

1 **Biological soil crusts inhibit seed germination in a temperate pine barren ecosystem**

2

3

**Jessica A. Gilbert<sup>1,2</sup> and Jeffrey D. Corbin<sup>1,3</sup>**

4

5

6

7

<sup>1</sup>Department of Biological Sciences, Union College, Schenectady, NY 12308

8

<sup>2</sup>Orchid ID: 0000-0002-5506-666X

9

<sup>3</sup>Corresponding Author: [corbinj@union.edu](mailto:corbinj@union.edu); 518-388-6097;

10

Orchid ID: 0000-0002-3377-5916

11

12

13

14

15

16  
17

18 **Keywords:** Albany Pine Bush Preserve; Cryptogamic crust; Bryophytes; Inland sand plain;  
19 *Lespedeza capitata* ; *Lupinus perennis*

20  
21

## 22 **Abstract**

### 23 Aims

24 Biological soil crusts (BSCs) are known to affect plants' germination and seedling  
25 establishment in arid ecosystems, but their ecological role in more mesic climates is not so  
26 well-known. We tested the effects of moss-crusts versus uncrusted soils on seed  
27 germination dynamics in a temperate pine barren ecosystem.

28

### 29 Methods

30 We conducted a 35-day laboratory assay of seed germination on moss-crusts versus  
31 uncrusted soils from the Albany (NY) Pine Bush Preserve. We tested total seed germination  
32 and the number of days to 50% of total germination (T50) of two herbaceous perennial  
33 forb species in each soil type.

34

### 35 Results

36 Three and five times more seeds germinated on uncrusted soil than on crusted soil for bush  
37 clover (*Lespedeza capitata*) and wild lupine (*Lupinus perennis*), respectively. Seeds of both

38 species also germinated approximately 10 days earlier on uncrusted soil than on crusted  
39 soil.

40

#### 41 Conclusions

42 This study, and others in similar habitats, show that BSCs in mesic climates can influence  
43 germination and other early life-history stages of plants. We hope that further study of the  
44 interactions between BSCs and vascular plants in mesic climates will contribute to our  
45 understanding of the ecology of BSCs outside the arid and semiarid climates where they are  
46 more extensively studied.

47

#### 48 **Abbreviations:**

49 Albany Pine Bush (APB); Biological soil crusts (BSCs)

50

51

52 **Introduction**

53 A variety of biotic and abiotic factors can strongly influence the rates of seed  
54 germination and other early plant life stages that, in turn, influence plant population  
55 structure and community composition (Crawley 1990; Eriksson and Ehrlén 1992; Harper  
56 1977). Understanding such factors, and how they vary in space and time, are critical if we  
57 are to understand ecosystem processes and resilience to disturbances (Hoffmann 1999;  
58 Platt et al. 1988; Prevéy and Seastedt 2015).

59 The combined effects of abiotic and biotic influences on plant establishment have  
60 been demonstrated in habitats supporting biological soil crusts (BSCs) worldwide. BSCs are  
61 aggregations of cyanobacteria, algae, lichens, and bryophytes that form thin layers on soil  
62 surfaces (Belnap 2003; Belnap and Lange 2001; Weber et al. 2016). They can play an  
63 integral role in soil stability (Belnap and Gillette 1997; Jimenez Aguilar et al. 2009), soil  
64 moisture retention (Bu et al. 2015; Chamizo et al. 2016) and the nitrogen cycle (Belnap  
65 2002; Castillo-Monroy et al. 2010). They can also influence the vascular plant community  
66 through their impacts on seed germination and seedling survival (Zhang et al. 2016). The  
67 direction and magnitude of BSCs' impacts on plants, however, has been shown to vary  
68 widely by plant species and crust community composition. For this reason, biocrust-plant  
69 interactions should be tested empirically rather than inferred from other studies.

70 BSCs have been most-often studied in arid to semi-arid ecosystems, but they can  
71 also occur in more mesic climates including the temperate and subtropical US (e.g. Hawkes  
72 and Flechtner 2002; Neher et al. 2003; Sedia and Ehrenfeld 2003; Smith et al. 2004; Thiet  
73 et al. 2014). BSCs in these habitats can be found in open barrens, pine barrens, pavement

74 barrens, sand plains, and dunes, and include a diverse assemblage of algae, cyanobacteria,  
75 lichens, and bryophytes (Corbin and Thiet, *unpublished data*). Many of these habitats are  
76 recognized as systems of high conservation value for their unique ecology and the presence  
77 of rare and threatened plants and animals (e.g. Edinger 2014; Gawler and Cutko 2010;  
78 Motzkin and Foster 2002; Sperduto and Kimball 2011).

