

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

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4 Jessica A. Gilbert^{1,2} and Jeffrey D. Corbin^{1,3}

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9 ¹Department of Biological Sciences, Union College, Schenectady, NY 12308

10 ²Orchid ID: 0000-0002-5506-666X

11 ³Corresponding Author: corbinj@union.edu; 518-388-6097;

12 Orchid ID: 0000-0002-3377-5916

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Abstract

Biological soil crusts (BSCs) are known to affect plants' germination and seedling establishment in arid ecosystems, but their ecological role in more mesic climates is not so well-known. We tested the effects of moss-crusts versus uncrusted soils on seed germination dynamics in a temperate pine barren ecosystem. We conducted a 35-day laboratory assay of seed germination on moss-crusts versus uncrusted soils from the Albany (NY) Pine Bush Preserve. We tested total seed germination and the number of days to 50% of total germination (T50) of two herbaceous perennial forb species in each soil type. Three and five times more seeds germinated on uncrusted soil than on crusted soil for bush clover (*Lespedeza capitata*) and wild lupine (*Lupinus perennis*), respectively. Seeds of both species also germinated approximately 10 days earlier on uncrusted soil than on crusted soil. This study, and others in similar habitats, show that BSCs in mesic climates can influence germination and other early life-history stages of plants. We hope that further study of the interactions between BSCs and vascular plants in mesic climates will contribute to our understanding of the ecology of BSCs outside the arid and semiarid climates where they are more extensively studied.

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

Introduction

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

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

BSCs have been most-often studied in arid to semi-arid ecosystems, but they can also occur in more mesic climates including the temperate and subtropical US (e.g. Hawkes and Flechtner 2002; Neher et al. 2003; Sedia and Ehrenfeld 2003; Smith et al. 2004; Thiet et al. 2014). BSCs in these habitats can be found in open barrens, pine barrens, pavement barrens, sand plains, and dunes, and include a diverse assemblage of algae, cyanobacteria,

lichens, and bryophytes (Corbin and Thiet, *unpublished data*). Many of these habitats are recognized as systems of high conservation value for their unique ecology and the presence of rare and threatened plants and animals (e.g. Edinger 2014; Gawler and Cutko 2010; Motzkin and Foster 2002; Sperduto and Kimball 2011).

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

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

Materials and Methods

Study Area

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

Biological soil crusts are abundant in areas of APB where fires or other recent disturbances maintain an open canopy. Vascular plants, BSCs, and uncrusted sand at APB and other pine barren ecosystems form a spatial mosaic at the scale of 0.5-10 m² per patch (Sedia and Ehrenfeld 2003; personal observation). Crust composition ranges from incipient algal mats to moss-dominated crusts that also contain lichens and cyanobacteria (Corbin and Thiet, *unpublished data*). Common species include the mosses *Ceratodon purpureus* and *Polytrichum piliferum* and the lichens *Cladonia cristatella* and *C. gracilis* ssp. *turbinata*, and *C. ochrochlora*.

