

1 **Seed bank changes with time-since-fire in Florida rosemary scrub**

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7 **ABSTRACT**

8 The soil seed bank plays a central role in the regeneration of obligate seeding species in fire
9 prone habitats. We evaluated how seed density and species composition changed with time-
10 since-fire in Florida rosemary scrub. Because fire affects habitat availability and plant
11 demographic variation, we predicted that soil seed density would be low in recently burned and
12 long-unburned stands and high at intermediate time-since-fire. Seed bank soil samples were
13 collected from a chronosequence of time-since-fire composited from two trials conducted in
14 1992-1993 and 2008-2009: two sites each of three, six, ten, and 24 years post-fire and three long-
15 unburned (>24 years). The seedling emergence method was used to determine species
16 composition of the seed bank. Across all time-since-fire age classes scrub herbs dominated the
17 seed bank, while long-lived subshrubs and shrubs were present in low densities. Seed banks
18 from sites three years post-fire were distinct from the other sites. Seed densities were associated
19 with time-since-fire for subshrubs and ruderal herbs, while densities of scrub herbs and
20 graminoids were independent of time-since-fire. Seed densities of *Ceratiola ericoides* Michx.
21 (only obligate seeding shrub in this community) were associated with time-since-fire and showed
22 highest densities at recently burned and long-unburned sites. The seed banks of two scrub herb

23 species, *Paronychia chartacea* Fernald and *Lechea cernua* Small, were associated with time-
24 since-fire, reaching peaks in density at six and ten years post-fire. Overall seed densities of scrub
25 herbs were highest in the first ten years post-fire, corresponding with changes in aboveground
26 abundances of these species with time-since-fire. This result indicated a close link between
27 above- and belowground scrub herb abundances. Soil seed densities of several species and
28 functional groups were associated with time-since-fire, but timing of peak seed density varied
29 depending on species' life span and age of reproductive maturity.

30 *Keywords:* chronosequence; disturbance; fire-prone; Florida scrub; Lake Wales Ridge; obligate
31 seeder; seed bank; seed density; shrubland; time-since-fire.

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34 **INTRODUCTION**

35 Disturbances play a central role in shaping species life history strategies (Pickett and White
36 1985). Life history characteristics such as dispersal mechanisms, ability to establish and grow,
37 and time necessary to reach critical life stages determine if a species will persist in a community
38 during and after disturbance (Noble and Slatyer 1980). Species within the same ecosystem often
39 evolve a variety of adaptive strategies to cope with frequent disturbance (Christensen 1985).

40 Fire is one of the most ubiquitous disturbances worldwide. It influences global vegetation
41 pattern and shapes species characteristics (Bond *et al.* 2005). In fire-prone communities like
42 African fynbos, Australian heaths, and California chaparral, species rely upon persistent soil seed
43 banks to regenerate after fire (Keeley 1991, Auld *et al.* 2000, Holmes and Newton 2004).
44 Recruitment from the soil seed bank is essential for obligate seeding species of which

45 aboveground individuals are killed by fire. Fire has been found to stimulate mass recruitment
46 events and seedling densities are generally highest in recently burned stands (Tyler 1995,
47 Carrington and Keeley 1999, Weekley and Menges 2003). High recruitment post-fire is
48 promoted by direct cues such as smoke, heat, or chemical leaching which break seed dormancy
49 or from indirect effects such as increased light, microhabitat availability, and release from
50 competition or allelopathic chemicals (Christensen 1985, Keeley 1991, Pierce and Cowling
51 1991, Tyler 1996, Keeley and Fotheringham 1998). Changes in aboveground species
52 abundances and composition as time-since-fire increases may affect seed bank characteristics in
53 pyrogenic communities. Available information indicates seed bank size can be low immediately
54 following fire when seedling recruitment is high and seed inputs are low (due to mortality of
55 reproductive plants), peak in size at intermediate years since fire, and decline in size in long-
56 unburned stands as aboveground populations senesce and seeds lose viability (Vaughton 1998,
57 Clemente *et al.* 2007).

58 Fire is the most important disturbance in Florida rosemary scrub and likely plays a central
59 role in determining the dynamics of the seed bank for many species, particularly those endemic
60 to this community. Florida rosemary scrub is a xeric upland sclerophyllous shrubland found on
61 relic sand dunes harboring a high diversity of endemic plant and animals (Abrahamson *et al.*
62 1984, Christman and Judd 1990). Understanding how species regenerate and respond to fire is
63 essential for proper management of plant populations (Menges 2007) since fire intervals that are
64 either too frequent or infrequent can lead to local population extinctions (Zedler *et al.* 1983).
65 Species characteristics such as life span, fire sensitivity, dispersal mechanism, and timing of
66 reproductive maturity strongly influence how species cope with fire (Keeley 1991, Ooi *et al.*
67 2006). One key requirement for maintaining healthy populations in fire-prone habitats is

68 implementation of appropriate fire return intervals. The interval for obligate seeders must be
69 long enough to insure that adult plants reach a reproductive life stage to replenish the seed bank;
70 however, it should not be so long that adult life span and/or the viability of the seed bank have
71 been surpassed (Zammit and Zedler 1988). In Florida scrub, population viability analyses have
72 been used to suggest fire regimes for different types of scrub vegetation (reviewed in Menges
73 2007), but no analyses of seed banks with varying time-since-fire have informed land managers.

74 In this study we evaluate seed bank changes with time-since-fire in Florida scrub using data
75 from a chronosequence composited from two trials conducted in 1992-1993 (trial I) and 2008-
76 2009 (trial II). We address the following questions: (1) Is there an association between time-
77 since-fire and soil seed density? (2) If so, how does this association vary among different
78 functional groups? (3) Which rosemary scrub species form persistent soil seed banks?

