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# Genetic change following fire in populations of a seed-banking perennial plant

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**Genetic change following fire in populations of a  
seed-banking perennial plant**

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41 **Abstract**

42 Disturbances such as fire have the potential to remove genetic variation, but seed banks  
43 may counter this loss by restoring alleles through a reservoir effect. We used allozyme  
44 analysis to characterize genetic change in two populations of the perennial *Hypericum*  
45 *cumulicola*, an endemic of the fire-prone Florida scrub. We assessed genetic variation  
46 before and one, two, and three years after fire that killed nearly all aboveground plants.  
47 Populations increased in size following fire, with most seedlings likely recruited from a  
48 persistent seed bank. Four of five loci were variable. Most alleles were present in low  
49 frequencies, but our large sample sizes allowed detection of significant trends. Expected  
50 heterozygosity increased, and allele presence and allele frequencies showed marked shifts  
51 following fire. The post-fire seedling cohort contained new alleles to the study and one  
52 new allele to the species. Population differentiation between the two study sites did not  
53 change. Our study is the first to directly documents genetic changes following fire, a  
54 dominant ecological disturbance worldwide, and is also one of the few to consider shifts  
55 in a naturally recruiting post-disturbance seedling cohort. We demonstrate the potential  
56 of seed banks to restore genetic variation lost between disturbances. Our study  
57 demonstrates that rapid genetic change can occur with disturbance and that fire can have  
58 positive effects on the genetics of rare species.

59

60

61

62 **Keywords**

63 allozymes, fire, Florida scrub, genetic variation, *Hypericum cumulicola*

64 **Introduction**

65 Rapid shifts in the genetic structure of populations are increasingly recognized as  
66 important responses of wild plants and animals to environmental changes such as global  
67 warming (Bradshaw and Holzapfel 2001), alterations in soil chemistry (Snaydon and  
68 Davies 1982), or invasion of exotic species (Groman and Pellmyr 2000). Ecological  
69 disturbances, by causing mass mortality and allowing prodigious recruitment, should also  
70 be capable of causing rapid genetic changes. However, this process remains virtually  
71 unstudied.

72

73 Fire is probably the predominant ecological disturbance worldwide, controlling much  
74 variation in vegetation, carbon, and nutrient dynamics (Bond and Keeley 2005).

75 However, no studies have investigated the effects of fire as a driver of genetic change.

76 For plant species that are generally killed by fire and recover via a persistent seed bank,

77 there is great potential for such change. Seed banks can be genetically distinct from

78 aboveground plants, and can serve as genetic reservoirs, harboring and replenishing

79 variation that has been lost aboveground (Del Castillo 1994). They have the potential to

80 affect the evolutionary potential of plant populations (McCue and Holtsford 1998; Mahy

81 et al. 1999) by dispersing genes through time (Tonsor et al. 1993). If built up over many

82 years, seed banks can store genetic memory of variation lost in aboveground plants

83 (Templeton and Levin 1979; Cabin 1996) due to inbreeding and drift. Yet, field studies of

84 seed bank genetics (Baskin and Baskin 1978; Tonsor 1993; Peroni and Armstrong 2001;

85 Mandák et al. 2006) and the genetics of naturally occurring seedling cohorts (Epperson

86 and Alvarez-Buylla 1997) are rare.

87

88 Florida scrub is a fire-prone, disturbance mediated habitat (Menges 2007). Fire reduces  
89 aboveground biomass and releases herbaceous species from competition (Quintana-  
90 Ascencio and Morales-Hernández 1997). Many of these herbaceous plants are killed by  
91 fire, but populations are rapidly restored by recruitment from seeds in a persistent seed  
92 bank (Menges and Kohfeldt 1995). Post-fire seeders are particularly well-represented  
93 among rare plants of Florida scrub, which is itself a hotspot for endemism (Christman  
94 and Judd 1990; Estill and Cruzan 2001).

