JT SCIENCE

A newsletter to promote a better understanding of the natural, physical, & cultural environment in Joshua Tree National Park.

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JT SCIENCE

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OUR MISSION
Joshua Tree National Park Association (*www.joshuatree.org*) works in partnership with Joshua Tree National Park to help in its achievement of programming goals in education and interpretation, along with scientific and historical research and activities.

BEING A PART OF THE ADVENTURE
We operate four visitor centers and two park stores that are often the first stop for visitors from around the world. We also offer a field institute with classes taught by experts in natural sciences, cultural history, and the arts; we raise funds via donations and our membership program. Visit a park store to learn about wildflower identification, birding, geology, stargazing, native plants and local history; pick up climbing and hiking guides; or sign up for a Desert Institute field class and make the park your classroom.

YOUR MEMBERSHIP MATTERS
As a member, you support scientific research, the park's historical collections, youth programs, and assist in the preservation of our fragile desert. Email **membership@joshuatree.org** to find out more!

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Welcome to JT Science

The mission of JT Science is to promote a better understanding of the natural, physical, and cultural environment in Joshua Tree National Park (JTNP). Each issue highlights scientific endeavors being conducted in JTNP and provides an opportunity for scientists, land managers, and the general public to know and appreciate this desert region.

In memory of Marian Huff Tremblay
In May of 2023, we lost one of our long-standing and ardent supporters, Marian H. Tremblay. Marian was the Director of Business Operations at Joshua Tree National Park Association for 18 years. While she performed her job with fervor and proficiency, she did more than manage budgets and programs for the park. Marian truly cared about the future of JTNP and all things desert. To honor Marian's many years of hard work and dedication to the previous iterations of the Graduate Student Research Grant, we have renamed the grant: it is now called the Marian Huff Tremblay Science Scholarship.

Joshua Tree National Park Association is providing funding for the JTNP Science Research Grant Program, directly supporting this science-based newsletter for the public, as well as annual funding for the Marian Huff Tremblay Science Scholarship. The goal of the scholarship is to support graduate student researchers conducting independent field studies in JTNP and more specifically to support high-priority research needs that inform park management of socio-cultural, natural, and wilderness resources identified by the park.

Grant awardees will participate in the Desert Institute lecture series, if possible, as well as provide manuscripts for *JT Science*, public outreach materials for JTNP Interpretation staff, and final reports summarizing their findings. By offering up to $5,000 to each student, this program provides opportunities for the student to gain experience with grant and report writing skills, budget management, and most importantly, to demonstrate how their research can apply to land management issues.

To date, we have supported over 40 students, through which we have gained insight into such things as visitor awareness of tortoises; conservation implications for fringe-toed lizards and Joshua trees; microbial diversity in soils; rare plant life history; insect inventories; and discoveries of new-to-science species of poppies and green algae. The impact of the JTNP Science Research Grant Program and the contributions made by these scientists have been richly rewarding.

Enjoy the newsletter.

EDITORIAL CORRECTION

In Volume 4, Fall 2024 issue, page 2, line 2, the year should be 1936, not 1939:

"Joshua Tree National Park (JTNP) was first designated as a National Monument in 1936..."

Tiny But Deadly: Surveying Joshua Tree National Park for a Plant Pathogenic Microbe and its Diminutive Insect Vectors

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SUMMARY STATEMENT

'*Candidatus* Liberibacter solanacearum' (CLso) is a bacterial plant pathogen that causes serious disease in California crops of the nightshade family, such as potatoes, tomatoes, and bell peppers. CLso is transmitted between plants by a tiny, sap-feeding insect called the potato psyllid (*Bactericera cockerelli*). In addition to feeding on crop plants, the potato psyllid is known to feed on a variety of wild plants in the nightshade family. However, the extent to which potato psyllids and CLso impact California native plants is largely unknown. Thus, in this study, surveys were conducted to determine whether potato psyllids associate with any of the unique native plants in the nightshade family that grow in Joshua Tree National Park, and whether these potato psyllids carry the damaging CLso pathogen.

BACKGROUND & OBJECTIVES

Extensive research in crop plants has demonstrated that vector-borne pathogens, such as viruses, fungi, and bacteria, can have drastic negative effects on the health of the plants they infect. Furthermore, neither these pathogens nor their vectors are restricted to agricultural fields; they often spill over into populations of closely related wild plants (*1, 2*). However, relatively few studies have investigated the distribution and impacts of vector-borne pathogens on native plants in the natural plant communities we strive to conserve (*3, 4*). As a result, it is unclear how to incorporate vector-borne plant pathogens and their vectors into natural ecosystem conservation plans. This is the case in Southern California with a plant pathogen called '*Candidatus* Liberibacter solanacearum' (CLso) and its insect vector, the potato psyllid (*Bactericera cockerelli*).

CLso is a bacterial plant pathogen that has been responsible for substantial vegetable crop losses throughout western North America over the past few decades. CLso affects a variety of plants in the nightshade family, Solanaceae, including bell pepper, tomato, eggplant, and tomatillo. However, it is most notorious as the causal agent of a condition called 'zebra chip disease' of potato (*5*). This disease causes malformation and discoloration of potato tubers that make them unpalatable for consumption. Moreover, in the most severe outbreak years, it can cause 100% potato crop failures (*6*). To manage this destructive disease, there has been a focused research effort aimed at understanding the biology and ecology of CLso in agricultural settings over the past couple of decades.

What we have learned from this research is that CLso relies on insect vectors to facilitate its spread between individual host plants, as well as between fields of crops distributed across large geographic distances. In North America, the insect species responsible for transmitting CLso between crop plants is the potato psyllid (*B. cockerelli*, Fig. 1) (*7*). The potato psyllid is a tiny, sap-feeding insect in the order Hemiptera, which is closely related to aphids and whiteflies. It's native to central and western

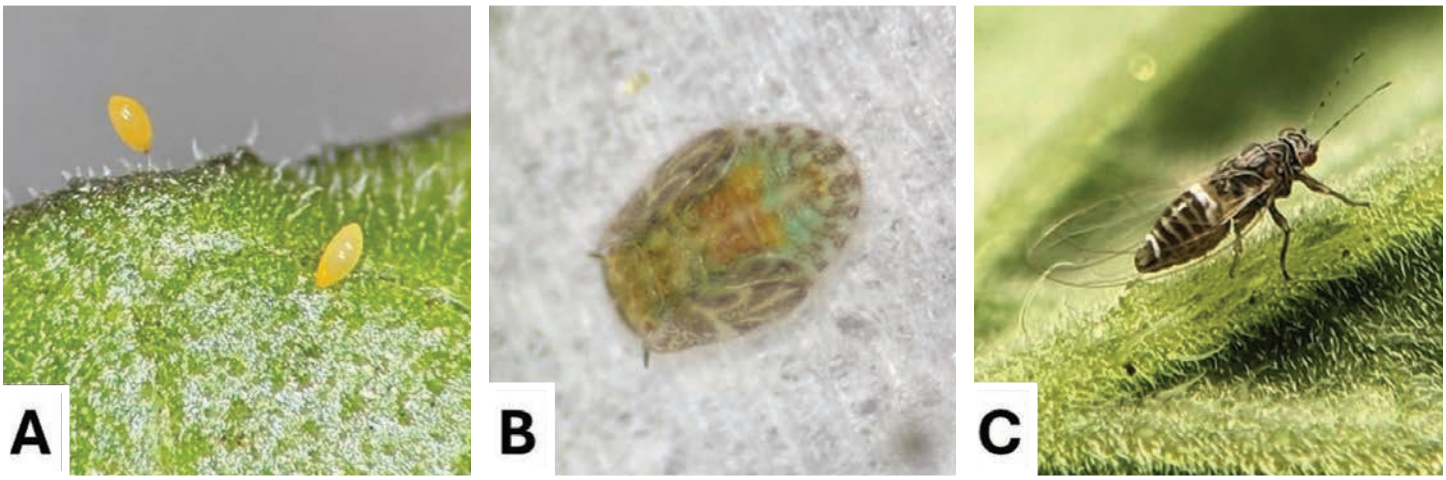

Figure 1. Potato psyllid (*Bactericera cockerelli*) (A) eggs, (B) juvenile, and (C) adult. **Photo credits: A & B: Jaimie Kenney, C: Kerry Mauck.**

North America, where it is known to feed and reproduce on a wide variety of plants in the nightshade family, including both crops and native species.

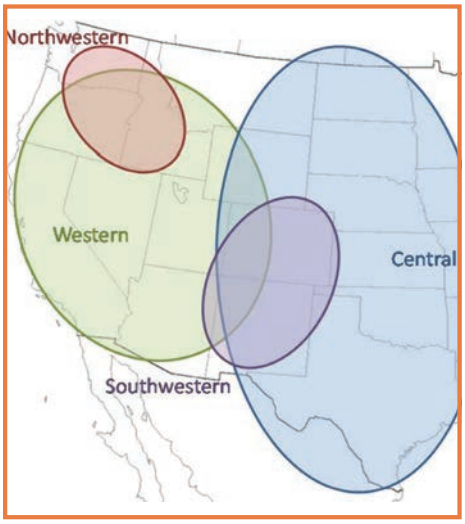

Figure 2. Map showing inferred distribution (based on data from 8–10) of four potato psyllid genetic groups (Central, Northwestern, Southwestern, and Western) in North America prior to our work in 2024 (*18*).

Four distinct genetic groups of the potato psyllid have been identified in North America (Fig. 2), and due to biological and ecological differences between these groups, they vary in their importance as vectors of CLso (*8, 9*). While the geographic ranges of these four genetic groups overlap to some extent (*10*), they are named after the regions of the U.S. where they are most often found in crops: the Central, Northwestern, Southwestern, and Western genetic groups. The groups that are most often associated with CLso transmission and disease in crops are the Central and Western groups, whereas there is evidence that the Northwestern group is a much less efficient vector of CLso (*11*). The Southwestern group's role in transmitting CLso is not well understood, as it is infrequently observed in crop systems, and, therefore, has received relatively little study.

Western potato psyllids and CLso have both been present in California pepper, potato, and tomato fields for at least 15 years, during which time their impact on crop plants has been the focus of a number of studies (*12–16*). However, the distribution, abundance, and diversity of CLso and potato psyllids in California natural plant communities, or how CLso might be affecting the health of these communities, had never been explored, despite the fact that native nightshades are widespread and abundant in California. We recently addressed this knowledge gap by surveying populations of the herbaceous, native nightshade *Solanum umbelliferum* in western Riverside County for potato psyllids and CLso. In that study, we used targeted PCR and Sanger sequencing to test individual plants and psyllids for CLso infection, as well as to determine the genetic group of the each CLso isolate and potato psyllid specimen. This work revealed that potato psyllids and CLso are virtually ubiquitous in natural plant communities in this region (*17, 18*). Furthermore, instead of detecting Western potato psyllids, we found Northwestern and Southwestern potato psyllids associated with these native plants, suggesting that although they may not be important vectors of CLso in crops, these genetic groups may be responsible for transmission of CLso among native plants.