79 **METHODS**

80 *Study Site*

81 Research was conducted at Archbold Biological Station (Archbold) located near the southern
82 end of the Lake Wales Ridge in Highlands County, Florida (Township 38S, Range 30E, Sections
83 5-8,18,19,29-32). The station experiences mean temperatures that range from 8.33° C in winter
84 to 34.05° C in summer and has an average annual rainfall of 1364 mm (Archbold weather data,
85 1932-2009). The Lake Wales Ridge is characterized by a mixture of wetlands, mesic flatwoods,
86 and more xeric upland communities found on relic sand dunes in central Florida. Rosemary
87 scrub is found at locally high elevations with well drained, low nutrient Archbold or St. Lucie
88 soils (Menges 1999). This habitat is dominated by Florida rosemary (*Ceratiola ericoides*
89 Michx.), an allelopathic shrub, but also includes patches of shrub species such as palmettos
90 (*Serenoa repens* (W. Bartram) Small, *Sabal etonia* Swingle ex Nash), and clonal oaks (*Quercus*

91 *chapmanii* Sarg., *Q. inopina* Ashe, *Q. geminate* Small) (Hunter and Menges 2002). Shrub
92 patches are separated by bare sand gaps where many herbaceous endemic species grow (Menges
93 *et al.* 2008). After fire most shrub species resprout from rhizomes or roots (Menges and
94 Kohfeldt 1995); obligate seeders such as the dominant shrub *C. ericoides* and several herbaceous
95 species recruit from the seed bank or from nearby unburned areas (Quintana-Ascencio and
96 Menges 2000).

97 *Seed Bank Sampling*

98 During trial I (1992-1993), we sampled eight rosemary scrub sites that consisted of two sites
99 in each of four age classes of time-since-fire: three, six, 24 years, and long-unburned (>24 years).
100 From each site, we collected 20 soil cores in a stratified random fashion along a 6 m transect
101 through the longest axis of each rosemary scrub site. Soil cores were collected in tins 10 cm in
102 diameter x 6 cm in depth (surface area per site = 0.079 m²). We collected six samples over a
103 one and a half year period in January, April, July, and October of 1992, and January and April of
104 1993. Over this period we collected a total of 120 soil cores per site.

105 During trial II (2008-2009), we established three 16 x 16 m macroplots in three separate
106 sites: two at ten years post-fire and one long-unburned (>24 years). Ten 2 x 2 m subplots were
107 randomly placed within each macroplot. Each subplot was subdivided into 40 x 40 cm quadrats
108 and samples were collected in a checkerboard pattern from every other quadrat (yielding thirteen
109 quadrats per subplot). In August 2008 and January 2009, we collected five 1.92 cm diameter by
110 3 cm deep soil cores from each quadrat and the cores were aggregated yielding 130 soil samples
111 per macroplot (surface area per plot = 0.188 m²). During both sampling periods, we collected
112 soil cores from the quadrats in a regular coring pattern and this pattern was alternated between
113 the two seasons to avoid coring the exact same locations.

114 We analyzed the two trials together to evaluate the effect of time-since-fire. Both trials
115 included samples representing the gradient of time-since-fire (Trial I = three, six, 24 and >24
116 years, Trial II = ten years and >24 years). In spite of the differences in soil depth employed
117 during the two trials (trial I = 6 cm, trial II = 3 cm) the volume of soil per sample unit was
118 approximately equivalent (trial I = 235.62 cm³, trial II = 217.15 cm³). Species composition has
119 been found to be consistent within this range of soil depth (J.J. Navarra, University of Central
120 Florida, unpublished data).

121 *Greenhouse Monitoring*

122 We used the seedling emergence method to determine species composition of the seed bank.
123 During trial I, we thoroughly mixed each soil core and half of the volume of soil was distributed
124 among four separate germination trays. In trial II, we sieved each soil sample to break up soil
125 structure and large litter and then potted the soil and litter on top of a white sand substrate. We
126 collected the substrate from fire lanes located within Archbold Biological Station and heated it to
127 85° C (minimum of 8 hours) to kill any seeds that may have been present in the soil. We
128 randomized placement of the samples within the greenhouses and the seedling flat locations were
129 regularly changed to minimize micro-environmental effects.

130 For both trials, we maintained samples in unheated greenhouses and watered them regularly
131 to keep the soil moist. Sterile soil controls were placed among the samples to detect
132 contamination from outside seed sources and, for trial II, to also ensure all seeds were killed
133 during soil heating. For trial I, we considered all seedlings in the analysis since a relatively small
134 portion of the emerging seedlings came from the controls (~1% of the total number of seedlings
135 emerged from the controls). For the second trial, we omitted species/seedlings from the analysis
136 that appeared to result from contamination based on the pattern of occurrence in the samples and

137 controls (~5% of the total number of seedlings emerged from the controls). For both trials, we
138 monitored the soil samples for germination at monthly intervals. Seedlings were removed once
139 they had been identified to the species level; however, some seedlings died before identification
140 was possible. Nomenclature follows the Atlas of Florida Vascular Plants online database
141 (<http://www.florida.plantatlas.usf.edu>).

142 For trial I, we carried out seedling monitoring from the time of soil collection until July 1994
143 (minimum time = 18 months, maximum time = 30 months). For trial II, we monitored the soil
144 samples for 8-12 months. Although the soil samples were monitored for different lengths of
145 time, this variation was unlikely to bias the results of the study since the majority of seedlings
146 emerged during the first two months after collection. For all sampling periods, germination rates
147 reached an asymptote before germination monitoring was discontinued.

