

Mycorrhizal colonization of *Palafoxia feayi* (Asteraceae) in a pyrogenic ecosystem

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Abstract Although it is known that a number of factors have predictable effects on mycorrhizal colonization, determining generalized patterns for some variables have remained elusive. In particular, fire has been identified as a major event that may influence plant–mycorrhiza interactions, yet efforts to date have yielded contradictory results. Here, we assess the impact of fire on mycorrhizal colonization in *Palafoxia feayi*, a plant commonly found in the fireswept, nutrient-poor scrub community of central Florida. We determined soil nutrient conditions and percent colonization patterns for plants growing in replicate plots that were burned 1 to 15 years previously. The results showed a negative relationship between mycorrhizal colonization and time since fire, but there was no effect of fire return interval (lapsed time between successive fires). Soil nutrient analyses corroborated previous studies and showed no change in soil nutrients following fire. In contrast to previous studies of mycorrhizal colonization in Florida scrub, we conclude that fire can affect arbuscular mycorrhizal fungi colonization and we speculate that this is mediated by light availability.

Keywords Mycorrhizal colonization · Fire ecology · Fire return interval · *Palafoxia feayi* · Soil analysis

Arbuscular mycorrhizal fungi (AMF) are crucial mutualists of many plant species (e.g., Hart and Klironomos 2002; Hartnett and Wilson 2002; Parniske 2008; Smith and Read 2008), especially in nutrient-limited ecosystems where plants may have enhanced mycorrhizal dependency (Harrison 2005; Smith and Read 2008; Johnson 2010). One such nutrient-limited environment is the scrub ecosystem of the Lake Wales Ridge in south-central Florida. Scrub is characterized by nutrient-poor, well-drained, sandy soils and is dominated by stands of xerophytic oaks, saw palmettos (*Serenoa repens*), and pines (*Pinus clausa* and *Pinus elliottii*). Not only are the soils nutrient-poor, but this ecosystem also experiences natural disturbance caused by relatively frequent fires. Fires are often stand-replacing, but do not generally affect species composition, as many species resprout from roots or regenerate from seeds (Abrahamson 1984; Schmalzer and Hinkle 1987).

Fire can influence a number of factors important to AMF colonization, such as the nutrient content of soils by rapid combustion and release of nutrients from herbaceous vegetation and accumulated organic matter. Ash deposition may create a nutrient pulse following fire (e.g., Kellman et al. 1985; Smithwick et al. 2005; Turner et al. 2007; Galang et al. 2010), or nutrients can be lost via volatilization and/or removal of ash by wind or water (Raison et al. 1985; Gray and Dighton 2006). Ultimately, soil nutrient content following fire will depend on fire intensity, duration of soil heating, and local conditions at a site (Raison et al. 1985; Certini 2005; Gray and Dighton 2006; Galang et al. 2010). In addition to changes in nutrient content, fire can also influence mycorrhizal inoculum potential or the ability of propagules to form mycorrhizal associations. Burning can reduce mycorrhizal inoculum potential (Vilariño and Arines 1991; Dhillion and Anderson 1993) and spore germination (Vilariño and Arines 1991) which, in turn, decreases AMF colonization. Alternatively, studies have also shown

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68 a range of effects from no change to increases in inoculum
69 potential with burning (Allsopp and Stock 1994; Korb et al.
70 2003); thus, the effects of fire on AMF colonization involve a
71 number of factors and may be ecosystem-specific.

72 This complexity makes it challenging to identify gener-
73 alized AMF colonization patterns correlated with fire dis-
74 turbance (Cairney and Bastias 2007), and not surprisingly,
75 previous research on the role of fire in mycorrhizal coloni-
76 zation has yielded contradictory results. For instance, stud-
77 ies have identified increased colonization (Bentivenga and
78 Hetrick 1991), decreased colonization (Klopatek et al. 1988;
79 Vilariño and Arines 1991; Dhillion and Anderson 1993;
80 Hartnett et al. 2004), and no change in AMF colonization
81 following fire (Bellgard et al. 1994; Anderson and Menges
82 1997; Eom et al. 1999; Haskins and Gehring 2004; Treseder
83 et al. 2004). Part of this variability in plant–AMF response
84 to fire is likely a result of differences in conditions and
85 methodology among studies, including the time frame of
86 the study, study sites, and plant–AMF species involved
87 (Cairney and Bastias 2007). The next step in resolving this
88 issue is to tease apart the myriad factors that determine AMF
89 colonization patterns following fire.

