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UNIVERSITY OF CALIFORNIA  
SANTA CRUZ

**SPECIES INTERACTIONS AND CLIMATE CHANGE IN THE LOSS OF  
JOSHUA TREES  
AND  
THE ROLE OF ECO-ART FOR UNDERSTANDING MULTISPECIES  
CONNECTIONS**

A dissertation submitted in partial satisfaction  
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Jennifer T. Harrower

June 2019

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## **Abstract**

### **Species interactions and climate change in the loss of Joshua trees and the role of eco-art for understanding multispecies connections**

**Jennifer T. Harrower**

Human induced global change has greatly contributed to species loss with profound consequences for humans and other organisms. With the rapid pace of climate change and the slow adoption of sustainable actions, I argue that art-science integrated research can enhance our understanding of interspecies connections and support the development of sustainable societies. Working with iconic Joshua trees as a symbol of the nature/culture interface, I take an ecological, eco-art, and multispecies studies approach to understand the ways that climate change impacts the important symbiotic interactions that regulate Joshua tree distribution and how art can provide a meaningful connection to that work. First, I characterize and quantify populations of Joshua trees and their key symbionts – moth pollinators and mycorrhizal fungi – across a climate gradient in Joshua Tree National Park, to understand how their context-dependent associations change with climate and the resulting implications for tree survival. I found that moth number, trees number, and all measures of tree vigor peaked around the same elevation, but that the moths were not present at Joshua tree range extremes even though the trees were flowering at those locations. I also found that the reproductive success of Joshua trees is tightly linked to pollinator abundance, and the conditional outcomes (magnitude of the fitness benefit) of the mutualism change depending on where it occurs on the



elevation gradient. Likewise, we found that fungal communities change with elevation, and that different fungal communities resulted in a spectrum of interaction outcomes from mutualism to parasitism that depended on the developmental stage of the plant. These are important examples of how climate change can impact species distributions directly (acting on either the moth, the fungi, or the Joshua tree) as well as indirectly by affecting the interactions between them. Next, I discuss my research findings in relation to the California Desert Protection and Recreation Act, highlighting areas where the Act falls short on Joshua tree protection and recommending future research and policy considerations. Finally, I discuss how those ecological findings, when colored by Donna Haraway's multispecies studies approach, influence my multimedia social-practice art work *Staying with the Trouble for Joshua Trees*. My art practice engages diverse communities in the experience and discourse of species loss in three media: an experimental and conceptual painted soil study, a stop motion animation, and a mock online dating site to meet Joshua trees. Through this work I discuss how art can be a powerful tool for social change, both as an inquiry-based practice and a platform to share complex environmental issues with a diverse public.

This dissertation is dedicated to:

Owen, Jack, Mom, and Dad

with my deepest gratitude.

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## **Introduction**

We are losing a great number of species at alarming rates because of the impacts of our collective behaviors on the Earth's ecosystems (Ceballos and Ehrlich 2018), yet we lack the magnitude of public response and behavioral shifts that are needed to address these issues. Most of the environmental issues that contribute to accelerated species loss come from systemic socioeconomic and cultural causes. They are embedded within our social institutions, structures, and social relations within our society, and their solutions will require a range of disciplinary approaches (Van Dooren 2014, Demos 2016, Haraway 2016, Tsing et al. 2017). Art is a powerful tool for social change, both as an inquiry-based practice as well as a platform to share complex environmental issues with a diverse public (Curtis et al. 2014, Curtis 2017). Narrative techniques through art can connect people to complex concepts at an emotional level, increasing public understanding and empathetic response to our role in the crisis of species loss (Harrison and Harrison 1993, Jacobson et al. 2007, Ballengée 2015, A'Bear et al. 2017, Curtis 2017). Art can play a transformative role by initiating behavioral shifts and inciting demand for environmental policy to move towards more sustainable and equitable societies (Miller 2014, Curtis 2017, Tsing et al. 2017, Harrower et al. 2018).

Rapid anthropogenic climate change is one of the biggest threats to ecosystems and greatly contributes to species loss through the disruption of species' phenology (Field et al. 2014, Melillo 2014), the decoupling of trophic relationships (Van der Putten et al. 2010), asynchronous species range shifts (Chen et al. 2011),

and differential outcomes of symbiotic interactions that can vary from mutualistic to parasitic (Johnson 1997, Tylianakis et al. 2008, Hegland et al. 2009, CaraDonna et al. 2017). We know that changes in abiotic conditions can affect the outcome of an interaction through direct effects on each interacting species as well as by modulation of the interaction itself. The outcomes of those species interactions can set geographical ranges (Afkhani et al. 2014) and influence population dynamics (Holland et al. 2002). But to uncover opportunities to manage the outcomes of symbiotic interactions under future climate scenarios, we need to know how these interactions determine range limits, and how effects varies across species and environmental gradients. Evaluating local variation in demographically important outcomes of target species interactions along geographical gradients may help to predict whether a species distribution range will decline, be stable, or expand in the face of climate change.

Iconic Joshua trees (*Yucca brevifolia*; Agavaceae) are threatened by the changing climate, and may be extinct from their namesake park within a century (Cole et al. 2011, Barrows and Murphy-Mariscal 2012). Pollinated exclusively and obligately by yucca moths (*Tegeticula synthetica* and *Tegeticula antithetica*; Prodoxidae), the moths provide a pollination service to the trees and then lay eggs inside of the fertilized flowers (Pellmyr 2003, Smith 2009). The developing moth larvae incubate within the seed pods that form from those fertilized flowers, consuming a fraction of the Joshua tree's fertilized seeds; this results in a tight codependence between the species for survival (Pellmyr and Huth 1994). But we

did not know how moth populations are impacted by the changing climate nor how changes in moth populations would impact Joshua tree reproductive success.

Fertilized seeds uneaten by moth larvae have an opportunity to become the next generation of Joshua trees. Upon landing in a hospitable area, the emerging seedling encounters different strains of mycorrhizal fungi depending on where it germinates in the soil. Arbuscular mycorrhizal fungi (AMF) form important symbiotic relationships with most plant species, providing improved access to soil nutrients and enhanced protection against pests, disease, and drought stress, which can be particularly important for young seedlings (Allen 1991, Smith et al. 2010). However, we did not know if AMF form associations with Joshua trees, how these associations impact tree functioning, or in what ways changes in environmental conditions could impact the outcomes of that symbiosis.

Beyond their ecological roles, Joshua trees are also socially and culturally important to many people, both traditionally and in modern times. They were used by the Cahuilla, Chemehuevi, and Serrano tribes (among others) as a food and/or fiber source (Bean and Saubel 1972). In popular culture, they have been featured in numerous music videos, films, advertising campaigns, fashion shoots, and across social media (Sizek 2017). JTNP is one of the most visited National Parks, and Joshua trees are the iconic species of the Mojave Desert (Rogers 2016), thus providing an opportunity to leverage Joshua tree iconography and focus public attention on the impacts that our actions have on the earth's ecosystems and species.



In this dissertation, I first address the complexities of species loss under climate change within the Joshua tree model system by combining ecological and molecular methods to understand how Joshua tree, fungal, and moth distributions vary across a climate gradient in Joshua Tree National Park (JTNP), and how the context-dependent outcomes of those symbioses impact Joshua tree population dynamics. Next, I discuss what the findings from my ecological research imply for Joshua trees when considered with the recently passed California Desert Protection and Recreation Act (CDPRA; S. 32 – 115th Congress: California Desert Protection and Recreation Act of 2018). Lastly, I integrate my ecological results with multispecies theories from scholars in the humanities (Tsing 2012, Haraway 2016, Van Dooren et al. 2016), to build theory that informs my multimedia arts practice. Through this interdisciplinary approach, I develop various platforms to communicate the complexity and ecological importance of multispecies interactions in the Joshua tree system with a diverse community.

In Chapter 1, I evaluated the spectrum of conditional outcomes of the Joshua tree yucca moth interaction, examining a range of performance measures and abiotic factors across the elevation range that spans the distribution of Joshua trees in JTNP. I found a strong concordance between tree size, moth and tree abundance, and reproductive success, with peak performance of both partners at intermediate elevation. Within sites, larger trees produced more flowers, attracted more pollinators, and had greater seed set. I found that the conditional outcomes of the interaction varied predictably along the gradient: seed set, as well as seed predation

were greatest at intermediate elevations where trees and pollinators were both at high abundance. At range margins the proportion of infertile seeds increased, possibly because low pollinator abundance led to pollen limitation. This suggests that the reproductive success of Joshua trees is tightly linked to pollinator abundance, and the conditional outcomes (magnitude of the fitness benefit) of the mutualism change depending on where it occurs on the elevation gradient.

In Chapter 2, I used next generation DNA sequencing to examine the changing AMF community of Joshua trees along a climate gradient in Joshua Tree National Park. I then used a range of performance measures and abiotic factors to evaluate how different AMF communities may impact Joshua tree fitness. I found that fungal communities change with elevation and that different fungal communities resulted in a spectrum of interaction outcomes from mutualism to parasitism that changed with the developmental stage of the plant. Nutrient accumulation and the mycorrhizal growth response (MGR) of the Joshua tree seedlings inoculated with fungi from the lowest (warmest) elevations was first negative, but after 9 months had surpassed that of plants with other fungal treatments. This indicates that low elevation fungi are costly for the plant to initiate symbiosis, yet confer benefits over time. The strong relationship between AMF community and plant growth suggests that variation in AMF community may have long term consequences for plant populations along an elevation gradient. This could be particularly important for the survival of desert seedlings that must establish and survive extreme temperatures and drought.

For Chapter 3, I reviewed the history of land preservation in the Mojave Desert and its relationship to JTNP, then considered my ecological research on Joshua trees and their key interacting species to describe how the CDPRA falls short on Joshua tree protection for current and future populations. I found that while the Act adds acreage directly to JTNP, it does not secure future areas where Joshua trees may need to establish as their local range shifts with the changing climate. I also found that the northern-most local range edge of Joshua trees straddles wilderness land and National Forest, an area governed by agencies with histories of conflicting management strategies and land use (Thomas 2003) which could present significant future management issues for Joshua tree populations. I conclude by recommending future research and next steps that guide management efforts, provide suggestions for collaborative governance strategies following examples from other systems (Thomas 2003, Ansell and Gash 2008), and argue that endangered species protection may be needed to regulate effective management of future Joshua tree populations as has been shown for other cases (Thomas 2003, Duane and Guerico 2010).