148 *Assessing Long-Term Persistence*

149 We determined which species form persistent seed banks using all of the data collected in
150 trial I. Those species that continued to germinate into the second year of greenhouse monitoring
151 and that were present in the seed bank during all six months of soil collection were considered to
152 form persistent seed banks. This dual approach to assessing the persistent seed bank ensured that
153 these species' seeds remained viable for at least one year and that their seeds remained in the
154 seed bank year round (Thompson and Grime 1979, Ortega *et al.* 1997, Arroyo *et al.* 1999). This
155 approach to assessing seed persistence is conservative and those species that do not meet both
156 criteria may still form persistent seed banks.

157 *Data Analysis*

158 We used regression to assess the association of time-since-fire with soil seed bank density
159 (number of seeds/total surface area per m⁻²) and species richness organizing the data by species
160 and functional groups. For these time-since-fire analyses, we only used seed bank data collected
161 from summer and winter seasons to combine comparable datasets from the two trials (trial I =
162 January and July 1992; trial II = August 2008 and January 2009). We divided the species into
163 functional groups based upon growth habit and, for herbaceous species, habitat preference. We
164 identified the following functional groups: (1) scrub herbaceous species; (2) scrub subshrubs; (3)
165 scrub shrubs; (4) graminoids (sedges, rushes, and grasses), and (5) ruderal herbs (species typical
166 of disturbed habitats, generally not found growing aboveground in Florida scrub). We only
167 analyzed species and functional groups that were present across at least 50% of the sites to
168 ensure occurrence was high enough along the time-since-fire chronosequence to reveal patterns.
169 Seed density was averaged across seasons.

170 We used a model selection approach for small samples (Akaike's information criterion; AIC_c)
171 to compare linear, quadratic and cubic models assuming negative binomial error distribution for
172 seed counts (Venable and Brown 1988, Crawley 2007). We calculated Akaike weights for each
173 model (Burnham and Anderson 2002) and analyses were conducted in R 2.9.1 (R Development
174 Core Team 2009).

175 We evaluated whether time-since-fire had an association with seed composition and density
176 at the community level using Non-metric Multidimensional Scaling (NMS) ordination based on
177 Sorensen distances (Kruskal 1964, Mather 1976). Species that occurred across less than 20% of
178 the sites and seasons were omitted from the NMS ordination to reduce noise in the data set
179 (McCune and Grace 2002). The data were analyzed using PC-ORD 5.0 (MjM Software Design,

180 Sweet Home, Oregon, USA). We started with a random configuration and 200 runs with real
181 data. Dimensionality of the data was assessed using autopilot and the stability of the solution
182 was evaluated using a NMS scree plot. We evaluated whether a similar final stress could be
183 obtained by chance with Monte Carlo tests. We compared species richness between summer and
184 winter seasons using a non-parametric Kruskal-Wallis one-way analysis of variance (Sokal and
185 Rohlf 1995).

186 **RESULTS**

187 *Species Composition*

188 We found 3,963 seedlings (trial I = 2,647; trial II = 1,316) belonging to 45 species in the seed
189 banks of the two trials (summer and winter seasons only) (

190). Approximately 15% of the emerging seedlings could not be identified. In both trials, the seed
191 banks were dominated by annual and short-lived perennial herbaceous species (Figure 1). The
192 two most abundant species in the seed bank were *Paronychia chartacea* Fernald and *Stipulicida*
193 *setacea* Michx., which comprised approximately 43% (trial I = 34%, trial II = 62%) of the
194 emerging seedlings (

195). Among long-lived species, the total seed count and number of species was significantly lower
196 when compared to short-lived herbs. A club moss, *Selaginella arenicola* Underw., comprised
197 approximately 50% of the propagules emerging from the samples collected in trial I (trial II = 1
198 %); however, this species was not considered in the regression or NMS ordination analyses since
199 it is a sporophyte. This species was observed to recruit from broken fragments and spores.

200 *Species Richness*

201 Species richness ranged between seven and 37 species and had a mean of 14 across all sites
202 and seasons. We did not find evidence of association between species richness and time-since-
203 fire; however, mean species richness was slightly higher in the three year (25 in summer, 16 in
204 winter) and long-unburned stands (15 in summer, 17 in winter). This slight increase was
205 primarily due to a greater number of ruderal species being present in these two time-since-fire
206 age classes. Species richness was higher in winter than in summer ($df = 1$, $p = 0.026$).

207 *Community Level Association with Time-since-fire*

208 NMS ordination of seed density for species occurring across ≥ 20 % of the seasons and sites
209 indicated that time-since-fire does explain some differences among the sites. While both axes
210 were significant (final stress = 11.55, # iterations = 43; axis 1 - $p = 0.032$, $R^2 = 0.562$; axis 2 - p
211 = 0.008, $R^2 = 0.317$), a NMS scree plot showed slight overlap between the stress for real and
212 randomized data indicating a weaker pattern for axis 1. The NMS ordination plot showed clear
213 separation of sites three years time-since-fire from all other sites, particularly for the winter
214 samples. The other time-since-fire age classes exhibited considerable overlap (Figure 2). Long-
215 unburned sites showed the greatest variation in species composition.

