assessed in the context of the expected

476 shortening of the fire-free interval to understand when erosion of serotinous forest resilience to
477 fire may occur.

478 CONCLUSION

479 Reproductive capacity recovered rapidly following high-severity fire in California
480 closed-cone pine forests, suggesting that the window for immaturity risk is relatively brief.
481 Differences in the canopy seed bank among stand trajectories suggest that high-density stands
482 are more buffered against immaturity risk than are low-density stands during the critical early
483 post-fire window. Evidence of decreased reproductive capacity and increased tree mortality
484 associated with moisture stress suggest that a demographic shift may further dampen seed
485 availability. Although the demographic mechanisms we investigate here are aligned to relatively
486 frequent high severity fires, continued climate warming and increased fire activity may
487 overwhelm these mechanisms. Understanding how fuels and associated fire hazard develop in
488 tandem with reproductive capacity is critical for predicting when and where serotinous forests
489 will persist under future conditions.

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716

717 TABLES

718 Table 1. Summary statistics for stand structure attributes, total trees measured, and mean cones
 719 per tree by stand age.

Stand age	Plots (n)	Species	Trees (n)	Mean cones per tree	Quadratic mean diameter (cm)		Stand density (live trees ha ⁻¹)		Live basal area (m ² ha ⁻¹)	
					median	range	median	range	median	range
4	4	PIMU	276	0	NA	NA	3932	1840–6068	0.41	0.06–0.93
5	2	PIAT	114	0	NA	NA	7582	6013–9151	1.06	0.97–1.15
5	3	PIMU	122	0.01	NA	NA	5659	3830–9549	0.75	0.44–2.31
6	2	PIAT	95	0.10	2.0	1.8–2.2	1837	640–3034	0.53	0.25–0.81
7	4	PIMU	585	0.14	1.2	1.0–1.5	54643	13440–82761	4.50	2.38–11.12
8	3	PIAT	150	0.53	3.0	1.0–3.7	7112	1890–29412	1.98	0.17–3.90
8	4	PIMU	225	1.01	2.8	1.5–5.4	6797	643–16977	2.62	1.31–9.09
10	8	PIAT	464	1.89	5.6	3.1–9.0	2763	671–11332	4.90	2.62–8.64
10	6	PIMU	475	9.85	3.6	2.7–7.0	1723	553–3631	2.45	0.69–5.71
14	9	PIAT	456	13.33	8.8	3.5–16.6	4106	943–18104	17.71	5.70–24.98
15	2	PIAT	110	2.08	6.6	6.1–7.0	3417	2236–4598	10.01	7.78–12.23
19	6	PIAT	341	17.23	8.9	6.0–11.1	2412	1297–16043	17.13	3.46–47.11
23	3	PIAT	189	62.74	12.2	8.1–12.6	2735	603–3979	20.02	7.48–32.48
23	10	PIMU	769	75.39	13.8	4.0–29.2	2910	147–28736	40.80	9.18–59.43
32	3	PIAT	202	47.06	10.4	10.3–12.6	2785	2288–3183	26.15	21.95–28.67

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722 LIST OF CAPTIONS

723 Figure 1. Cumulative stand-level cone density estimates by stand age for (A) all cone class
724 (closed, open, or damaged) by tree status (live or dead) combinations and (B) closed cones only
725 (cones presumed to contribute to the canopy seed bank) by tree status. Colors represent averages
726 of plot-level ($n = 69$) estimates of each cone category for each measured stand age interpolated
727 across the chronosequence using a loess smoother ($\text{span} = 0.5$).

