Linking Avian pollination and frugivory to Cactaceae seed dispersal and successful facilitation.

Malory Owen and Chris Lortie

November 27th, 2018

# Timeline

Table 1: A proposed timeline of the three chapters

|  |  |  |  |
| --- | --- | --- | --- |
| Chapter | Title | Goal | Timeline |
| 1 | Fruiting metrics in Cactaceae- A meta-analysis | Identify and isolate the combined results of relevant studies in Cactaceae in regards to fruiting patterns. | Derived data extracted by December 2018. Paper written by January 2019. |
| 2 | Strength of birds as pollinators and seed dispersers in Cactaceae | Connect bird interactions with flowering and fruiting in cacti of different endangerment status. | Flowering field season January-Febuary April-May 2019. Fruiting field season August 2019. Paper written by January 2020. |
| 3 | Avian pollination and seed dispersal influence on seed shadow of Cactaceae obligatory facilitatees | Determine the role of birds as pollinators and seed dispersers for Saguaro ssp. | Flowering field season April-May 2020. Fruitnig field season August 2020. Paper written by December 2020. |

# Introduction

Desert ecosystems are threatened by a variety of circumstances. Results of anthropogenic actions like climate change and habitat fragmentation are perpetuating arid ecosystem degradation. Specifically, climate change increases severe precipitation changes such as droughts and flooding (Nielsen and Ball 2015; Pfahl, O’Gorman, and Fischer 2017; Singh et al. 2013; Smith 2011) and human development like roads, solar panels, and land use change fragments and destroys habitats (Gutzwiller and Barrow 2003; Hernandez et al. 2014; Rodriguez-Estrella 2007). In the American Southwest, arid ecosystems are home to dozens of endangered plants and animals (StateofCaliforniaa 2018; StateofCaliforniaa 2018), provide ecosystem services to humans (Taylor et al. 2017), and have cultural significance to indigenous peoples. In order to restore the region and mitigate the effects of climate change and human development, we must understand the connections which proliferate life in the desert.

Positive interactions are any associative action between interspecifics where one species benefits another’s fitness in some capacity (M. D. M. Bertness and Callaway 1994). The further scientists determine the prevalence and strength of positive interactions in determining an ecosystem, the more communities are viewed as interconnected in a non-random way (R. M. Callaway 1997). Similarly, but perhaps in a more narrow sense, facilitation is the process by which a foundational species perpetuates the success of many other individuals within an ecosystem which interact with that foundational species, particularly in years of high stress F. T. Maestre et al. (2009)]. This suggests that facilitation amongst plants and animals by foundational species are one of the driving forces behind an ecosystem’s development (Angelini et al. 2011). For this reason, identifying the mechanisms of facilitation is an avenue to understanding how certain ecosystems disperse and form.

In arid ecosystems, this takes the form of providing water and shade from excessive solar radiation (Flores-Torres and Galindo-Escamilla 2017; Miranda-Jacome, Montaña, and Fornoni 2013), or, to a lesser extent, preventing physical damage from herbivory, wind, and freezing temperatures (Gomez-Aparicio et al. 2008; Parker 1989; Tewksbury and Lloyd 2001; P. S. Nobel 1980). Nurse plants provide these amenities to seedlings, and improve recruitment, germination, and growth in juvenile plants (Franco and Nobel 2009). This makes nurse plants important facilitators for many species. Some of these patient plants are even obligated to be deposited under the canopy of a nurse plant to germinate at all (Taly D. Drezner and Garrity 2003; T. Dawn Drezner 2010). Therefore, the nurse plant is a limiting factor in the growth of many plant species.

However, before a nurse plant can “offer its services” to a germinating seedling, the seed must arrive under the canopy of a nurse plant. Because plants are sessile lifeforms, the movement of seeds must rely of some abiotic or biotic vector of transportation (Nathan and Muller-landau 2000). Seed rain is the placement of of a seed after being deposited either through endozoochory, exozoochory, wind dispersal, or mechanical dispersal, whereas seed shadow refers to the placement of daughter seeds relative to the mother plant (Willson 1993). There is ample research in regards to the successful recruitment and germination of seed rain based on the nurse plant as well as the effect of the endozoochorous disperser’s gut on germination rate and success (M. Verdu and Traveset 2004; A. Traveset, Riera, and Mas 2001; A. Traveset and Verdu 2002). However, there is a gap in knowledge on the relative importance of dispersers, particularly in arid ecosystems and to the end of deposition at facilitating nurse plants.