216 *Species and Functional Group Associations with Time-since-fire*

217 Thirteen species and four functional groups (graminoids, ruderal herbs, scrub herbs, and
218 subshrubs) had enough occurrences to be considered in the time-since-fire analysis. We
219 identified different associations between time-since-fire and seed densities for several species
220 and functional groups. A quadratic model was the best model for ruderal herbs and subshrubs.
221 Their seed densities were highest three years post-fire and declined in the later time-since-fire
222 age classes (Figure 3a and b). For scrub herbs, highest seed densities were generally observed at
223 three to ten years post-fire (Figure 3c); however, we do not have statistical evidence to discard
224 the null model. A cubic model of time-since-fire was found to be best for *C. ericoides*, *Lechea*
225 *cernua* Small, *P. chartacea*, and *Phyllanthus tenellus* Roxb. *C. ericoides* showed highest seed
226 density at recent and long-unburned time-since-fire (Figure 4a). Two scrub endemics, *L. cernua*
227 and *P. chartacea*, showed low densities in recently burned and long-unburned sites and high
228 densities at short to intermediate (six, ten year) times-since-fire (Figure 4b and c). *P. tenellus*
229 showed highest density in long-unburned sites (Figure 4d).

230 *Seed Persistence*

231 Given our conservative criteria five scrub herbs (*Eryngium cuneifolium* Small, *Hypericum*
232 *cumulicola* (Small) W.P.Adams, *L. cernua*, *P. chartacea*, and *S. setacea*), one subshrub (*Lechea*
233 *deckertii*), one shrub (*C. ericoides*), two graminoids (*Cyperus spp.*, Poaceae), and five ruderal
234 herbs (*Euthamia caroliniana* (L.) Greene ex Porter & Britton, *Eupatorium spp.*, *Gamochaeta*
235 *purpurea* (L.) Cabrera, *Linaria floridana* Chapm., and *Oxalis corniculata* L.) formed persistent
236 soil seed banks. Several species had germinants emerging into the third year, suggesting the
237 possibility of a long-term persistent seed bank (*C. ericoides*, *E. caroliniana*, *Eupatorium spp.*, *H.*

238 *cumulicola*, *L. floridana*, *P. feayi*, *P. chartacea*, and *S. setacea*). *S. arenicola*, a club moss, was
239 also found across all seasons of sampling and had propagules after the second year.

240 **DISCUSSION**

241 Our results indicate that disturbances can influence seed bank dynamics. In Florida rosemary
242 scrub, time-since-fire affects seed density for some species and functional groups. In fire-prone
243 communities with a significant association between seed density and time-since-fire, there is a
244 gradual increase in seed bank size in recently burned stands followed by a decline in long-
245 unburned sites (Vaughton 1998, Clemente *et al.* 2007). In this study we found that association of
246 seed density with time-since-fire varied depending on life history and timing of reproductive
247 maturity. Long-lived species such as shrubs generally showed peaks in density at recent and
248 long-unburned time-since-fire, while short-lived scrub species reached density peaks at early to
249 intermediate times-since fire. For *C. ericoides* (only obligate seeding shrubs in this community)
250 the pattern of high seed densities at recently burned and long-unburned sites and low seed
251 densities or absence at six and ten years post-fire is not surprising since this species takes ten
252 years to reach reproductive maturity (Johnson 1982). The pattern observed for scrub herbs such
253 as *P. chartacea* and *L. cernua* corresponds with changes in abundances of these two species
254 aboveground (Menges and Kohfeldt 1995) and suggests seed densities and vegetation
255 abundances are closely linked. These results agree well with what is already known about the
256 demography of some scrub endemic herbs. For example, in *E. cuneifolium*, seedling recruitment
257 after fire is much higher than at other times. The plants reach maturity very quickly post-fire
258 (Menges and Quintana-Ascencio 2004) and probably replenish the seed bank rapidly. The
259 population declines with time-since-fire and the seed bank likely decays fairly quickly (Menges
260 and Kimmich 1996, Menges and Quintana-Ascencio 2004).

261 The majority of herbaceous species in rosemary scrub are “gap specialists” and are most
262 abundant, have the greatest survival, and highest seed production in the years immediately
263 following fire (Hawkes and Menges 1996, Menges and Kimmich 1996, Menges 1999). As time-
264 since-fire increases, gaps close while shrub, litter and lichen covers increase and herbaceous
265 species are outcompeted (Menges and Hawkes 1998). Gap sizes are smallest in long-unburned
266 areas and largest between six and ten years post-fire; herb cover increases with gap area (Menges
267 *et al.* 2008). Menges *et al.* (2008) found sites greater than ten years post-fire have a wide amount
268 of variation in gap area. Site-to-site variation in microhabitat cover may help to explain variation
269 in seed density among different time-since-fire age classes (Navarra *et al. unpublished*
270 *manuscript*). Environmental variables such as elevation may explain why some sites retain
271 greater amounts of open space than others (Hawkes and Menges 1996) and thus sustain higher
272 cover of herbs leading to larger yearly inputs into the seed bank. Increased variability of gap
273 area as time-since-fire increases and dominance of the seed banks by scrub herbs may explain
274 why at the community level only recently burned sites showed distinctive pattern of seed density,
275 while sites ranging from six years post-fire to long-unburned exhibited considerable overlap and
276 more variation.

277 The high seed density of ruderal herbs at recent and long-unburned sites remains
278 unexplained, as these species are not found aboveground in rosemary scrub. This pattern may be
279 a result of location rather than response to time-since-fire. Archbold Biological Station is
280 surrounded by a variety of human modified habitats (primarily orange groves and pastures).
281 Since sites belonging to the same time-since-fire age class were generally in close proximity to
282 each other, these sites may have also experienced similar rates of dispersal of weedy species
283 from surrounding areas.