Overall, these results suggest that potato psyllids and CLso may be common members of a variety of southern California ecosystems, and that further research is needed to fully understand the risk this pathogen and vector may pose to California's unique native flora.

The inland deserts of Southern California, in particular, are home to a number of unique native perennial plants in the nightshade family that may be at high risk of CLso infection, as they are closely related to other known potato psyllid and CLso host plant species. These include plants in the genera *Lycium* (relatives of Goji berry) (*19, 20*) and *Physalis* (wild tomatillos) (*21, 22*), such as *L. andersonii* (Anderson's wolfberry; Fig. 3A), *L. cooperi* (Cooper's box thorn; Fig. 3B), and *P. crassifolia* (thick-leaf groundcherry; Fig. 3C). All three of these plants are common throughout Joshua Tree National Park (JTNP). However, prior to the present study it was completely unknown whether potato psyllids visited *L. andersonii*, *L. cooperi*, or *P. crassifolia* in California, or what implications this might have for the conservation of these native perennial plants in JTNP and other natural reserves in this region.

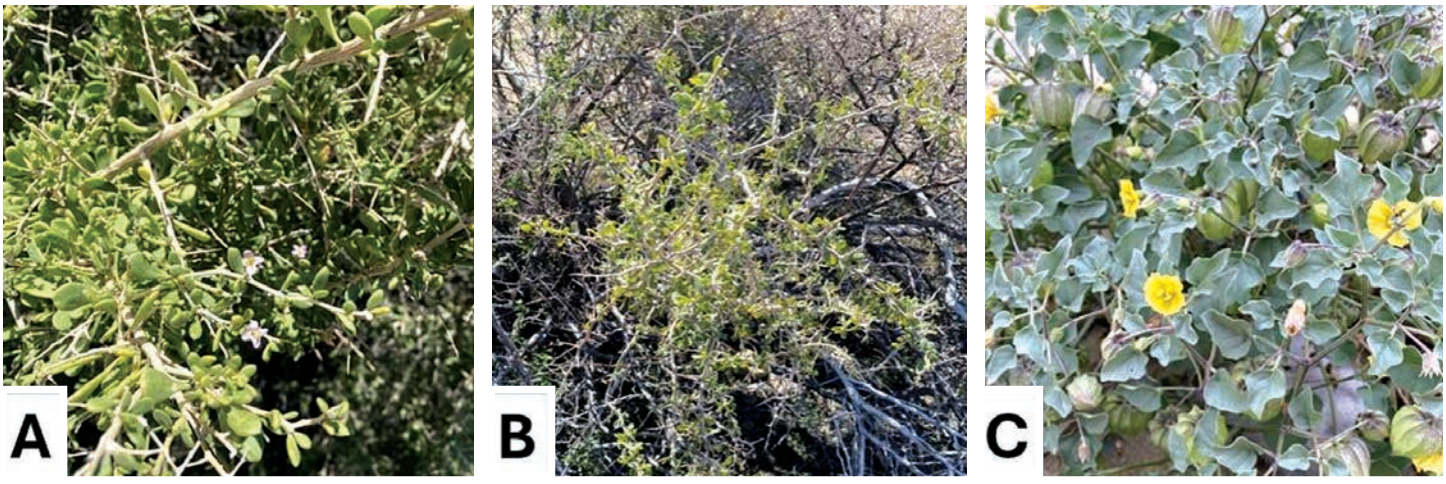

Figure 3. Three native species from the Solanaceae found in Joshua Tree National Park: (A) *Lycium andersonii* (Anderson's wolfberry), (B) *Lycium cooperi* (Cooper's box thorn), and (C) *Physalis crassifolia* (thick-leaf groundcherry). **Photo credits: Jaimie Kenney.**

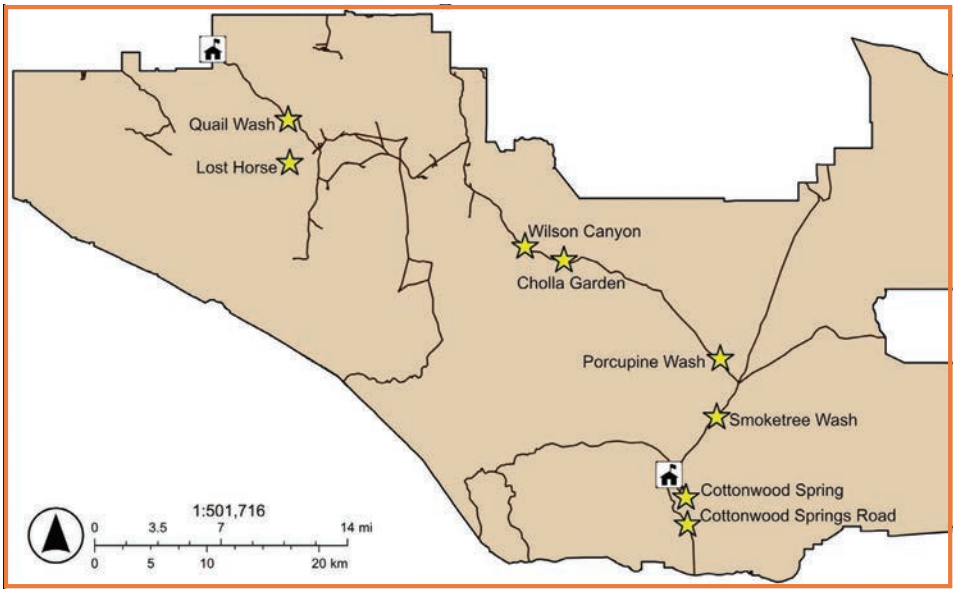

Figure 4 (left). Map of psyllid sampling sites in Joshua Tree National Park. Quail Wash and Lost Horse were manually surveyed in November of 2023. At all other locations a combination of manual surveys and trapping were used to monitor psyllids from February to April of 2023.

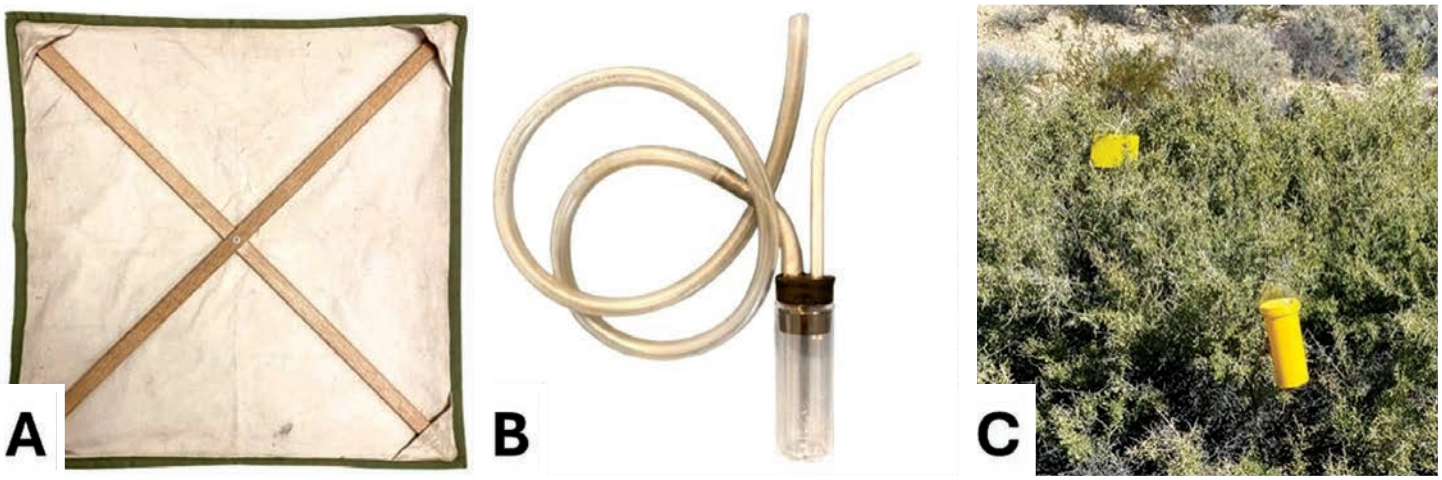

Figure 5 (below). Manual collection of insects required shaking the plant over top of (A) a canvas sheet for collecting insects, then collecting the psyllids from the sheet with an (B) insect aspirator. For trapping, we used (C) yellow sticky cards and cylindrical psyllid traps attached to the canopy of the shrub. **Photo credits: Jaimie Kenney.**

This study aimed to address this knowledge gap to help evaluate the risk posed to native California desert plants by potato psyllids and CLso, via two primary objectives:

1. Determining whether potato psyllids visit three common plants of the nightshade family in JTNP (*Lycium andersonii*, *L. cooperi*, or *Physalis crassifolia*), and if so, which of the four genetic groups these potato psyllids belong to (Central, Northwestern, Southwestern, or Western).

2. Quantifying the proportion of these psyllids that carry the CLso pathogen.

Here it should be noted that it can be very difficult to directly detect CLso infections in wild plants, which is due to a couple of key reasons. Firstly, the most effective way to diagnose CLso infection in any organism is by collecting a tissue sample, extracting DNA from that tissue, and then running a PCR test. However, wild plants often contain large amounts of chemical compounds, such as polysaccharides and phenolics, in their tissues to protect themselves from attack by insects and other forms of biotic and abiotic stress. These chemical compounds are difficult to remove from DNA samples and are notorious for inhibiting the functioning of PCR tests (*23, 24*). Furthermore, the distribution of CLso bacteria within the tissues of a plant is often not consistent (*25, 26*). In large, woody perennials, such as *L. andersonii* or *L. cooperi*, evidence from close relatives suggests that CLso may colonize one stem of the plant, but be undetectable in stems or leaves on another portion of the same plant (*27, 28*). Thus, when testing wild plants for CLso infection, there is a very high chance of false negative results.

Fortunately, these problems do not exist when it comes to testing psyllids for CLso. Therefore, instead of directly testing native plant tissue samples for CLso, we opted to test the tissues of psyllids collected from these plants. What's more, rather than simply determining how many plants are infected at the present moment, assessing rates of CLso in psyllid vectors can give us an idea of how fast the pathogen is likely spreading to new host plants.