In my final chapter, I return to the ecological results from Chapter's 1 and 2 to reframe my findings using a multi-species studies approach, and I discuss how this critical theory informs my art practice. For Chapter 4, I asked: how can art-science-integrated research build understanding of interspecies connections for Joshua tree communities (e.g., trees, fungi, moths and culture)? How might this approach provide an enhanced platform with which to capture a diverse public

interest, building understanding and motivating sustainable behaviors more effectively than either discipline on its own? With this work I endeavored to co-create meaning and understanding of these interdisciplinary concepts by creating art for diverse communities of artists and scientists, the local Joshua tree community, and the greater community of people concerned about Joshua tree loss. Building on critical theorist Donna Haraway's challenge for societies to commit to doing the best we can with what we have, while expressly seeking solutions that value above all equity and sustainable practices – or as she calls it, “staying with the trouble” (Haraway 2016), my art and science practice engaged multilayers of species and cultural entanglements, and are collectively titled “*Staying with the trouble for Joshua trees*”. This social practice artwork of alternative communication and seeking meaning offered new possibilities through interdisciplinary and liminal spaces to understand ecosystems and generate connection. With this work, I invited the audience to participate in Joshua tree *knowing*, through an interdisciplinary fusion that takes place across three core projects: *Soil Symbiosis*, *A Joshua Tree Love Story*, and *Hey Jtree*.

For the first of these projects *Soil Symbiosis*, I created a conceptually driven and medium-pushing painting experiment to explore the tension existing in Joshua tree and fungal symbiosis. Drawing on materials gathered from my study organisms and incorporating my ecological data into the composition, this work is a window into the beauty and complexity of symbiotic interactions. Paintings from that work became backdrops in the second project, *A Joshua Tree Love Story*. This

collaborative stop-motion animation drew on my experiences while doing research in JTNP to demystify the science process, and provide an emotional narrative that engage viewers on themes of climate change, species loss, and motherhood. For the last project, *Hey Jtree*, I created a mock-online dating site and curatorial art project where participants can interact with the Joshua trees from my field sites through science, art, and play. Through these various projects I brought attention to the Joshua tree ecosystem's unique form, content, and symbols. By developing concepts and theories that informed and resonated with a diverse public I created new opportunities for science engagement while also pointing to the role that the artist plays in the evolving relationship between society and nature. I found that an arts practice is both a form of inquiry-based research and a tool for meaning making from ecological research, and that art can powerfully and effectively engage diverse audiences with complex science concepts.

This dissertation contributes 1) empirical evidence that climate change can impact species both directly and indirectly by influencing the outcomes of their key species interactions, 2) novel findings that demonstrate plant-mycorrhizal associations are both dependent on the species associating as well as the time since the interaction begins, 3) timely policy analysis that directly relates my ecological discoveries to recently enacted policies while pointing to key management considerations, and 4) successful examples for how an art practice can enhance science research and communication possibilities. Firstly, while other work has demonstrated that climate can drive the range of focal species, I find that obligate

species interactions are instrumental for setting species ranges and that climate can act on the outcomes of those interactions, indirectly impacting each partner.

Secondly, I characterized the unique fungal community for Joshua trees and demonstrated that plant-fungal associations can vary from mutualistic to parasitic depending on the different fungal communities associating, but also the concurrent stage of plant developmental. This work establishes the importance of AMF associations for the Joshua tree system. When taken together and in light of the recent passing of the CDPRA, I identified important considerations for Joshua tree management utilizing a multi-species approach and suggested key next steps to secure future, contiguous Joshua tree populations. Finally, I demonstrated that by utilizing narrative through art I could convey complex concepts and inspire emotional response across diverse communities thus increasing opportunities for science engagement and environmental empowerment. By engaging science concepts, artists can act as agents of change by advocating for communities and organisms not represented by economic interests or political parties and through developing new ways to communicate the complex nature-culture relationship.

## Chapter 1

### **Context-dependent mutualisms in the Joshua tree-yucca moth system shift along a climate gradient**

#### **Introduction**

The outcome of mutualistic species interactions can set geographical ranges (Afkhami et al. 2014) and influence population dynamics (Holland et al. 2002). Changes in abiotic conditions can affect the outcome of an interaction through direct effects on each interacting species as well as by modulation of the interaction itself. Abiotic changes can enhance a mutualism, convert it to antagonism, disrupt it, or force migration of one or both species (Bronstein 1994, Warren and Bradford 2014, Rafferty et al. 2015).

Rapid anthropogenic climate change is one of the biggest threats to ecosystems, visible as disruption of species' phenology (Field et al. 2014, Melillo 2014), the decoupling of trophic relationships (Van der Putten et al. 2010), asynchronous species range shifts (Chen et al. 2011), and differential outcomes of symbiotic interactions (Tylianakis et al. 2008, Hegland et al. 2009, CaraDonna et al. 2017). We have already witnessed shifts in species ranges to higher elevations and towards the poles (Parmesan and Yohe 2003, Poloczanska et al. 2013, Mason et al. 2015). Numerous forecasts suggest future changes in climate conditions will continue to shift species distributions and change the direction and magnitude of the outcomes of key species interactions (Burkle et al. 2013, Chamberlain et al. 2014, Schmidt et al. 2016).

Species ranges are determined simultaneously by abiotic factors such as temperature, moisture, and nutrients, and by positive and negative species interactions (Bronstein 1994, Afkhami et al. 2014, Louthan et al. 2015, Tylianakis and Morris 2017).

To understand limits and uncover opportunities to manage the outcomes of mutualistic interactions under future climate scenarios, we need to know how these interactions determine range limits, and how the effect varies across environmental gradients. Elevation gradients function as ‘natural experimental systems’ through systematic variation in abiotic and biotic factors, and provide opportunities to gain needed insight into the context-dependence of mutualisms (Sundqvist et al. 2013, Rasmann et al. 2014). Changes in weather patterns or in soil temperature, moisture, and nutrients can impact the outcomes of species interactions (Forrest 2015a, McQuillan and Rice 2015, Rafferty et al. 2015). Evaluating local variation in demographically important outcomes of species interactions along geographical gradients may help to predict whether a species distribution range will decline, be stable, or expand in the face of climate change.

The iconic Joshua tree (*Yucca brevifolia*; Agavaceae) is a monocotyledonous tree distributed throughout the Mojave Desert of North America. Joshua trees produce bisexual flowers that occur in dense panicles, flowering once yearly between February and April, and can reproduce sexually or via clonal growth from sprouts from the root system (Fig. 1). Pollinated exclusively and obligately by yucca moths (*Tegeticula synthetica* and *Tegeticula antithetica*; Prodoxidae), the



female oviposits her eggs into the Joshua tree floral ovary and then actively pollinates the flower using specialized tentacles (Trelease 1893, Pellmyr 2003). The yucca moth is the tree's only pollinator and her growing larvae consume a fraction of the fertilized seeds; this results in a tight codependence between the species for survival (Pellmyr and Huth 1994). Bogus yucca moths (*Prodoxus weethumpi* and *Prodoxus sordidus*; Prodoxidae) are the sister genus of *Tegeticula* (Darwell et al. 2018) and will parasitize this system by ovipositing eggs into plant tissue and forming galls in the fruits and stalks (respectively) without providing a pollination service (Pellmyr et al. 2006).

Obligate mutualisms like the Joshua tree-yucca moth interaction are acutely sensitive to changes in climate. The interacting partners may respond differently, creating an asynchrony in species phenology that can lead to population decline and local extinction (Pellmyr and Huth 1994, Geib and Galen 2012, Rafferty et al. 2015). Environmental changes that shift the outcome to fewer viable seeds or greater seed predation could be detrimental to both species. However, the climate envelope within which this mutualism currently exists is narrow, and climate change effects in the Mojave Desert are expected to limit this envelope to only the highest elevations in Joshua Tree National Park (JTNP) within 90 years, greatly reducing habitat with suitable climate and potentially extirpating the species from its namesake park (Dole et al. 2003, Cole et al. 2011, Barrows and Murphy-Mariscal 2012). Abiotic changes will likely affect Joshua trees, their pollinators, and/or the interaction between them (Fig. 1.1). We do not know how either the Joshua tree or

the yucca moths respond directly to the expected changes to climate conditions, or how the interaction may be affected.

A key step towards anticipating how the Joshua tree-yucca moth mutualism may respond to environmental change is to examine how each organism varies across its geographic range, and how the outcomes of those interactions vary along that range. These mutualisms can be considered context-dependent when either the sign ( $-$ ,  $0$ ,  $+$ ) or the magnitude (strong to weak) of the interaction changes (Chamberlain et al. 2014). It is unknown if the performance of Joshua trees and their moths have independent optima and minima at the same environmental conditions, or if the geographic distribution of the mutualism is primarily determined by abiotic effects on just one of the partners and the other partner just follows along.

Here we examine how the abundance of each species varies by elevation, and quantify how the outcome of the Joshua tree-yucca moth interaction shifts depending on the context of where it occurs. We then develop and test a conceptual model that characterizes the drivers and structure of this context-dependent pollination mutualism (Fig. 1.2). This descriptive framework provides a structured approach for thinking about the factors contributing to mutualism outcomes in the Joshua tree-yucca moth system and aims to provide a tool to describe processes and context-dependent outcomes along an abiotic gradient.

In this study we sampled the abundance of Joshua trees and their moth pollinators across an elevation gradient to determine what impact species density and/or location has on the outcomes of this species interaction and the resulting

Joshua tree fitness. Specifically, we ask: 1) How do processes that are demographically important for Joshua trees change along an elevation gradient across the tree range in Joshua Tree National Park? 2) Does the abundance of yucca moth pollinators of Joshua trees vary predictably across the Joshua tree range in JTNP ? 3) To what degree is the reproductive success of Joshua trees explained by pollinator abundance versus environmental conditions? 4) Do the outcomes of the Joshua tree-yucca moth mutualism vary predictably along an elevation gradient?