284 *Seed Persistence*

285 Seed persistence was generally well predicted by fire adaptive strategy (obligate seeders,
286 seeders and resprouters) and seed morphology (seed size). Many of the species, particularly
287 endemic herbs, have small seed size which is a characteristic known to promote formation of
288 persistent seed banks (Thompson *et al.* 1993, Funes *et al.* 1999, Moles *et al.* 2000, Thompson *et*
289 *al.* 2001, Stromberg *et al.* 2008). Of the seven scrub herbs found in the seed bank, five were
290 present year round and germinated into the second year. While formation of a persistent seed
291 bank is a common mechanism species used to cope with frequent disturbance, not all obligate
292 seeding herbs were found in the seed bank. For example, *Polygonella basiramia* (Small
293 G.L.Nesom and V.M.Bates can form only a limited persistent seed bank (Maliakal-Witt *et al.*
294 2005) and relies on dispersal from unburned areas to re-colonize post-fire (Menges 1999,
295 Quintana-Ascencio and Menges 2000).

296 The seed banks were largely dominated by short-lived herbaceous species, while long-lived
297 species were present in far fewer numbers of species and much lower densities. Absence of
298 long-lived species in the seed bank is not uncommon because adult-longevity has been found to
299 be negatively correlated with seed persistence (Rees *et al.* 1996, Clemente *et al.* 2007). The
300 majority of long-lived species in Florida scrub habitats resprout after fire and are less dependent
301 on sexual reproduction (Menges and Kohfeldt 1995). These results contrast with other fire-prone
302 communities such as California chaparral and Australian heaths which report higher species
303 richness and seed densities of resprouting and obligate seeding shrubs (Zammit and Zedler 1994,
304 Wills and Read 2007). In contrast, a study conducted in the fire-prone Mediterranean Aleppo
305 pine forest also reported absence of long-lived species in the seed bank (Ne'eman and Izhaki
306 1999).

307 Species specific knowledge on which obligate seeding specie from transient versus persistent
308 seed banks and how seed bank densities change with time-since-fire has important implications
309 for implementing appropriate prescribed fire regimes. Due to differences in species' life
310 histories such as juvenile period, fire sensitivity and microhabitat requirements, not all species
311 will be favored by the same fire regime (Quintana-Ascencio and Menges 2000, Ooi *et al.* 2006,
312 Menges 2007). Implementation of low intensity patchy fires has been suggested as a solution
313 that allows for coexistence of species with varying fire requirements because smaller portions of
314 the aboveground populations will be killed (Ooi et al. 2006). This fire regime is fitting for
315 obligate seeding species that rely on dispersal for post-fire recruitment but do not form persistent
316 seed banks, as well as for species that have long juvenile periods before they reach reproductive
317 maturity and replenish the seed bank (e.g. *C. ericoides*).

318 *Conclusion*

319 The results of this study support previous findings that obligate seeding species respond to
320 time-since-fire. Greatest seed densities were observed in the first ten years post-fire; however,
321 significant site-to-site variation did occur even in recently burned stands. Many of the obligate
322 seeding species in Florida rosemary scrub rely on persistent soil seed banks to recover after fire.
323 Considerable variation in seed bank size in relationship to time-since-fire are likely linked to
324 differences in life history characteristics such as plant life span, dispersal mechanism, seed size,
325 germinability, and length of juvenile period (Pierce and Cowling 1991). The majority of studies
326 evaluating seed bank dynamics in fire-prone communities have reported dominance of obligate
327 seeding shrubs. In contrast, herbaceous species appear to dominate the seed bank in Florida
328 rosemary scrub. While these findings have broadened our understanding of how rosemary scrub

329 changes with time-since-fire, further research is necessary to fully understand the role of the seed
330 bank in this unique pyrogenic community.

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- 465

466 Figure 1. Percent seed density of functional groups comprising the seed bank for each time-
467 since-fire age class.

468 Figure 2. NMS ordination of species seed density. Each number indicates time-since-fire, LU =
469 long-unburned, s = summer, and w = winter.

470 Figure 3. Negative binomial regression models for functional groups showing significant
471 association between mean seed density (m^{-2}) and time-since-fire: (a) Ruderal herbs, quadratic
472 model (ratio of residual deviance/degrees of freedom = 1.4), (b) Subshrubs, quadratic model
473 (ratio = 1.7), and (c) Scrub herbs, cubic model (ratio = 1.6, not selected as the best model).
474 Analyses were conducted using centered time-since-fire values but graphed using original
475 values.

476 Figure 4. Cubic negative binomial regression models for species showing significant association
477 between mean seed density (m^{-2}) and time-since-fire: (a) *C. ericoides* (ratio of residual
478 deviance/degrees of freedom = 1.8), (b) *L. cernua* (ratio = 1.9), (c) *P. chartacea* (ratio = 1.6), and
479 (d) *P. tenellus* (ratio = 1.7). Analyses were conducted using centered time-since-fire values but
480 graphed using original values.

481 Table 1. Mean seed density (m^{-2}) rounded to the nearest integer (\pm standard error) for species in
 482 different time-since-fire age classes. LU = Long unburned.