But what characteristics of a cacti might drive frugivory by birds? As allocation theory suggests, cacti have evolved to allocate energy and resources to anatomical features which best increase their fitness (Obeso 2004). Perhaps these traits that are attractive to frugivorous birds also improve fitness beyond just ability to be dispersed. For example, fruit size/number and seed size/number are reproductive organ characteristics which may determine both frugivory, and by extension, fitness in plants.

Fruit and frugivory are not the only ways birds increase fitness of cacti. Fruiting is dependent on pollination, a service which birds (particularly hummingbirds) provide. According the the magnet species hypothesis, pollinators are drawn to “showier” flowering displays, thereby increasing hummingbird pollinator frequency in a physical space, which other cacti species benefit from (Thomson 1978; Johnson et al. 2003; Wolf and Hainsworth 1990). However, size (specifically height) of plants are another contributing factor to hummingbird pollinator visitation, as higher flowers are more likely to be seen by flying hummingbirds (Wolf and Hainsworth 1990; Mitchell 1994). If larger cacti have more flowers and produce more fruit, it may stand that pollinators are important for the cactus of interest to produce offspring.

Member of the Cactaceae family in the *Opuntia* and *Clyndropuntia* genuses, which are both facilitators and facilitatees, may rely heavily on positive interactions with birds in order to reproduce. In these studies, we will identify the strength of birds as pollinators and as seed dispersers for different species and reproductive characteristics of cacti. These findings will increase our understanding of the importance in community-level positive plant-animal interactions in determining an ecosystem’s biotic structure.

## Study Sites

**Mojave Desert: Sweeney Granite Mountains Desert Reseach Center** A preservation with use exclusive to researchers, the Sweeney Granite Mountains Desert Research Center in the Mojave Desert (34.8056°N, 115.6639°W) is located in San Bernadino Country. It boasts a high species richness of 504 vascular plant, 156 birds, 42 mammals, and 2 amphibians. The site has an average of 23 cm of precipitation annually. The July maximum and minimum mean temperature of 33 degrees C and 20 degrees C, respectively, and a December maximum and minimum mean temperature of 8 degrees C and -1 degrees C, respectively. The elevation range is 1,128 to 2,071 meters. It is home to two species of interest, Buckhorn Cholla (*Cylindroputia acanthocarpa*) and Beavertail Prickly Pear (*Opuntia basilaris* var. *basilaris*).

**Wind Wolves Preserve** Self identifying as the West Coast’s largest nonprofit preserve at 93,000 acres, the Wind Wolves Preserve (34.9943°N, 119.1854°W) is located within Kern County, CA. The site’s elevation ranges between 640 and 6,005 feet. The site is home to several endangered species, including the Bakersfield cactus (*Opuntia basilaris* var. *treleasei*). The preserve is dominated by invasive grasses, particularly Brome Grass (*Bromus* ssp.) with the management conducting studies to remove those invasives.

**TBD Arizona Site** We must conduct a team expedition to find suitable sites in the Sonoran Desert, where the Saguaro Cactus (*Carnegiea gigantea*) is found.

# Study Species

***Opuntia basilaris*** var. ***basilaris***, also known as Beavertail, is a frequently occurring species of the family Cactaceae. Found at 800-1900 meters above sea level in gravelly bajadas, washes, and pinyon-juniper woodland (a common habitat in the Granite Mountains) , this species is more easily accessible than some other *Opuntia* species (Andre 2006). Like other members of the *Opuntia* genus, this species is distinct for its “paddle” shaped leaves and bright pink flowers. It is listed as secure by The Nature Conservancy.

***Cylindropuntia acanthocarpa***, or Buckhorn Cholla, is another member of the Cactaceae family found in the Mojave desert and Granite Mountains. Found commonly in gravelly bajadas at 900-1500 meters above sea-level, it has similar accessibility as *O. basilaris* Andre (2006)]. With an appearance more like a small, spiky tree and large red flowers, the genus *Cyclindropuntia* was recently split from the *Opuntia* genus (P. Nobel 2002).