## **Materials and Methods**

### *Study sites*

The study was conducted between spring 2016 and summer 2017 across a 1,200-m elevation gradient (ranging from 1,004 to 2,212 m) in Joshua Tree National Park, in south-western California, USA (located at 33.8734° N, 115.9010° W), with two additional sites located north west of JTNP to include the northernmost point of the local Joshua tree distribution (Fig. A1.1). Biogeographically, JTNP is situated at the transition zone between the Mojave and Colorado deserts. We selected 11 sampling sites from a continuous Joshua tree population that ranged from the southernmost point of the global Joshua tree distribution to the northern end of its continuous local range. These sites encompass 4 broad eco-regional vegetation types: Sonoran-Colorado Desert scrub, Mojave-Sonoran creosote bush scrubland, Mojave mid-elevation desert, and pinyon-juniper woodland (Sawyer et al. 2009). We obtained climate and soil moisture data for sites from 7 HOBO Pro V2

datalogger weather stations (Onset Computer, Cape Cod, Massachusetts, USA). Although the sites experience a similar cismontane influence along the western margin, they experience different climate conditions on average and vary across the gradient from very hot and dry at the lowest elevation to seasonal freezing temperatures at the highest elevation (Table 1.1).

### *Joshua tree demography*

To determine whether Joshua tree demographic parameters change across an elevation gradient in Joshua Tree National Park, we sampled two 20x200-m belt transects randomly positioned and separated by 50 m, and running from south-east to north-west at each of the 11 sites (Fig. A1.1). Since Joshua trees are monocots and do not produce annual growth rings, we measured the height of each tree using a digital clinometer (Haglöf HEC2), and counted the number of branches and flower panicles. All juveniles (<0.5m tall) were considered to be clonal if they occurred next to another tree and if rhizomes connected to the tree were found by digging under ground; otherwise seedlings were considered to be the products of sexual reproduction. Any dead trees were counted separately from live trees.

### *Soil sampling*

At each of the eleven sites, three soil cores (5-cm diameter and 15-cm length) were collected along each of the two transects and then bulked (six cores per site). Soil texture is sandy loam at all sites with varying amounts of rock and gravel.

Soil was dried, ground, and analyzed for total carbon and total nitrogen following the combustion method (AOAC 1997), pH (in H<sub>2</sub>O), total extractable ammonium and nitrate content by flow injection analyzer method (Keeney and Nelson 1982, Hofer 2003), extractable phosphorus using the Olsen method (OLSEN 1982), and percentage soil moisture following the gravimetric method (Black 1965) at the UC Davis Analytical Lab (<http://anlab.ucdavis.edu>) (Table 1.1).

### *Moth sampling*

To determine if the abundance of moth pollinators varies predictably over the distribution of Joshua trees along an elevation gradient, we used moth traps (clear plastic acetate painted with tangle-trap (Contech Inc., Victoria, BC) and secured to unopened blooms at the peduncle) (Smith et al. 2009) to sample flower panicle visitation across the 11 sites. The traps were randomly attached to three flower panicles per tree, three trees per site, or to the maximum number of blooms available at that location. The traps remained in place for 28 days to be exposed during peak pollinator emergence, and then they were removed and the captured moths were morphotyped to species by comparison to the collection at the Essig Museum of Entomology (<https://essig.berkeley.edu>).

### *Seed collection*

To determine if seed production varies with elevation, tree size, or pollinator abundance, we collected a maximum of six pods per tree, six trees per site from

each transect. If a tree had fewer than six pods, the total number available were collected and then we moved to the next tree, attempting to collect at least 36 pods per site. The total number of all pods available in each transect was recorded. For each site the collected pods were weighed and measured, split open, and all seeds were counted, noting the number of fertile and infertile seeds in each.

### *Data analysis*

We conducted simple linear regressions to evaluate the relationships between tree, site, and pollinator characteristics and compared different combinations of interactions both within and across sites. We then used generalized additive models (GAM) because we expected a non-linear and potentially idiosyncratic relationship between plant and pollinator numbers across elevation as well as between tree performance characteristics and elevation. GAMs are nonparametric extensions of linear models that allow the expected response to vary smoothly with a set of predictor variables (Yee and Mitchell 1991). We also used multiple regression to identify the most important combinations of characteristics for explaining moth abundance and seed set. This was done with stepwise regression to identify a model that parsimoniously explained the variability in the response variable for each combination of variables. We used the following criteria to select the best model: 1) the model had the lowest Akaike information criterion (AIC) value, 2) the model explained the most variability in the response variable, 3) individual variables in the model were significant at  $\alpha=0.10$  or better, and 4)

variables had low multicollinearity (Burnham and Anderson 2003). When all four criteria were not met, we selected the best model possible from the remaining criteria.

To determine the conditional variance of the outcomes of the pollination mutualism, we counted the number of fertile seeds (seeds are black), infertile seeds (seeds are small and white), and eaten seeds (seeds with visible predation damage) across the elevation gradient. As the positive outcome for the tree is the number of fertile seeds, and the positive outcome for the moth is proportional to the number of consumed seeds, we used a generalized additive model to examine the ratio of fertile seeds to eaten seeds to determine how the mutualism outcomes shift. All calculations were performed using the R language for statistical computing (The R Development Core Team 2017).

## **Results**

### *Weather conditions and soil properties along the elevation gradient*

Average summer temperature per site declined steadily along the elevation gradient with the warmest site at a daily average of 30.2°C and the coolest at 19.9°C ( $r^2=0.9$ ) (Table 1.1). Relative humidity generally increased with elevation ( $r^2=0.636$ ), as did the soil moisture at 10 cm ( $r^2=0.8$ ), increasing from 0.005 m<sup>3</sup>/m<sup>3</sup> to 0.14 m<sup>3</sup>/m<sup>3</sup>. Soil nutrients did not follow any noticeable trend with elevation, although pH declined from 8.06 to 6.63 with increasing elevation ( $r^2=0.827$ ).

### *Demography and reproduction across the elevation gradient*

Joshua trees are distributed across a 1200-m elevational range in JTNP, peaking at intermediate elevations (Table 1.1). The number of dead Joshua trees peaks at both the lowest (1004 m) and highest (2212 m) elevations across the range (Fig. 1.3). At the lowest and highest elevations in the range, there were no seedlings that were the product of sexual reproduction. Trees were small and few, and with few flowers, and we encountered no moths, seedpods, or seedlings at those sites, so reproduction was limited to clonal spread. Generalized additive models highlight a marked peak at around 1250 m where the trees were numerous and large and produced many flowers; this peak coincided with a high abundance of moths, as well as high production of pods, seeds, fertile seeds, and seedlings that grew from seeds (Fig. 1.3).

In the generalized additive models, the effect of elevation was highly significant for 12 of the 14 evaluated response variables, all except tree branches ( $p=0.109$ ) and number of seedlings ( $p=0.282$ ). The deviance explained by the models varied from 57.8% for the number of seedlings to 99% for the percent of eaten seeds (Table 1.2).

### *Joshua tree performance across the elevation gradient*

Within each site (Fig. 1.4), as well as for all sites combined ( $r^2=0.787$ ,  $p=0.0003$ ), larger Joshua trees produced more flower panicles. This reflects the developmental relationship between branch nodes and inflorescence production.



While there was a positive relationship between tree size and the percent of fertile seeds per pod across sites ( $r^2=0.67$ ,  $p=0.007$ ), there was no consistent relationship between tree size and fertile seeds within sites (Fig. 1.4). Likewise, there was no relationship between tree size and the pod length within sites, suggesting that seed production was not a simple function of plant vigor (Fig. 1.4).

#### *Joshua tree and yucca moth interaction across the elevation gradient*

The number of pods produced was significantly positively correlated with the mean pollinator density per trap ( $r^2=0.87$ ,  $p\leq 0.026$ ); similarly, the percent fertile seeds per pod ( $r^2=0.8$ ,  $p\leq 0.0012$ ), and total number of seeds per pod ( $r^2= 0.43$ ,  $p\leq 0.056$ ) were correlated with pollinator abundance, suggesting that areas with more moths will have greater sexual reproduction of Joshua trees. There was no correlation between pod length and the number of moths ( $r^2=0.26$ ,  $p\leq 0.16$ ).

Moth abundance was significantly correlated with tree size ( $r^2=0.826$ ,  $p\leq 0.0001$ ), tree abundance, and number of flower panicles per tree ( $r^2=0.764$ ,  $p\leq 0.0004$ ). Bigger trees had significantly more flower panicles ( $r^2=0.787$ ,  $p\leq 0.0002$ ). Moth abundance increased with the local abundance of trees but dropped off abruptly at the site with the most trees (61 trees/800m<sup>2</sup>) (Fig. 1.5). This site (1494 m) had a high number of trees, however many of those trees were clumped in clonal reproduction groups. With all sites combined there was a strong correlation between number of moths and total flower panicle numbers per site ( $r^2=0.914$ ,  $p\leq 4.3\times 10^{-6}$ ); however, within sites, only those sites in the middle of the elevation

range showed a positive correlation with more moths associated with more flowers on individual trees (Fig. 1.6).

#### *Combinations of factors explain fertile seeds and moth abundance across sites*

While different factors were the best predictors of fertile seeds or of moth abundance in pairwise correlations, when taken together, certain combinations of factors resulted in the strongest explanatory models. The best multivariate model to explain percent fertile seeds included elevation, the total number of flower panicles, and the number of trees ( $r^2=0.85$ ,  $p=0.0176$ ). Moth abundance was best explained by the total number of flower panicles, the number of trees, and the number of pods ( $r^2=0.9468$ ,  $p=2.292 \times 10^{-5}$ ). The predictor variable “tree height” did not appear in any of the final models, probably because tree height and panicle number are strongly colinear and functionally linked. Together these models indicate that reproductive success of both Joshua trees and the yucca moths are greatest where the Joshua trees are abundant and vigorous.