METHODS

To accomplish these objectives, we sampled psyllids visiting *Lycium andersonii*, *L. cooperi*, and *Physalis crassifolia* across eight field sites (Fig. 4) during two key seasons at JTNP. From February to April of 2023, we performed manual sampling and biweekly trapping at six sites. In November 2023, we noticed a second wave of vegetative growth in response to summer rains, so we performed manual sampling at two additional sites in the northern portion of the park (Lost Horse and Quail Wash).

Manual surveys for psyllids consisted of shaking plants over a sheet of canvas (Fig. 5A) to dislodge insects and then collecting live psyllids from the canvas directly into vials using a special apparatus called an insect aspirator (Fig. 5B). Trapping was performed with yellow sticky card traps, as well as cylindrical psyllid traps specifically designed to funnel insects directly into vials of nontoxic preservative solution and protect them from the elements (Fig. 5C) (*29*). At trapping sites, one 4" x 6" yellow sticky card and one cylindrical psyllid trap were hung at canopy height on one representative plant of each species at each sampling site. The sticky cards and vials of preservative inside the cylindrical traps were collected and replaced every two weeks from February 11 to April 11, 2023. In total, we captured 871 *Bactericera cockerelli* in JTNP over the course of this study.

Upon returning to the laboratory at UC Riverside, all collected psyllids were examined under a dissecting scope, identified to species, photographed, and temporarily stored in vials of ethanol in the freezer. A representative subset of the psyllid specimens collected, spanning all sampling sites and dates from February to April of 2023, were then selected for DNA extraction. DNA was isolated from individual psyllids using a commercially available Qiagen DNEasy Blood & Tissue DNA extraction kit according to the manufacturer's recommendations for use with insect specimens. The resulting DNA samples were used to perform targeted PCR reactions and Sanger sequencing to determine which of the four genetic groups (Central, Northwestern, Southwestern, or Western) each psyllid specimen belonged to, as well as to screen each individual psyllid for infection with the CLso pathogen.

Host Plant Species	Sampling Period	
	February-April 2023	November 2023
Ericameria cooperi	*N/A*	19
Ericameria cuneata	*N/A*	4
Lycium andersonii	664	8
Lycium cooperi	35	69
Physalis crassifolia	72	*N/A*

Table 1. Total number of potato psyllids (*Bactericera cockerelli*) collected from each host plant species during each of two sampling periods.

RESULTS

Our psyllid surveys and trapping revealed that potato psyllids (*Bactericera cockerelli*) commonly visit native perennials in the nightshade family in JTNP. *Bactericera cockerelli* were present in JTNP throughout the entire primary sampling period of February to April, as well as in November of 2023. We frequently collected *B. cockerelli* from *Lycium andersonii* (Figs. 3A, 6A, and Table 1) and *Physalis crassifolia* (Fig. 3A and Table 1) throughout the park from February to April of 2023. In February and March, we observed evidence that *B. cockerelli* was reproducing on these two host plant species (presence of eggs and juveniles). Additionally, we recovered small numbers of *B. cockerelli* from *L. cooperi* in February–April and many more in November 2023 (Table 1). However, no signs of reproduction were ever observed on this host.

In addition to *B. cockerelli*, our surveys revealed the presence of two other closely-related psyllid species associated with native *Lycium* in JTNP: *Bactericera dorsalis* (Fig. 6B) and *Bactericera lobata* (Fig. 6C). A total of 14 *B. dorsalis* were found co-occurring with *B. cockerelli* on *L. andersonii* in February and April, and a total of two *B. lobata* were captured together with *B. cockerelli* from *L. cooperi* in November of 2023. Another interesting observation from the November 2023 sampling was that we found some specimens of *B. cockerelli* on two shrubs from the Asteraceae family (i.e. not Solanaceae): *Ericameria cuneata* and *E. cooperi*.

Ultimately, we were able to extract DNA from 213 of the potato psyllids we captured throughout the February to April 2023 sampling period, approximately 25% of the total specimens we had collected. DNA sequencing revealed that all 213 of these potato psyllids

Figure 6. (A) A potato psyllid (*Bactericera cockerelli*) on *Lycium andersonii* in JTNP. (B) *Bactericera dorsalis* and (C) *Bactericera lobata* captured in JTNP. **Photo credits: Jaimie Kenney.**

belonged to the Southwestern genetic group. Of the 213 potato psyllid (*B. cockerelli*) specimens tested for the CLso pathogen, zero tested positive.

DISCUSSION & MANAGEMENT IMPLICATIONS

Our results revealed that potato psyllids not only occasionally visit native perennials in the nightshade family in JTNP, but large populations of them likely reproduce on these plants throughout the late winter and spring each year. Therefore, opportunities for potato psyllids to potentially transmit the CLso pathogen among populations of *Lycium andersonii*, *L. cooperi,* and *Physalis crassifolia* in JTNP are plentiful. Nonetheless, none of the potato psyllids that we screened tested positive for CLso. Furthermore, all of the potato psyllids we tested belonged to the Southwestern genetic group, and unlike the Central and Western groups, the Southwestern group is not known to be an important vector of CLso in crops (*8*). These results suggest that the current risk of CLso transmission to native plants in JTNP is probably low, despite the presence of a large potato psyllid population within the park. However, because CLso prevalence in psyllid populations can vary greatly across seasons and years, repeated, broader sampling is recommended to confirm JTNP's pathogen-free status.

In addition to potato psyllids, we discovered two additional psyllid species feeding on native *Lycium* species in JTNP that could potentially serve as vectors of CLso in desert plant communities, *Bactericera dorsalis* and *B. lobata* (Fig. 5). This is the first record of *B. dorsalis* in California (*30*). However, *B. dorsalis* is known to associate with *Lycium* species in Arizona, Florida, and Texas, and in controlled greenhouse experiments it has been demonstrated to be capable of acquiring the CLso pathogen from infected *Lycium* plants (*19*). While *B. lobata* has previously been documented on *Lycium* spp. in California, Arizona, Colorado, Nevada, New Mexico, and Wyoming (*30*), it is unknown whether this species can transmit CLso. However, the presence of both *B. dorsalis* and *B. lobata* co-occurring with *B. cockerelli* on native *L. andersonii* and *L. cooperi*, respectively, could present opportunities for CLso to jump from *B. cockerelli* to *B. dorsalis* or *B. lobata* in the future, should CLso become introduced into JTNP populations of *B. cockerelli*.

Overall, the results of this study suggest that the risk of harm to native plants in JTNP via infection with CLso is probably low at this time, and no management action is currently necessary. However, the proximity of commercial fields of potatoes, bell peppers, and tomatoes in the Coachella and Imperial Valleys, as well as native *S. umbelliferum* populations harboring Western and Northwestern potato psyllids infected with CLso (*18*), present opportunities for CLso to potentially become introduced into JTNP plant and potato psyllid populations in the future. If this should occur, the high density of resident potato psyllids feeding on *L. andersonii*, *L. cooperi*, and *P. crassifolia* in both the early spring and fall could facilitate the rapid spread of CLso through populations of these native plants in JTNP. Furthermore, the presence of *B. dorsalis* and *B. lobata* in these same plant populations could potentially exacerbate the spread of this pathogen. Therefore, controlled CLso transmission assays directly evaluating the effect of CLso infection on *L. andersonii*, *L. cooperi*, and *P. crassifolia* are still recommended, and intermittent screening of JTNP psyllid populations for CLso should be considered. Moreover, if symptoms of disease are observed affecting *L. andersonii*, *L. cooperi*, and *P. crassifolia* in JTNP in the future, CLso should be considered first as a likely potential culprit.

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A Perspective: Biocrust Cyanobacteria as a Fundamental Desert Resource

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CYANOBACTERIA AS A FUNDAMENTAL DESERT RESOURCE

Deserts are home to diverse animals, plants, and microscopic life (*1*). Among this biodiversity, cyanobacteria are a group of bacteria that play key roles in maintaining desert ecosystems. They influence the availability of essential nutrients such as carbon, nitrogen, and phosphorus. Like plants, cyanobacteria can photosynthesize, transforming atmospheric carbon dioxide into sugars and other organic molecules (*2*). In the desert, this is an essential pathway that channels carbon into a system where it's otherwise scarce.

In addition to photosynthesis, some cyanobacteria can carry out a specialized process called nitrogen fixation. Through this process, they can capture nitrogen from the air and sequester it into their biomass because it is a key component of proteins and nucleic acids (*3*). Upon cyanobacterial cell death and waste excretion, this "fixed" nitrogen is released to the soil and becomes available to other microbes and plants (*4*). Similarly, phosphorus is another nutrient essential for life; it is the backbone of nucleic acids, lipids, and the energy currency of cells (*5*). In the desert, phosphorus is often a limiting soil nutrient because highly abundant calcium carbonate minerals bind with phosphorus, forming insoluble compounds that limit its bioavailability (*6*). Cyanobacteria can excrete organic acids such as citric acid that release the phosphorus from the minerals, locally increasing available phosphorus in desert soils (*7, 8*). In sum, cyanobacteria represent key players in desert soil biogeochemistry, mediating the cycling of carbon, nitrogen, and phosphorus.

Besides increasing the availability of essential nutrients to other desert organisms, cyanobacteria are pioneer species, colonizing bare and disturbed soils (*9*). Cyanobacteria do this by forming thread-like chains of cells surrounded by a protective jelly-like layer, collectively forming filaments that can weave through the soil matrix. The jelly layer is made of excreted long, sugar-based molecules called exopolysaccharides (EPS) that are very sticky, causing soil particles to bind together, promoting soil aggregation, and ultimately stabilizing the desert soil (*10*). Consequently, filamentous soil cyanobacteria are now recognized as keystone species, and are responsible for forming important microhabitats known as biological soil crusts (hereafter biocrusts, Fig. 1) (*9*). Biocrusts are living soil aggregates in the topsoil of deserts

Figure 1. Soil crust with lichens in JTNP. **Photo credit: Paul DeLey.**

and can contain cyanobacteria, lichens, mosses, green algae, free-living fungi, other bacteria, and even diatoms (*11*). Biocrusts are important for desert ecosystems because they hold soil in place, improve water retention, and can impact plant germination (*12, 13*). In Joshua Tree National Park (JTNP), the most common biocrust types are cyanobacteria-dominated crusts with *Microcoleus*, *Symplocastrum*, *Nostoc*, *Oculatella*, *Spirirestis*, *Kalymmatonema*, *Trichocoleus*, *Myxacorys*, and *Trichotorquatus* species being the prominent cyanobacterial taxa (*14, 15*). Lichen and moss-dominated crusts are patchy; *Collema coccophorum*, *Clavascidium lacinulatum*, and *Heppia* spp. being commonly found lichen taxa (*16*), while species of *Syntrichia*, *Pterygoneurum*, and *Bryum* are common mosses (*17*).