***Opuntia basilaris*** var. ***treleasei***, or the Bakersfield Cactus, is a state and federally listed endangered variation of *Opuntia basilaris*. At the time of listing, it was considered its own species, *Opuntia treleasei* (StateofCaliforniab 2018). Like the *basilaris* variation, the *treleasei* is found in gravelly soil (Hoover 1970).

***Carnegiea gigantea***, commonly known as Saguaro, is a columnar cactus found in the Sonoran Desert. A distinctive species, it’s large, white, waxy flowers bloom at the apex of the arms or spire of the plant. While they can live between 150-200 years, they are obligated to be facilitated by nurse plants (Taly Dawn Drezner 2014). They also require wet environments for germination, a limiting factor in the American Southwest (Turner et al. 1966).

# Chapter 1: Fruiting metrics in Cactaceae: A meta-analysis

## Purpose

This meta-analysis will provide a comprehensive analysis of studies related to fruit and seeds of plants within the Cactaceae family. It will seek to synthesize reports on allocation theory.

## Research Questions

1. Do larger cacti individuals within the same species produce more fruits and/or larger fruits?
2. Do larger cacti individuals within the same species produce more seeds and/or larger seeds?
3. Do larger fruits produce more seeds compared within the same species?

## Strategy of the systematic review

Using combinations of search terms in Web of Science, I will perform a systematic review of fruiting cacti and their size, isolating the relevant studies as data points for a meta-analysis through a series of filtering mechanisms (Fig 1). The search terms include different combinations of: “cact”, “seed”, “fruit”, “allocat”, and “size”. To be included in the meta-analysis, papers must have been published in the past 5 years, be ecological in discipline, and report a regression or correlation coefficient.

## Progress to date

At this time, 302 papers have been compiled after removing duplicates. Next steps include identifying papers as fitting requirements prefaced above, and then compiling the data points (regression and correlation coefficients). Finally, we will summarize the pooled results of the relevant papers.

Fig 1: A PRIMSA statement identifying the workflow completed to date for the systematic review of papers to be included in the meta-analysis (Moher et al. 2009).

# Chapter 2: Strength of birds as pollinators and seed dispersers in Cactaceae

## Purpose

This chapter will test the strength of pollinating/frugivorous bird interactions to observed and experimentally manipulated characteristics with and between 3 cacti species.

## Research Questions

1. Is cactus size an indicator for fruit mass/abundance? For flower abundance?
2. Is there a positive relationship between number of seeds per fruit and fruit size in the cacti of interest?
3. Are frugivorous birds stronger dispersers for larger cacti?
4. Are pollinating birds (hummingbirds) optimally foraging at larger cacti?

## Hypotheses and Predictions

1. Cacti size and flower, fruit, and seed production are positively related. Predictions:

* Larger cacti will produce more flowers, fruits, and seeds, as well as more massive fruits and seeds.
* This will be true within species, but not between species.

1. Fruit mass and seed abundance are positively related.

* Larger individual fruits will have more seeds than smaller fruits.

1. Frugivorous and pollinating birds optimally forage at cacti. Predictions:

* Birds will more frequently pollinate larger cacti, which have more flowers.
* Birds will more frequently eat fruit at larger cacti, which have larger/more fruits.

## Explanatory Variables

* **Mesohabitat**: Open/Cactus
* *Open is the control for cactus presense*
* **Species of cactus**: *Opuntia basilaris* var. *basilaris*, *Opuntia basiliaris* var. *treleasei*, or *Cylindropuntia anthrocarpa*
* **Size of cactus individual**: Large, medium, small
* **Percentage of flower/fruit on cactus**: 0%, 50%, 100%
* *0% fruit on cactus is the negative control, 100% fruit on cactus is positive control for fruit abundance*

## Response variables

* Mass of individual fruits
* Mass of individual seeds
* Number of fruits per cactus
* Number of seeds per fruit
* Species richness and diversity per cactus
* Proportion of frugivous birds present relative to non frugivorous birds

## Methods and Experimental Design

### Site specific metrics

For one week (4 days at the Mojave, 2 days at Wind Wolves), I will complete a preliminary field season where I measure the size of each cactus (x, y, and z dimensions of the cactus) and count its branches. I will do this for 100 individuals of each study species. I will also perform a density survey of cactus species. To do this, I will randomly choose one location within my study site, and create a 100m transect starting from that point in a random direct. Every 5m, I will record the distance to the nearest cactus of each species. I will repeat this transect 6 times total, 10m a part for each “starting” point of the transect. This week will only be to collect data to ensure my sample size and time frame is reasonable, so that I have ample time to redesign any issues in my methods.