Species	Time-Since-Fire				
	3 yrs	6 yrs	10 yrs	24 yrs	LU
Scrub Herbs					
<i>Balduina angustifolia</i>					
(Pursh) B.L.Rob.	3 (3)	-	-	-	-
<i>Eryngium cuneifolium</i>					
Small	38 (38)	3 (3)	-	16 (16)	2 (2)
<i>Helianthemum nashii</i>					
Britton	38 (38)	-	-	-	-
<i>Hypericum cumulicola</i>					
(Small) W.P.Adams	3 (3)	57 (29)	3 (2)	13 (13)	86 (29)
<i>Lechea cernua</i> Small	10 (5)	70 (41)	13 (3)	-	8 (4)
<i>Lechea spp.</i> Small	13 (9)	60 (56)	-	-	2 (2)
<i>Paronychia chartacea</i>					
Fernald	32 (11)	395 (71)	357 (134)	99 (26)	154 (38)
<i>Polanisia tenuifolia</i>					
Torr. & A.Gray	-	-	3 (3)	-	1 (1)
<i>Polygonella basiramia</i>					
(Small) G.L.Nesom & V.M.Bates	-	-	3 (2)	-	-

<i>Stipulicida setacea</i>					
Michx.	735 (639)	573 (135)	610 (69)	226 (56)	435 (170)
All scrub herbs	872 (611)	1159 (166)	988 (115)	353 (65)	688 (161)
Subshrubs					
<i>Calamintha ashei</i>					
(Weath.) Shinnery	-	-	-	-	2 (2)
<i>Lechea deckertii</i> Small	10 (3)	60 (29)	-	-	6 (6)
<i>Palafoxia feayi</i> A.Gray	41 (20)	-	5 (2)	3 (3)	4 (3)
<i>Polygonella robusta</i>					
(Small) G.L.Nesom & V.M.Bates	38 (38)	3 (3)	-	-	-
All subshrubs	89 (38)	64 (32)	5 (2)	3 (3)	13 (6)
Shrubs					
<i>Ceratiola ericoides</i>					
Michx.	67 (17)	3 (3)	-	16 (6)	28 (12)
<i>Lyonia sp.</i>	-	-	-	-	2 (2)
All shrubs	67 (17)	3 (3)	-	16 (6)	30 (13)
Graminoids					
<i>Bulbostylis warei</i>					
(Torr.) C.B.Clarke	3 (3)	3 (3)	-	-	-
<i>Cyperus spp.</i>	22 (10)	51 (25)	100 (38)	29 (17)	51 (18)
<i>Dichanthelium spp.</i>	3 (3)	-	-	-	-
<i>Juncus sp.</i>	-	-	8 (3)	-	2 (2)

<i>Panicum repens</i> L.	6 (6)	-	-	3 (3)	-
<i>Paspalum notatum</i>					
Flüggé	3 (3)	-	-	-	-
<i>Paspalum setaceum</i>					
Michx.	10 (6)	-	-	-	-
Poaceae	45 (24)	16 (8)	7 (3)	48 (6)	45 (26)
All graminoids	92 (48)	70 (32)	114 (44)	80 (18)	98 (16)
<hr/>					
Ruderal Herbs					
<hr/>					
<i>Conyza canadensis</i> (L.)					
Cronquist	10 (6)	48 (36)	-	-	4 (4)
<i>Emilia fosbergii</i>					
Nicolson	6 (4)	3 (3)	-	13 (13)	-
<i>Eupatorium</i> spp.	29 (11)	13 (5)	17 (13)	19 (8)	29 (10)
<i>Euthamia caroliniana</i>					
(L.) Greene ex Porter &					
Britton	10 (6)	-	-	6 (6)	2 (2)
<i>Gamochaeta purpurea</i>					
(L.) Cabrera	1623 (862)	-	33 (5)	-	104 (55)
<i>Houstonia procumbens</i>					
(J.F.Gmel.) Standl.	3 (3)	-	-	-	1 (1)
<i>Linaria floridana</i>					
Chapm.	54 (36)	293 (196)	43 (15)	13 (7)	92 (44)
<i>Oldenlandia</i>	3 (3)	-	1 (1)	3 (3)	2 (2)

<i>corymbosa</i> L.					
<i>Oldenlandia</i> spp.	6 (4)	57 (27)	-	-	2 (2)
<i>Oldenlandia uniflora</i> L.	10 (10)	-	3 (2)	3 (3)	2 (2)
<i>Oxalis corniculata</i> L.	67 (29)	-	-	-	17 (11)
<i>Phyllanthus tenellus</i>					
Roxb.	38 (38)	-	-	-	-
<i>Physalis</i> sp.	22 (11)	6 (6)	-	57 (22)	34 (31)
<i>Pilea microphylla</i>					
(L.) Liebm.	10 (6)	6 (4)	-	-	2 (2)
<i>Polypremum</i>					
<i>procumbens</i> L.	-	-	5 (2)	-	6 (4)
<i>Richardia scabra</i> L.	3 (3)	-	-	-	4 (4)
<i>Ruellia blechum</i> L.	6 (4)	-	-	16 (10)	8 (3)
<i>Scoparia dulcis</i> L.	-	-	4 (4)	-	4 (2)
All ruderal herbs	1900 (822)	427 (244)	106 (29)	131 (50)	314 (100)
Unknown					
Dicot - long hair	140 (56)	73 (31)	-	45 (25)	38 (15)
Solanaceae Family	10 (10)	-	-	-	2 (2)
Unidentified	162 (74)	535 (194)	145 (31)	350 (47)	248 (69)
All unknowns	312 (68)	608 (224)	145 (31)	395 (45)	288 (78)
Overall Total	3333 (1101)	2330 (419)	1359 (172)	977 (116)	1430 (254)