728 Figure 2. Effects of covariates from the model: Tree-level probability of reproductive maturity ~
729 Stand age + DBH + Species + Disease incidence + Heat load index + Stand density (log
730 transformed) + Mean growing season precipitation (ppt) + DBH:Stand density (log transformed)
731 + DBH:Stand age. (A) Partial effect of DBH. The solid line represents the median estimate with
732 all other covariates held at their means. Points are shaded by stand age and each point represents
733 a tree ($n = 3,855$). (B) Effects of tree-level and stand-level covariates on tree-level probability of
734 reproductive maturity. Here, and for subsequent figures, dots represent medians and horizontal
735 lines represent 95% confidence intervals. The effects for each continuous predictor are per two
736 standard deviations. Strength of evidence for effect sizes are indicated by: *** ($P < 0.001$), ** (P
737 < 0.01), * ($P < 0.05$), + ($P < 0.10$). (C-E) Change in stand age or stand density and tree-level
738 probability of reproductive maturity across gradients of significant tree-level and stand-level
739 covariates. Here, and for subsequent figures, solid lines represent median estimates and shaded
740 areas represent 95% confidence intervals. Predictions consider the effect of each covariate
741 combination individually, holding all other covariates at their means.

742 Figure 3. Effects of covariates from the model: Tree-level cone production ~ Stand age + DBH +
743 Species + Heat load index (HLI) + Stand density (log transformed) + Soil clay (%) + Mean
744 growing season cumulative moisture deficit (CMD) + Disease incidence + Shrub cover +

745 DBH:Stand age + DBH:Stand density (log transformed). (A) Partial effect of DBH. The solid
746 line represents the median estimate with all other covariates held at their means. Points are
747 shaded by stand age and each point represents a tree (n = 1,806). (B) Effects of tree-level and
748 stand-level covariates on tree-level cone production on reproductively mature trees. (C-H)
749 Change in stand age and tree-level cone production across gradients of significant tree-level and
750 stand-level covariates.

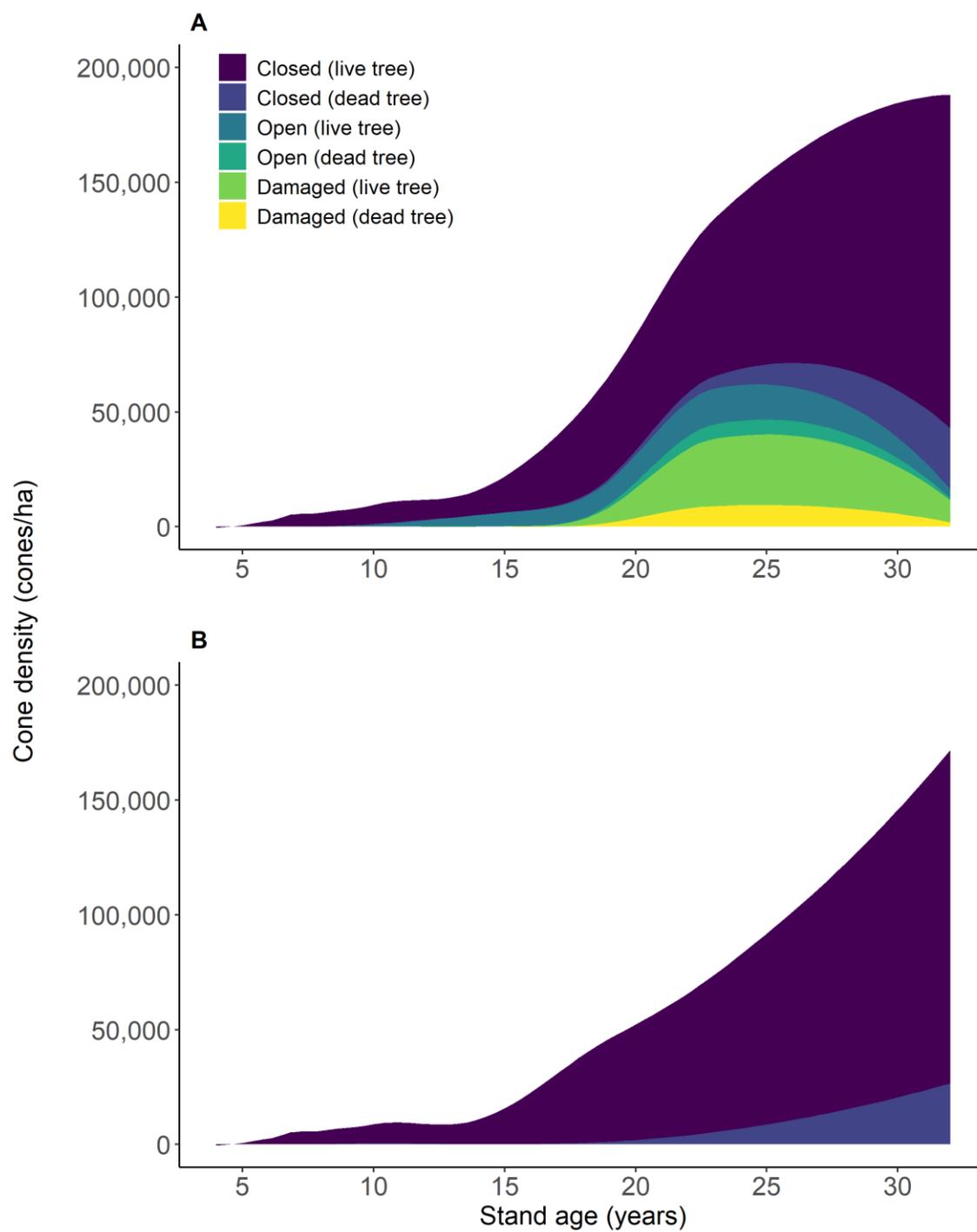
751 Figure 4. Effects of covariates from the model: Stand-level proportion mature ~ Stand age +
752 Stand density (log transformed) + Species + Mean growing season precipitation (ppt) + Soil clay
753 (%) + Stand age:Stand density (log transformed). (A) Partial effect of stand age. The solid line
754 represents the median estimate with all other covariates held at their means. Points are shaded by
755 stand density (log-transformed) and each point represents a plot (n = 69). (B) Effects of stand-
756 level covariates on stand-level proportion mature. (C-E) Change in stand age and stand-level
757 proportion mature across gradients of significant covariates.