In addition to surveying cactus density and diversity, we will also be conducting density and diversity surveys of birds at the site. While walking 1km transects, we will record the presence and transect meter for all birds seen or heard, and identify them to the best of our ability. Doing this once every 7 days will give us a better idea of the total bird diversity/density of the site.

### Flowering Experiment

Pending the exploratory week, we will return in April/May during the flowering season to observe pollinating birds interactions with cacti. The cacti will have different levels of manipulated “showiness” (percent of flowers) at different sized cacti. First, we will choose 270 cacti (10 replicates of each combination of species, size, and percent flower), and remove 0%, 50%, and 100% of flower buds from 10 individuals of each size class and species.

While the flowering season for our study cacti is in May, the cactus individual itself only blooms for 1-2 days throughout the season. Additionally, we are most interested in hummingbirds as pollinators, which are nearly impossible to document on camera traps and difficult to identify by eye in the field (especially female/juveniles). Because of these constraints, we will primarily rely on focal observations aided by a 200-500mm digital camera. We will do 1 hour observations in mornings or evenings at each combination of variables 4 times and at an open, cactusless site (40 hours of observations). During this time, we will also be equipped with audio recorders with parabolic shields to make recordings of bird calls *ad libitum*.

### Fruiting Experiment

Next, in August, we will begin the fruiting observation and experiment–it will be nearly identical to the flowering experiment, but with some added components. Each combination of variables (species, size, and fruit percent) will again have 10 replicates, meaning 270 cacti will be a part of the study. We will remove 0%, 50%, and 100% of fruits from small, medium, and large cacti for all three species. We will immediately place each cactus’s fruit in a sealed zip lock bag to prevent desiccation while in the field. Post collection, we will weigh the fruits and sieve the seeds for weighing and counting.

We will place two camera traps at an individual sample cactus for all combinations of variables, one facing the cactus (>5m away from the cactus) and one facing the open (18 total cameras). We will leave this camera to record movement for 5 days taking still images. After 5 days, we will randomly choose a new cactus/open site for each treatment combination to place camera traps at. We will replicate this process 5 times, over 25 days. Because camera traps may be unreliable recorders of bird abundance, we will also use audio recordings to measure bird presence. We will record during our focal observations (see below) *ad libitum* during both the cactus and open observations. Sound recorders have been shown to be as reliable a measurement of bird presence compared to walking point transects, and are more time and cost effective (Darras et al. 2018). To identify bird calls, we will classify the calls by ear, and then use a audio software program, like Sound Analysis Pro 2011 to identify the many hours of audio data (L. A. Grieves, Logue, and Quinn 2014; Leanne A. Grieves, Logue, and Quinn 2015).

In addition to passive monitoring, we will also perform focal observations, equipped with 200-500mm digital cameras. We will be at least 10 meters from the cactus, so as not to impact bird abundance. These focal observations will last for 1 hour in mornings or evenings, and be performed 4 times at each combination of treatments and in an open, cactusless site (40 total hours of focal observation). We will record each bird individual’s species and behavior (using an ethogram). Should there be more than one individual present, we will record the visiting species, but continue behavior observation for the first arrival birds (for up to 10 minutes, although this time limit is unlikely to be surpassed considering bird movement).

We will give seeds taken from *Opuntia basilaris* var. *treleasei* to the management at the Wind Wolves Preserve, should they desire to use these seeds in restoration projects (as they do with many native species at the site). I will have a team of 4-6 undergraduate assistants to help me, particularly with fruit collection and focal observations.

## Paired Flower and Fruit Observations

Because the manipulated flowering and fruiting cacti will not be paired, we will also perform a paired observational study. To link flowering number to fruiting number, we will find 20 individuals of each species (60 cacti total) in flowering season, and count the number of flowers/buds, determine the branching pattern, and measure their volume (x, y, z axis). We will also measure the sucrose content of the nectar for each plant using a radiometer, as sucrose is the nutritional source in nectar for hummingbirds (Martinez Del Rio 1990). These cacti will be geographically logged, and revisited in the fruiting season. In August, we will similarly collect and count the number of fruit. These data will allow us to compare flowering patterns with fruiting patterns in paired individuals across species.