95

96 Although the effects of fire on the demography of several Florida scrub endemics have  
97 been documented (e.g., Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio  
98 2004; Menges et al. 2006), no previous study has examined the effects of fire on genetic  
99 change in a Florida scrub plant. We used allozyme markers to study genetic changes  
100 following fire in the federally-endangered *Hypericum cumulicola* (Small) P. Adams  
101 (Clusiaceae) at two sites on the Lake Wales Ridge in central Florida. Complete censuses  
102 were conducted pre-fire at both sites. Fires the following year killed almost all  
103 aboveground plants. We then sampled all seedlings emerging each of the next three  
104 years. These seedlings were assumed to have derived from the seed bank based on the  
105 extremely limited seed dispersal documented for this species (Quintana-Ascencio et al.  
106 1998). Congruent spatial patterns within populations pre-fire vs. post-fire (Quintana-  
107 Ascencio et al. in preparation) also suggest limited dispersal. Thus, we were able to track  
108 genetic changes occurring post-fire by comparing genetic variation in pre-burn  
109 aboveground populations with that in cohorts of emerging post-fire seedlings.

110

111 Seed banks are notoriously difficult to study, but can be very important life stages when  
112 considering metapopulation dynamics and genetic structure. This is especially true in  
113 rare plants with few populations, where the seed bank may represent a significant  
114 proportion of the gene pool. Prior genetic studies of seed banks relied on meticulously  
115 recovering seeds from soil cores and germinating them in greenhouses under artificial  
116 conditions (e.g., McGraw 1993; Cabin 1996; McCue and Holtsford 1998; Mandák et al.  
117 2006). Our study system overcomes several shortcomings of this approach: 1) seed  
118 banks can be large and aggregated, making it hard to know where to collect samples at a  
119 site (Cabin 1998); 2) recovery of seeds from seed cores often results in few available  
120 seeds to grow into seedlings, so previous studies looked at few seed genotypes and  
121 therefore lacked statistical power to detect low frequency alleles (e.g., Mahy et al. 1999).  
122 Our *in situ* system and large sample sizes make our study one of the most comprehensive  
123 studies of genetic change in a wild plant species yet conducted.

124 **Materials and Methods**

125 **Study species**

126 *Hypericum cumulicola*, the Highlands scrub hypericum, is a short-lived perennial herb. It  
127 is a federally listed endangered plant endemic to the Lake Wales Ridge in central Florida  
128 (Christman and Judd 1990). It grows in xeric, open areas of well-drained white sand in  
129 Florida scrub dominated by Florida rosemary (*Ceratiola ericoides*) and scrub oaks  
130 (*Quercus* spp.) (Menges 1999). Populations tend to occur in discrete patches that are  
131 separated by large patches of unsuitable habitat (Quintana-Ascencio and Menges 1996).  
132 Plants are self-compatible and have high rates of inbreeding (Dolan et al. 1999)  
133 Pollinators of *H. cumulicola* are bees that forage locally in a trap-line fashion and are  
134 unlikely to travel between patches of occupied habitat (Boyle and Menges 2001). Seeds  
135 and fruits disperse on average less than a meter (Menges et al. 1998). Consequently, most  
136 seedlings are found in the vicinity of fruiting plants (Quintana-Ascencio et al. 1998,  
137 Quintana-Ascencio et al. in preparation). Interpopulation gene flow, via either pollen or  
138 seeds, is therefore quite unlikely. As a consequence,  $F_{ST}$ , the proportion of genetic  
139 variation found among populations, at patch level, is extremely large (0.72; Dolan et al..  
140 1999; this study included 34 populations including the two populations included in this  
141 study). No populations were in Hardy-Weinberg equilibrium.

142

143 Florida rosemary scrub probably burns infrequently, about every 15-30 (Menges 2007) or  
144 20-80 years (Menges and Hawkes 1998). Fire kills aboveground *H. cumulicola* plants  
145 (Menges and Kohfeldt 1995) as well as the dominant Florida rosemary (Johnson 1982).  
146 Reestablishment of both species occurs primarily from a persistent seed bank (Quintana-



147 Ascencio et al. 1998), with *Hypericum cumulicola* establishment enhanced during wet  
148 winters (Quintana-Ascencio et al. 2007). Survival and growth are greatest in recently  
149 burned patches (Quintana-Ascencio 1997), where there is less competition due to the  
150 temporary removal of aboveground shrub biomass and ground lichens (Quintana-  
151 Ascencio and Morales-Hernández (1997).