758 Figure 5. Effects of covariates from the model: Stand-level closed cone density ~ Stand age +
759 Species + Stand density (log transformed) + Soil clay (%) + Mean growing season cumulative
760 moisture deficit (CMD) + Stand age:Stand density (log transformed). (A) Partial effect of stand
761 age. The solid line represents the median estimate with all other covariates held at their means.
762 Points are shaded by stand density (log-transformed) and each point represents a plot (n = 69).
763 (B) Effects of stand-level covariates on stand-level closed cone density. (C-D) Change in stand
764 age and stand-level closed cone density across gradients of significant covariates.

765 Figure 6. Effects of covariates from the model: Stand-level tree mortality ~ Stand age + Stand
766 density (log transformed) + Species + Heat load index + Mean growing season CMD. (A) Partial
767 effect of stand age. The solid line represents the median estimate with all other covariates held at

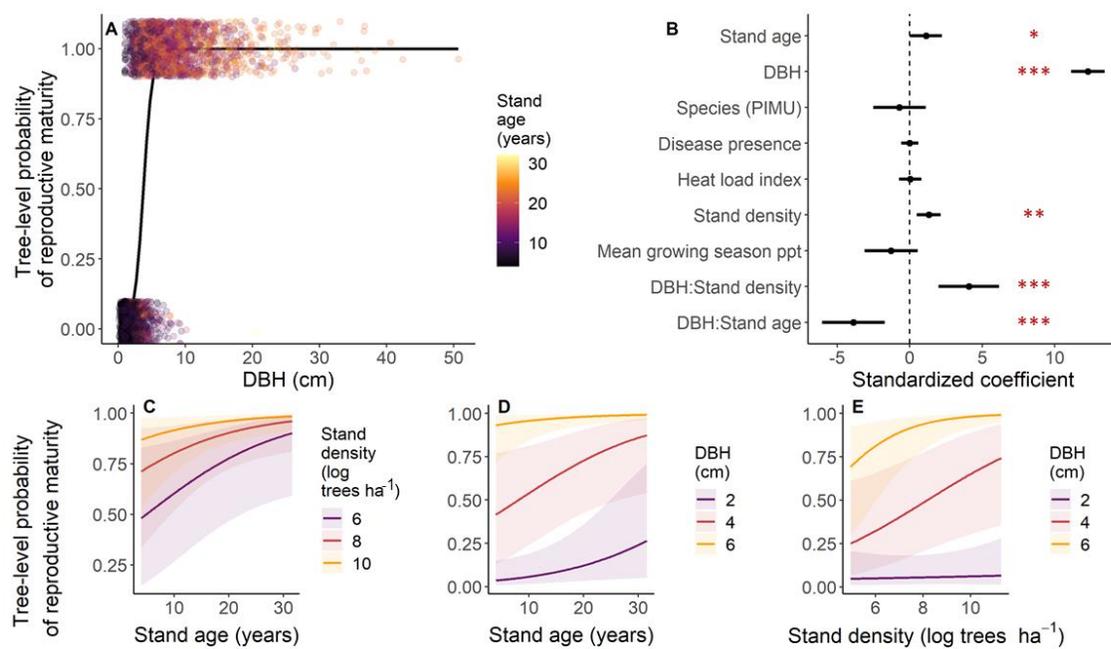
768 their means. Points are shaded by stand density (log-transformed) and each point represents a
769 plot ($n = 47$). Note: Two points at 49,400 and 85,100 trees ha^{-1} were omitted from the figure for
770 interpretability. (B) Effects of stand-level covariates on stand-level tree mortality. (C-E) Change
771 in stand age and stand-level tree mortality across gradients of significant covariates.