# Chapter 3: Avian pollination and seed dispersal influence on seed shadow of Cactaceae obligatory facilitatees

## Purpose

This chapter will test the importance of birds as seed dispersers for cacti which are, at different life stages, beneficiaries and benefactors of nurse plants and animals respectively. Specifically, the Saguaro cactus. This chapter has nearly the same methods as Chapter 2, except an additional step to link birds to saguaro facilitators.

## Research Questions

1. Does flower number predict fruit number?
2. Do larger cacti produce more flowers/fruits, or higher mass fruits than smaller cacti?
3. Do larger fruits produce more seeds, or higher mass seeds than smaller fruits?
4. Are frugivorous birds more frequent at for larger cacti?
5. Are pollinating birds (hummingbirds) optimally foraging at larger cacti?
6. Do birds produce seed rain in favorable habitats for germinating seedlings (under a nurse shrub canopy)?

## Hypotheses

1. Cacti size and flower, fruit, and seed production are positively related. Predictions:

* Larger cacti will produce more flowers, fruits, and seeds, as well as more massive fruits and seeds.

1. Bird frugivory and pollination optimally forage at cacti. Predictions:

* Birds will more frequently pollinate larger cacti, which have more flowers.
* Birds will more frequently eat fruit at larger cacti, which have larger/more fruits.

1. Frugivorous birds are perching in spaces for depositing seed rain in optimal germination habitats (under nurse plant shrubs). Predictions:

* Frugivorous birds will be found more often perching above nurse plant canopies than in open areas.

## Treatments

* **Mesohabitat**: Open/Cactus
* *Open is the control for cactus presense.*
* **Mesohabitat**: Open/Nurse Shrub
* *Open is the control for nurse shrub presense.*
* **Size of cactus individual**: Large, medium, small
* **Percentage of fruit on cactus**: 0%, 50%, 100%
* *0% fruit on cactus is the negative control, 100% fruit on cactus is positive control for fruit abundance*

## Response variables

* Mass of individual fruits
* Mass of individual seeds
* Number of flowers per cactus
* Number of fruits per cactus
* Number of seeds per fruit
* Species richness and diversity per cactus/shrub
* during both flowering and fruiting season
* Proportion of frugivorous birds present relative to other species per cactus
* during both flowering and fruiting season
* Species richness and diversity per nurse shrub
* Proportion of frugivorous birds present relative to other species per nurse shrub

## Methods

All methods in regards to density, flowering, fruiting, and seed manipulations/measurements will be the same as in Chapter 2. Additionally, the methods to monitor bird species will also remain the same (camera trapping, audio recording, focal observations, and walking surveys).

What will differ, however, is an additional component where we explore the saguaro’s need to germinate under a nurse plant’s canopy (Turner et al. 1966). To do this, we will randomly select 100 shrub individuals, and count the number of Saguaro juveniles having germinated under the shrub canopy. We will then measure 100 paired open spaces 5m from a measured shrub. To determine bird abundance at these two sites, we will place 2 camera traps at 20 of the shrub/open sites (one camera facing the shrub, one facing the open), and 2 unidirectional audio recorders, one facing the shrub and one facing the open. We will only perform this protocol during the fruiting season.

# Future Work

This study opens up at least two side projects, potentially to be conducted by an undergraduate research assistant. One would be linking bird frugivory to seed shadow using seed trays placed under different mesohabitats. For example, the trays could be placed under nurse shrubs, cacti, and open spaces. This would help complete the circle of my thesis chapters. Additionally, by collecting fruit and seed samples, a collaborator could identify nutrition offered to bird species by facilitating cactus species. This would offer a better understanding of the importance of these cactus species to the community structure.

# References

Andre, J. M. 2006. “Vascular Flora of the Granite Mountains, San Bernardino County: An Annotated Checklist.” *Crossosoma* 32 (2): 38–74.

Angelini, Christine, Andrew H. Altieri, Brian R. Silliman, and Mark D. Bertness. 2011. “Interactions Among Foundation Species and Their Consequences for Community Organization, Biodiversity, and Conservation.” *BioScience* 61 (10): 782–89. doi:[10.1525/bio.2011.61.10.8](https://doi.org/10.1525/bio.2011.61.10.8).