79 To date, only a few studies have examined how BSCs in these more mesic climates  
80 influence plant dynamics, and, as has been observed for BSC-plant dynamics in general, the  
81 results are system- and species-specific. BSCs in New Jersey's Pine Barrens inhibited  
82 germination of three perennial species (Sedia and Ehrenfeld 2003), but in a Florida sand  
83 scrub, BSCs promoted germination of three short-lived perennial herbaceous species and  
84 an annual/occasional perennial (Hawkes 2004). Meanwhile, BSCs in a German sand  
85 ecosystem inhibited perennial species' germination but had either a positive effect or no  
86 effect on annual species' germination (Langhans et al. 2009). Thiet et al. (2014) found that  
87 algal and lichen-moss crusts from a coastal sand dune increased seedling survivorship and  
88 growth of a perennial grass and a woody shrub; but moss-only crusts decreased seedling  
89 performance. The range of results demonstrates that a general relationship between crusts  
90 and plant demography in such habitats is not possible.

91 This study contributes to the growing but still small body of research investigating  
92 the role of BSCs on early-stage plant population dynamics in mesic climates. We assessed  
93 seed germination on moss-crusts versus uncrusted (sand) substrate in an inland pine  
94 barren ecosystem in New York, USA. This is the first known examination of BSCs in such a  
95 habitat, and adds needed understanding to the ecology of BSCs in temperate ecosystems.

96

## 97 **Materials and Methods**

### 98 *Study Area*

99           The Albany Pine Bush (APB) Preserve (42° 42' N; 73° 52' W; Figure 1) is an inland  
100 pine barren that is formed of deep, sandy, glacial outwash soils (Barnes 2003). Though its  
101 cold temperate climate supports nearby eastern deciduous forest, vegetation cover at the  
102 APB is relatively sparse due to the edaphically xeric conditions and frequent fires. Native  
103 vegetation is dominated by scrub oak (*Quercus ilicifolia*), blueberry (*Vaccinium* spp.), and  
104 scattered pitch pine (*Pinus rigida*). Areas of APB were invaded by the non-native black  
105 locust tree (*Robinia pseudoacacia*) in the latter 20<sup>th</sup> Century and subsequently restored  
106 with mechanical removal of locust stems and roots (Rice et al. 2004). Both native pine-oak  
107 scrub and areas from which black locust trees have been removed are managed using  
108 prescribed fire (Bried et al. 2015).

109           Biological soil crusts are abundant in areas of APB where fires or other recent  
110 disturbances maintain an open canopy. Vascular plants, BSCs, and uncrusted sand at APB  
111 and other pine barren ecosystems form a spatial mosaic at the scale of 0.5-10 m<sup>2</sup> per patch  
112 (Sedia and Ehrenfeld 2003; personal observation). Crust composition ranges from incipient  
113 algal mats to moss-dominated crusts that also contain lichens and cyanobacteria (Corbin  
114 and Thiet, *unpublished data*). Common species include the mosses *Ceratodon purpureus* and  
115 *Polytrichum piliferum* and the lichens *Cladonia cristatella* and *C. gracilis* ssp. *turbinata*, and  
116 *C. ochrochlora*.

117

118

119

## 120 *Sample collection*

121           In June 2017, we collected the substrate for our germination trials from a single site  
122 that had been cleared of the black locust tree in 2008 and subsequently replanted with a  
123 native species mix including little bluestem (*Schizachyrium scoparium* (Michx.) Nash), wild  
124 perennial lupine (*Lupinus perennis* L.) and round-headed bush clover (*Lespedeza capitata*  
125 Michx.). We collected mature moss-dominated BSCs by inserting 40, 3.5-cm diameter  
126 plastic Petri dishes into the soil to a depth of 2 cm. We also collected 40 dishes of bare sand,  
127 hereafter referred to as “uncrusted” samples, from the same site and within meters of our  
128 crusted samples. Collections were approved by the Albany Pine Bush Preserve  
129 Commission. Crusted samples were dominated by the mosses *C. purpureus* and *P. commune*.  
130 Lichens made up a minor component, though in several dishes they increased in cover  
131 during experimental watering. Though the uncrusted samples were free of visible mosses  
132 and lichens and had a loose-sand texture, some turned green during the experiment,  
133 indicating that algae and perhaps cyanobacteria were present.

134           All dishes were stored in a refrigerator (4°C) for three weeks until the experiment  
135 began.

136

## 137 *Germination Procedure*

138           We tested germination rates of three herbaceous species – lupine, bush clover, and  
139 little bluestem. These three species are abundant in both mature pine barren habitat and  
140 also in the post-black locust removal sites such as where we collected our soil samples.  
141 Lupine and bush clover seeds were collected from wild populations at APB in 2016. Little  
142 bluestem was grown by Ernst Conservation Seeds, Inc. (Meadville, PA) using traditional

143 agricultural techniques and harvested in 2016. The source for the Pennsylvania-grown  
144 little bluestem seeds was a 2014 collection from APB. All seeds were stored in a freezer (-  
145 20 °C) between cleaning and use.