#### *Conditional variance of the mutualism across elevation*

Across the elevation gradient, the number of fertile seeds varied with respect to the number of eaten seeds (Fig. 1.7) ( $r^2=0.98$ ,  $p=0.007$ ). There were more fertile seeds per pod than the eaten seeds per pod at each of the elevation extremes. Conversely, the trees had a higher percentage of infertile seeds at either end of the elevation range compared to the seed pods occurring in the middle of the range (Fig.

1.7), yet seed predation increased as an inverse of the production of infertile seeds ( $r^2=0.918$ ;  $p=4.7 \times 10^{-5}$ ).

## **Discussion**

### *Effect of elevation on tree demography and reproduction*

Our results showed that tree death was greatest at the lowest elevations, with tree abundance and performance peaking at intermediate elevation. The ratio of dead to living trees was greater at the lower elevations where the sites are warmer and drier than sites at higher elevation. These sites fall in a transitional ecotone between the Colorado and Mojave Desert where plant communities change significantly in response to local climate (Barrows et al. 2014). Vegetation in transition zones such as these are predicted to be particularly sensitive to changes in climate (Ackerly et al. 2010). Patterns of size and reproduction across the elevation gradient were consistent with expectations from the models (Cole et al. 2011, Barrows and Murphy-Mariscal 2012) with Joshua trees dying and not reproducing at lower elevations. These results also agree with a recent demographic analysis of Joshua trees that found a negative relationship between warming temperatures and stand density, potentially constraining tree establishment (Clair and Hoines, 2018).

Elevation in JTNP is a surrogate for strong gradients in precipitation, temperature, soil type, and pH. Desert precipitation is low, so local differences in precipitation strongly affects the spatial and temporal patterns of desert biodiversity (MacMahon 1979, Barrows and Murphy-Mariscal 2012). Soil moisture was very

low at the lower, warmer elevations and may have contributed to Joshua tree death. Our results agree with model predictions (Cole et al. 2011, Barrows and Murphy-Mariscal 2012) and suggest that the range of Joshua trees is contracting at the lower elevations where there was no seedling recruitment and high tree mortality. As the hot, dry conditions extend upward, future generations of trees may only thrive at cooler, higher elevations.

We also found that a high proportion of trees were dying at the highest elevations, where there are strong winds and freezing temperatures. However, the high mortality at the highest site may be an artifact of small sample size; there were only four trees present at the upper range limit. Expected warming may make higher elevations more hospitable to Joshua trees in the future, but there is very limited land area at such high elevations in Joshua Tree National Park and those locations are also areas of high fire threat within the park (DeFalco et al. 2010).

At elevation extremes, Joshua tree reproduction is almost exclusively clonal. This agrees with studies which found that Joshua tree clonality increases with elevation (Simpson 1977, Rowlands 1978), but the lack of seedling recruitment and enhanced clonality at low elevations has not been previously reported. Seedlings may be unable to establish due to drought stress and heat at the lower elevation and freezing temperatures at the higher elevation (Reynolds et al. 2012). Trees produced flowers at both of the extremes, but we found no moths, no fruit development, and no seed set. Therefore, the lack of seedlings could also be explained by the lack of

pollinators and viable seeds. This could be tested with experimental outplanting of seeds.

Most species ranges occur along environmental gradients of variable habitat quality, with reduced fitness at range limits (Eckert 2002, Sagarin and Gaines 2002, Sexton et al. 2009). Clonal reproduction may allow plants to better forage for nutrients and water at the range margins; clonality may be due to an absence of pollinators and failed sexual reproduction; and clonality may dominate where environmental conditions are difficult for seedling establishment (Barrett 2015). A contracting range edge is typically a product of declining fitness and local extinction (Jump et al. 2009). If trailing edge populations of (mostly clonal) Joshua trees are also those in the population that are best adapted to deal with the highest local temperatures, a lack of sexual outcrossing with populations at higher elevations could threaten overall species persistence due to reduced fitness of seedlings as the climate warms (Dlugosch and Parker 2008, Dlugosch and Hays 2008). Clones have reduced reproductive fitness, which could increase susceptibility to local extinction of the trees (Hampe and Petit 2005). The lack of pollinators, seed set, and seedlings at higher elevations suggests that Joshua trees are not currently expanding their range upslope, however this trend would be better established by examining tree demography across several years. Common garden experiments with genotypes from different elevations, planted at different elevations could uncover any local adaptation to higher temperatures.

We found considerable Joshua tree seedling recruitment at intermediate elevations, peaking around 1300m, near the lower part of their range. This area of high seedling recruitment is also where the trees were biggest, produced the most flowers, pods and seeds, and had the biggest branches. Other studies have found that Joshua tree seeds germinate best following a heat treatment and that seedlings grow best following a cold treatment; however these impacts are bounded by temperature extremes (Went 1948). This suggests that the Joshua trees will have the greatest reproductive success with a combination of heat to stimulate seed germination and cold to support seedling establishment, but temperature extremes in either direction may result in death.

*The relationship between moth abundance and tree abundance*

Populations of both trees and moths were most vigorous near the middle of their elevation range. In many ecosystems, the number of individuals within a species is lower and performance is suboptimal towards their range edges (Eckhart et al. 2011). In JTNP, populations of both trees and moths peaked at approximately the same elevation, as did all measures of tree vigor. This may be either because the two species coincide in their environmental preferences, or because the mobile moths are able to congregate where robust tree hosts produce many flowers.

Large trees may derive more resources from their environment, allowing them to potentially support a larger population of organisms that depend on them for survival (Greene and Johnson 1994). Except at extreme elevations, bigger Joshua

trees, which had more flowers, hosted more pollinators (Fig. 1.6). They did not, however, produce more seeds (Fig. 1.4). This suggests that there are site level characteristics across the elevation gradient, other than moth abundance, that contribute to tree reproductive success.

The number of flowers is linked to tree size both across and within sites. This relationship makes sense developmentally because after flowering, a Joshua tree produces a branch from the flower node; more branches can then support more flower panicles in flowering years (Rowlands 1978).

We found that the density of both pollinating moths and bogus yucca moths generally increase with the densities of live trees just as pollinator moths do. Curiously, there was a low abundance of both moth species at the sites (elevation 1500-1600m) with the highest density of trees. These higher elevation sites were dominated by trees reproducing asexually. It is not clear whether moths are unable to thrive at these higher elevations or if the low numbers of flowers meant that location was unable to attract or support the moths. In either case, the low moth numbers mean low seed set for the trees. This elevation range, from 1500-1600m, where trees thrive but moths do not, may be an important transition zone for future work on the details of the Joshua tree-yucca moth climate mismatch.

While tree density does not appear to drive moth abundance directly, we found a very strong relationship between moth and flower numbers. Yucca moths are directly dependent on flowers and use their resulting fruit as nurseries for their larva (Pellmyr 2003). Areas where the moth populations exceed the ability of plants

to produce seed could lead to a loss of the next generation for both trees and moths, as one way the mutualism is kept in check is through abscission of flowers carrying excessive egg loads (Pellmyr and Huth 1994). However, we only found a relationship between moth and flower numbers within sites at middle elevations from 1240 to 1625. At extreme elevations, having more flowers did not correspond to higher moth numbers, which may indicate that in those areas, moth numbers are limited by site-specific conditions other than the number of flowers. For some insects that use fruit as a larval nursery, temperature can impact larval development (Krishnan et al. 2014). Temperature fluxuations may impact other stages of plant and animal life cycles in addition to flowering and pollinator emergence (Forrest 2015b); yucca moths continue a portion of their life cycle underground and may be limited by temperature changes that they encounter in the soil at extreme elevation.

#### *The relationship between moth abundance and seed production*

We found that seed production was strongly dependent on moth numbers. The areas with no moths failed to produce any seeds, even though there were flowering Joshua trees present. Areas with a greater number of moths produced pods with more fertile seeds than in areas with low moth numbers, suggesting that seed production is pollen limited. These results are consistent with findings of pollen-limited seed set in other yucca-yucca moth systems (Aker and Udovic 1981, Aker 1982, Addicott 1985, James et al. 1994). The decreased moth numbers and



seed set at Joshua tree range margins suggests that these pollinators may play a key role in setting range limits.

Pod size however was not correlated with moth numbers. In many systems, fruit production can be resource limited, and is linked to factors such as plant size or availability of key resources (Stephenson 1981, Fenner 2012). This is also found in other species of yucca where variance in fruit production was explained by geographic region as opposed to pollinator visitation (Udovic 1981). In Joshua trees, while the total number of fertile seeds may be dependent on the availability of pollinators, the size of the pods and seeds was smaller at range margins (Fig. 1.3), suggesting resource limitation. This appears to be more dependent on where the tree is growing and the resources it has available than tree size or pollinator number, because pod size does not vary consistently with changes in moth number or tree size. Small seed size could also contribute to the low seedling numbers towards range margins, but was not examined here. These results suggest that both pollinator abundance and tree access to resources are key for producing large seed pods with high numbers of fertile seeds.

Trees growing at the elevation extremes of the range produced a higher percentage of infertile seeds than did trees at the middle elevations. Inside of the pods, developing moth larvae consume seeds by moving down a chamber within a locule until they encounter an infertile seed, at which point they exit the pod by chewing out through the side and drop to the ground to burrow and pupate (Ziv and

Bronstein 1996). Thus having some number of infertile seeds spaced amongst the fertile seeds can actually improve overall seed survival.

Moth density is linked with pod number and to the percent of fertile seeds across the sites, but is weakly related to the total number of seeds per pod or pod length. One explanation could be that moth numbers remain low until around 1250 m elevation whereas total seed production (both fertile and infertile seeds) climbs before that. The flowers receive enough pollen to make infertile seeds but fertile seed set is low, either due to pollen quality or low abundance of pollen. Joshua trees may be producing large pods due to abundant available resources (soil, water and light). At either elevation extreme the pods have a much higher percentage of infertile seeds. A lack of available pollinators could result in large pods with more infertile seeds due to the low number of pollination events, suggesting that reproduction is pollen limited in these locations. This would occur if the environmental envelope of the moth's range does not extend as far as the Joshua tree's range, so that the number of pollinators is lower towards the range edges, resulting in lower numbers of fertile seeds and higher infertile seeds. This idea is consistent with other studies of systems involving specialized pollinators (Wilcock and Neiland 2002, Trunschke et al. 2017).