In this Perspective, we highlight how biocrust cyanobacteria, with their unique physiological characteristics, represent a fundamental but poorly understood and rarely recognized desert resource with immense potential to yield nature-based solutions for desert restoration. Additionally, we emphasize the need for and importance of studying the physiology of biocrust cyanobacteria, especially when exposed to environmental stresses of desert ecosystems, while also highlighting current obstacles of such research. Finally, we share insights from our research investigating how nutrients such as phosphorus can limit the growth of biocrust cyanobacteria, with implications for restoration in JTNP and other desert ecosystems.

CYANOBACTERIA DIVERSITY AND FUNCTIONAL TRAITS ARE IMPORTANT FOR DESERT SOIL

Our knowledge of desert cyanobacteria diversity is rapidly expanding due to advancements in microscopy, DNA sequencing, and other molecular characterization tools. For example, in JTNP, several species were discovered in the past two decades with the descriptions of *Oculatella coburnii* (Fig. 1C) (*18*), *Symplocastrum flechtnerae* (*19*), *Roholtiella mojaviensis* (*20*), *Myxacorys californica* (*21*), *Trichotorquatus ladouxae* and *T. andrei* (*22*), and *Kalymmatonema desertorum* (*23*). These previous studies not only revealed cyanobacterial biodiversity but also highlighted the presence of unique phenotypic traits such as specialized cells used to track light (e.g., *Oculatella* spp.), cells to fix nitrogen (e.g., *Roholtiella* and *Kalymmatonema* spp.), dark pigments that act as sun protection (e.g., *Kalymmatonema* spp.), and a slimy EPS layer around the cells to retain water or bind nutrients (e.g., *Symplocastrum*).

These fascinating traits are often recognized as functional traits — they are vital for the survival of cyanobacteria in deserts and contribute to ecosystem processes (*21*, *24*, *25*, and *26*). One of the most important functions cyanobacteria perform is photosynthesis. Through photosynthesis, cyanobacteria convert atmospheric carbon dioxide into glucose and other organic molecules, providing energy for their growth (*2*). These organic molecules contribute to the buildup of cyanobacteria biomass, which can then serve as a food source for desert microfauna such as protists, nematodes, tardigrades, and rotifers, supporting the base of the desert food web (*27*). However, the rates at which carbon dioxide is fixed and turned into biomass vary by species due to their specific life history strategies and the biogeochemical processes in the soil. In addition, some cyanobacteria develop specialized cells called heterocytes (*28*). These cells can fix atmospheric nitrogen and transform it into ammonia or related inorganic compounds that cyanobacteria use for their growth (*29*). When cyanobacterial cells die or leak cellular contents, some of the inorganic nitrogen compounds become available to plants and other microbes in the surrounding soil (*3*). Another functional trait is the production of EPS, which acts as a shield protecting cyanobacterial cells against desiccation and UV-radiation (*29*). The sticky nature of EPS promotes soil stabilization and water retention (*3, 30*). Given their critical roles in carbon and nitrogen cycling and soil stabilization, integrating cyanobacteria in restoration efforts may be a promising strategy for managing degraded desert ecosystems.

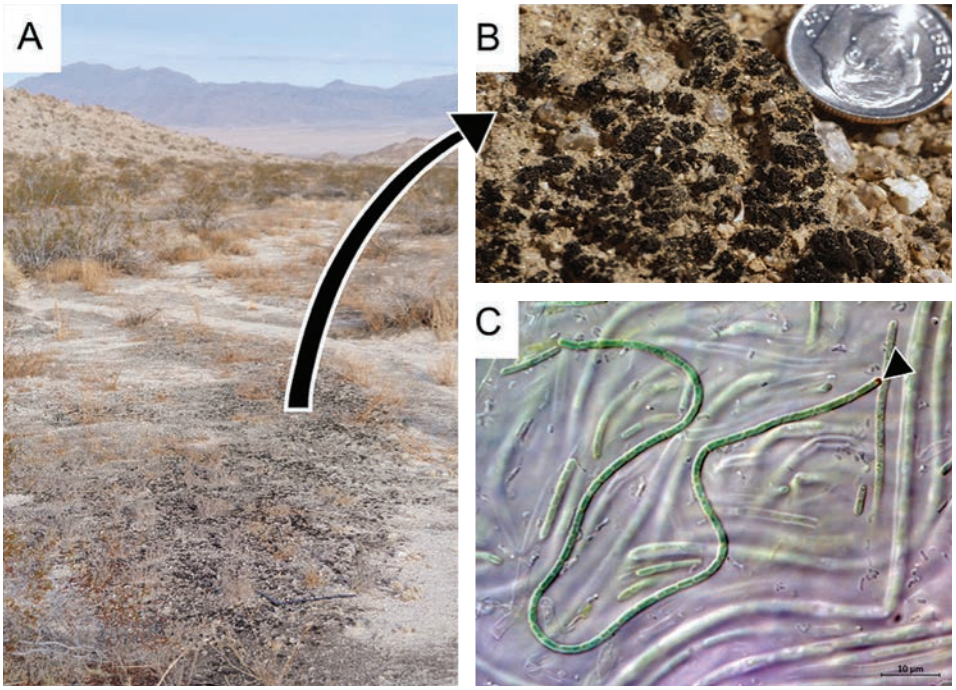

Figure 2. Cyanobacteria from biocrusts in Joshua Tree National Park (JTNP). (A) A typical biocrusted landscape in JTNP. (B) Close-up view of a biocrust dominated by cyanobacteria and the lichen *Collema coccophorum*. (C) A micrograph of the filamentous biocrust cyanobacterium, *Oculatella coburnii* strain WJT66-NPBG6A, showing a specialized pigment containing cell at the end used to track light (black triangle). This pigment inclusion is a diagnostic character of the genus *Oculatella* (*18*). **Photo credits: Paul De Ley.**

APPROACHES AND LIMITATIONS OF BIOCRUST CYANOBACTERIA INOCULATION FOR DESERT RESTORATION

Due to their ecological importance in deserts and their key roles in biocrust formation, cyanobacteria are used to restore degraded desert soils (*31*, *32*). However, inoculation efforts of cyanobacteria in soils under natural field conditions often fail to establish new biocrusts due to the low survival of cyanobacteria caused by environmental stressors such as UV-radiation and high light intensity (*33*, *34*). Hence, studying how cyanobacteria tolerate different stressors might give insights into their survival in desert soils, which can inform and enhance restoration practices. Contemporary

restoration projects in many deserts around the world are now investigating how to promote the formation of biocrusts with cyanobacteria using laboratory, greenhouse, and field experiments (*31*, *32*).

Laboratory experiments use controlled stressors to improve cyanobacterial inoculation success. Exposing lab-grown strains to stressors similar to those in natural environments is called preconditioning. One study exposed biocrusts to wet-dry cycles and a gradual increase in light intensity in the lab to precondition biocrust cyanobacteria from the Chihuahuan Desert (*35*). This was designed to help cyanobacteria survive after being moved from the controlled laboratory environment to a natural setting. Thirteen of the twenty preconditioned cyanobacteria cultures had higher growth than nonconditioned cultures after inoculation into field-collected soils under outdoor conditions. Four cultures were indifferent to preconditions, and three had lower growth than nonconditioned cultures. This experiment, conducted by Giraldo-Silva et al. (*35*), suggested that preconditioning cyanobacteria may be an important step to enhance the success of inocula establishment in future restoration efforts. Their results also highlight that not all cyanobacteria respond equally to environmental stresses, indicating that the selection of cyanobacteria that tolerate local environmental conditions could improve restoration efforts.

Greenhouse experiments are used to propagate cyanobacteria in conditions closer to natural conditions rather than laboratory experiments, as a greenhouse environment is more variable than a laboratory environment. For example, one experiment collected biocrusts from the Chihuahuan Desert and grew them in greenhouse nursery facilities to evaluate whether the biocrust microbial communities, particularly cyanobacteria, could be propagated at larger volumes to produce effective inoculum for restoration (*36*). After 90 days in the greenhouse, the researchers analyzed the microbial community composition to assess which microbial groups became dominant. Cyanobacteria were the dominant bacterial group under these conditions. These results suggest that greenhouse incubation may promote cyanobacterial growth under semi-natural conditions. Beyond the greenhouse, field experiments aim to determine how cyanobacterial inocula perform under natural conditions. For example, Chiquoine et al. (*37*) inoculated biocrusts, which were previously collected and stored dry for two years, in disturbed soils of the Mojave Desert. After eighteen months in natural field conditions, they subsampled the inoculated biocrust and quantified the cyanobacterial density. They found that biocrust inoculation increased the cyanobacteria density and soil stability compared to treatments without biocrust inoculation. However, in natural conditions, success is not guaranteed. For example, Kubečková et al. (*33*) inoculated *Microcoleus vaginatus* JT-15, a filamentous cyanobacterium, in specific soil plots of Fort Irwin National Training Center, Mojave Desert, California. They took samples of the soil plots at 6-, 12-, and 18-months post-inoculation to examine cyanobacterial biomass. Cyanobacterial biomass was not detected after 18 months, and the authors suggested that the UV radiation present in hot desert habitats likely killed the inoculated cyanobacteria.

In addition to UV radiation, other stressors, such as low availability of nutrients, particularly nitrogen and phosphorus, might also limit cyanobacterial growth, as these elements are key components of proteins and nucleic acids, and are often scarce in desert soils (*5*, *8*). Yet, the physiological response of biocrust cyanobacteria to phosphorus limitation remains poorly understood. Research suggests that phosphorus limitation can inhibit the growth of aquatic cyanobacteria and may increase the production of EPS to enhance phosphorus availability (*38*). However, this hypothesis remains untested in biocrust cyanobacteria and requires empirical validation.

Another challenge facing cyanobacteria restoration is the uncertainty of population ranges, which could increase risk of non-native cyanobacteria introductions to the target restoration site (*39-42*). This often occurs because well-characterized or readily culturable strains from other locations are used as inocula, while the native cyanobacterial communities of the restoration site remain poorly documented (*39*). The use of non-native cyanobacteria may lead to changes in the diversity and composition of indigenous microbes of the target area, affecting the ecosystem health in the long term (*43*). Laboratory, greenhouse, and field experiments exhibit many challenges in using cyanobacteria for dryland restoration. They highlight the importance of better characterizing the physiology of candidate cyanobacteria under desert stressors, especially those cyanobacteria native to the target restoration site (*39*).