146 Our experiment was a full factorial experiment with two soil types – moss-crust  
147 and uncrusted – and four plant species types – lupine, bush clover, little bluestem, and no  
148 seeds. There were 10 replicates of each soil type x plant species treatment combination.  
149 Each dish except the no seeds treatments received 20 seeds of a single species scattered  
150 onto the surface; seeds were not buried so as to best mimic natural wind-dispersal. The no  
151 seed treatments on each soil type were established as a control for seeds emerging from a  
152 potential buried seed bank; no seeds were added to this latter treatment.

153 Dishes were laid out randomly on a light table under 12-hour white light beginning  
154 July 2, 2017, and were rotated once a week to eliminate discrepancies in light conditions.  
155 All dishes were watered with 5 ml of water every day, which was the quantity that evenly  
156 moistened the soil or crust surface through the base of the dish. Germinating seeds, judged  
157 by the emergence of the radicle, were recorded every 1-2 days for 35 days. Once a seed  
158 germinated, it was removed. We recorded the total number of seeds that germinated in  
159 each dish and the number of days it took for each dish to reach 50% of total germination  
160 (T50). T50 was not calculated for any experimental dishes in which total germination was  
161 zero.

162

### 163 *Data Analysis*

164 We used two-way ANOVA (R version 3.4.1) to analyze the effect of soil type (moss-  
165 crusted versus uncrusted), plant species, and the interaction between soil type and plant



166 species on total germination and T50 ( $\alpha = 0.05$ ). Little bluestem germination was  
167 extremely low in both soil conditions, and thus was omitted from data analysis. Otherwise,  
168 the data were found to meet assumptions of normality and homogeneity of variance.

169

## 170 **Results**

171 There was a strong effect of soil type on the number of bush clover and lupine seeds  
172 that germinated, as three and five times more bush clover and lupine, respectively,  
173 germinated on uncrusted soil than on moss-crusted soil (Table 1; Figure 2A). Seeds on  
174 uncrusted soil reached T50 approximately 10 days earlier than seeds on crusted soils. Bush  
175 clover seeds' T50 was approximately 5 days earlier than lupine seeds' T50 on both crusted  
176 and uncrusted soils (Table 1; Figures 2B and 3). There was no interaction between soil type  
177 and plant species on T50 (Table 1). By the end of the experiment, total germination did not  
178 differ between the two species, nor was there a significant interaction between soil type  
179 and plant species on total germination (Table 1; Figures 2 and 3).

180 No seeds germinated in either our crusted or uncrusted control (“no seeds”) dishes  
181 that would indicate the presence of a stable seed bank.

182

## 183 **Discussion**

184 Moss-covered BSCs at the Albany Pine Bush clearly inhibited seed germination in  
185 our experiment. Fewer seeds germinated, and they took longer to do so, on moss crusts  
186 than they did on uncrusted sand. Though some germination assays have found that BSCs  
187 can enhance rates of germination (Godínez-Alvarez et al. 2012; Hawkes 2004), our findings  
188 are consistent with other studies in mesic and arid climates in which BSCs inhibited

189 germination (Deines et al. 2007; Jeschke and Kiehl 2008; Langhans et al. 2009; Serpe et al.  
190 2008; Thiet et al. 2014; Zaady et al. 1997).

191        Though we were only able to test the effects of BSCs on two species, both of which  
192 were herbaceous perennial forbs, they both responded in similar ways. We saw no  
193 interaction between plant species and the type of soil for either total germination nor the  
194 time it took for germination to reach 50% of total (T50). The lone grass we tested, little  
195 bluestem, did not germinate in any conditions. A number of other studies have reported  
196 mixed effects of crusts on germination: crusts had negative effects on germination of some  
197 species and no effect or positive effects on others (e.g. Godínez-Alvarez et al. 2012; Hawkes  
198 2004; Langhans et al. 2009; Zaady et al. 1997; Zhang and Belnap 2015). However, until  
199 more species with a wider range of life history traits are assayed for their response to  
200 crusts in our system, we have no evidence that there are species-specific effects of BSCs on  
201 seed germination.

202        BSCs' negative effects on seed germination have been explained, in part, by the  
203 physical barrier that they can create between seeds and soil (Jeschke and Kiehl 2008; Serpe  
204 et al. 2008; Song et al. 2017; Zhang and Belnap 2015). The mosses in our BSC treatments  
205 quickly absorbed the added water and thus seeds were more likely to dry out. Many of the  
206 seeds that did germinate on BSC treatments did so in cracks or gaps in the moss canopy, as  
207 has been observed in other studies (e.g. Langhans et al. 2009). By contrast, bare soil in the  
208 uncrusted treatments provided seeds with a larger area of soil contact and potentially  
209 more moisture as described by Song et al. (2017).