Bertness, Mark D. M.D., and Ragan Callaway. 1994. “Positive Interactions in Communities.” *Tree* 9 (5): 191–93. doi:[10.1016/0169-5347(94)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4).

Callaway, Ragan M. 1997. “Positive Interactions in Plant Communities and the Individualistic-Continuum Concept.” *Oecologia* 112: 143–49.

Darras, Kevin, Péter Batáry, Brett Furnas, Antonio Celis-Murillo, Steven L. Van Wilgenburg, Yeni A. Mulyani, and Teja Tscharntke. 2018. “Comparing the Sampling Performance of Sound Recorders Versus Point Counts in Bird Surveys: A Meta-Analysis.” *Journal of Applied Ecology*, no. June: 2575–86. doi:[10.1111/1365-2664.13229](https://doi.org/10.1111/1365-2664.13229).

Drezner, T. Dawn. 2010. “Nurse Tree Canopy Shape, the Subcanopy Distribution of Cacti, and Facilitation in the Sonoran Desert.” *The Journal of the Torrey Botanical Society* 137 (2–3): 277–86. doi:[10.3159/09-RA-069R1.1](https://doi.org/10.3159/09-RA-069R1.1).

Drezner, Taly D., and Colleen M. Garrity. 2003. “Saguaro Distribution Under Nurse Plants in Arizona’s Sonoran Desert: Directional and Microclimate Influences.” *Professional Geographer* 55 (4): 505–12. doi:[10.1111/0033-0124.5504008](https://doi.org/10.1111/0033-0124.5504008).

Drezner, Taly Dawn. 2014. “The Keystone Saguaro (Carnegiea Gigantea, Cactaceae): A Review of Its Ecology, Associations, Reproduction, Limits, and Demographics.” *Plant Ecology* 215 (6): 581–95. doi:[10.1007/s11258-014-0326-y](https://doi.org/10.1007/s11258-014-0326-y).

Flores-Torres, Arnoldo, and Andrea Galindo-Escamilla. 2017. “Pollination Biology of Agave Horrida (Agavaceae) in the Chichinautzin Mountain Range, in Central Mexico“.” *Botanical Sciences* 95 (3): 423–31.

Franco, Author A. C., and P. S. Nobel. 2009. “Effect of Nurse Plants on the Microhabitat and Growth of Cacti Published by : British Ecological Society Stable URL : Http://Www.jstor.org/Stable/2260991” 77 (3): 870–86.

Gomez-Aparicio, Lorena, Regino Zamora, Jorge Castro, and Jose A. Hódar. 2008. “Facilitation of Tree Saplings by Nurse Plants: Microhabitat Amelioration or Protection Against Herbivores?” *Journal of Vegetation Science* 19 (2): 161–72. doi:[10.3170/2008-8-18347](https://doi.org/10.3170/2008-8-18347).

Grieves, L. A., D. M. Logue, and J. S. Quinn. 2014. “Joint-Nesting Smooth-Billed Anis, Crotophaga Ani, Use a Functionally Referential Alarm Call System.” *Animal Behaviour* 89. Elsevier Ltd: 215–21. doi:[10.1016/j.anbehav.2014.01.008](https://doi.org/10.1016/j.anbehav.2014.01.008).

Grieves, Leanne A., David M. Logue, and James S. Quinn. 2015. “Vocal Repertoire of Cooperatively Breeding Smooth-Billed Anis.” *Journal of Field Ornithology* 86 (2): 130–43. doi:[10.1111/jofo.12096](https://doi.org/10.1111/jofo.12096).

Gutzwiller, Kevin J., and Wylie C. Barrow. 2003. “Influences of Roads and Development on Bird Communities in Protected Chihuahuan Desert Landscapes.” *Biological Conservation* 113 (2): 225–37. doi:[10.1016/S0006-3207(02)00361-0](https://doi.org/10.1016/S0006-3207(02)00361-0).

Hernandez, R. R., S. B. Easter, M. L. Murphy-Mariscal, F. T. Maestre, M. Tavassoli, E. B. Allen, C. W. Barrows, et al. 2014. “Environmental Impacts of Utility-Scale Solar Energy.” *Renewable and Sustainable Energy Reviews* 29. Elsevier: 766–79. doi:[10.1016/j.rser.2013.08.041](https://doi.org/10.1016/j.rser.2013.08.041).