CHALLENGES IN STUDYING THE PHYSIOLOGY OF BIOCRUST CYANOBACTERIA

Despite the critical need to understand the basic biology of biocrust cyanobacteria, several bottlenecks challenge physiological studies of these enigmatic organisms. These include difficulties in taxonomic identification, methodological limitations in measuring their growth, and the paucity of species records. The first challenge is the accurate identification of cyanobacteria. Historically, cyanobacteria were classified and named based on morphological traits (*44*). However, cyanobacteria with similar morphological traits do not necessarily belong to the same species, and sometimes not even to the same genus. Many lineages represent what taxonomic experts call cryptic species and cryptogenera (*45*). Cryptic species found in the Mojave Desert include *Oculatella coburnii* and *Oculatella mojaviensis*. They are morphologically indistinguishable from each other, and only genetic traits reveal their evolutionary distinction as separate lineages (*18*). Without accurate taxonomic identification, researchers can overgeneralize the physiological responses of one cyanobacterial species to others that are genetically distinct. This may lead to incorrect assumptions about how different species respond to environmental stressors. One method, called the polyphasic approach, combines morphological, molecular, and ecological data and has been proposed as a gold standard to improve the identification of cyanobacteria (*44*).

Another challenge includes the methodological limitation of measuring cyanobacterial growth. Biocrust cyanobacteria usually grow as colonies leading to clump formation, and produce EPS that promote adherence to surfaces when grown in liquid media. In consequence, their biomass is often unevenly distributed between the liquid media and flask surfaces, making standard growth measurements such as optical density (OD), which is measured by spectrophotometry, inaccurate. Since OD relies on the absorbance of a homogeneous solution at a specific wavelength, it is not a reliable method for organisms that grow as aggregates, as biocrust cyanobacteria do.

The third challenge is the limited number of

cyanobacterial records and associated living specimens readily available for physiological investigations. Cyanobacterial culture collections, which preserve and provide access to cyanobacterial strains for future research (*46*), contain relatively few representatives from terrestrial environments compared to aquatic ones. Floyd et al. (*47*) reported that the American Type Culture Collection (ATCC) has a larger number of cyanobacterial records from freshwater than terrestrial ones. Although Floyd et al. (*47*) did not mention the exact number of cyanobacterial records, cyanobacteria accounted for 8% of all freshwater microbe records, while cyanobacteria collected from soil comprised less than 1% of the total soil microbes. This underrepresentation of terrestrial cyanobacteria might be linked to a higher research and public health focus on bloom-forming cyanobacteria in aquatic environments, particularly those that produce toxins harmful to humans and animals (*48*). Together, this highlights the paucity of biocrust cyanobacteria strains available in culture collections for physiological research and limits the detection of general rules of terrestrial cyanobacteria life.

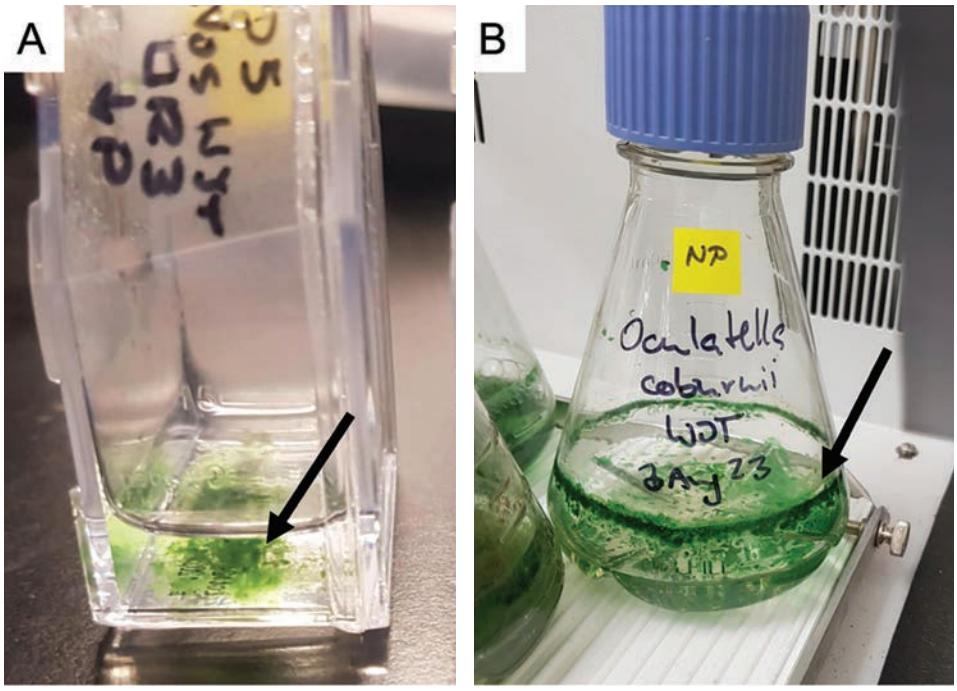

Figure 3. Biocrust cyanobacteria grow as colonies, forming clumps, and producing exopolysaccharides (EPS), which limit the methods to measure cyanobacterial growth. (A) *Nostoc* sp. forming clumps in liquid media inside a culture flask (black arrow). (B) *Oculatella coburnii* adhering to the surface of the culture flask (black arrow).

CASE STUDY: PHOSPHORUS LIMITATION INHIBITS THE GROWTH OF BIOCRUST CYANOBACTERIA FROM JOSHUA TREE NATIONAL PARK

To contribute to the knowledge of desert cyanobacteria physiology, we studied the effect of phosphorus (P) limitation on the growth, photosynthetic activity, and EPS production of biocrust cyanobacteria from the Mojave and Chihuahuan Deserts (*49*). In this Perspective, we present findings for the influence of P availability on biocrust cyanobacteria isolated from JTNP. Cyanobacterial cultures were previously isolated from a 2007 biocrust inventory campaign in JTNP. Cultures have been maintained since 2007 and are housed at the University of Nevada, Las Vegas Terrestrial Cyanobacterial Culture Collection. The cyanobacterial cultures have been identified as *Nostoc* sp. strain WJT66-NPBG18A (hereafter *Nostoc* sp.) and *Oculatella coburnii* strain WJT66-NPBG6A (hereafter *Oculatella coburnii*).

In our experiment, we examined how the two species of cyanobacteria grew with two different phosphate (PO_4^{3-}) concentrations to test the influence of P availability on cyanobacterial growth. One treatment contained the optimal amount of phosphate (25 mg/L PO_4^{3-}), and the other contained less phosphate than the cyanobacteria need (0.5 mg/L PO_4^{3-}). Both *Nostoc* sp. and *Oculatella coburnii* eventually grew in clumps and attached themselves to the surfaces of the flasks (Fig. 2). This made it difficult to measure their biomass. Therefore, we measured their chlorophyll *a* (Chl *a*) concentrations as a proxy for biomass (*50*) rather than counting cells, allowing us to compare the growth of each species in both P conditions. We also extracted the EPS (*50*) to find out if the amount of sticky, aggregate-forming sugars decreased when the cyanobacteria were limited by phosphorus. From the EPS extractions, we determined how much of the EPS was released to the external environment and how much remained tightly bound to the cell (*51*).

We found that both *Nostoc* sp. and *Oculatella coburnii* under phosphorus limitation had a lower biomass than the same cyanobacteria under optimal growth conditions (Fig. 3). This was expected because phosphorus is an essential nutrient for life. It serves as a fundamental building block of biological molecules, forming part of nucleic acids, cell membranes, and energy currency molecules such as ATP in most organisms (*52*). Additionally, we found the EPS-to-biomass ratios between optimal growth conditions and P-limited conditions were not significantly different (Fig. 4 shows the results for released polysaccharides). This suggests that cyanobacteria maintain a proportional balance between EPS production and biomass rather than completely halting EPS production. The production of EPS may be important to continue forming biofilms or aggregates even under P limitation. In general, biofilm or aggregate formation is a strategy employed by bacteria to overcome the impact of environmental stressors such as water and nutrient deficits (*53*, *54*). A constant EPS-to-biomass ratio under phosphorus limitation may represent a potential adaptive mechanism, allowing cyanobacteria to maintain EPS production even when growth is inhibited. EPS plays a key role in enhancing adherence to soil particles, keeping cyanobacterial cells hydrated, and protecting against UV-radiation (*55*, *56*). This highlights the potential role of EPS for the survival of biocrust cyanobacteria, despite nutrient limitation. Although our research was performed under controlled laboratory conditions, it provides relevant insights into the physiology of biocrust cyanobacteria under an important desert stressor such as phosphorus limitation. Future studies need to evaluate the effect of phosphorus on biocrust cyanobacteria in an outdoor setting.

CONCLUSION

Desert cyanobacteria, such as those forming biocrusts in JTNP, are ecologically and evolutionarily intriguing, but they remain poorly studied in their basic biology. They exhibit different functional traits that strongly influence nutrient cycling, soil stabilization, and water retention. These traits make cyanobacteria promising inoculants to restore degraded desert areas. However, the lack of success in establishment after cyanobacteria inoculation is still a common outcome of restoration efforts. One of the primary barriers to success is the limited knowledge of cyanobacteria physiology under environmental stressors. For instance, the effect of phosphorus limitation on biocrust cyanobacteria growth and health remains poorly understood. Our work showed that phosphorus limitation inhibits the growth but not the production of EPS in biocrust cyanobacteria from JTNP (*49*). These findings raise pivotal questions about how and why EPS is still produced under nutrient limitation. Looking forward, we advocate for comprehensive investigations to study biocrust cyanobacteria. For example, determining how multiple environmental stressors, such as UV radiation, desiccation, and nutrient limitation, interact to affect cyanobacterial survival, and identifying the tolerance thresholds of different species, are both important future research directions. Increasing the understanding of the basic biology and physiology of native cyanobacteria, such as those found in understudied locations like JTNP, might improve cyanobacteria survival after inoculation in restoration field experiments. Altogether, basic research on cyanobacteria needs to become a priority in efforts to conserve and restore desert ecosystems in a changing world.

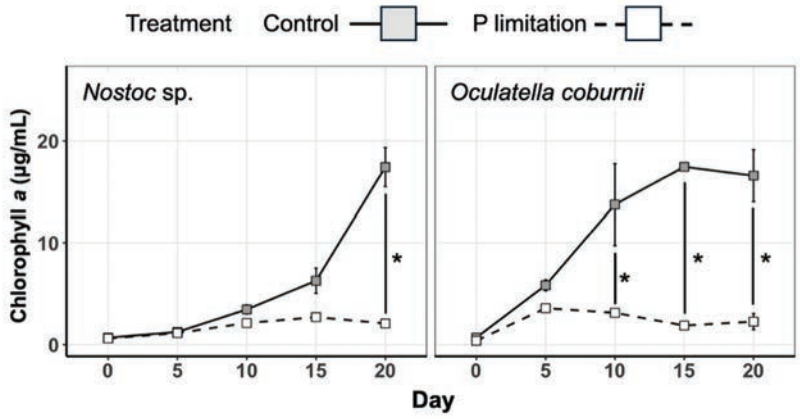

Figure 4. Chlorophyll a concentration, a proxy for growth and biomass, for *Nostoc* sp. and *Oculatella coburnii* during 20 days under control and phosphorus (P) limitation conditions. Solid lines and gray symbols represent control conditions, and dashed lines indicate P-limited conditions. Each symbol denotes the mean of three replicates, with error bars representing the standard error. A linear mixed-effects model was applied, followed by estimated marginal means (emmeans) comparisons between treatments (control vs P-limited). Asterisks indicate statistically significant differences based on a *post-hoc* Tukey test (*P*-value < 0.05).