210        Our study did not consider the impact of BSCs on subsequent plant life stages, yet a  
211 variety of other studies have shown distinct effects on seedling growth and survival as well.

212 Mosses and other crust components can limit root penetration and therefore plants' access  
213 to moisture and nutrients (Deines et al. 2007; Serpe et al. 2008). This can be a major source  
214 of mortality for seedlings that germinate on crust surfaces (Jeschke and Kiehl 2008).  
215 However, if seedling roots can reach through the crust to the soil, they may find enhanced  
216 growing conditions. BSCs have been shown to positively affect seedling performance,  
217 perhaps through the higher nutrient and organic content of the soil under BSCs (Godínez-  
218 Alvarez et al. 2012; Langhans et al. 2009; Thiet et al. 2014).

219 BSCs' influence on the distribution and abundance of plant species may also have  
220 broader effects on the APB ecosystem. For example, lupines host the larvae of the federally  
221 endangered Karner blue butterfly (*Lycaeides melissa samuelis*) (Barnes 2003).  
222 Furthermore, both lupines and bush clover form symbioses with nitrogen-fixing bacteria,  
223 and N inputs from such plants are known to influence the nitrogen status of other  
224 components of the ecosystem (Rascher et al. 2012). Finally, BSCs in temperate (Sedia and  
225 Ehrenfeld 2003; Thiet et al. 2005) and dryland (Belnap 2002) systems are known to,  
226 themselves, affect soil C, N, micronutrients, and moisture. BSCs' role in northeastern barren  
227 and dune ecosystems is worthy of further study.

228 Our study is evidence that intact BSC communities can influence the plant  
229 community of pine barren ecosystems by affecting the fate of seeds. This mechanism likely  
230 contributes to the mosaic of BSC patches interwoven with vegetated patches and is likely a  
231 significant source of habitat heterogeneity. Sedia and Ehrenfeld (2003) hypothesized that  
232 BSCs and vascular plants form alternative stable states in pine barren ecosystems,  
233 potentially mediated by seasonal weather conditions. Until recently, there were relatively  
234 few efforts to further explore the interactions between BSCs and vascular plants in mesic

235 climates, and how those interactions vary over space in time (but see Büdel et al. 2014;  
236 Langhans et al. 2009; Thiet et al. 2014). We hope that further awareness of crusts outside  
237 of the arid and semiarid climates where they are more extensively studied will encourage  
238 more exploration.

239

#### 240 **Acknowledgements**

241 This research was made possible by funding from Union College in support of JAG. The  
242 Albany Pine Bush Preserve allowed us to collect crust samples and generously provided  
243 seeds for our experiment. We highlight the Preserve staff's dedicated stewardship on  
244 behalf of this unique ecosystem. Rachel Thiet made helpful suggestions on a previous  
245 version of this paper and also identified lichens found at APB. Lorinda Leonardi identified  
246 bryophytes. Jacqueline Sharry and Samantha Williams assisted with field collection.

247

248 **References**

- 249 Barnes JK (2003) Natural history of the Albany Pine Bush. New York State Museum, Albany,  
250 USA
- 251 Belnap J (2002) Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biology*  
252 *and Fertility of Soils* 35:128-135. doi:10.1007/s00374-002-0452-x
- 253 Belnap J (2003) The world at your feet: desert biological soil crusts. *Frontiers in Ecology*  
254 *and the Environment* 1:181-189. doi:doi:10.1890/1540-  
255 9295(2003)001[0181:TWAYFD]2.0.CO;2
- 256 Belnap J, Gillette DA (1997) Disturbance of biological soil crusts: impacts on potential wind  
257 erodibility of sandy desert soils in southeastern Utah. *Land Degradation &*  
258 *Development* 8:355-362. doi:doi:10.1002/(SICI)1099-145X(199712)8:4<355::AID-  
259 LDR266>3.0.CO;2-H
- 260 Belnap J, Lange OL (2001) *Biological soil crusts: Structure, function, and management.*  
261 *Ecological Studies* 150. Springer, Berlin
- 262 Bried JT, Gifford NA, Robertson KM (2015) Predicted Crown Fire Risk Adds Incentive to  
263 Restore Open-Canopy Pine Barrens at the Wildland-Urban Interface. *Journal of*  
264 *sustainable forestry* 34:147-167
- 265 Bu C, Wu S, Han F, Yang Y, Meng J (2015) The Combined Effects of Moss-Dominated  
266 Biocrusts and Vegetation on Erosion and Soil Moisture and Implications for  
267 Disturbance on the Loess Plateau, China. *PLOS ONE* 10:e0127394.  
268 doi:10.1371/journal.pone.0127394