Hoover, Robert F. 1970. *The Vascular Plants of San Luis Obispo County, California*. 1st ed. Berkley: University of California Press.

Johnson, Steven D., C. I. Peter, Anders Nilsson, and Jon Agren. 2003. “Pollination Success in a Deceptive Orchid Is Enhanced Co-Occurring Rewarding Magnet Plants.” *Ecology* 84 (11): 2919–27. doi:[10.1890/1](https://doi.org/10.1890/1).

Maestre, Fernando T., Ragan M. Callaway, Fernando Valladares, and Christopher J. Lortie. 2009. “Refining the Stress-Gradient Hypothesis for Competition and Facilitation in Plant Communities.” *Journal of Ecology* 97 (2): 199–205. doi:[10.1111/j.1365-2745.2008.01476.x](https://doi.org/10.1111/j.1365-2745.2008.01476.x).

Martinez Del Rio, Carlos. 1990. “Sugar Preferences in Hummingbirds : The Influence of Subtle Chemical Differences on Food Choice.” *The Condor* 92 (4): 1022–30.

Miranda-Jacome, Antonio, Carlos Montaña, and Juan Fornoni. 2013. “Sun/Shade Conditions Affect Recruitment and Local Adaptation of a Columnar Cactus in Dry Forests.” *Annals of Botany* 111 (2): 293–303. doi:[10.1093/aob/mcs255](https://doi.org/10.1093/aob/mcs255).

Mitchell, Randall J. 1994. “Effects of Floral Traits , Pollinator Visitation , and Plant Size on Ipomopsis Aggregata Fruit Production Author ( S ): Randall J . Mitchell Source : The American Naturalist , Vol . 143 , No . 5 ( May , 1994 ), Pp . 870-889 Published by : The University O” 143 (5): 870–89.

Moher, David, Alessandro Liberati, Jennifer Tetzlaff, Douglas G. Altman, and the PRISMA Group. 2009. “Academia and Clinic Annals of Internal Medicine Preferred Reporting Items for Systematic Reviews and Meta-Analyses :” *Annals of Internal Medicine* 151 (4): 264–69. doi:[10.1371/journal.pmed1000097](https://doi.org/10.1371/journal.pmed1000097).

Nathan, R., and H. C. Muller-landau. 2000. “Spatial Patterns of Seed Dispersal, Their Determinants and Consequences for Recruitment.” *Trends in Ecology & Evolution* 15 (7): 278–85. doi:[10.1016/S0169-5347(00)01874-7](https://doi.org/10.1016/S0169-5347(00)01874-7).

Nielsen, Uffe N., and Becky A. Ball. 2015. “Impacts of Altered Precipitation Regimes on Soil Communities and Biogeochemistry in Arid and Semi-Arid Ecosystems.” *Global Change Biology* 21 (4): 1407–21. doi:[10.1111/gcb.12789](https://doi.org/10.1111/gcb.12789).

Nobel, Park. 2002. *Cacti Biology and Uses*. University of California Press 1.

Nobel, Park S. 1980. “Morphology , Nurse Plants , and Minimum Apical Temperatures for Young Carnegiea Gigantea Author ( S ): Park S . Nobel Published by : The University of Chicago Press Stable URL : Http://Www.jstor.org/Stable/2474851 Accessed : 16-05-2016 19 : 34 UTC Your Us.” *Botanical Gazette* 141 (2): 188–91.

Obeso, José Ramón. 2004. “A Hierarchical Perspective in Allocation to Reproduction from Whole Plant to Fruit and Seed Level.” *Perspectives in Plant Ecology, Evolution and Systematics* 6 (4): 217–25. doi:[10.1078/1433-8319-00080](https://doi.org/10.1078/1433-8319-00080).

Parker, Kathleen C. 1989. “Nurse Plant Retationships of Columnar Cacti in Arizona.” *Physical Geography* 10 (4): 322–35. doi:[10.1080/02723646.1989.10642386](https://doi.org/10.1080/02723646.1989.10642386).