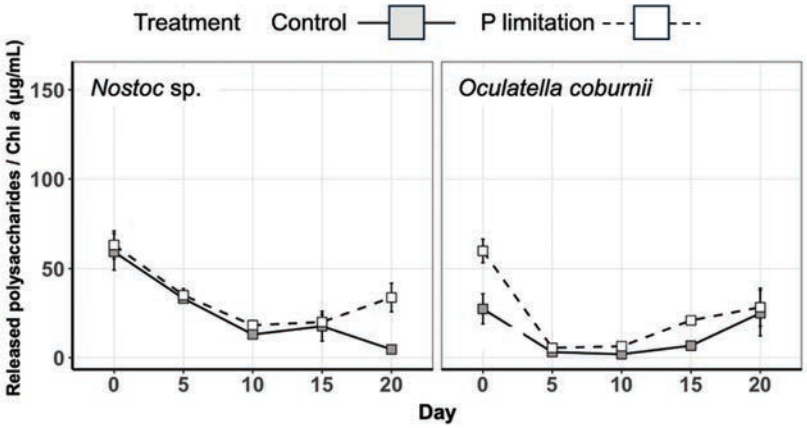

Figure 5. Ratio of released polysaccharides and chlorophyll a (Chl a) concentration for *Nostoc* sp. and *Oculatella coburnii* during 20 days under control and phosphorus (P) limitation conditions. Solid lines and gray symbols represent control conditions, and dashed lines indicate P-limited conditions. Each symbol denotes the mean of three replicates, with error bars representing the standard error. A linear mixed-effects model was applied, followed by estimated marginal means (emmeans) comparisons between treatments (control vs P-limited). The absence of asterisks indicates non-statistically significant differences based on a *post-hoc* Tukey test (*P*-value < 0.05).

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Benjy Sedano-Herrera recently graduated with his Master of Science from the School of Life Sciences at UNLV. He has a big passion for cyanobacteria, evolution, and bioinformatics. During his Master's, Benjy worked in Dr. Nicole Pietrasiak's lab. His research focused on the effect of nutrient scarcity, particularly phosphorus, on the production of exopolysaccharides in desert cyanobacteria. Additionally, he investigated the genes involved in the production of exopolysaccharides in terrestrial cyanobacteria and compared them with those in aquatic cyanobacteria. Currently, he is a PhD student at Paris-Saclay University in France, where he studies the evolution of early cyanobacteria.

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The Subtle But Profound Changes of a Desert Plant Community in Joshua Tree National Park

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INTRODUCTION

The striking changes in the landscape that occur during a spring bloom offer a rare glimpse of plant activity in arid lands. Limited water availability in deserts causes processes of birth, growth, and death in the perennial shrub community to be very gradual and long-lasting and those in the annual plant community to be very rapid and ephemeral. For this reason, desert landscapes exhibit a sense of timelessness and stasis. Long-term monitoring of desert shrubs, however, exposes dramatic changes in species composition that are masked by the "invisible present" (*1*) that reflects the combination of slow demographic change and sometimes extreme longevity of large and conspicuous species such as *Larrea tridentata* (creosote bush) or *Yucca brevifolia* (Joshua tree).

Deserts are harsh habitats for plants, receiving <25 cm of rain annually. All plants require water and a similar suite of nutrients, nitrogen chief among them, which are absorbed by roots. Plants also require light and carbon that, with a few exceptions (*2*), are absorbed by leaves. Unlike animals that can acquire water and basic nutrients from multiple sources and can move around to forage, plants must forage from a single location determined by where a seed successfully germinates and grows. Common species should possess advantages in acquiring limiting resources (*3*) or have greater reproductive success than other co-occurring species (*4*). These constraints provide opportunities for plant ecologists to understand adaptations, interactions, and growth strategies that permit survival under extreme conditions.

Within Joshua Tree National Park (JTNP), a shrub community near Cottonwood Springs has been monitored for 40 years (Fig. 1). During these four decades, dramatic episodes of seedling regeneration, local extinction of a common species, and extreme drought mortality have been observed. The monitored community occurs on a gently sloping bajada northwest of the Eagle Mountains, which are visible from the Cottonwood campgrounds. Unlike the north end of JTNP, which is within the Mojave Desert, this site occurs in the Colorado Desert, which is at the western edge of the Sonoran Desert. As is characteristic of all deserts, rainfall is sparse and highly variable. Total annual rainfall ranged from 3.76–24.52 cm between 2006–2025 near the study site (Table 1). Rainfall primarily occurs during the cold season (October–March), with minimum temperatures of -2.7° C, although summer rains (July–September) are not unusual with minimums of 0 cm/month and maximums of 8.7 cm/month recorded near the study site (Fig. 2, Tables 1 and 2). Maximum temperatures in the summer months range between 38.2–42.0° C (Table 1). Common shrub species include *Ambrosia dumosa* (white bur-sage), *Larrea tridentata* (creosote bush), *Simmondsia chinensis* (jojoba), and *Tetracoccus hallii* (Hall's shrubby spurge). Beginning in 1984, all perennial plants were tagged and mapped by S. Joseph Wright and Henry F. Howe (see *5*). Regular censuses followed every five years, with a few exceptions. Maria N. Miriti joined the research team in 1994, adding longitudinal and demographic analyses to the site research portfolio (e.g. 6–9). Each census documented 23–26 species of mostly shrub species as well as two species of cholla, *Cylindropuntia ramosissima* and *C. echinocarpa*, and a relative of the Joshua tree, *Yucca schidigera* (Mojave yucca). To date, data from >10,000 individual plants have been captured on one hectare of land and has contributed to 17 research articles and hundreds of citations.

This amazing dataset has revealed novel insights on the roles of plant distributions, plant interactions to the species diversity, and coexistence in this desert community. Below I highlight what has been learned over the years.

THE IMPORTANCE OF SPATIAL DISTRIBUTION

High temperatures and scarce water limit the number of individuals in desert plant communities; for these reasons, the spatial distribution of plant species is conspicuous. Because plants cannot move throughout their lifetime, their spatial distributions (i.e., arrangement in space), can offer insights into what locations are favorable for survival and which neighbors are friends or foes. For example:

> Specific locations of high plant abundance may identify regions where resource availability is higher, whereas wide spacing among neighbors may indicate strong competition for resources, such as water or nutrients.

Early studies of desert plant spatial distributions asserted that plant immobility and harsh living conditions should promote antagonistic interactions evidenced by wide spacing among plants; dense aggregations could occur if neighbors possessed complementary growth traits (*10–14*). These studies revealed strategies, such as:

1) variation in root architecture among species that permits aggregation of species with complementary architectures;
2) release of chemicals to repel heterospecific neighbors; and
3) contrasting patterns of individual resource allocation to growth or reproduction;

all of which either support species coexistence or offer mechanisms for patterns of dominance among species. Underlying these discoveries is the examination of plant spatial distributions.

Many desert shrub species appear to be distributed uniformly, like trees in an orchard, with individuals separated by empty spaces (Fig. 3). Such spatial distributions are

unusual in non-arid plant communities, but commonplace in deserts. Early inferences of the cause of this unique pattern suggested it to be a consequence of limiting water that imposed intense belowground competition among roots of neighboring plants causing wide and uniform spacing between neighbors (e.g. *14*). Unfortunately, some of these inferences were not derived from quantitative analyses of plant distributions, relying largely on perceived distributions. Subsequent quantification of plant spatial distributions shows that most species have random or clumped patterns whether determined from a single observation (*11*) or multiple observations of the same plants over time (*5, 6*). These outcomes invite consideration of the role of other kinds of interactions among plants in desert communities. If competition explains the regular patterns of shrub distribution, what processes explain other kinds of distribution?

Quantitative analyses of spatial distributions are important because they can help scientists generate hypotheses about the ways plants interact with near neighbors. Observations of death and recruitment over time can help refine inferences of the ways these patterns are created and how they relate to interactions within and between species. For example, if individuals in a plant cluster experience higher mortality than those occurring in a widely spaced group, competition for limiting resources is supported. In contrast, if mortality is greater among widely spaced plants compared to clustered plants, a benefit from close neighbors is supported (Fig. 4). Analyses of spatial pattern at the Cottonwood site have shown that most of the species have random or clustered distributions and that clustering is common among juvenile plants even when the overall species distribution is not (*5, 6*). Within species, changes in spatial patterns over time occur because of mortality and recruitment. These processes suggest a relationship between survival, recruitment, and pattern. Such analyses at the Cottonwood site show that juvenile mortality after five years is related to distance from a conspecific adult for some species and that the benefit or detriment of clustering around adults is species dependent (*6*). This result invites further examination of the kinds of interactions juveniles may have with adult plants. For example, how does high juvenile density influence mortality of juveniles and adults in both positive and negative ways (e.g. *15*)? Furthermore, studying how juvenile density varies with distance from conspecific adults could lead to a better understanding of the consequences of such interactions for population persistence. These studies also highlight what can be learned by linking demographic processes with spatial distributions.