- 269 Büdel B et al. (2014) Improved appreciation of the functioning and importance of biological  
270 soil crusts in Europe: the Soil Crust International Project (SCIN). *Biodiversity and*  
271 *Conservation* 23:1639-1658. doi:10.1007/s10531-014-0645-2
- 272 Castillo-Monroy AP, Maestre FT, Delgado-Baquerizo M, Gallardo A (2010) Biological soil  
273 crusts modulate nitrogen availability in semi-arid ecosystems: insights from a  
274 Mediterranean grassland. *Plant and Soil* 333:21-34. doi:10.1007/s11104-009-0276-  
275 7
- 276 Chamizo S, Cantón Y, Rodríguez-Caballero E, Domingo F (2016) Biocrusts positively affect  
277 the soil water balance in semiarid ecosystems. *Ecohydrology* 9:1208-1221.  
278 doi:doi:10.1002/eco.1719
- 279 Crawley MJ (1990) The population dynamics of plants. *Phil Trans R Soc Lond B* 330:125-  
280 140
- 281 Deines L, Rosentreter R, Eldridge DJ, Serpe MD (2007) Germination and seedling  
282 establishment of two annual grasses on lichen-dominated biological soil crusts.  
283 *Plant and Soil* 295:23-35. doi:10.1007/s11104-007-9256-y
- 284 Edinger GJ, D. J. Evans, S. Gebauer, T. G. Howard, D. M. Hunt, and A. M. Olivero (2014)  
285 *Ecological Communities of New York State. Second Edition. A revised and expanded*  
286 *edition of Carol Reschke's Ecological Communities of New York State. Albany, NY*
- 287 Eriksson O, Ehrlén J (1992) Seed and microsite limitation of recruitment in plant  
288 populations. *Oecologia* 91:360-364
- 289 Gawler SC, Cutko A (2010) *Natural landscapes of Maine: a guide to natural communities*  
290 *and ecosystems. Maine Natural Areas Program, Department of Conservation,*

- 291 Godínez-Alvarez H, Morín C, Rivera-Aguilar V (2012) Germination, survival and growth of  
292 three vascular plants on biological soil crusts from a Mexican tropical desert. *Plant*  
293 *Biology* 14:157-162. doi:doi:10.1111/j.1438-8677.2011.00495.x
- 294 Harper JL (1977) *Population biology of plants*. Academic Press, London
- 295 Hawkes CV (2004) Effects of biological soil crusts on seed germination of four endangered  
296 herbs in a xeric Florida shrubland during drought. *Plant Ecology* 170:121-134.  
297 doi:10.1023/b:Vege.0000019035.56245.91
- 298 Hawkes CV, Flechtner VR (2002) Biological soil crusts in a xeric Florida shrubland:  
299 Composition, abundance, and spatial heterogeneity of crusts with different  
300 disturbance histories. *Microbial Ecology* 43:1-12. doi:10.1007/s00248-001-1017-5
- 301 Hoffmann WA (1999) Fire and population dynamics of woody plants in a neotropical  
302 savanna: Matrix model projections *Ecology* 80:1354-1369. doi:doi:10.1890/0012-  
303 9658(1999)080[1354:FAPDOW]2.0.CO;2
- 304 Jeschke M, Kiehl K (2008) Effects of a dense moss layer on germination and establishment  
305 of vascular plants in newly created calcareous grasslands. *Flora - Morphology,*  
306 *Distribution, Functional Ecology of Plants* 203:557-566.  
307 doi:<https://doi.org/10.1016/j.flora.2007.09.006>
- 308 Jimenez Aguilar A, Huber-Sannwald E, Belnap J, Smart DR, Arredondo Moreno JT (2009)  
309 Biological soil crusts exhibit a dynamic response to seasonal rain and release from  
310 grazing with implications for soil stability. *Journal of Arid Environments* 73:1158-  
311 1169. doi:<https://doi.org/10.1016/j.jaridenv.2009.05.009>
- 312 Langhans TM, Storm C, Schwabe A (2009) Biological soil crusts and their  
313 microenvironment: Impact on emergence, survival and establishment of seedlings.