Sample collection

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

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

Germination Procedure

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

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

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

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

Data Analysis

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

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

Results

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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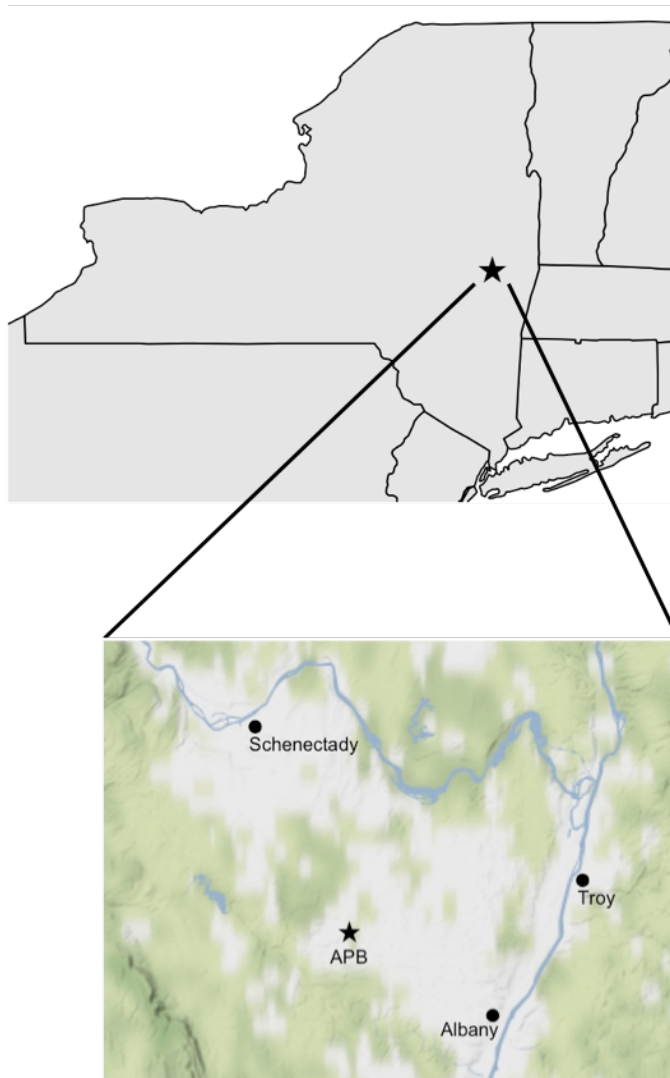
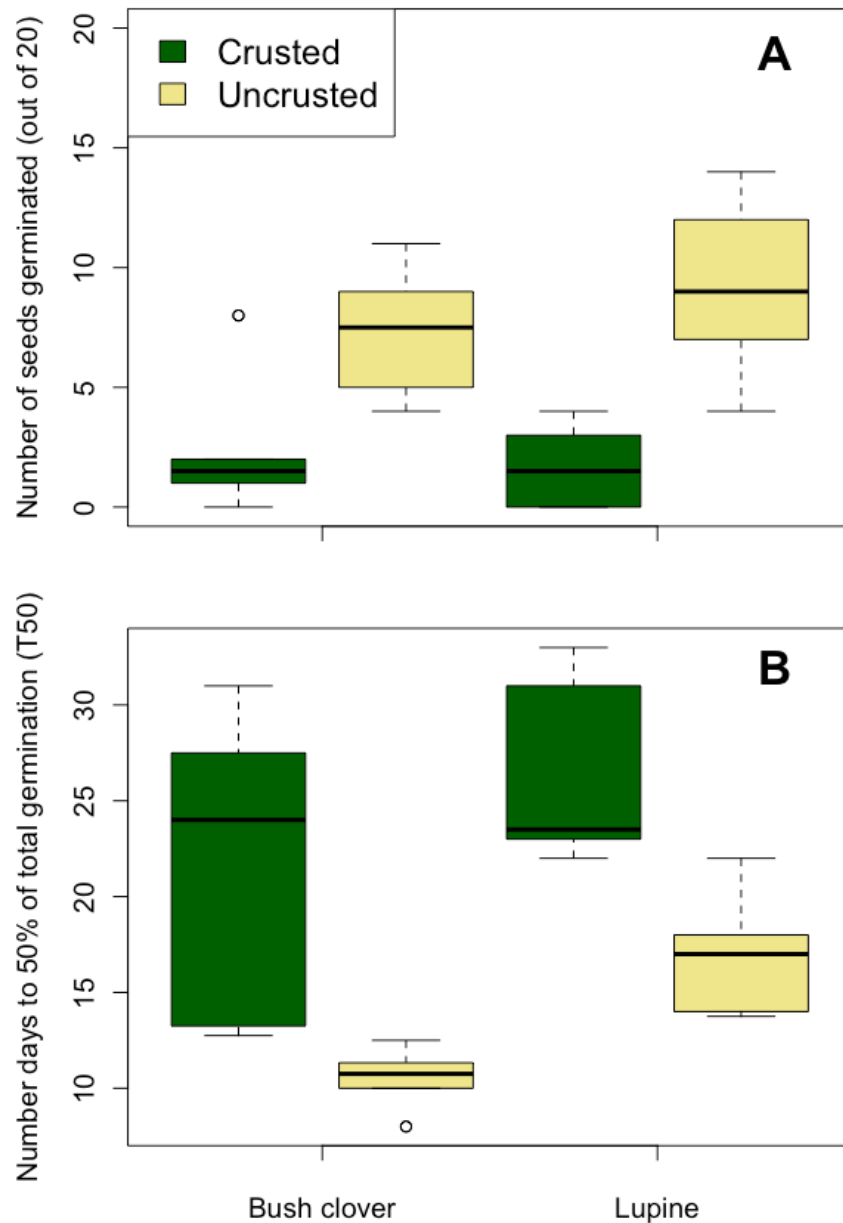


Figure 1 – Study area at Albany Pine Bush Preserve in New York State, indicated by the stars.