152

### 153 **Study sites**

154 We studied genetic shifts in *H. cumulicola* with fire at two sites: Archbold Biological  
155 Station (ABS) and Lake Placid Scrub (LPS). At each site, *H. cumulicola* occurs  
156 primarily in rosemary scrub, and periodic fires have been part of the recent history of  
157 each site. The patch at Archbold extends for *ca.* 400 m from north to south and is 80 m at  
158 its widest. The patch at Lake Placid Scrub extends for *ca.* 90 m from northwest to  
159 southeast and is 35 m at its widest. Sites are 6 km apart and suitable habitat is  
160 discontinuous between the sites due to wetlands and human-caused habitat fragmentation.  
161 For both sites, complete pre-fire censuses for *H. cumulicola* were conducted in  
162 preparation for planned prescribed fires.

163

164 At ABS, an accidental fire ignited by a passing train burned over the study site in  
165 February, 2001. This was a high intensity fire burning during an extreme drought  
166 (Weekley et al. 2007). Unlike most landscape fires over the years, this fire burned  
167 completely through seasonal ponds (that were bone dry) In addition, it produced  
168 unusually little variation in fire intensity in xeric uplands such as rosemary scrub (ABS  
169 fire data and Menges, personal observations). In particular, this fire burned >99% of the

170 area in the patch, killing most standing *H. cumulicola*. Fewer than 1 % (8 of 842) of all  
171 plants survived through 2002; only three of them survived to 2003. The surviving plants  
172 were unburned and located in a single gap at the south end of the patch. Because of the  
173 large scale and homogeneity of this fire, along with the poor dispersal of *H. cumulicola*  
174 fruits, we believe the vast majority of post-fire seedlings derived from on-site seeds in the  
175 persistent seed bank.

176

177 At LPS, the prescribed fire occurred as planned in July, 2001, just after the 2001 drought  
178 (Weekley et al. 2007). Because of higher humidity, this prescribed fire resulted in a  
179 patchy burn. Nevertheless, most standing *H. cumulicola* plants in this patch were also  
180 killed. Fourteen plants (7.5 % of 186 total plants in the patch) in 6 gaps that did not burn  
181 on the eastern part of the Lake Placid patch survived through 2002; 4 of them survived  
182 through 2004.

183

184 Recruitment of new seedlings began during the winter of 2001-2002. We located, marked  
185 and mapped with a laser (Impulse, Laser Technology Inc., Englewood, Colorado, USA, 1  
186 cm accuracy) every new recruit between July and September of 2002, 2003 and 2004  
187 within all gaps at Archbold and Lake Placid scrub patches (a total of over 1700 seedlings)  
188 Sites were visited 2-3 times every other week during peak germination time to increase  
189 chances of finding seedlings.

190

191 **Allozyme analysis**

192 Small samples of leaf and stem or flower buds were collected from each plant larger than  
193 2 cm at both study sites (ABS and LPS) during the summer of 2000 (pre-fire) and 2002  
194 (post-fire) Additionally, during 2003 and 2004, samples from newly established  
195 seedlings were collected. Almost all plants were large enough to be sampled (Table 1).

196

197 Material was sent to Butler University via overnight mail, where standard procedures for  
198 starch gel electrophoresis for allozymes were conducted with recipes following Dolan et  
199 al. (1999). Gels were stained for the five variable loci identified in our previous,  
200 extensive, species-wide survey of *H. cumulicola* (Dolan et al. 1999): isocitrate  
201 dehydrogenase (*IDH*), malate dehydrogenase 1 (*MDH1*), malate dehydrogenase 3  
202 (*MDH3*), menadione reductase (*MNR*), and 6-phosphoglucomutase (*6PGD*) We used  
203 the GDA software of Lewis and Zaykin (1999) for genetic analysis. Because sample  
204 sizes were large (at least 699 at ABS and 172 at LPS for each year) and nearly complete  
205 we applied no cut-off criterion for considering a locus polymorphic, including all alleles  
206 detected in our analyses. The few plants that survived the fire at either site were included  
207 in pre-fire genetic analyses but not the post-fire analyses.