- 314 Flora - Morphology, Distribution, Functional Ecology of Plants 204:157-168.  
315 doi:<https://doi.org/10.1016/j.flora.2008.01.001>
- 316 Motzkin G, Foster DR (2002) Grasslands, heathlands and shrublands in coastal New  
317 England: historical interpretations and approaches to conservation. Journal of  
318 Biogeography 29:1569-1590. doi:doi:10.1046/j.1365-2699.2002.00769.x
- 319 Neher DA et al. (2003) Biological soil crust and vascular plant communities in a sand  
320 savanna of northwestern Ohio. The Journal of the Torrey Botanical Society 130:244-  
321 252. doi:10.2307/3557543
- 322 Platt WJ, Evans GW, Rathbun SL (1988) The Population Dynamics of a Long-Lived Conifer  
323 (*Pinus palustris*). The American Naturalist 131:491-525. doi:10.1086/284803
- 324 Prevéy JS, Seastedt TR (2015) Effects of precipitation change and neighboring plants on  
325 population dynamics of *Bromus tectorum* Oecologia 179:765-775.  
326 doi:10.1007/s00442-015-3398-z
- 327 Rascher KG, Hellmann C, Máguas C, Werner C (2012) Community scale <sup>15</sup>N isoscapes:  
328 tracing the spatial impact of an exotic N<sub>2</sub>-fixing invader. Ecology Letters 15:484-491
- 329 Sedia EG, Ehrenfeld JG (2003) Lichens and mosses promote alternate stable plant  
330 communities in the New Jersey Pinelands. Oikos 100:447-458.  
331 doi:doi:10.1034/j.1600-0706.2003.12058.x
- 332 Serpe MD, Zimmerman SJ, Deines L, Rosentreter R (2008) Seed water status and root tip  
333 characteristics of two annual grasses on lichen-dominated biological soil crusts.  
334 Plant and Soil 303:191-205. doi:10.1007/s11104-007-9498-8



- 335 Smith SM, Abed RMM, Gercia-Pichel F (2004) Biological soil crusts of sand dunes in Cape  
336 Cod National Seashore, Massachusetts, USA. *Microbial Ecology* 48:200-208.  
337 doi:10.1007/s00248-004-0254-9
- 338 Song G, Li X, Hui R (2017) Effect of biological soil crusts on seed germination and growth of  
339 an exotic and two native plant species in an arid ecosystem *PLOS ONE* 12:e0185839.  
340 doi:10.1371/journal.pone.0185839
- 341 Sperduto D, Kimball B (2011) *The Nature of New Hampshire: Natural Communities of the*  
342 *Granite State*. University Press of New England, Hanover, NH
- 343 Thiet RK, Boerner REJ, Nagy M, Jardine R (2005) The effect of biological soil crusts on  
344 throughput of rainwater and N into Lake Michigan sand dune soils. *Plant and Soil*  
345 278:235-251. doi:10.1007/s11104-005-8550-9
- 346 Thiet RK, Doshas A, Smith SM (2014) Effects of biocrusts and lichen-moss mats on plant  
347 productivity in a US sand dune ecosystem. *Plant and Soil* 377:235-244.  
348 doi:10.1007/s11104-013-2002-8
- 349 Weber B, Büdel B, Belnap J (2016) *Biological soil crusts: an organizing principle in*  
350 *drylands*. vol 226. Springer,
- 351 Zaady E, Gutterman Y, Boeken B (1997) The germination of mucilaginous seeds of *Plantago*  
352 *coronopus*, *Reboudia pinnata*, and *Carrichtera annua* on cyanobacterial soil crust  
353 from the Negev Desert. *Plant and Soil* 190:247-252. doi:10.1023/a:1004269031844
- 354 Zhang Y, Aradottir AL, Serpe M, Boeken B (2016) Interactions of biological soil crusts with  
355 vascular plants. In: *Biological soil crusts: an organizing principle in drylands*.  
356 Springer, pp 385-406

357 Zhang Y, Belnap J (2015) Growth responses of five desert plants as influenced by biological  
358 soil crusts from a temperate desert, China. *Ecological Research* 30:1037-1045.  
359 doi:10.1007/s11284-015-1305-z

360

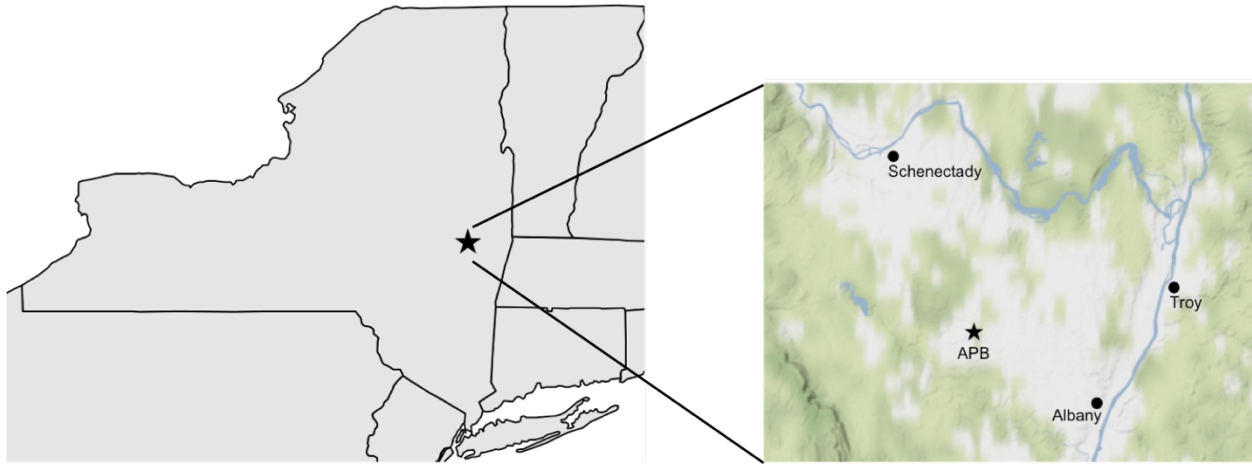
361  
 362 **Table 1:** Analysis of variance comparing the effects of soil type (crusted versus uncrusted)  
 363 and plant species (bush clover versus lupine), and their interaction, on total germination  
 364 and time to 50% of total germination (T50). Significant p-values are indicated by bold text.  
 365