772 FIGURES



773

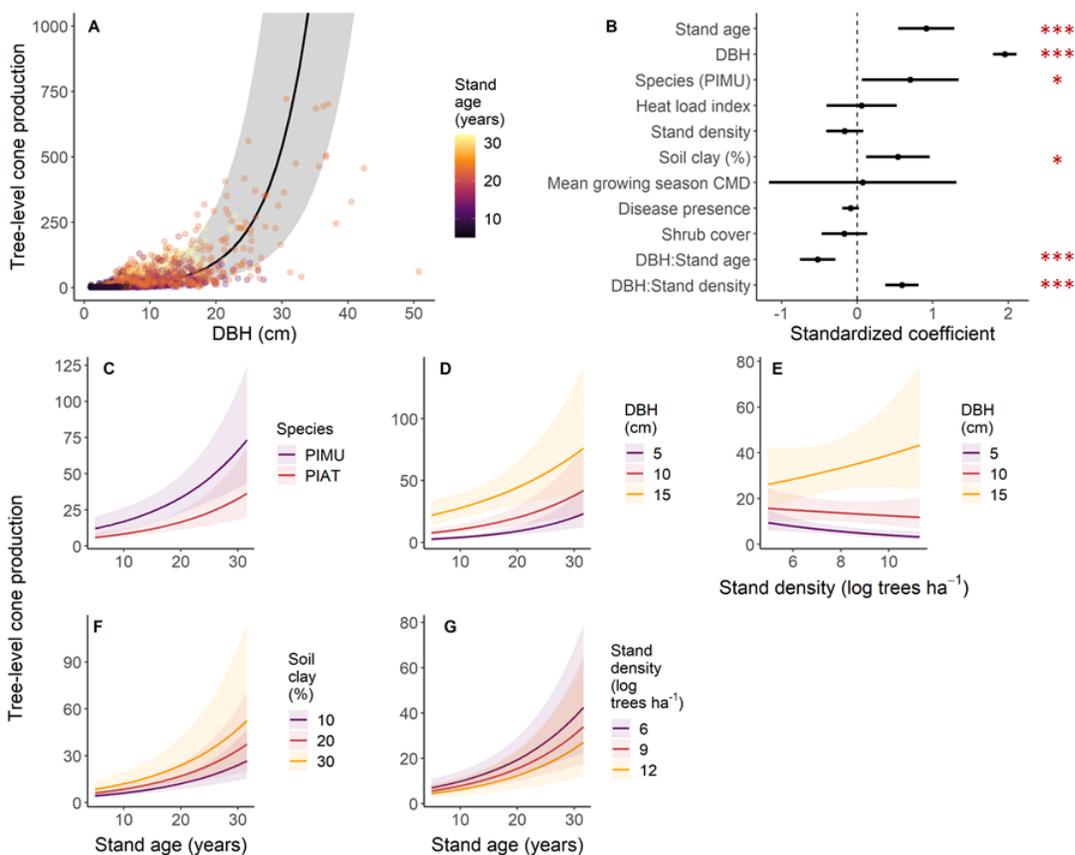
774 Figure 1.