#### *Summarizing the outcomes of the mutualism across the elevation gradient*

Our results suggest that the outcome of the Joshua tree – yucca moth mutualism varies with respect to its location on the elevation gradient, in agreement

with other research that demonstrates context dependency in mutualistic interactions (Bronstein 1994, Chamberlain et al. 2014, Cass et al. 2016, Ji and Bever 2016, Tylianakis and Morris 2017). Specifically, the outcome of the mutualism (viable seed set) is congruent with optimum host vigor under current conditions, around the middle of the elevation range. Joshua trees seem to be dying back at low elevations as predicted, but they do not seem to be moving successfully into higher elevations, where the mutualism is not successful. Having robust, dense, flowering trees is important to support and attract enough moths for successful seed set, leading to a higher percentage of fertile seeds per pod and a higher magnitude positive interaction outcome (Fig. 1.2). It remains to be seen if Joshua tree performance can improve at higher elevations and if it will be able to attract enough moths to successfully reproduce, or if moths can migrate to and survive at those locations.

As this study only considers a single elevational transect with one study site per elevation, other variables such as genetic similarity and weather patterns could co-vary with elevation, presenting a limitation inherent in the study design. However, the measures of growth and reproduction (except for flowers and moths) are integrated across many years at those sites, and while there will undoubtedly be temporal variation, these flower and fruit observations are consistent with those expected from the integrated data, thus supporting a temporal variability argument.

With species distribution information, we can focus on the key variables and conditions that influence population numbers and promote favorable mutualistic outcomes, as well as quantify the outcome of the association in different locations

and the potential for species to track the changing climate. Future work with species distribution modeling that predicts how moths may respond to the changing climate could help us gauge if Joshua trees and their pollinators might overlap under future climate scenarios and how the local conditions may effect the outcomes of their mutualism.

## Tables

**Table 1.1 Characteristics of the eleven sites along an elevation gradient in JTNP.**

Variable	Site										
	1	2	3	4	5	6	7	8	9	10	11
Lat °N	34.24	34.11	33.55	34.13	34.47	33.58	33.59	33.55	34.14	34.14	34.14
Long °W	116.1	116.0	116.3	116.1	116.2	116.1	116.7	116.1	116.2	116.4	116.4
Elevation(m)	1004	1049	1114	1240	1290	1331	1402	1494	1625	2076	2212
Summer Tav(°C)	30.2	29.3	-	-	27.3	-	24.4	23.1	-	-	19.9
Summer RH(%)	32.1	34.9	-	-	34.7	-	46.1	45.6	-	-	42.2
Num of trees	7	26	14	48	34	42	39	61	35	38	4
Summer ppt(m)	0.01	0.23	-	-	0.12	-	0.25	0.01	-	-	0.003
Soil H <sub>2</sub> O(m <sup>3</sup> /m <sup>3</sup> )	0.01	0.02	-	-	0.05	-	0.11	0.05	-	-	0.14
C (total)(%)	3.03	0.19	0.20	0.31	0.21	0.96	0.34	0.25	0.29	0.47	0.52
NH <sub>4</sub> -N(ppm)	1.89	1.44	1.17	1.43	1.20	1.86	1.61	1.06	1.59	1.93	1.51
NO <sub>3</sub> -N(ppm)	5.53	2.03	3.06	4.26	2.19	39.1	2.41	2.19	4.02	4.42	1.90
Olsen-P(ppm)	10.9	6.30	8.00	9.10	5.40	19.3	11.4	7.50	12.9	22.7	14.9
K(ppm)	339	203	251	174	116	263	231	79.0	277	476	135
Na(ppm)	7	5	5	6	6	6	4	5	4	7	14
Ca(meg/100g)	27.2	3.16	2.63	3.2	3.03	7.41	3.75	4.58	2.85	3.56	7.47
Mg(meg/100g)	1.44	0.93	1.05	0.81	0.86	1.09	0.91	1.12	0.82	1.66	2.27
CEC(meg/100g)	29.5	4.62	4.34	4.49	4.22	9.20	5.26	5.93	4.39	6.47	10.2
OM(%)	2.87	0.45	0.42	0.40	0.40	1.72	0.58	0.62	0.81	1.01	1.28
pH	8.06	8.09	8.00	7.90	7.92	7.28	7.65	7.41	7.32	7.26	6.63

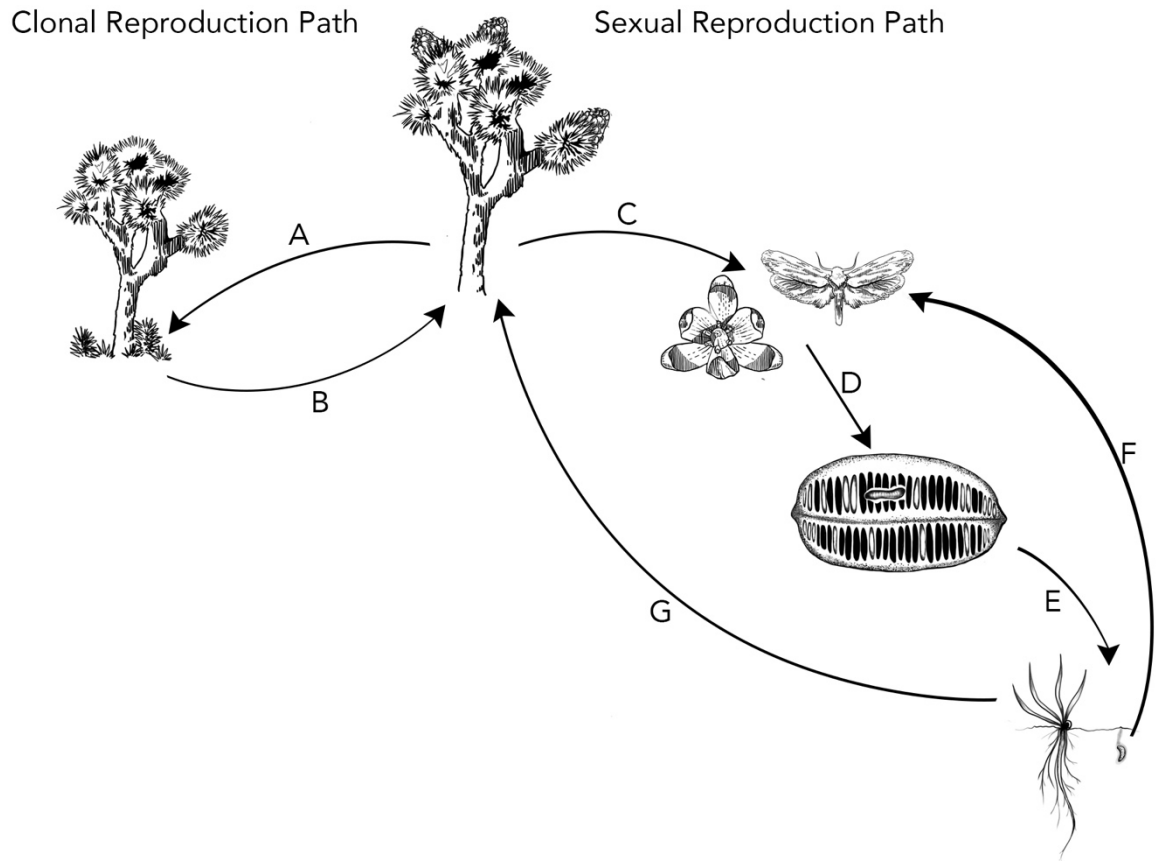
Notes: Tav, average temperature; RH, relative humidity; ppt, precipitation; C, carbon; NH<sub>4</sub>-N, ammonium; NO<sub>3</sub>-N, nitrate; P, phosphorus; K, potassium; Na, sodium; Ca, calcium; Mg, magnesium; CEC, cation exchange capacity; OM, organic matter; pH, potential of hydrogen.

**Table 1.2 Statistics associated with the generalized additive modeling (GAM) for the 14 different response variables as a function of elevation.**

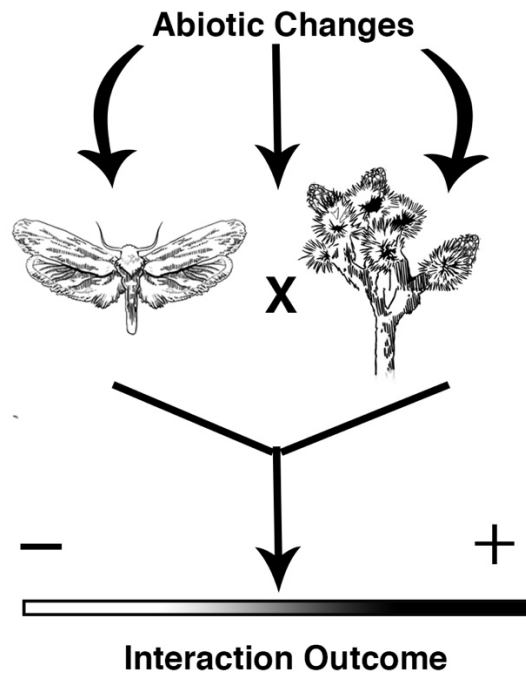
Species variables	D (%)	r <sup>2</sup>	c <sub>r</sub>	edf	f	p
Number of living trees/8000m <sup>2</sup>	96.9	0.941	0.8263	4.801	28.21	7.2x10 <sup>-5</sup>
Mean tree height	99.7	0.982	2.5855	8.589	62.25	0.006
Mean number of branches/tree	63.1	0.477	5.7150	2.954	2.686	0.109
Number of seedlings/site	57.8	0.353	0.9091	3.481	1.557	0.282
Number of juvenile clones/site	96.9	0.919	3.2727	6.21	15.92	0.01
% Juvenile clonal trees/site	99.5	0.96	0.7500	8.77	27.52	0.104
Mean number of flowers/tree	76.5	0.619	2.5289	3.85	3.615	0.073
Mean number of pollinators/tree	93.4	0.847	3.7543	5.694	8.813	0.022
Mean number of pods/tree	99.2	0.958	3.3458	8.117	26.21	0.044
Mean pod length/tree	98.6	0.972	6.5133	3.973	58.32	1.6x10 <sup>-5</sup>
Mean number seeds/pod	97.4	0.944	215.70	4.269	26.71	0.003
% Fertile seeds/pod	99.6	0.976	0.6664	6.631	44.03	0.062
% Infertile seeds/pod	99	0.999	0.2299	7.811	693.3	0.032
% Eaten seeds/pod	99	0.999	0.104	7.999	6840	2x10 <sup>-5</sup>

Notes: D, deviance explained; r<sup>2</sup>, the coefficient of determination; c<sub>r</sub>, intercept of the model in the response scale; edf, estimated degrees of freedom; f, f ratio statistic; p, calculated probability.