If spatial distributions impact plant survival and growth, it is possible that plant distributions and their consequences for individual plants also impact whether population growth is increasing, decreasing, or persisting at a stable size. Survival and individual growth provide essential information for demographic

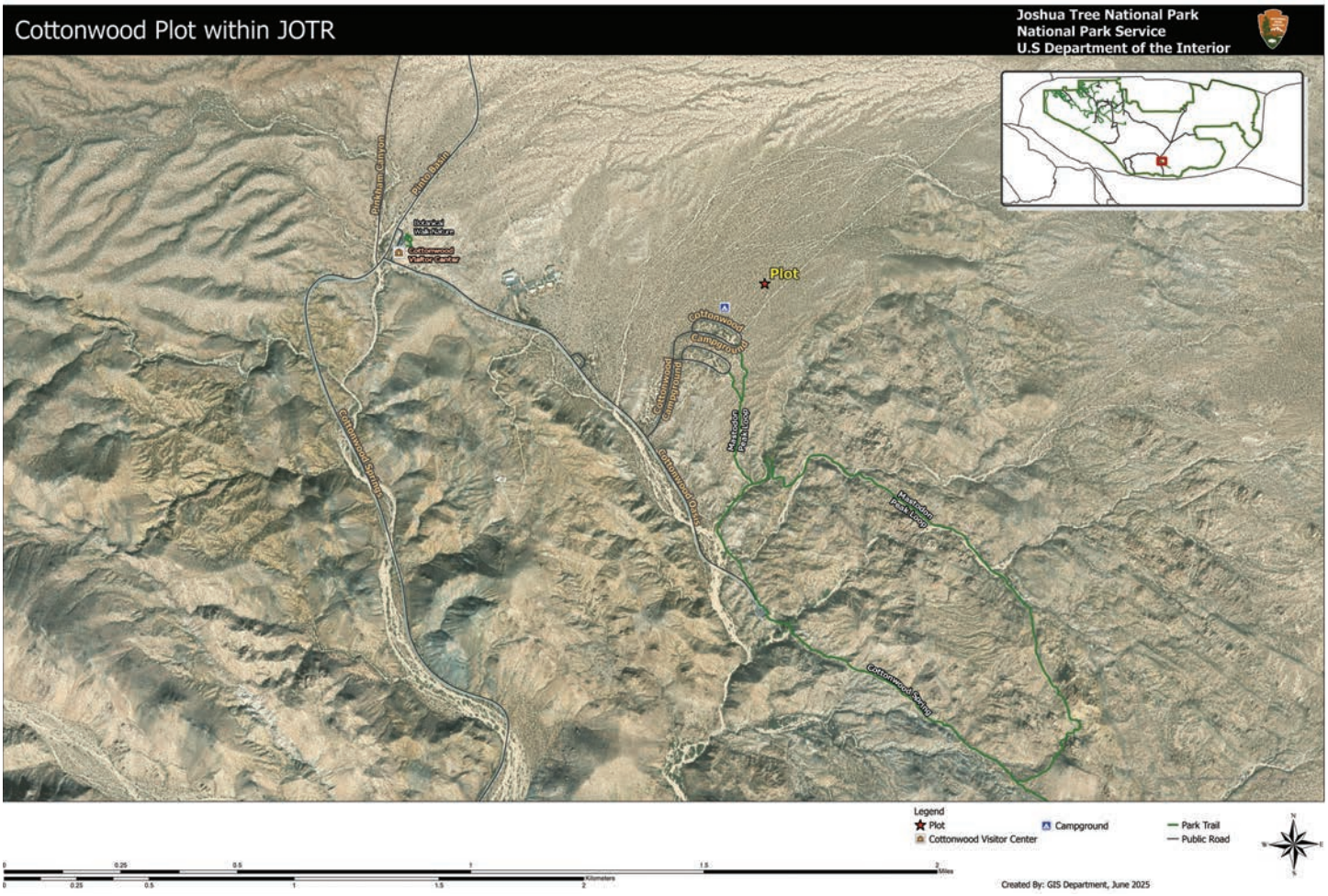

Figure 1. Location of the study site in relation to the Cottonwood Campground. The site is indicated by a red star within a wilderness area north of the campground, and east of the Cottonwood visitor center. Park trails are indicated by green lines, and public roads are indicated by gray lines. The inset on the upper right side of this figure shows the position of the Cottonwood region (red square) toward the south-central boundary of JTNP. **Image created by A. Ramos (NPS JTNP).**

analyses, which are the formal analysis of the fate or well-being of a population. To understand the population-level consequences of spatial distribution and juvenile mortality, we conducted demographic analyses to examine if spatial patterns within a species could influence population growth. These analyses require large numbers of individuals at all of the important life history stages present within a population. At the Cottonwood site, *Ambrosia dumosa* meets this requirement and also has enough individuals in distinct spatial configurations to understand if there is a relationship between population growth and spatial pattern. We found that although the most common spatial configuration of *A. dumosa* is aggregated, individuals without near conspecific neighbors, especially larger, reproductive plants, contribute most significantly to population fate. In other words, isolated individuals were the most important contributor to population persistence (*7*). Small changes in the growth or mortality of these individuals more strongly impact population growth or decline.

This result does not mean that aggregated plants are unimportant. Limited seed dispersal in deserts (*16*) indicates that most seeds land or get trapped in the litter under maternal adults. Further, plant requirements vary with plant size (see *17*). Most surviving, young *A. dumosa* plants have an adult neighbor nearby because smaller plants are more vulnerable to high temperatures, coupled with scarce water, when compared to larger plants. The needs of large, isolated plants are distinct from those of small, recently germinated plants. Facilitation of juveniles by adults (*18*) is seen in harsh environments including deserts and high alpine regions, but is also observed in some temperate habitats. Our results from the Cottonwood site support that a lower number of juveniles manage to survive on their own and reach reproductive size without facilitation, but they experience growth and survival advantages. In a separate study, this trade-off between the impacts of near adult neighbors with plant size was confirmed (*8*). Small juveniles benefit from near adult proximity, but as plants grow, this benefit reduces and changes such that larger plants perform better without near neighbors. Nevertheless, the frequency of new plants surviving without facilitation is rare, especially under unusually harsh climate conditions.

Our findings demonstrate the ways in which ecological interactions depend upon external circumstances (e.g. *19*). Plant size impacts the benefit or detriment of having near neighbors, but climate is another factor that can influence the pros or cons of aggregation. Subsequent analyses revealed that regions of high and low plant density respond differently to climate variations (*20*). Some plants are more likely to survive when clustered during typical climate conditions, but high density regions do not persist during severe drought that causes a major mortality event (*9*). Further, our analyses suggest that *A. dumosa* not only protects its own but also the juveniles of other species. This means that the preponderance of *A. dumosa* may support higher species diversity than if it were absent. These findings also raise questions about how facilitation responds to increasing habitat severity.

In summary, analyses of spatial distributions offer inferences that may support or refute paradigms of desert plant ecology, and they offer one method to develop hypotheses of the dynamics regulating plant communities. These

	Ambient Temperature (degrees C)			Precipitation (cm)
Year	Average	Maximum	Minimum	Annual Total
2013	21.5	40.5	-1.8	10.7
2014	21.4	39.4	-1.8	3.76
2015	20.1	39.0	-1.7	6.75
2016	20.1	42.0	0.5	14.68
2017	20.4	41.2	1.3	13.55
2018	20.1	40.5	-0.9	24.52
2019	17.3	38.9	-2.7	24.33
2020	19.4	40.9	-2.2	14.9
2021	19.6	41.6	-1.1	8.31
2022	19.1	38.2	-2.4	24.27
2023	18.5	40.5	-0.2	14.27

Table 1. Annual maximum, minimum, and average temperatures, and total rainfall near the Cottonwood study site. Data presented in this table only range from 2013–2023 in order to demonstrate the range of annual precipitation (3.76–24.52 cm) and the strong differences between annual high and low temperatures. Data were collected from the Cottonwood Campground (2013–2017) and Cottonwood Visitor Center (2018–2023) climate stations; both are <1 km from the study site.

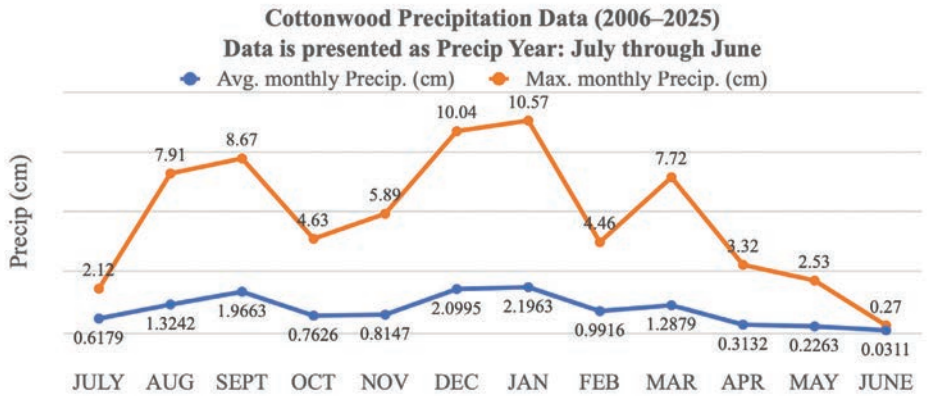

Figure 2. Average (blue) and maximum (orange) monthly precipitation from 2006–2025 near the study site. The figure illustrates the influence of summer precipitation with September and August having the 3rd and 4th highest averages and maximums annually. Data were collected from the Cottonwood Campground (2013–2017) and Cottonwood Visitor Center (2018–2023) climate stations; both are <1 km from the study site.

Figure 3. (*Left*) An aerial view of the landscape that includes the Cottonwood Springs research site. Plants appear as distinct units that are surrounded by open ground. (*Right*) The bare ground is also very evident at ground level and is a unique characteristic of desert landscapes.
Photo credits: Left image, Google Earth. Right image, M. Miriti.

Figure 4. (*Left*) A cluster of tightly aggregated plants, and (*Right*) more uniformly spaced shrubs. Early hypotheses of plant interactions in deserts emphasized plant competition as the most important driver of plant distributions. Over time, studies documenting the frequency of plant aggregations motivated considerations of alternative interactions among desert plants. **Photo credits: M. Miriti.**

hypotheses can guide the development of experiments that can reveal the mechanisms of coexistence in desert plant communities.

CLIMATE VARIATION AND WHAT DROUGHT TEACHES US

Deserts, including those found in the Desert Southwest, have been enduring severe drought for more than 20 years (*21*), which has caused extensive mortality in these regions (*9, 22, 23*). At the Cottonwood site, drought mortality occurring between 1999-2004 resulted in the local extinction of *Sphaeralcea ambigua* (desert globemallow), near local extinction of *Eriogonum fasciculatum* (California buckwheat), and left only 25% of the dominant *Ambrosia dumosa* alive (*9*) (Fig. 5). Other species suffered less, most notably *L. tridentata*, which experienced negligible mortality. Further, among species that suffered high mortality, mortality was nonrandom; plants in dense clusters suffered greater mortality (*20*).

The resultant drastic change in species composition and relative abundance offers an opportunity to better understand how climate affects predominant interactions among arid plants. Although established plants may compete more with near neighbors under extreme conditions, the conditions favoring recruitment of new juveniles are unclear. Taken together with our previous observations at the Cottonwood site, plant responses during drought can help anticipate community recovery potential and the permanence of changes in community composition.