Pfahl, S., P. A. O’Gorman, and E. M. Fischer. 2017. “Understanding the Regional Pattern of Projected Future Changes in Extreme Precipitation.” *Nature Climate Change* 7 (6): 423–27. doi:[10.1038/nclimate3287](https://doi.org/10.1038/nclimate3287).

Rodriguez-Estrella, Ricardo. 2007. “Land Use Changes Affect Distributional Patterns of Desert Birds in the Baja California Peninsula, Mexico.” *Diversity and Distributions* 13 (6): 877–89. doi:[10.1111/j.1472-4642.2007.00387.x](https://doi.org/10.1111/j.1472-4642.2007.00387.x).

Singh, Deepti, Michael Tsiang, Bala Rajaratnam, and Noah S. Diffenbaugh. 2013. “Precipitation Extremes over the Continental United States in a Transient, High-Resolution, Ensemble Climate Model Experiment.” *Journal of Geophysical Research Atmospheres* 118 (13): 7063–86. doi:[10.1002/jgrd.50543](https://doi.org/10.1002/jgrd.50543).

Smith, Melinda D. 2011. “The Ecological Role of Climate Extremes: Current Understanding and Future Prospects.” *Journal of Ecology* 99 (3): 651–55. doi:[10.1111/j.1365-2745.2011.01833.x](https://doi.org/10.1111/j.1365-2745.2011.01833.x).

StateofCaliforniaa, Natural Resource Agency. 2018. “State and Federally Listed Endangered and Threatened Animals of California.”

StateofCaliforniab, Natural Resource Agency. 2018. “State and Federally Listed Endangered, Threatened, and Rare Plants of California.”

Taylor, Nathan T., Kendall M. Davis, Helena Abad, Maureen R. McClung, and Matthew D. Moran. 2017. “Ecosystem Services of the Big Bend Region of the Chihuahuan Desert.” *Ecosystem Services* 27. Elsevier B.V.: 48–57. doi:[10.1016/j.ecoser.2017.07.017](https://doi.org/10.1016/j.ecoser.2017.07.017).

Tewksbury, Joshua J., and John D. Lloyd. 2001. “Positive Interactions Under Nurse-Plants: Spatial Scale, Stress Gradients and Benefactor Size.” *Oecologia* 127 (3): 425–34. doi:[10.1007/s004420000614](https://doi.org/10.1007/s004420000614).

Thomson, James D. 1978. “Insect Visitation in Two-Species Mixtures of Hieracium Author ( S ): James D . Thomson Source : The American Midland Naturalist , Vol . 100 , No . 2 ( Oct ., 1978 ), Pp . 431-440 Published by :” 100 (2): 431–40.

Traveset, A., and M. Verdu. 2002. “A Meta-Analysis of the Effect of Gut Treatment on Seed Germination.” *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. Third International Symposium-Workshop on Frugivores and Seed Dispersal, São Pedro, Brazil, 6-11 August 2000*, 339–50. doi:[10.1079/9780851995250.0339](https://doi.org/10.1079/9780851995250.0339).

Traveset, A., N. Riera, and R. E. Mas. 2001. “Passage Throgh Bird Guts Causes Interspecific Differences in.PDF,” 669–75.

Turner, Raymond M., Stanley M. Alcorn, George Olin, and John A. Booth. 1966. “The Influence of Shade , Soil , and Water on Saguaro Seedling Establishment.” *Botanical Gazette* 127 (2-3): 95–102. doi:[10.1016/j.apmr.2013.01.024](https://doi.org/10.1016/j.apmr.2013.01.024).

Verdu, Miguel, and Anna Traveset. 2004. “Bridging Meta-Analysis and the Comparative Method: A Test of Seed Size Effect on Germination After Frugivores’ Gut Passage.” *Oecologia* 138 (3): 414–18. doi:[10.1007/s00442-003-1448-4](https://doi.org/10.1007/s00442-003-1448-4).

Willson, M. F. 1993. “Dispersal Mode, Seed Shadows, and Colonization Patterns.” *Vegetatio* 107-108 (1): 261–80. doi:[10.1007/BF00052229](https://doi.org/10.1007/BF00052229).

Wolf, Author L. L., and F. R. Hainsworth. 1990. “Non-Random Foraging by Hummingbirds : Patterns of Movement Between Ipomopsis.” *Functional Ecology* 4 (2): 149–57.