Variable	Total Germination			T50		
	d.f.	F	p-value	d.f.	F	p-value
Soil type	<b>1, 36</b>	<b>54.4</b>	<b>&lt;0.0001</b>	<b>1, 30</b>	<b>42.2</b>	<b>&lt;0.0001</b>
Plant species	1, 36	0.2	0.6	<b>1, 30</b>	<b>13.0</b>	<b>0.002</b>
Soil type x Plant species	1, 36	2.4	0.13	1, 30	0.4	0.6

366

367

368



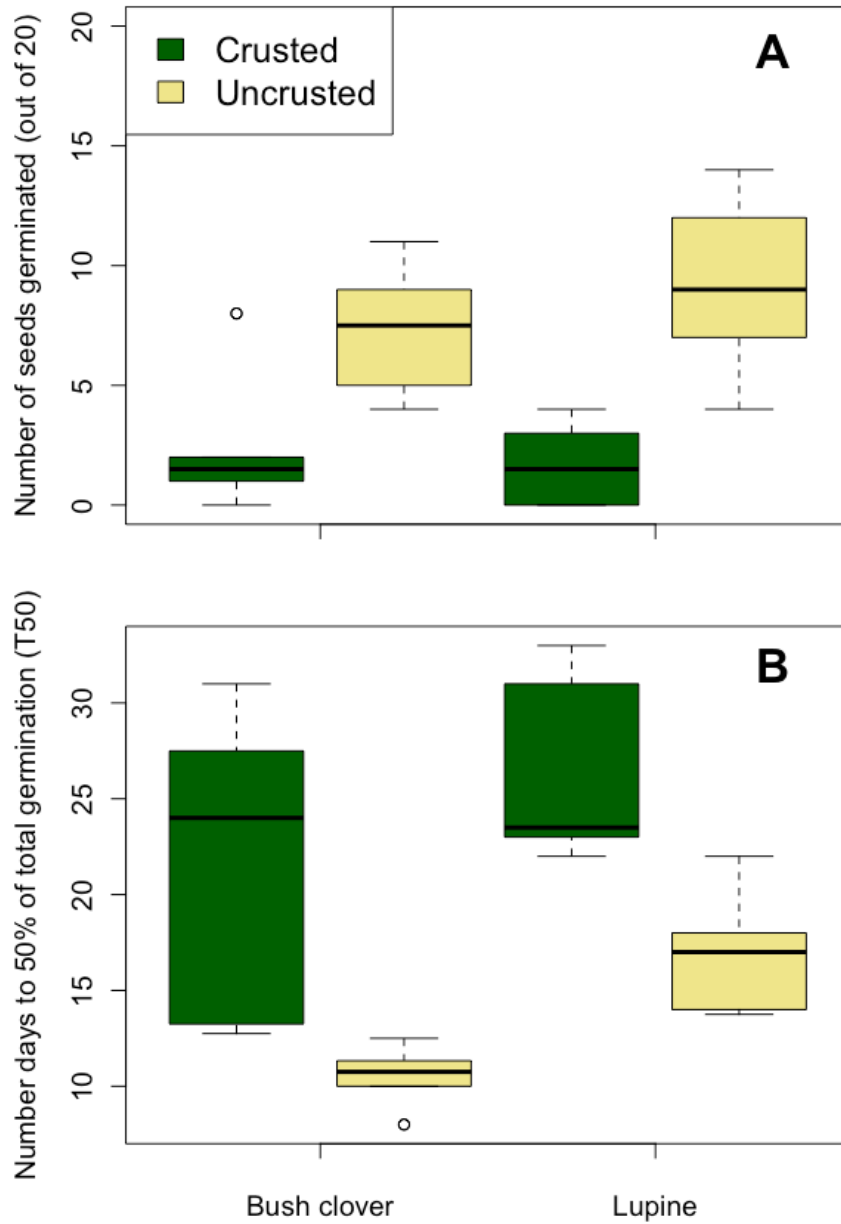
369

370

371 **Figure 1** – Study area at Albany Pine Bush Preserve in New York State, indicated by the

372 stars.