## Figures

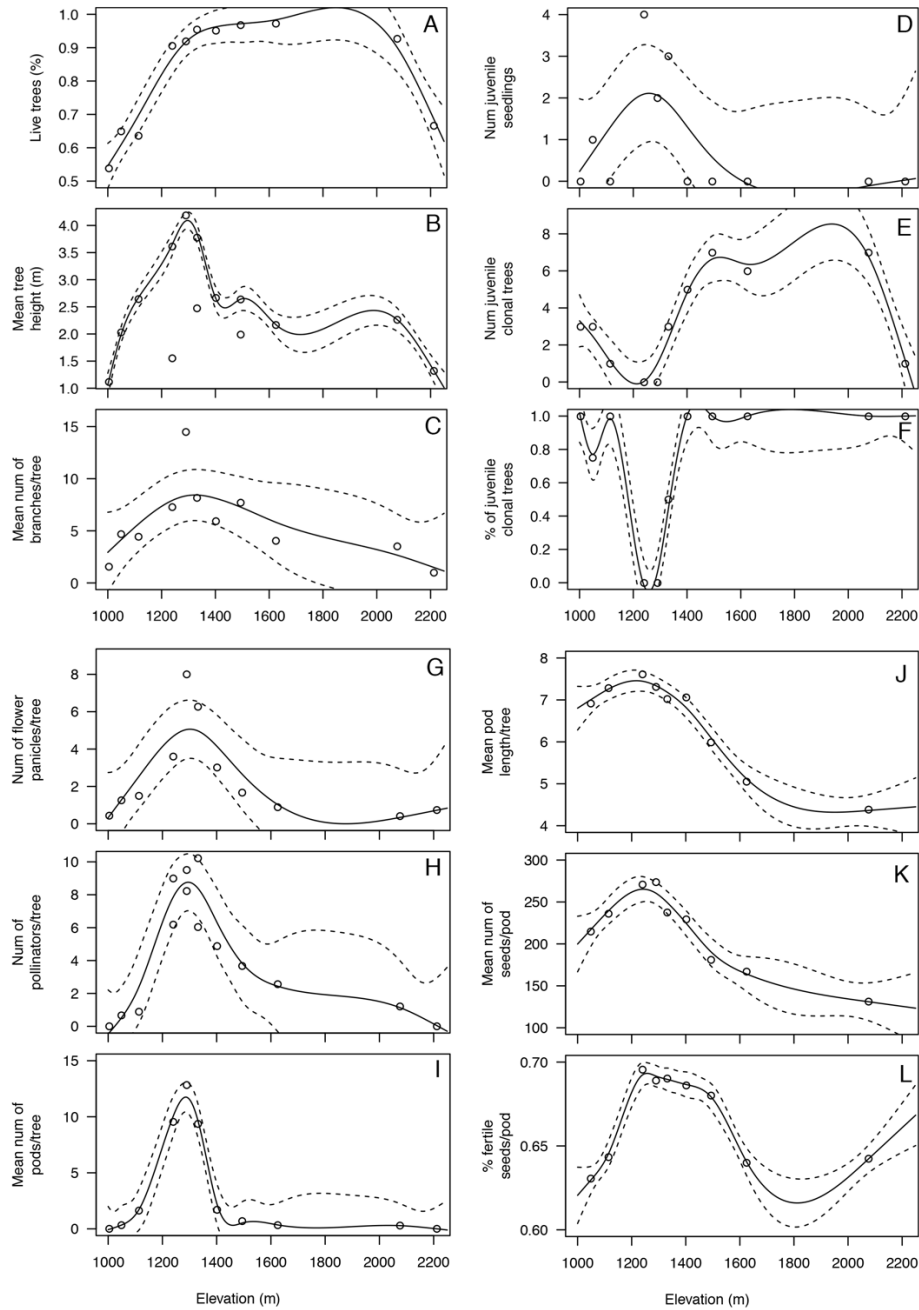


**Figure 1.1 The clonal reproductive path and the sexual reproductive path in Joshua tree reproduction.** In the clonal path, (A) the Joshua tree creates a juvenile clone via underground ramets. This juvenile may grow into an adult (B) and then follow the clonal, sexual, or both reproductive paths. In sexual reproduction, the adult tree flowers and a moth emerges from a cocoon to pollinate and oviposit eggs in Joshua tree flower (C). The flower forms a seedpod containing both fertile and infertile seeds. Developing moth larvae consume a fraction of the fertile seeds (D), exit the pod and form a cocoon in the soil (E). Larva pupate for at least a year and emerge from soil as adult moths during the next flowering cycle of Joshua trees (F). Seeds land in hospitable area and grow into a new Joshua tree for the cycle to begin again (G).

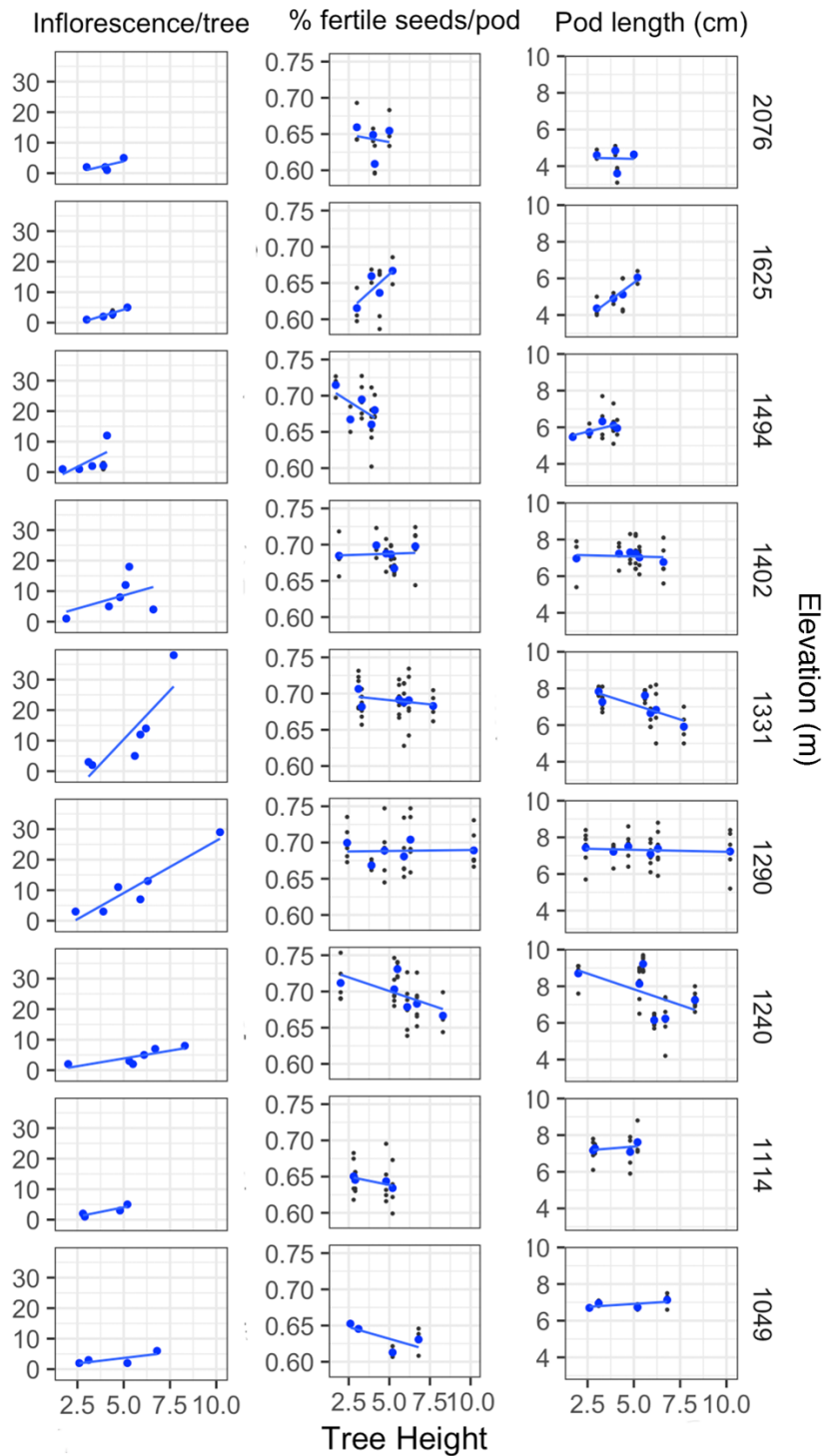


**Figure 1.2 Conceptual model of the hypothesized factors influencing plant fitness in the Joshua tree/yucca moth symbiotic relationship across an elevation gradient in JTNP.** Top black arrows represent three specific hypotheses tested; abiotic factors can influence the moth directly, the Joshua tree directly, or influence the interaction between them through sign (–, 0, +) or magnitude (strong to weak). A resulting positive interaction outcome refers to positive fitness effects for the moth and tree (more moths and/or seeds), while a negative interaction outcome refers to hypothetical negative fitness effects (less moths and/or seeds).