90 The Florida scrub ecosystem offers an opportunity to ex-
91 amine the role of fire in AMF colonization. Although fire can
92 clearly have an impact on soil nutrient dynamics, in scrub,
93 such changes may be less important in determining the extent
94 of AMF colonization. Short-term increases in soil nitrogen
95 and phosphorus have been observed; however, these changes
96 in nutrient content are ephemeral, lasting only a few months
97 before returning to pre-burn levels (Abrahamson 1984;
98 Anderson and Menges 1997; Schafer and Mack 2010). Fur-
99 thermore, mycorrhizal inoculum potential of Florida scrub
100 also appears to be unaffected by fire (Anderson and Menges
101 1997). Consequently, the relatively constant nutrient status of
102 soils and mycorrhizal inoculum potential of scrub allows us to
103 examine alternative factors that influence AMF colonization
104 in pyrogenic ecosystems.

105 Previous work in Florida scrub has shown no effect of
106 fire on AMF colonization and three of four species exam-
107 ined were either not colonized or were only weakly col-
108 onized (Anderson and Menges 1997). These results were
109 somewhat surprising given the expectation that this
110 nutrient-limited ecosystem would facilitate strong depen-
111 dency on AMF and that fire would impact colonization.
112 The root structure of these species suggested that only
113 *Balduina angustifolia* would be strongly dependent on
114 AMF; however, comparisons of colonization before and
115 after burning were limited by the short-term nature of the
116 study and that *B. angustifolia* must regenerate from seed
117 following fire (Anderson and Menges 1997). Furthermore,
118 only one burned and unburned site were used in the study.
119 Consequently, we currently lack statistical power to assess
120 the effects of fire on AMF colonization in the Florida scrub.

121 Here, we take advantage of a series of controlled, repli-
122 cate burns at the Archbold Biological Station (ABS) to
123 determine the relationship between time since fire and
124 AMF colonization. We assessed total colonization of *Pala-*
125 *foxia feayi* (Asteraceae), a small, perennial shrub endemic to
126 the scrub, scrubby flatwood, and pineland ecosystems of
127 south-central Florida (Carrington 1999). This plant has
128 adapted to fire by establishing seedlings between fires and
129 resprouting postfire from the root system (Ostertag and
130 Menges 1994; Menges and Kohfeldt 1995; Carrington
131 1999), thus making it an excellent candidate to assess the
132 impact of fire on AMF colonization. We address three
133 questions: (1) Is there a relationship between time since fire
134 (time since the most recent burn) and AMF colonization
135 patterns? (2) Is there a relationship between fire return
136 interval (elapsed time between successive burns) and AMF
137 colonization patterns? (3) Is there a relationship between
138 AMF colonization and soil nutrient content?

139Q2 Materials and methods

140 Site information and sample collection

141 *P. feayi* was collected from 24 sites at the ABS, Highlands
142 County, Florida (27°10'50" N, 81°21'00" W). ABS main-
143 tains a 2,101-ha preserve located on the Lake Wales Ridge
144 in south-central Florida that is dominated by fire-adapted
145 scrub habitat with sandy, nutrient-poor soils. The station has
146 been subdivided into a series of discrete plots of varying
147 sizes; these plots are independently burned according to the
148 ABS fire management plan (Main and Menges 1997). The
149 fire return interval for each plot or the time lag between
150 successive fires is determined following Abrahamson
151 (1984) and the intervals range from 2 to 5, 6 to 9, 10 to
152 14, 15 to 19, 20 to 59, and 60 to 100 years between fires.
153 Thus, sites with a 6- to 9-year fire return interval are burned
154 every 6–9 years. The sites selected for this study spanned
155 the breadth of fire return intervals and ranged from 1 to
156 15 years postfire (Table 1). As a consequence of the fire
157 management plan at ABS, fire return interval and time since
158 fire (the number of years passing since the most recent fire)
159 vary independently. For example, a plot that was burned 1 year
160 ago could have a fire return interval of 2–5 or 60–100 years
161 depending on the prescribed burn schedule for that particular
162 plot. This independence between the two measures of fire
163 history was accounted for in our statistical analysis.