775

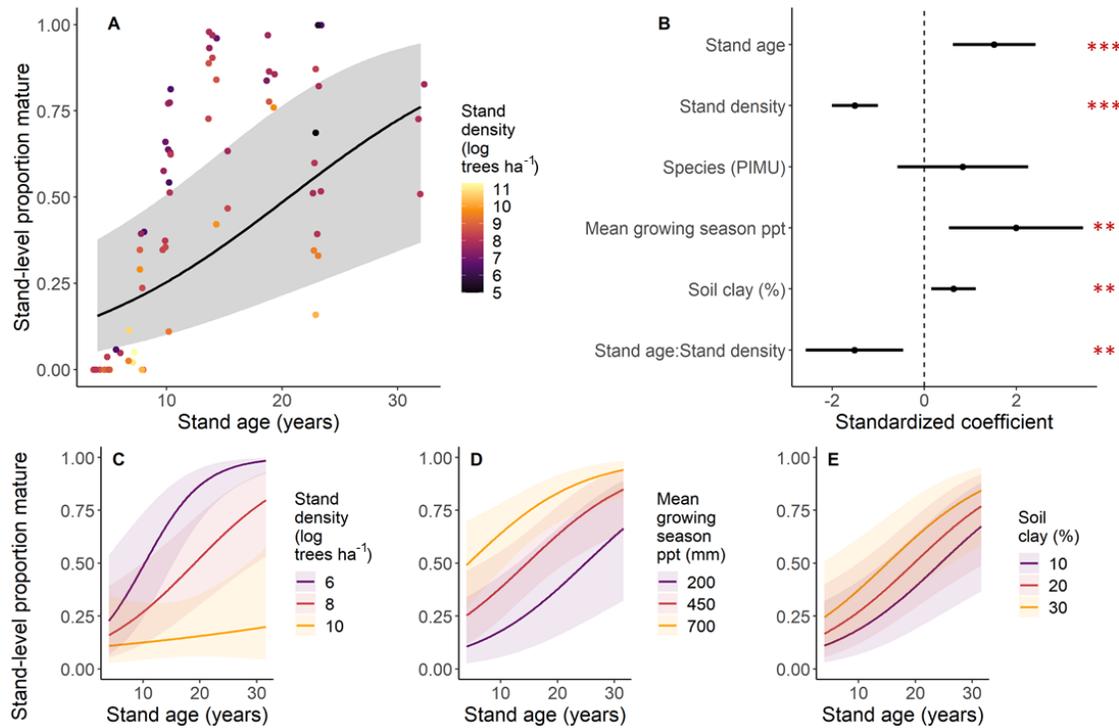
776 Figure 2.