208

### 209 **Statistical Analyses**

210 Expected heterozygosity was calculated for each study site pre-fire (2000) and post-fire  
211 (2002, 2003, 2004). We used contingency chi-square tests (recommended by Ryman and  
212 Jorde 2001 over other tests) generated by Systat software (Academic Distributing, Inc.,  
213 Dewey, AZ, USA) to compare allele frequencies between pre-fire plants and 2002 post-  
214 fire plants derived from the seed bank. Alpha levels are adjusted via Bonferroni

215 correction to reduce the likelihood of type I errors. Genetic structure between the two  
216 sites was analyzed using  $\theta_p$ , a measure of the extent to which populations are  
217 differentiated (Weir 1996).

218

219

220

221

222 **Results**

223 We found several changes in allele presence during our study. A total of 12 alleles were  
224 detected for the 5 loci assayed (Table 1). *MDH1*, surveyed because it was variable at  
225 some sites in our previous work (Dolan et al. 1999) was not variable in either site in any  
226 year. The population at ABS had greater allelic richness, with alleles for *IDH* and *6PGD*  
227 that were not present during any sample years at LPS. The very low frequency *IDH-b*  
228 allele was lost from ABS following the fire. Three alleles were detected in our study sites  
229 only after the fire: *MDH3-c* and *6PGD-a* at ABS and *MNR-c* at LPS. *6PGD-a* is a  
230 globally new allele; not being found in our previous species-wide survey (Dolan et al  
231 1999).

232

233 Quantitative shifts in allele frequencies following fire were often marked, were present in  
234 seedlings recruited the first year post-fire, and persisted throughout our study. At ABS,  
235 three of the four variable loci had significant allele frequency shifts in 2002, the first year  
236 seedlings were present following the burn (Table 1). *MDH3-a* increased almost five-fold  
237 while *6PGD-b* decreased by about one-third. *6PGD-d*, present at 0.4% frequency pre-  
238 fire, was not detected in the first survey year post-fire, but was found the next two years.  
239 At LPS, one of the two variable loci had significant allele frequency differences  
240 following the burn compared to pre-fire. There was a 42% reduction in frequency of  
241 *MDH3-b* in the first sample year post-burn. All significant allele frequency shifts were  
242 robust enough that they continued to be significant ( $p < 0.05$ ) even when alpha levels are  
243 adjusted via Bonferroni correction to reduce the likelihood of type I errors.

244

245 Population size at ABS increased 75% after the fire, increasing for at least three years,  
246 through 2004 (Fig. 1). Similarly, population size at LPS increased 95% after the fire,  
247 peaking two years post-fire in 2003 (Fig. 1). Both sites experienced increases in expected  
248 heterozygosity (that mostly paralleled population size increases) by the end of the study  
249 period (50% at ASB, 62.5% at LPS), following slight drops in the first post-fire census  
250 year, 2002 (Fig. 1).

251

252 Populations at ABS and LPS were significantly differentiated genetically in all sample  
253 years (95% confidence intervals of  $\theta_p$  did not overlap zero; Fig. 2). The magnitude of  
254 the differentiation was similar in all sample years(95% confidence intervals overlap).

255

256 **Discussion**

257 The seed bank of *Hypericum cumulicola* has the potential to serve as a genetic reservoir,  
258 storing and accumulating genes of the fittest plants over many years and under a range of  
259 environmental conditions. The formation of a persistent seed bank allows *H. cumulicola*  
260 to reverse population declines that occur between fires in Florida scrub (Quintana-  
261 Ascencio et al. 2003, 2007). The moderate (15-30 years) fire return frequency proposed  
262 for rosemary scrub (Menges 2007) allows sufficient time for a fecund species such as *H.*  
263 *cumulicola* to build up a very large seed bank. Although the longevity of its seed bank is  
264 not known (it is at least two years; Quintana-Ascencio et al. 1998), other species found in  
265 rosemary scrub may have seeds that can persist for at least 7 years (Menges and  
266 Quintana-Ascencio 2004).