164 To standardize fire intensity, plots were selected that were
165 heavily burned, with fire consuming surface litter, dead
166 leaves, small twigs, and palmetto leaf blades (Main and
167 Menges 1997). At this intensity, the aboveground portions
168 of *P. feayi* are completely removed, although the root system
169 is typically left intact. Plants quickly regrow following fire

t1.1 **Q3** **Table 1** Site information for *P.*
t1.2 *feayi* roots

	Plot ID	No. plants sampled	Time since fire (years)	Fire return interval (years)	Plot size (m ²)
t1.3	49A	5	2	2–5	191,449
t1.4	49B	5	2	2–5	307,911
t1.5	60A	5	3	2–5	75,185
t1.6	OA	5	4	2–5	18,644
t1.7	61A	4	5	2–5	161,812
t1.8	41C	2	1	6–9	232,746
t1.9	42	1	1	6–9	181,894
t1.10	42A	2	1	6–9	15,084
t1.11	36	5	2	6–9	42,594
t1.12	39A	5	3	6–9	138,646
t1.13	41A	5	7	6–9	582,404
t1.14	42B	5	7	6–9	92,138
t1.15	46	5	8	6–9	710,268
t1.16	18D	5	10	6–9	8,188
t1.17	26A	5	7	10–19	58,613
t1.18	26B	5	7	10–19	31,376
t1.19	45C	5	8	10–19	329,868
t1.20	30A(4)	5	4	20–59	145,370
t1.21	45A	5	8	20–59	198,384
t1.22	17E	5	10	20–59	38,290
t1.23	30A	5	15	20–59	26,953
t1.24	13A	5	10	60–100	86,731
t1.25	19	5	10	60–100	47,673
t1.26	20	5	10	60–100	51,322

170 and often reproduce within 1 year (Ostertag and Menges
171 1994). Due to a paucity of recently burned plots with fire
172 return intervals of 10–14 and 15–19 years, we combined
173 these two categories in our analyses. One plot in the 6- to 9-
174 year fire return interval (plot 18D) was not burned on
175 schedule due to poor burning conditions.

176 To test whether time since fire and fire return interval
177 affect AMF colonization in *P. feayi*, roots were collected
178 from approximately 5 plants per plot, sampling across 24
179 plots differing in fire history. Because the treatment (fire)
180 was applied at the plot level, plots represent the experimen-
181 tal unit in this study; thus, replication was achieved by
182 sampling from 24 plots (Table 1). Multiple plants were
183 collected per plot to obtain a plot mean. To standardize plant
184 collections, a line transect was established in each plot. On
185 each transect, roots were harvested from plants separated by
186 at least 10 m. Prior to root collection, the maximum height
187 and number of lateral branches were determined on each
188 individual to assess plant size. These measures were includ-
189 ed in subsequent statistical analyses to account for potential
190 effects of plant size on AMF colonization (see below).
191 Following measurement, each plant was partially uprooted,
192 approximately 30 cm of root length was sampled, and each
193 plant was carefully buried again. This sampling scheme was

used to minimize impact to the *P. feayi* population at ABS. 194
Once the roots were harvested, they were placed into plastic 195
bags and were immediately returned to the laboratory. Roots 196
were thoroughly rinsed with tap water and stored in 70 % 197
ethanol at 4 °C until analysis (Brundrett et al. 1996). All 198
collections were made during late May to mid-June 2009. 199

Analysis of AMF colonization patterns 200

Roots were cut into approximately 1 cm pieces and cleared 201
in 10 % potassium hydroxide by soaking them for 20 min at 202
121 °C in an autoclave. Once cleared, the roots were stained 203
by autoclaving at 121 °C for 15 min in a 0.03 % w/v 204
Chlorazol Black E solution (Brundrett et al. 1996). After 205
clearing and staining, segments were stored in 50 % glycerol 206
at 4 °C. Thirty-centimeter segments were haphazardly sel- 207
ected from each plant and mounted in 50 % glycerol, and 208
each segment was viewed at ×40 magnification using a light 209
microscope. Following McGonigle et al. (1990), we used 210
the cross-section intersection method to assess percent root 211
colonization. Each plant was viewed 150 times (30 seg- 212
ments viewed 5 times each), with the exception of 1 plant 213
that had insufficient root material (viewed 105 times on 214
segments). For each view, the presence of AMF intraradical 215

216 hyphae, coils, vesicles, and arbuscules were scored separately.
 217 In total, 16,305 views were examined across 109 plants in 24
 218 plots.