373



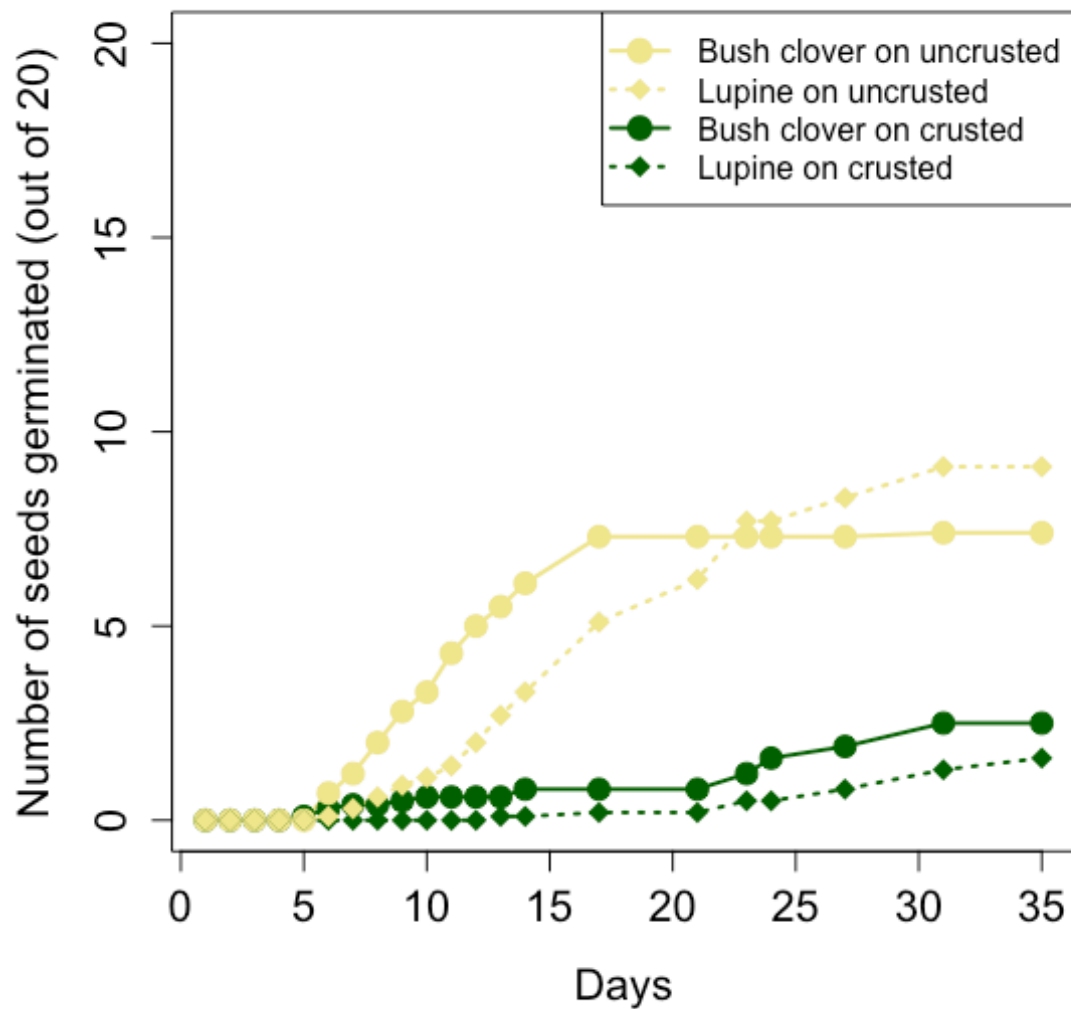
374

375 **Figure 2** – Boxplots of (A) total seed germination and (B) number of days to 50% of total  
376 germination (T50) for each soil type x plant species combination. The box in each box- and-  
377 whiskers plot represents the 25th and 75th percentiles, while the line in the middle of the

378 box is the median (50th percentile). The top and bottom whiskers extend to the most  
379 extreme data points that are no more than 1.5 times the interquartile range from the box.  
380 The open circle is an outlier beyond the whiskers. Total seed germination was lower, and  
381 T50 was longer, on crusted soils compared to uncrusted soils. A similar number of seeds  
382 germinated for each plant species, but bush clover seeds germinated significantly faster  
383 than lupine seeds.

384

385



386

387

388 **Figure 3** – Cumulative number of germinated seeds for bush clover and lupine on each soil

389 type during the 35-day experiment.

390