267

268 Recruitment in *H. cumulicola* is highest just after fire, although some germination occurs  
269 every year (Quintana-Ascencio et al. 2003). Although the initial flush of plants must have  
270 come from the persistent seed bank, some seedlings may have subsequently been  
271 produced from early-flowering post-fire plants. Therefore, we do not know how many of  
272 seedlings we analyzed arose from the seed bank. Therefore, continued seedling  
273 recruitment may dilute the seed bank reservoir effect. Nonetheless, even these additional  
274 seedlings may harbor alleles that owe their post-fire existence to prior storage in the soil  
275 seed bank.

276

277 Qualitative and quantitative differences in alleles between aboveground plants and their  
278 associated seed banks have been found in several other studies. Cases of both alleles

279 present aboveground and missing belowground and vice-versa have been reported (Cabin  
280 et al. 1998; McCue and Holtsford 1998; Tonsor 1993; Mahy et al. 1999; Mandák et al.  
281 2006). Alleles involved were rare and usually found in very low frequency, as were the  
282 one lost aboveground and three gained in our study (mean frequency = 0.4%). Alleles  
283 with frequencies this low would likely have been missed in studies with smaller sample  
284 sizes.

285

286 Long-term seed banks play an important role in *H. cumulicola* demography, being critical  
287 to reduce risks of decline or extinction during unfavorable years in fire-suppressed  
288 habitats (Quintana-Ascencio et al. 2003) For *H. cumulicola*, environmental conditions  
289 decline between fires as growing shrubs become more competitive neighbors (Quintana-  
290 Ascencio and Morales-Hernandez 1997; Quintana-Ascencio et al. 1998). Seedling  
291 recruitment declines greatly with time since fire (Quintana-Ascencio et al. in  
292 preparation,). Emigration from unfavorable patches is unlikely because dispersal  
293 distances are small and suitable patches usually too far away.

294

295 Matrix models of *H. cumulicola* indicate that seeds constitute 90-99 % of population  
296 stable stage distributions in most habitats (particularly long unburned habitats; Picó et al.  
297 2003), and that seed transitions have large influences on population growth (Quintana-  
298 Ascencio et al. 2003). Since seeds are the dominant stage both in terms of numbers and  
299 in terms of their impact on population growth, small evolutionary changes in seed  
300 survival and seed dormancy can have profound consequences for *H. cumulicola*  
301 persistence.



302

303 Our study demonstrates that rapid and significant genetic change can occur with  
304 disturbance. Fire, the principal disturbance responsible for shaping community structure  
305 in rosemary scrub vegetation, can also significantly influence genetic patterns in  
306 individual species. Fire both kills all (aboveground) *H. cumulicola* plants and triggers a  
307 flush of germination from a persistent seed bank. In so doing, it also triggers rapid  
308 genetic change and allows genetic material stored in the soil seed bank to once again be  
309 expressed in growing plants.

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319

320 **References**

- 321 Baskin JM, Baskin CC (1978) The seed bank in a population of an endemic plant species  
322 and its ecological significance. *Biol. Cons.* 14:125-130.
- 323 Bond WJ, Keeley JE (2005) Fire as a global “herbivore”, the ecology and evolution of  
324 flammable ecosystems. *Tr. In Ecol. and Evol.* 20:387-394.
- 325 Boyle O, Menges ES (2001) Pollinator visitation to *Hypericum cumulicola*  
326 (*Hypericaceae*), a rare Florida scrub endemic. *Fl. Sci.* 64:107-117.
- 327 Bradshaw WE, Holzapfel CM (2001) Genetic shift in photoperiod response correlated  
328 with global warming. *Proc. of the Nat. Acad. of Science* 98:14509-14511.
- 329 Cabin RJ (1996) Genetic comparisons of seed bank and seedling populations of a  
330 perennial desert mustard, *Lesquerella fendleri*. *Evolution* 50:1830-1841.
- 331 Cabin RJ, Mitchell, JR, Marshall DL (1998) Do surface plant and soil seed bank  
332 populations differ genetically? A multipopulation study of the desert mustard  
333 *Lesquerella fendleri* (*Brassicaceae*). *Amer. J. of Bot.* 85:1098-1109.
- 334 Christman S P Judd WS (1990) Notes on plants endemic to Florida scrub. *Fl. Sci.* 53:52-  
335 73.
- 336 Del Castillo RF (1994) Factors influencing the genetic structure of *Phacelia dubia*, a  
337 species with a seed bank and large fluctuations in population size. *Heredity* 72:  
338 446-458.
- 339 Dolan RW, Yahr R, Menges ES, Halfhill MD (1999) Conservation implications of  
340 genetic variation in three rare species endemic to Florida rosemary scrub. *Amer.*  
341 *J. of Bot.* 86:1556-1562.