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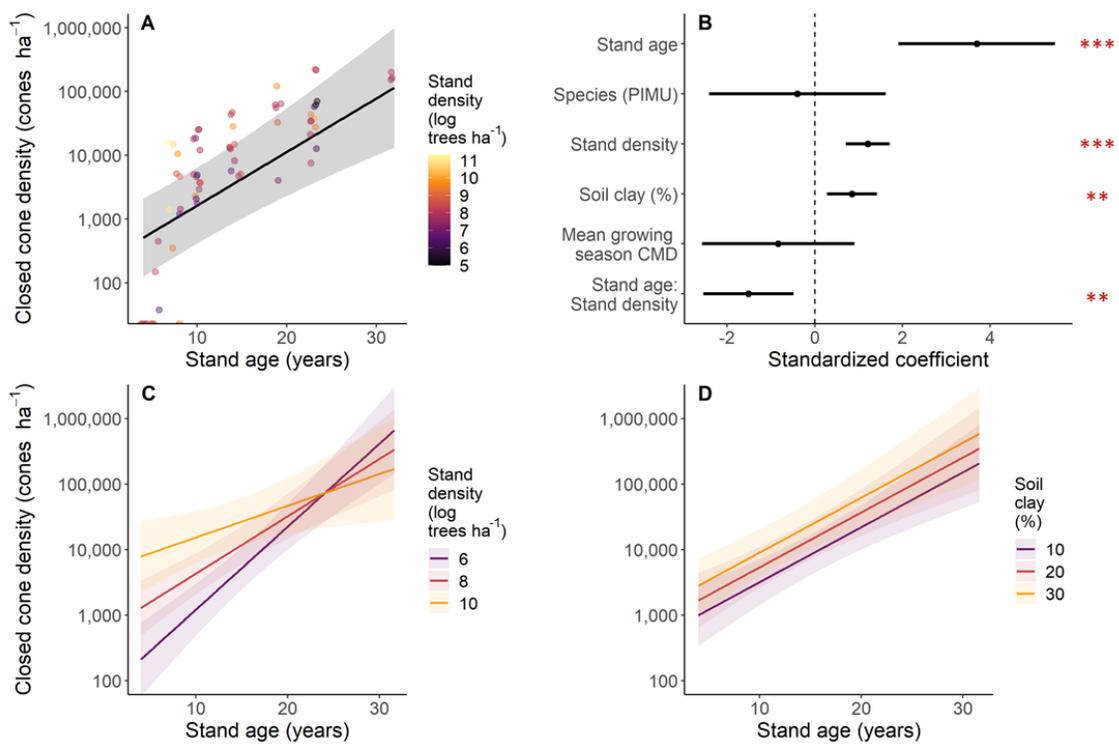
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779 Figure 3.



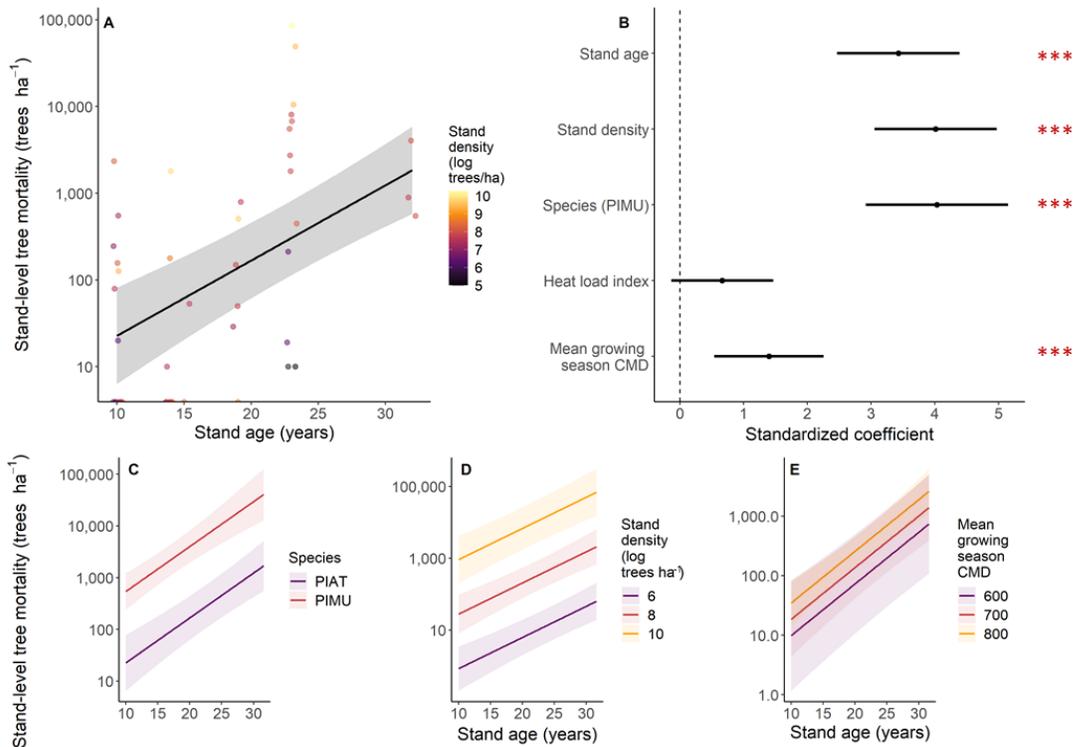
780

781 Figure 4.



782

783 Figure 5.



784

785 Figure 6.