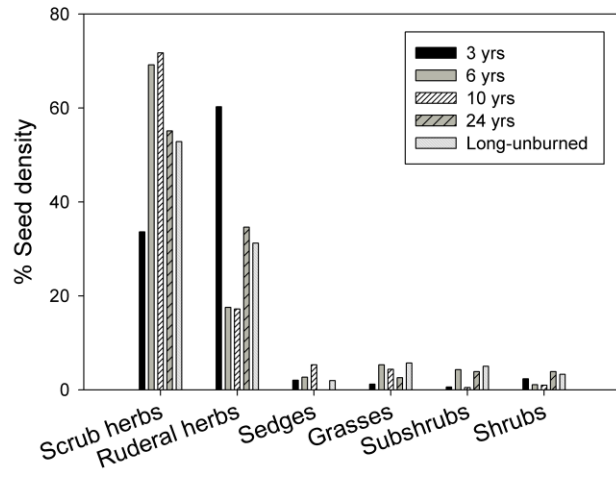


Figure 1

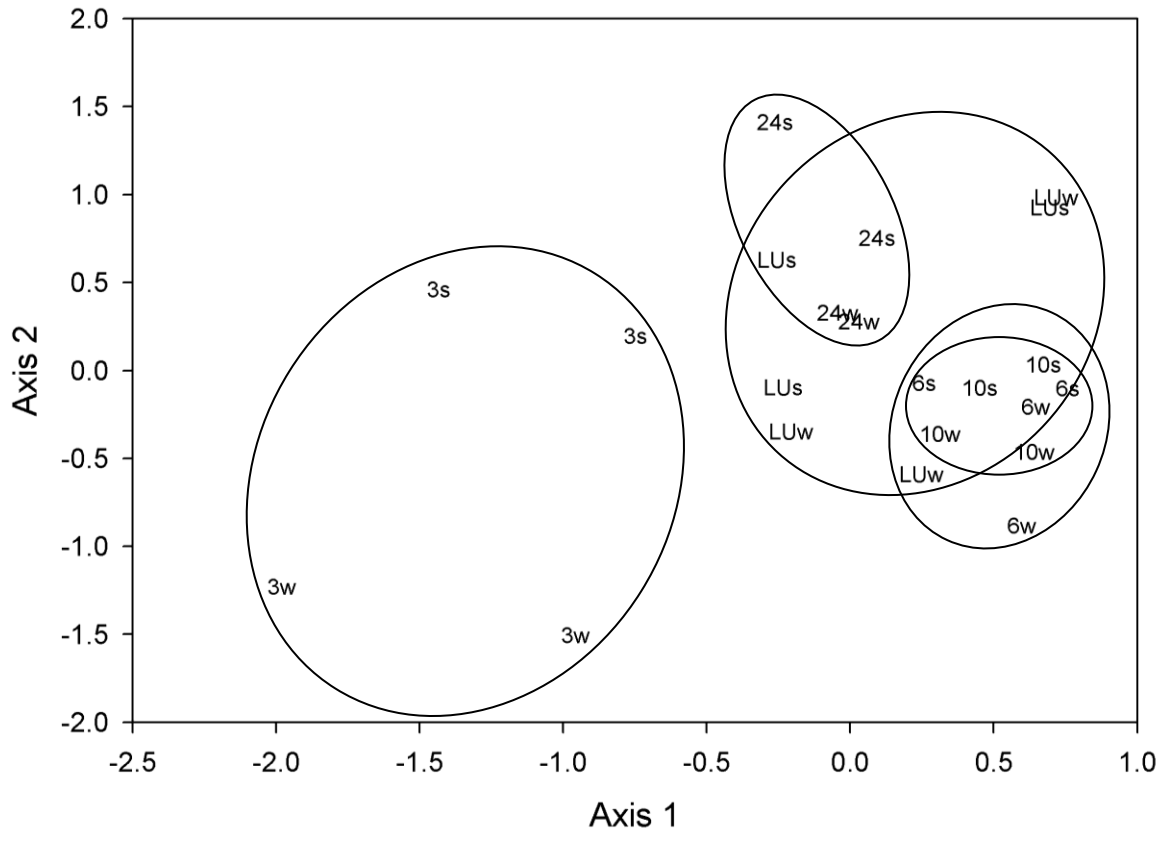


Figure 2.