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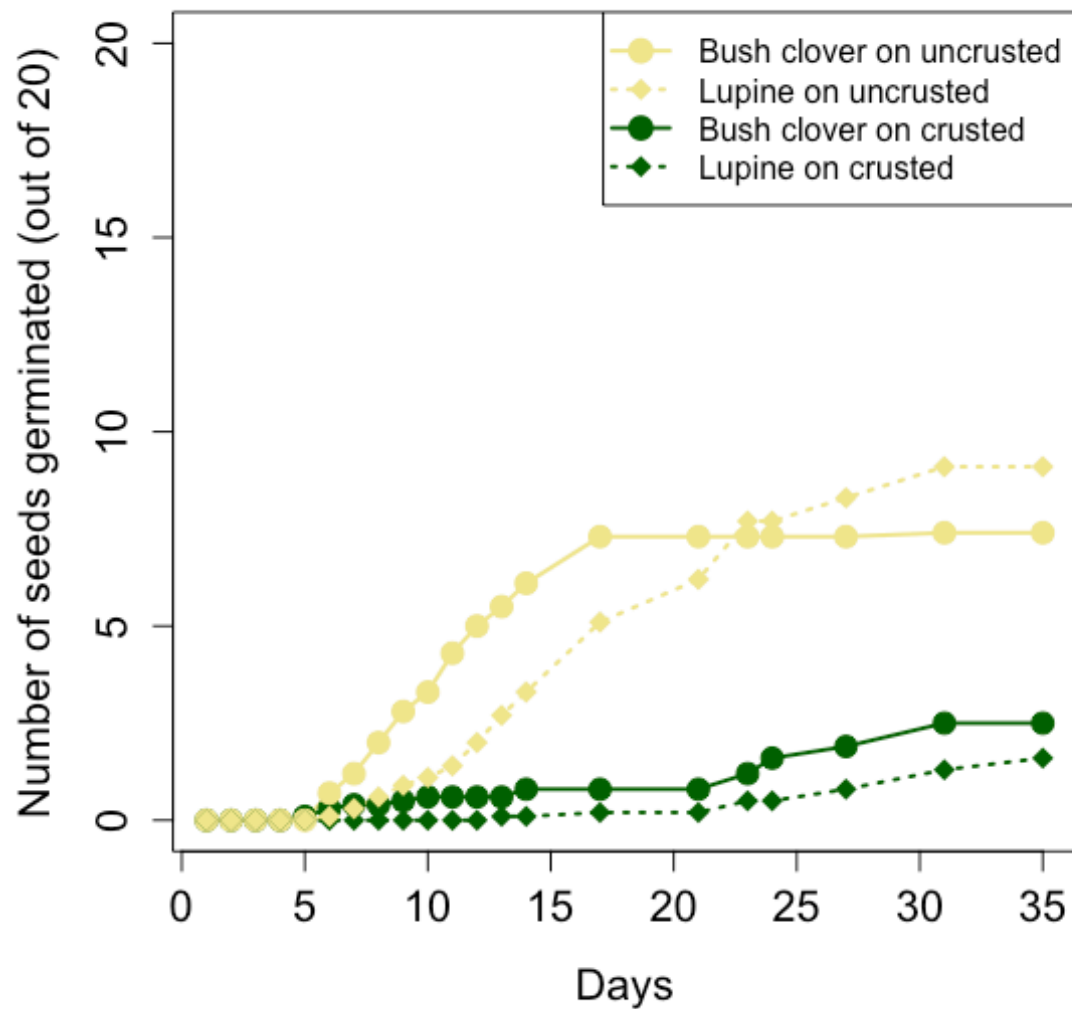
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361 **Figure 2** – Boxplots of (A) total seed germination and (B) number of days to 50% of total
 362 germination (T50) for each soil type x plant species combination. The box in each box- and-
 363 whiskers plot represents the 25th and 75th percentiles,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

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

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374 **Figure 3** – Cumulative number of germinated seeds for bush clover and lupine on each soil
375 type during the 35-day experiment.

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