342 Epperson BK, Alvarez-Buylla ER (1997) Limited dispersal and genetic structure in life  
343 stages of *Cecropia obtusifolia*. *Evolution* 51:275-282.

344 Estill JC, Cruzan MB (2001) Phylogeography of rare plant species endemic to the  
345 southeastern United States. *Castanea* 66:3-23.

346 Groman JD, Pellmyr O (2000) Rapid evolution and specialization following host  
347 colonization in a yucca moth. *J. of Evol. Biol.* 13:223-236.

348 Johnson A F (1982) Some demographic characteristics of the Florida rosemary *Ceratiola*  
349 *ericoides* Michx. *Amer. Midl. Nat.* 108:170-174.

350 Lewis PO, Zaykin D (1999) Genetic Data Analysis version 1.0d15. Available at:  
351 <http://lewis.eeb.uconn.edu/lewishome/gda.html>.

352 Mahy G, Vekemans X, Jacquemart A (1999) Patterns of variation within *Calluna*  
353 *vulgaris* populations at seed bank and adult stages. *Heredity* 82: 432-440.

354 Mandák B, Bímová K, Mahelka V, Plačková I (2006) How much genetic variation is  
355 stored in the seed bank? A study of *Atriplex tatarica* (Chenopodiaceae). *Mol.*  
356 *Ecol.* 11:2653-2663.

357 McCue KA, Holtsford TP (1998) Seed bank influences on genetic diversity in the rare  
358 annual *Clarkia springvillensis* (Onagraceae) *Amer. J. of Bot.* 85:30-36.

359 McGraw JB (1993) Ecological genetic variation in seed banks. IV. Differentiation of  
360 extant and seed bank-derived populations of *Eriophorum viginatum*. *Arctic and*  
361 *Alpine Res.*25:45-49.

362 Menges ES (1999) Ecology and conservation of Florida scrub. In: Anderson RC, Fralish  
363 JS, Baskin J (eds) *The savanna, barren, and rock outcrop communities of North*  
364 *America*. Cambridge University Press, Cambridge, pp 7-22.

365 Menges ES (2007) Integrating demography and fire management, an example from  
366 Florida scrub. *Aust. J. of Bot.* 55:261-272.

367 Menges ES, Dolan RW, Gordon DR, Evans MEK, Yahr R. (1998) *Demography, ecology,*  
368 *and preserve design for endemic plants of the Lake Wales Ridge, Florida.* Final  
369 Report to The Nature Conservancy's Ecosystem Research Program.

370 Menges ES, Dolan RW, Yahr R., Gordon, DR (2001) Comparative genetics of seven  
371 plants endemic to Florida's Lake Wales Ridge. *Castanea* 66:98-114.

372 Menges ES, Hawkes CV (1998) Interactive effects of fire and microhabitat on plants of  
373 Florida scrub. *Ecol. App* 8:935-946.

374 Menges ES, Kohfeldt N (1995) Life history strategies of Florida scrub plants in relation  
375 to fire. *Bull. of the Tor. Bot. Club* 122:282-297.

376 Menges ES, Quintana-Ascencio PF (2004) Evaluating population viability analysis with  
377 fire in *Eryngium cuneifolium*, deciphering a decade of demographic data. *Ecol.*  
378 *Mono.* 74:79-100.

379 Nunney, L. (2002) The effective size of annual plant populations: the interaction of a  
380 seed bank with fluctuating plant numbers. *Amer. Natur.* 160:195-204.

381 Pake CE, Venable DL (1996) Seed banks in desert annuals, implications for persistence  
382 and coexistence in variable environments. *Ecology* 77:1427-1435.