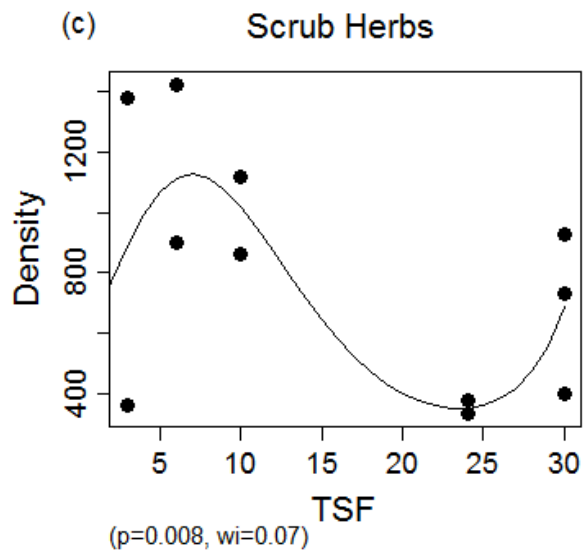
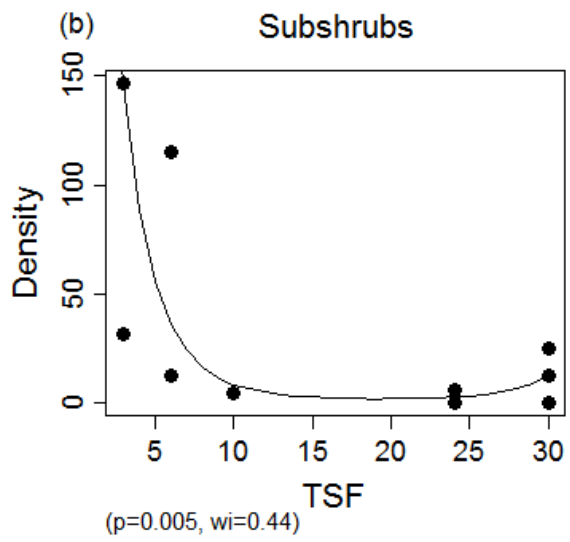
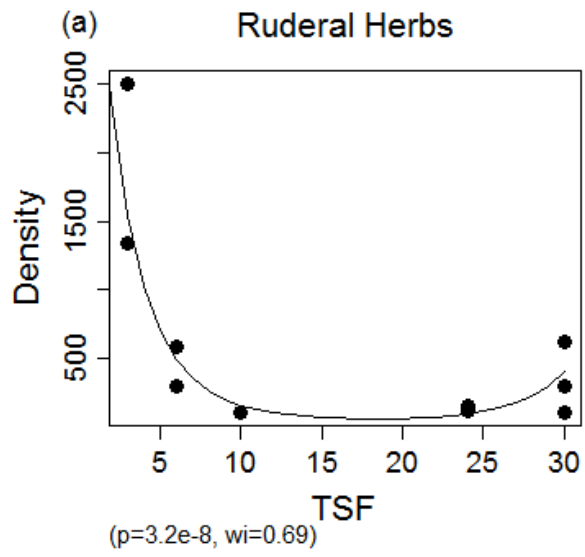


Figure 3

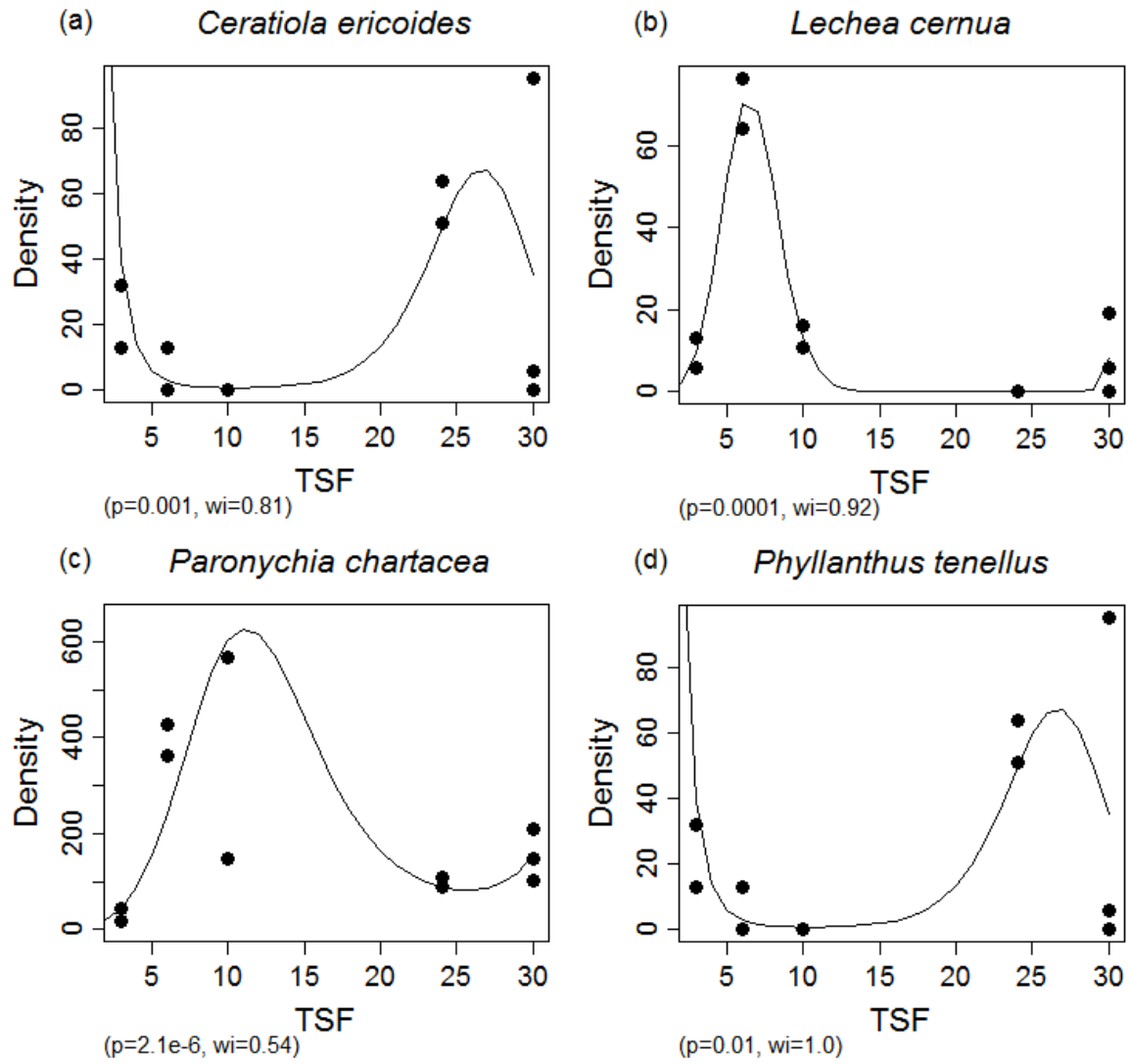


Figure 4