FACILITATION AND GERMINATION

Under typical climate conditions, survival of young plants can benefit from facilitation by adults of the same or different species (*6, 20, 24*). The ability of adults to facilitate juvenile growth and survival during periods of extreme habitat severity, such as severe drought, has been debated with evidence both in favor of and against facilitation decreasing with increasing habitat severity

(*25, 26*). In communities like the Cottonwood site, facilitation has been an important interaction that allows new juveniles to germinate and survive (*20*), but the frequency of facilitation under extreme conditions, such as the millennial drought (*22*) that was captured beginning with the 2004 census, is undetermined. Arguably, if seedling establishment benefits from facilitation under typical conditions, it seems unlikely to occur without facilitation under harsher conditions.

A second consideration is that not all shrub species are associated with facilitation. Studies at other desert locations emphasize the benefits received from specific facilitator species (*24, 27, 28*). At the Cottonwood site, *Ambrosia dumosa* adults are in close proximity to perennial seedlings of several species, but adults of other species are not. This may be because *A. dumosa* is the most common species at the site or because it offers unique advantages to seedlings that other species do not. To test this, we conducted an experiment to examine the facilitative ability of *A. dumosa*, *Tetracoccus hallii*, and *Larrea tridentata* to enhance germination of four beneficiary species: *A. dumosa*, *Sphaeralcea ambigua*, *Eriogonum fasciculatum*, and *L. tridentata*. Seed packets of 100 seeds, per beneficiary species, were placed in the canopy, canopy edge, and in the open interspace between shrubs (Fig. 6).

Our data support that, at least for seed germination, there is no special benefit conferred by *A. dumosa* compared to two other abundant, co-occurring shrubs, *L. tridentata* and *T. hallii* (29).

This field experiment did not distinguish the effects of limiting water, but despite significant differences in nitrogen availability, seeds of the four beneficiary species germinated equally well after two weeks under each facilitator canopy. Only *E. fasciculatum*, which had the highest germination percentage among the beneficiary species, significantly benefited from facilitation for germination.

Germination is the first step in seedling establishment, and in many instances, seeds may germinate and die before they are observed in field censuses. It is important, nevertheless, to recognize that germination does not appear to be the limiting factor for juvenile establishment.

UNDERSTANDING SEEDLING INTERACTIONS

Studies of facilitation generally consider advantages gained by established seedlings under facilitated versus non-facilitated conditions. These include protection from herbivores (*24*) and improved abiotic conditions, such as availability of nutrients

Figure 5. (*Left*) The Cottonwood Springs site (1994) before the onset of drought, which was first noted in 2004. (*Right*) Cottonwood Springs site post drought (2015). Open spaces are larger due to plant mortality, and many plants are dormant. **Photo credits: M. Miriti.**

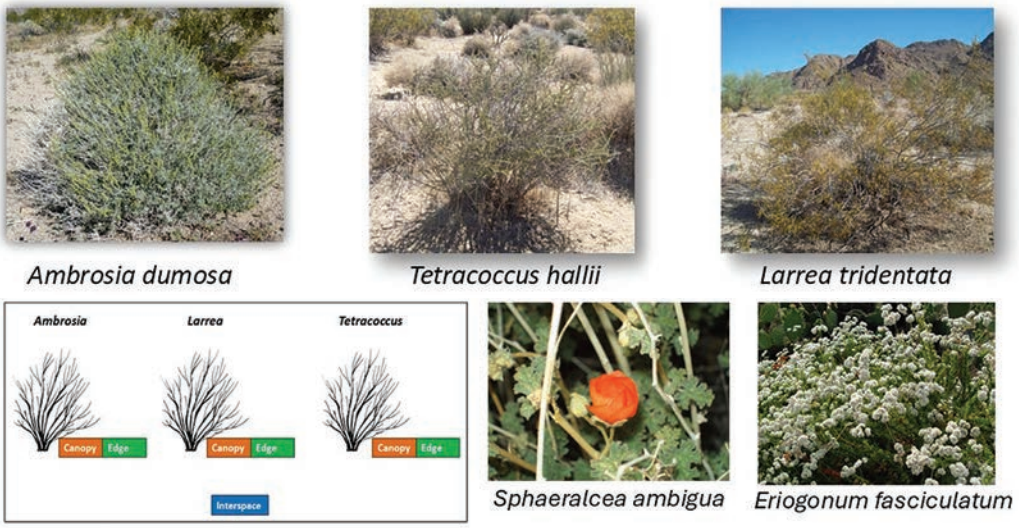

Figure 6. Graphic showing experimental layout of a facilitator-benefactor germination test conducted at the Cottonwood site. Data from this experiment did not support a difference between the facilitative ability of the canopy microsite for *A. dumosa*, *T. hallii*, and *L. tridentata* (shown in top photos) to enhance germination of four beneficiary species tested, *A. dumosa*, *L. tridentata*, *S. ambigua* and *E. fasciculatum* (latter two are shown on the bottom right).
Photos and graphic by N. Woods.

Figure 7. (*Left*) Juvenile plants being facilitated by *Ambrosia dumosa* during typical conditions in 1994 and (*Right*) during drought conditions in 2004. Although some research challenges the occurrence of facilitation during unusually harsh conditions, seedlings can still benefit from facilitation. Facilitation under harsh conditions may be important for post-drought community recovery. **Photo credits: M. Miriti.**

and soil moisture (e.g. *18, 24*). Generally speaking, the canopy space below facilitators offers a "safe site" (*sensu 30*) that contributes to community structure by providing reliable locations for regeneration (e.g. *17*), which can maintain community diversity.

Aside from supporting germination and early survival, safe sites may harbor high densities of seedlings, thereby creating a competitive environment. When this is the case, the competitive ability of seedling species is a determining factor of future community composition.

A seedling competition study conducted at the Cottonwood site found that the outcomes of competition among *Larrea tridentata*, *Ambrosia dumosa*, and *Tetracoccus hallii* were contingent on the relative abundance, species composition, and density of co-occurring species (*31*). Interestingly, seedling competitive ability was not correlated with the relative abundance of adults of the same species in the study hectare. Notably, *L. tridentata* seedlings had the weakest competitive ability, performing best in the absence of any other species. *Eriogonum fasciculatum* was a reasonably strong competitor, but outcomes were dependent on the presence of and relative abundance of *A. dumosa*, with high abundance of *A. dumosa* combined with high density of *L. tridentata* most negatively impacting *E. fasciculatum* seedling growth. Such non-hierarchical dynamics in which species impacts respond to multiple factors are important to maintain diversity because they eliminate the overriding superiority of any individual species. For example, the prevalence of *L. tridentata* at the Cottonwood site may be explained by its extreme longevity and competitive ability during later life history stages.

INTEGRATING WHAT WE HAVE LEARNED

As presented above, the frequency of facilitation may decrease as increasing habitat severity increases competition between adults and juveniles, albeit with some caveats (*25*). Nevertheless, it is unlikely that novel regeneration can occur under conditions of prolonged drought without facilitation (Fig. 7). In assessing the contributions of facilitation to community structure, it is important to recognize that seedling establishment is irregular and pulsed in deserts (*32*). This is in part due to very localized distribution of soil moisture, which controls resource availability (*32, 33*). Therefore, assessments should occur over a sufficiently large region to accommodate resultant variation in habitat quality at smaller, localized scales (e.g. *34*). A final consideration is that novel regeneration has been modeled to occur after the liberation of space caused by mortality events (*35*). The canopy of a dead adult plant may still offer improved soil moisture and nutrient availability without competition from the adult itself. This is partially supported by the research of Lortie and colleagues (*27*), who found that *Ephedra californica* (California jointfir) can facilitate seedlings with simulated canopy damage under drought conditions. Although an emphasis of that study was the ability of damaged plants to resprout ("Groot effect"), facilitation by *E. californica* remained significant throughout the experiment.

Considering our research at the Cottonwood site, drought recovery is likely to depend on

Figure 8. The potential for community recovery will likely depend on the persistence of *Ambrosia dumosa*. This *A. dumosa* seedling first observed in 2024 has survived at least one growing season despite persistent drought.
Photo credit: M. Miriti.

the persistence of *Ambrosia dumosa* and the occurrence of bouts of winter precipitation to support seedling establishment. As with other parts of the Desert Southwest, JTNP is experiencing drought that is indicated by continuous increases in temperature combined with reduced precipitation (*36*). Our field research shows that germination of all focal species can occur with soil moisture that persists for two weeks (*29*). Although a gap in our research is the survival of new seedlings from spring germination through the summer months, we observed 23% survival from a cohort of 162 seedlings composed of 11 species. Due to our monitoring interval, we cannot determine the rate of mortality per season. The seedlings established in 2015 and were monitored for three growing seasons through 2018. With the exception of 2015, which only received 51% of average rainfall, the plot appears to have received sufficient amounts of rain throughout 2016–2018 (Table 2). Beginning in 2023, we have documented perennial seedlings including *Sphaeralcea ambigua*, *Eriogonum fasciculatum*, *Larrea tridentata*, and *A. dumosa*, with the latter being the most abundant over two years of observation (Fig. 8). Data from these recent observations have not been quantified. Although seedling competition should determine which species survive over the long term, the contingencies of local density and seedling species competition are a promising mechanism to ensure the maintenance of diversity.

Monthly Precipitation (cm) during seedling recruitment study; data from Cottonwood Climate Stations. Average based on data from 2006 to 2025.

	2015 Rainfall	2016 Rainfall	2017 Rainfall	2018 Rainfall	Average Rainfall
JAN	0.67	5.1	6.91	9.23	2.37
FEB	1.07	0	2.28	0	0.99
MAR	1.56	0.03	0	0.17	1.12
APR	0.06	1.41	0	0	0.46
MAY	0.49	0	0	0.05	0.23
JUN	0	0.27	0	0.06	0.04
JUL	1.24	0	0.87	2.12	0.59
AUG	0	0.35	1.67	0	1.29
SEPT	0.56	1.84	1.82	1.56	2.06
OCT	1.07	0.99	0	4.63	0.74
NOV	0	0.13	0	0	0.94
DEC	0.03	4.56	0	10.04	2.15
Total	6.75	14.68	13.55	27.86	13.14

Table 2. Average monthly rainfall compared to monthly rainfall during the seedling cohort study years (2015–2018). With the exception of 2015, which only received 51% of average rainfall, the plot appears to have received sufficient amounts of rain throughout 2016–2018. Due to our monitoring interval, we cannot determine the rate of mortality per season, only that 23% survived until 2018. Average annual and monthly rainfall is based on data from 2006–2025. Data are from the Cottonwood Campground and Cottonwood Visitor Center climate stations located <1 km from the study site.

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Front cover: Evening Light Near Cottonwood. **Photo credit: NPS/Kurt Moses**
Back cover: *Lycium andersonii*, Joshua Tree National Park. **Photo credit: Tasha La Doux**

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