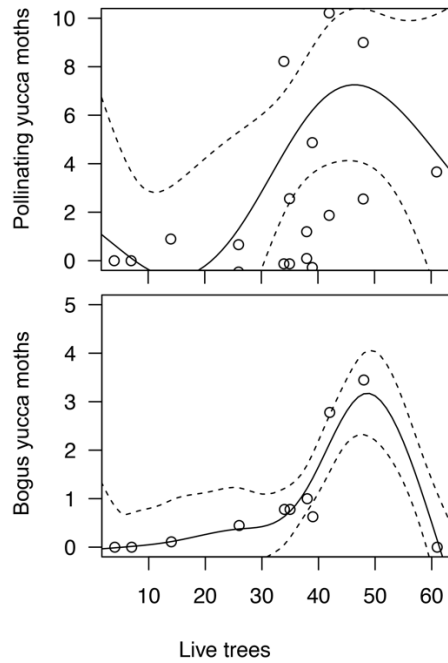




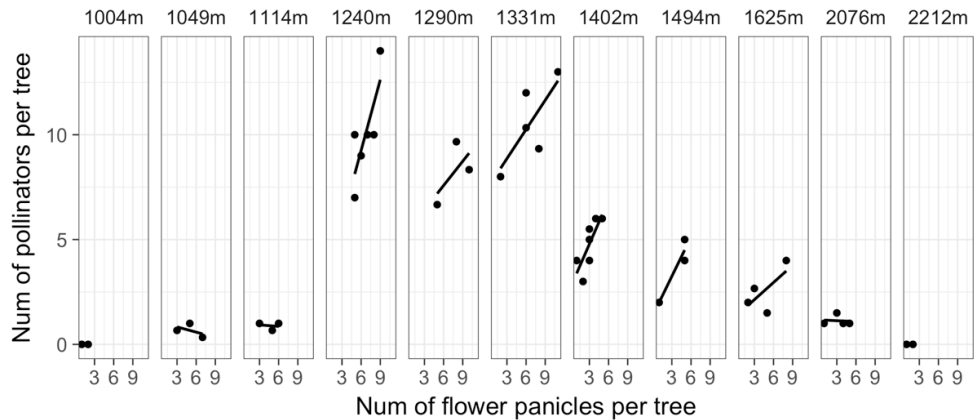
**Figure 1.3 Joshua tree performance measured as a function of elevation.** Solid lines represent the fitted values from a generalized additive model that estimates the form of a relationship between twelve performance measures and elevation. Dotted lines represent 95% confidence intervals. Top left panel (A-C) reflects measures of tree growth characteristics. Top right panel (D-F) includes measures of juvenile tree performance. Bottom left (G-I) reflects measures of tree reproductive potential. Bottom right (J-L) shows pod characteristics.



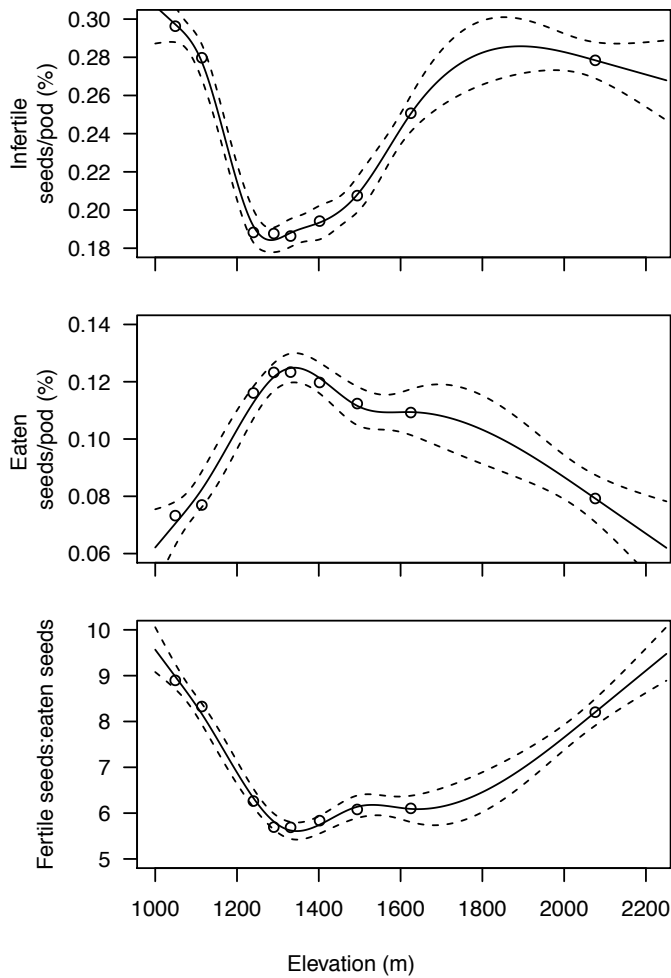
**Figure 1.4** Flower panicles per tree, percent fertile seeds per pod, and pod length, as a function of tree height, across the elevation gradient. There was no sexual reproduction at either the low (1004m) or high (2212m) elevation extremes.



**Figure 1.5** Pollinating yucca moth (*Tegeticula*) and bogus yucca moth (*Prodoxus*) abundance increases with density of live Joshua trees. At the highest tree density moth abundance was low despite high tree abundance; this was the highest elevation site at 2212m (site 11), which had no successful sexual reproduction.



**Figure 1.6** Linear analysis within site for each of the eleven sites of the number of pollinators versus the number of flower panicles per tree. Pollinator number per tree increases with the number of flower panicles on that tree, except at elevation extremes.



**Figure 1.7** The percent infertile seeds per pod, percent eaten seeds per pod across an elevation gradient and the conditional variation of the ratio of the percent of fertile seeds and percent eaten seeds across the elevation gradient. There were no seeds produced at the extreme elevations of 1004m and 2212m. Solid line shows a fit from a GAM model; Dotted lines represent a 95% confidence interval.

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## Chapter 2

### **Parasitism to mutualism continuum for Joshua trees inoculated with different communities of arbuscular mycorrhizal fungi from a desert elevation gradient**

#### **Introduction**

Symbioses between plants and mycorrhizal fungi are ubiquitous in nature and incredibly diverse. This ancient interaction evolved over 450 million years ago, and is credited with assisting the early colonization of land by plants (Pirozynski and Malloch 1975, Simon et al. 1993, Remy et al. 1994, Redecker et al. 2000). In exchange for carbon, the fungi help plants resist stress, disease, salinity, and drought, and provide greater access to soil nutrients, thereby playing a key role in plant fitness, productivity and community composition (Allen 1991, van der Heijden et al. 1998b, Smith et al. 2010). However, these fungal symbionts are not always beneficial to the plant host; the fungi can sometimes function as parasites, reducing performance of their plant partners (Johnson et al. 1997, Jin et al. 2017, Hoeksema et al. 2018) depending on the species involved (Maherali and Klironomos 2007, Van der Putten 2012), the environmental conditions where the interaction occurs, (van der Heijden et al. 1998b, Smith and Smith 2013, Nouri et al. 2014) as well as developmental and phenological factors (Kiers et al. 2011, Johnson and Graham 2013). The outcomes of the interactions are mutualistic when net benefits are greater than net costs for both partners, commensal when one partner benefits but the other receives neither benefit nor harm, and parasitic for either partner when

costs exceed the benefits received (Bronstein 1994, Johnson et al. 1997, Johnson and Graham 2013).

The distribution of arbuscular mycorrhizal fungal (AMF) is regulated by environmental parameters such as soil nutrients, texture (del Mar Alguacil et al. 2016) and pH (Jansa et al. 2014, Xu et al. 2017), as well as availability of suitable plant host (Lekberg and Waller 2016, Xu et al. 2017). As plant performance (Van Der Heijden et al. 2008) and symbiotic outcomes (Jin et al. 2017, Hoeksema et al. 2018) are linked to fungal community composition, understanding how local abiotic and biotic factors affect fungal distribution will inform management decisions for specific ecosystems and targeted species (Van Der Heijden et al. 2008).

Most plants form symbiotic associations with a diverse assemblage of mycorrhizal fungi, and while progress has been made to elucidate the ecological factors impacting fungal distribution and abundance (Davison et al. 2015), the mycorrhizal outcomes of different partners interacting across different locations remains poorly understood. Determining the numbers, identities, and distributions of the fungi involved is the first step towards understanding their ecosystem role and host impacts, as different communities of fungi can have very different outcomes for the host plant (van der Heijden et al. 2015b, Xu et al. 2017). For example, inoculating the host plant *Medicago truncatula* with three different AMF species resulted in different outcomes depending on the AMF species (Kiers et al. 2011). Even different isolates of the same fungal species can differ greatly in their ability to reward the host plant, with great variability in functional response of a single

species of AMF depending on biotic and abiotic factors (Hart and Reader 2002, Avio et al. 2006). In another study, a single pair of symbiotic partners (*Petunia hybrida* and *Rhizophagus irregularis*) generated the entire range of mutualistic to parasitic outcomes depending on the nutritional conditions under which the interaction occurs (Nouri et al. 2014). A series of experiments to understand mycorrhizal function in grassland plants inoculated with native and foreign AMF also resulted in the entire spectrum of outcomes (Klironomos 2003).

AMF community patterns have been studied across changing environmental and elevational gradients (Gai et al. 2012a, Geml et al. 2014, Liu et al. 2015, Egan et al. 2017, Kotlínek et al. 2017), yet knowledge about fungal community composition along elevation gradients in desert environments is limited (Kotlínek et al. 2017, Wang et al. 2018). Elevation gradients can correspond to temperature gradients over short geographic distances where variation in the biotic and abiotic environment, such as changes in weather patterns, soil moisture, nutrients, and species distributions, can vary with elevation (Sundqvist et al. 2013, Egan et al. 2017, Kotlínek et al. 2017). Symbiosis could be particularly important in extreme environments, helping to ameliorate stressful conditions such as climate and drought (Wang et al. 2018).

The conditional nature of these symbioses makes predicting how climate change will affect the outcomes of mycorrhizal interactions difficult. The benefit to a plant host species depends on the assemblage of fungi available in the location and the conditions that shape the interaction, both of which vary spatially. This points to

the need for habitat and species-specific investigations. With recent advances in molecular technology we can more accurately identify the fungi present in species interactions, but need many new case studies to establish the functional patterns between different species under varying conditions.