219 **Soil analysis**

220 To ensure that soil nutrient content (carbon, nitrogen, and
 221 phosphorus) did not differ significantly across plots, one soil
 222 sample was collected per plot. Samples were taken from the
 223 rhizosphere at approximately the root depth of *P. feayi* and
 224 were located near the center of the transect line used to
 225 collect root material. Samples were dried at 50 °C before
 226 transport to Syracuse, NY for analysis. Total carbon and
 227 nitrogen in each soil sample was determined by Dumas
 228 combustion in a CE Elantec Flash EA 1112 CN analyzer.
 229 Total carbon was measured to determine if there were any
 230 differences in organic matter and soil quality among plots
 231 differing in fire history. The methods of Bickelhaupt and
 232 White (1982) and Lajtha et al. (1999) were used to determine
 233 the concentration of inorganic (plant available) phosphorus in
 234 each sample.

235 **Statistical analysis**

236 Because the application of the treatment (fire) was con-
 237 ducted at the plot level, the experimental units were the
 238 plots ($N=24$ plots); thus, mean percent colonization per plot
 239 was used as the response variable for the analyses. Percent-
 240 age data were arcsine square root transformed prior to
 241 analysis. A general linear model (GLM) was used to assess
 242 the relationship between the total percent root length colo-
 243 nized by AMF and fire history. The model included time
 244 since fire, fire return interval, and measures of plant size
 245 (height and lateral branching) as factors. An additional
 246 analysis with time since fire, fire return interval, and plot
 247 size was also conducted to ensure that plot size had no
 248 influence on colonization. Similar GLMs were used to de-
 249 termine whether the percentage of root length with arbus-
 250 cles, coils, vesicles, and intraradical hyphae were affected
 251 by fire history. These models also included time since fire,
 252 fire return interval, and plant size as factors. To determine
 253 whether the concentration of carbon, nitrogen, and phospho-
 254 rus varied among plots differing in fire history, we used a
 255 GLM that included time since fire and fire return interval.
 256 Finally, linear regression was used to determine the relation-
 257 ship between soil nutrients and AMF colonization and between
 258 plant size and time since fire.

259 **Results**

260 *Palafoxia feayi* roots were consistently colonized by AMF,
 261 with more than 98 % of plants colonized. Total colonization

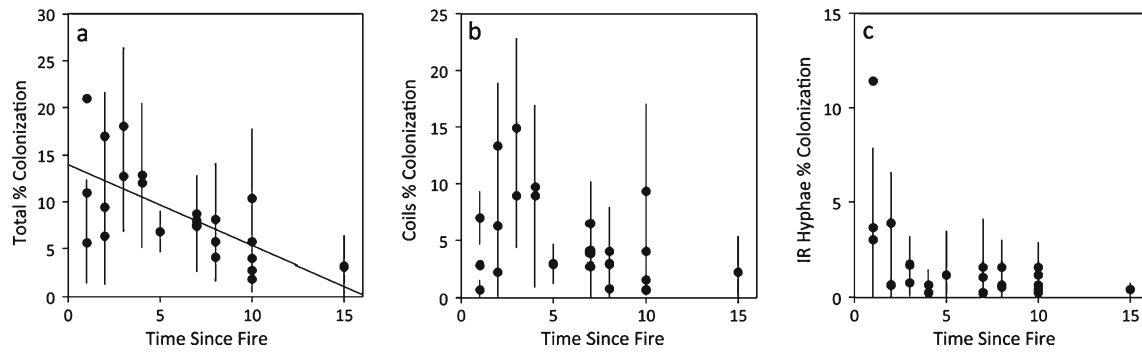
within plants ranged from 0.7 to 29.3 %. Percent root length
 containing arbuscules was 0 to 8 %, coils was 0 to 23 %,
 vesicles was 0 to 11 %, and intraradical hyphae was 0 to
 11 %. The GLM assessing the relationship between total
 colonization, fire history, and measures of plant size was
 significant ($F_{7,16}=2.77$; $P=0.04$); however, only the time
 since fire factor had a significant effect ($F_{1,16}=10.98$; $P=$
 0.004). Fire return interval, plant height, and lateral branch-
 ing were nonsignificant ($P>0.6$ for all factors). There was a
 negative relationship between time since fire and total col-
 onization (Fig. 1), and there was no relationship between
 time since fire and plant height ($F_{1,22}=2.22$; $P=0.16$). Sim-
 ilarly, the GLM assessing the relationship between total
 colonization, fire history, and plot size was significant
 ($F_{6,17}=3.16$; $P=0.03$) with time since fire having the only
 significant effect ($F_{1,17}=10.49$; $P=0.005$). Plot size had no
 effect on colonization levels ($F_{1,17}=0.10$; $P=0.75$).