383 Peroni PA, Armstrong RT (2001) Density, dispersion and population genetics of a *Silene*  
384 *latifolia* seed bank from southwestern Virginia. *J. of the Torr. Bot. Soc.* 128:400-  
385 406.

386 Picó FX, Quintana-Ascencio PF, Menges ES, López-Barrera F (2003) Recruitment rates  
387 exhibit high elasticity and high temporal variation in populations of a short-lived  
388 perennial herb. *Oikos* 103:69-74.

389 Quintana-Ascencio PF, Dolan RW, Menges ES (1998) *Hypericum cumulicola*  
390 demography in unoccupied and occupied Florida scrub patches with different  
391 time-since-fire. *J. of Ecol.* 86:640-651.

392 Quintana-Ascencio, PF, Menges, ES (1996) Inferring metapopulation dynamics from  
393 patch level incidence of Florida scrub plants. *Cons. Biol.*10:1210-1219.

394 Quintana-Ascencio PF, Menges ES, Weekley CW (2003) A fire-explicit population  
395 viability analysis of *Hypericum cumulicola* in Florida rosemary scrub. *Cons. Biol.*  
396 17:433-449.

397 Quintana-Ascencio PF, Morales-Hernández M (1997) Fire-mediated effects of shrubs,  
398 lichens, and herbs on the demography of *Hypericum cumulicola* in patchy Florida  
399 scrub. *Oecologia* 112:263-271.

400 Quintana-Ascencio PF, Weekley CW, Menges ES (2007) Comparative demography of a  
401 rare species in Florida scrub and road habitats. *Biol. Cons.*137:263-270.

402 Ryman N, Jorde PE (2001) Statistical power when testing for genetic differentiation.  
403 *Mol. Ecol.*10:2361-2373.

404 Shimono S, Ueno S, Tsumura Y, Washitani I (2006) Spatial genetic structure links  
405 between soil seed banks and above-ground populations of *Primula modesta* in  
406 subalpine grassland. *J. of Ecol.* 94:77-86.

407 Snaydon RW, Davies TM (1982) Rapid divergence of plant populations in response to  
408 recent changes in soil conditions. *Evolution* 36:289-297.

- 409 Templeton AR, Levin DA (1979) Evolutionary consequences of seed pools. Amer. Nat.  
410 114:232-249.
- 411 Tonsor SJ, Kalisz S, Fisher J, Holtsford TP (1993) A life-history based study of plant  
412 genetic structure, seed bank to adults in *Plantago lanceolata*. Evolution 47:833-  
413 843.
- 414 Venable DL, Brown JS (1988) The selective interactions of dispersal, dormancy, and  
415 seed size as adaptations for reducing risk in variable environments. Amer. Nat.  
416 131:360-384.
- 417 Weekley CW, Gagnon D, Menges ES, Quintana-Ascencio PF, Saha S (2007) Variation in  
418 soil moisture in Florida scrub. EcoScience 14:377-386.
- 419 Weir BS (1996) Genetic Data Analysis II. Sinauer Associates, Sunderland.

Table 1. Allele frequencies for the four polymorphic loci, for entire aboveground populations by site and year. Pre-fire = 2000. The fires occurred in 2001, but no plants emerged that year. N = number of plants sampled. % = percent of total population. Contingency analysis Chi-square ( $X^2$ ) values are given for loci that differed significantly in allele frequencies between pre-fire and 2002. Allele frequencies in subsequent years were not significantly different from those present in 2002.  $X^2$  results are not included for *IDH* at ASB and *MNR* at LPS due to the presence of sparse cells.