Fire history also had significant effects on the presence of
 specific AMF structures. The GLMs examining the role of
 fire history on the percent root length containing intraradical
 hyphae ($F_{7,16}=3.50$; $P=0.02$) and coils ($F_{7,16}=2.68$; $P=$
 0.05) were significant. In both instances, time since fire
 and plant height were the only significant effects (all $P\leq$
 0.05). The presence of coils and intraradical hyphae de-
 clined with increasing time since fire (Fig. 1), and the roots
 of taller plants contained fewer of these structures. Neither
 of the GLMs examining the relationship between fire history
 and percent root length containing vesicles or arbuscules
 were significant (vesicles: $F_{7,16}=1.56$, $P=0.22$; arbuscules:
 $F_{7,16}=1.52$, $P=0.23$).

Soil nutrient levels were similar across sites. Nitrogen
 content ranged from 0 to 0.06 %, carbon content had a range
 of 0.17 to 1.23 %, and phosphorus content ranged from 3.37 to
 9.31 $\mu\text{g/g}$. The GLMs testing for differences in soil chemistry
 associated with fire history were not significant (nitrogen:
 $F_{5,18}=0.81$, $P=0.56$; phosphorus: $F_{5,18}=0.82$, $P=0.55$; car-
 bon: $F_{5,18}=0.65$, $P=0.66$). There was also no relationship
 between soil nutrient content and total AMF colonization
 (nitrogen: $R^2=0.001$, $P=0.88$; phosphorus: $R^2=0.003$, $P=$
 0.80 ; carbon: $R^2=0.001$, $P=0.86$).

Discussion

The results indicated a strong decrease in total AMF colo-
 nization with time since fire that cannot be explained by
 changes in nutrient availability across sites. Total coloniza-
 tion was greatest 1 year postfire, gradually declining as time
 since fire increased, and as expected, we observed no differ-
 ences in soil nutrients across plots. The decrease in total
 percent colonization also cannot be explained by changes in
 plant size as we found no relationship between plant height
 and fire regime. *P. feayi* quickly resprouts following



Q4 Fig. 1 Relationship between mycorrhizal colonization of *P. feayi* roots and time since fire (years). Each circle represents the mean value for a plot (\pm SD). **a** Total colonization ($R^2_{23}=0.50$; $P<0.0001$), **b**

colonization by coils ($R^2_{23}=0.19$; $P=0.03$), **c** colonization by intraradical hyphae ($R^2_{23}=0.29$; $P<0.01$)

312 fire-preventing stratification of plant height across plots
 313 differing in burn history. The decline in total colonization
 314 was also mirrored by a decline in specific AMF structures.
 315 The results showed a negative relationship between fire and
 316 colonization by coils and intraradical hyphae. Interestingly,
 317 not all AMF structures changed with time since fire (e.g.,
 318 arbuscules and vesicles), although the reason for this is
 319 unclear.

320 In contrast, there was no effect of fire return interval, the
 321 time lapse between subsequent fires. Given that scrub
 322 undergoes no successional change following fire, this result
 323 was expected. Scrub fires can completely eliminate above-
 324 ground vegetation, as was the case in our experimental
 325 plots, but most of the vegetation resprouts from protected
 326 root systems. As a consequence, the regrowth of scrub
 327 vegetation following a fire returns the system to the prefire
 328 community (Abrahamson 1984; Schmalzer and Hinkle
 329 1987); thus, the length of time between successive fires is
 330 unlikely to affect colonization patterns.

331 One possible explanation for the observed relationship
 332 between time since fire and patterns of colonization is that
 333 fire temporarily removes dominant vegetation and increases
 334 light availability for *P. feayi*. The sites selected for this study
 335 were heavily burned with aboveground vegetation com-
 336 pletely removed; thus, light availability will be greatest
 337 immediately postfire and will decline as the vegetation
 338 resprouts. Indeed, at our field sites, canopy cover is posi-
 339 tively correlated with time since fire, and plots with in-
 340 creased canopy cover have lower light availability
 341 (Abrahamson 1999). Shading has been shown to decrease
 342 AMF colonization as plants allocate more resources to
 343 aboveground parts and have fewer resources to support
 344 AMF (e.g., Whitbeck 2001; Gehring 2003). Canopy cover
 345 strongly influenced flowering in the scrub plants *S. repens*
 346 and *Sabal etonia*, suggesting that light availability is an
 347 important factor limiting growth and reproduction in this
 348 ecosystem (Abrahamson 1999). Furthermore, there is also
 349 evidence that growth patterns of *P. feayi* change in response

to fire; *P. feayi* exhibits peak reproduction during the first 350
 year following fire and sharply declines 1 year postfire 351
 (Ostertag and Menges 1994). This growth response may 352
 be caused by the ephemeral nutrient pulse associated with 353
 scrub fires (e.g., Schafer and Mack 2010) and/or by changes 354
 in light availability. The combination of maximal light 355
 availability and a nutrient pulse may explain the increased 356
 AMF colonization patterns immediately following fire, and 357
 thus, we might expect to observe a gradual decline in 358
 colonization over time if plant carbon production is reduced 359
 by shading. 360

Even so, the hypothetical scenario described assumes that 361
 root colonization level reflects the mutualistic functioning of 362
 the interaction. Unfortunately, the relationship between colo- 363
 nization and mycorrhizal function is complex (e.g., Johnson 364
 2010), thus our conclusions are somewhat limited. The colo- 365
 nization levels observed in *P. feayi* are relatively low, suggest- 366
 ing that the modest changes in colonization following fire may 367
 have little functional consequence for the plant. The present 368
 study is also limited in the sense that we have examined only 369
 one measure of the interaction: root colonization. Assessing 370
 extraradical hyphal abundance or AMF species composition 371
 across the fire timeline may help to explain the observed 372
 patterns in colonization. The finding of decreased colonization 373
 associated with time since fire was surprising given the results 374
 from a previous study conducted at the same sites. Anderson 375
 and Menges (1997) showed no change in colonization asso- 376
 ciated with fire in three scrub herbs (a fourth species was 377
 examined, but plants did not survive the fire). Contradictory 378
 results among studies of AMF colonization have been attrib- 379
 uted to a number of factors including differences in plant 380
 community composition, plant adaptation to fire, and soil 381
 nutrient conditions (Cairney and Bastias 2007). However, 382
 since both studies were conducted at the same field sites on 383
 plants that resprout following fire, none of these factors can 384
 explain the strikingly different pattern observed in *P. feayi*. 385
 Two obvious differences between these studies are plant 386
 growth form and AMF colonization levels. *P. feayi* is a small 387

388 woody shrub in contrast to the herbs examined by Anderson
 389 and Menges (1997). *P. feayi* also had higher levels of coloni-
 390 zation as more than 98 % of plants examined were colonized,
 391 and total colonization ranged upwards of 29 %. Very low
 392 (~2 %) colonization was observed in both *Liatris tenuifolia*
 393 and *Pityopsis graminifolia*, and *Aristida stricta* lacked AMF
 394 completely (Anderson and Menges 1997). Consequently, dif-
 395 ferences between the studies may be attributed to differences in
 396 growth form and colonization level.

397 In addition to the dissimilarities among the study plants
 398 themselves, there also exist several differences in experi-
 399 mental design. Anderson and Menges (1997) compared
 400 colonization of plants in two plots: one site that was burned
 401 about 8 months prior to the final sampling date and one
 402 “unburned” site (burned previously but not as recently as the
 403 burned site). In contrast, the present study used 24 plots
 404 ranging from 1 to 15 years postburn. Since the timing of the
 405 last fire for the unburned site is unknown, comparing these
 406 two studies is challenging. If Anderson and Menges’ (1997)
 407 burned and unburned sites were more similar in burn age
 408 (e.g., the unburned site was burned about 5 years previous-
 409 ly), detecting differences in colonization may have been
 410 difficult. By comparing multiple plots differing in fire history,
 411 the present study has greater statistical power.

412 Overall, the present study shows a negative relationship
 413 between percent colonization and time since fire in this
 414 pyrogenic ecosystem. We hypothesize that this pattern may
 415 be a result of increased shading as vegetation resprouts after
 416 a burn. Controlled experiments to assess this possibility will
 417 be useful in making progress towards determining the factors
 418 most important in shaping colonization patterns.

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