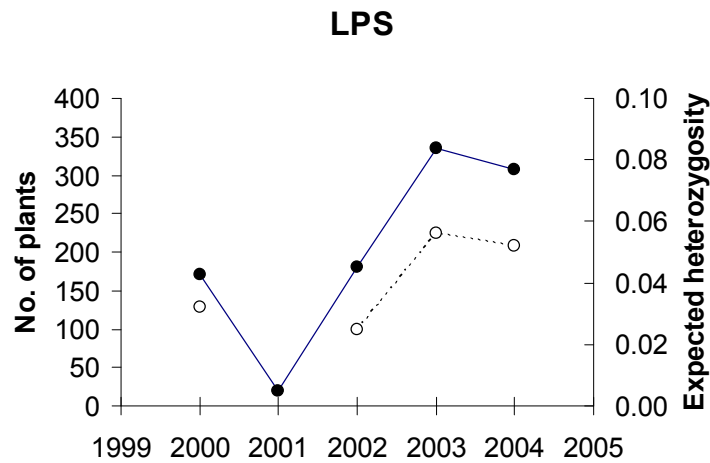
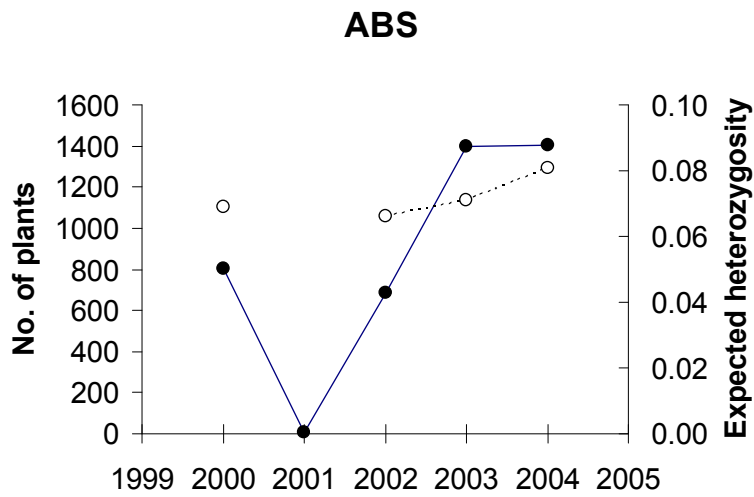
		ABS					LPS				
		Pre-fire	2002	$X^2$	2003	2004	Pre-fire	2002	$X^2$	2003	2004
N		816	699		1430	1454	172	182		337	309
%		100	86.6		88.9	99.7	100	95.7		92.3	99.7
Locus	Allele										
<i>IDH</i>	a	0.995	1.000		1.000	1.000	1.000	1.000		1.000	1.000
	b	0.005	-		-	-	-	-		-	-
<i>MDH3</i>	a	0.016	0.076	66.6***	0.084	0.084	0.018	0.092	97.3***	0.071	0.074
	b	0.984	0.924		0.910	0.910	0.836	0.483		0.564	0.570
	c	-	-		0.006	0.006	0.146	0.424		0.365	0.356
<i>MNR</i>	b	0.807	0.862	15.9***	0.815	0.816	1.000	0.995		0.977	0.977



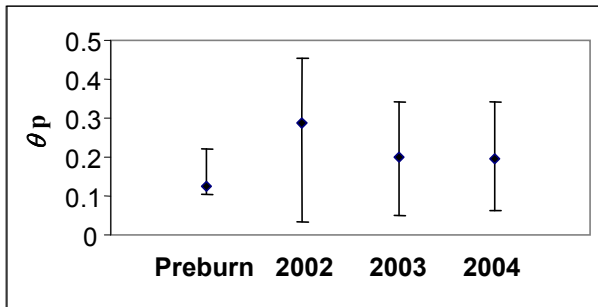
	c	0.193	0.138		0.185	0.184	-	0.005		0.023	0.023
<i>6PGD</i>	a	-	-		0.001	0.001	-	-		-	-
	b	0.169	0.055	107.0***	0.076	0.098	-	-		-	-
	c	0.823	0.945		0.908	0.886	1.000	1.000		1.000	1.000
	d	0.009	-		0.015	0.015	-	-		-	-

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\*\*\* =  $p < 0.001$



**Figure 1** Population size (closed circles and solid lines) and expected heterozygosity (open circles and dashed lines) for study populations ABS and LPS pre-fire (2000), the year of the fire (2001) and the three sample years post-fire. Expected heterozygosity was not calculated in the fire year.



**Figure 2** Degree of population differentiation ( $\theta_p$ ), with 95% confidence intervals indicated, between study populations ABS and LPS, pre-fire (2000) and the three sample years post-fire.  $\theta_p$  values greater than zero indicate significant differentiation.