To better understand how the role of climate, soil conditions, and fungal species influence symbiotic outcomes on a culturally significant plant in a desert environment, we focused on the mycorrhizal community of the Joshua tree (*Yucca brevifolia*) along an elevation gradient in Joshua Tree National Park (JTNP). Joshua trees are icons of the Mojave Desert, and are threatened by the rapidly changing climate (Harrower and Gilbert 2018). The temperature in the Mojave has been steadily increasing, and models predict the climate in JTNP will soon be outside of the range of tolerance of Joshua trees, leading to the potential extirpation of Joshua trees from their namesake park within the next century (Cole et al. 2011, Barrows and Murphy-Mariscal 2012).

Predicting symbiotic outcomes under future climate scenarios requires first understanding current species distributions and their ecological factors, and then the functional outcomes of those symbiotic interactions. As the Southernmost portion of the Joshua tree range occurs within JTNP, there is a unique opportunity to study these mycorrhizal interactions across a climate stress gradient within the park. This will allow us to better understand how population structure and abiotic conditions influence the spectrum of symbiotic outcomes from parasitic to mutualistic, and how that may impact current and future populations of threatened plant species. For

many plants, changes in AMF community result in changes to a plants mycorrhizal growth response (MGR) and ability to accumulate nutrients (Van Der Heijden 2004, Menzel et al. 2017, van der Heijden et al. 2015a), but we do not know what role these fungi play for Joshua trees.

In this study we examined how the AMF community that associates with Joshua trees varies across an elevation gradient in JTNP and how those different fungal partners may impact Joshua tree fitness. We then develop and test a conceptual model (Fig. 1) that characterizes the drivers and structure of the range of symbiotic outcomes on a parasitism-mutualism spectrum. Specifically, we ask: 1) Does the AMF community composition in Joshua tree roots change along an elevation gradient? 2) Does variation in the AMF community correspond to different outcomes of the symbiosis for Joshua trees? 3) Do those outcomes change with time as the plants grow?

## **Materials and Methods**

### *Study site and sampling methods*

The study was conducted across a 1,200-m elevation gradient in Joshua Tree National Park (JTNP) (located at 33.8734° N, 115.9010° W) southwestern California, USA, in Spring 2016. JTNP encompasses both the Mojave and Colorado deserts, and varies from hot and dry at low elevations, to seasonal freezing at high elevations (see Harrower 2018 and Barrows 2016 for a complete description of the area and sites). Eleven study sites were selected for analysis, from the low elevation



southern Joshua tree range limit, to the high elevation northern end of the local distribution. To collect and identify AMF communities, we sampled Joshua tree roots and associated soil from 3 randomly chosen individuals at each of the 11 sites. Soil for nutrient and fungal molecular analysis was sampled in triplicate at the base of each tree using a soil core (5 or 10 cm diameter, 15 cm deep), and then pooled for each site (9 cores/site; see Chapter 1, Table 1.1). To collect fungal inoculum, fine roots and bulk soil were collected from each tree by digging along large roots and collecting 3 samples of root/soil mix from around the tree, thus ensuring that sampled roots belonged to the Joshua tree (0.5 gallon/tree), 3 trees per site, and then pooled by site. After collection, samples were placed into individual bags and kept on ice, until they were either transferred to a -20°C freezer where they were stored until the roots were used in DNA extraction, or used for in soil nutrient analysis. Soil was dried, ground, and analyzed for total carbon and total nitrogen following the combustion method (AOAC 1997), pH (in H<sub>2</sub>O), total extractable ammonium and nitrate content by flow injection analyzer method (Keeney and Nelson 1982, Hofer 2003), extractable phosphorus using the Olsen method (Olsen 1982), and percentage soil moisture following the gravimetric method (Black 1965) at the UC Davis Analytical Lab (<http://anlab.ucdavis.edu>; see Chapter 1, Table 1.1).

#### *Intraradical AMF colonization*

We used root staining to visually determine the extent of root colonization of AMF in root samples taken from each individual Joshua tree at each site. We

washed roots free of debris using a 0.7mm soil sieve, cleared the roots in boiling 10%KOH, neutralized in 5% HCl, and stained in 0.1% trypan blue to visualize colonization by AMF (Philips and Hayman, 1970). Stained roots were selected randomly and placed on a slide, and percent root colonization was estimated using the modified line-intercept method (Philips and Hayman 1970, McGonigle 1990), scoring the quantity of AM fungal structures (hyphae, vesicles, and arbuscules).

#### *Plant inoculation, sampling, and nutrient extraction methods*

Seeds of *Y. brevifolia* were collected and pooled from Joshua tree pods collected across the elevation gradient in JTNP in September 2014 (lowest and highest elevation sites did not have seed pods – see Harrower and Gilbert 2018 for a discussion on this). The seeds were surface sterilized with 70% ethanol followed by a 0.5% sodium hypochlorite solution diluted in de-ionized water, and then rinsed with sterile, de-ionized water and germinated on moist filter paper in complete darkness for 3 days.

To establish the mycorrhizal symbiosis, three germinated seeds were placed in each of 144 Ray Leach UV-stabilized Cone-tainers (164ml) (Stuewe and Sons., Inc. Oregon, USA) filled with a twice-autoclaved mixture (1 hour, 120° C, and then again after 24 hours of rest) of sand (70% quartz sand, 0.125-0.25 mm) and greenhouse soil (30% Pro-mix HP). Seedlings were thinned to 1 per pot after 2 weeks. A 1-g band of AMF community inoculum (roots and soil) collected at each of the 11 sites, was added 2 cm below the soil surface, one treatment per pot

(Anacker Brian et al. 2014). Each pot received 1 ml of an AMF-free microbial filtrate wash produced from a mix of all samples, to correct for possible differences in microbial communities (Koide and Li 1989), with non-mycorrhizal controls receiving only the AMF-free filtrate, resulting in a total of 144 experimental units with 6 replicates per treatment. The inoculated seedlings were grown in a randomized complete block design at the UC Santa Cruz Greenhouses, and rotated every 3 weeks to minimize differences for environmental effects in the greenhouse (Potvin 1993). Soils were watered twice per week and fertilized at 2, 5, and 8 months with a half-strength Hoaglands solution (Sikes Benjamin et al. 2012).

Plants were destructively harvested (in triplicate) at 1, 3, 6, and 9 months. Plant biomass was assessed as a proxy for plant fitness (Johnson, 2010). Whole plants (roots and shoots) were oven dried at 55°C for 3 days and then weighed. After weighing, a subsample of roots from each plant was rehydrated, washed, stained with 0.05% Trypan Blue and examined at 40x to confirm AMF colonization (McGonigle, 1990).

Dried whole plants were ground with a Wiley Mill to pass through a 40-mesh screen, and then analyzed for total nitrogen following the combustion method coupled with gas chromatography (AOAC 2006), total phosphorus and potassium utilizing a nitric acid/hydrogen peroxide microwave digestion and determined by Inductively Coupled Plasma Atomic Emission Spectrometry (Meyer et.al. 1992, Sah et. al, 1992) at the UC Davis Analytical Lab (<http://anlab.ucdavis.edu>).

### *Molecular analysis of fungal inoculum*

We extracted DNA from 30-80 mg of field sampled and frozen roots for each pooled sample with a PowerSoil-htp soil DNA isolation kit (MO BIO laboratories, Inc., Carlsbad, CA, USA) with two modifications: to increase DNA yield, bead plates were shaken at an elevated temperature (60° C as suggested by the manufacturer), and the final elution was performed twice.

DNA from root samples was sequenced using the amplicon-based Illumina MiSeq platform. Nuclear SSU rRNA amplicons were generated with primers NS31 and AML2 (Simon et al. 1992, Lee et al. 2008) to identify AM fungi (Öpik et al. 2013) from previous citation). Amplified DNA was purified with the Qiagen QIAquick Gel Extraction kit (Qiagen GmbH, Hilden, Germany) following the manufacturer's protocol, and quantified with a Qubit 2.0 Fluorometer (Invitrogen, Grand Island, USA). DNA was processed for sequencing libraries with the Illumina Nextera XT sample preparation kit (Illumina, San Diego, USA) following the manufacturer's protocol, including tagmentation to fragment and tag DNA, and followed by a 12-cycle PCR to add sequencing indices, PCR cleanup, and normalization. Libraries were then sequenced on Illumina MiSeq with 2 x 250 bp paired-end reads at the RFLgenome sequencing facility in Lubbock Texas.

For bioinformatics analysis, we generated multiple sequence alignments with MAFFT (v7.306 Katoh and Standley 2013) and combined paired-end reads with FLASH (v1.2.10, Magoč and Salzberg 2011). The reads were quality-filtered by removing sequences with Nextera adapter contamination from tagmentation, and

where average quality was  $<30$  (Cock 2010). Paired-end reads were trimmed to retain the most variable section of the amplicon, and combined using FLASH with the default parameters (minimum overlap between paired reads = 10bp, maximum mismatch density in overlap = 0.25). We then removed chimeric reads with USEARCH (v7.0.1090, Edgar et al., 2011) in reference database mode (MaarjAM database, Öpik et al 2010), clustered sequences with blastclust (BLAST v2.2.26, Altschul et al. 1990) and identified sequences with BLAST (BLAST+ v2.5.0, Camacho et al. 2009). The MaarjAM database contains sequences covering the NS31/AML2 amplicon which are classified into virtual taxa (VT) (Öpik 2009). A virtual taxon is a phylogenetically defined group of closely related SSU rRNA gene sequences with sequence identity equal to or higher than 97%, and anchored to type sequences. From the 11 sites, we had 7,678,300 raw reads in total – with 210,035 to 1,100,345 reads per sample. After adapter removal and quality filtering, 799,748 quality filtered sequences remained. Paired reads were quality filtered and trimmed to the most variable region of the amplicon (following Vasar 2017) leaving 210,106 sequences. Taxonomic assignment was given by blasting the representative sequences against the MaarjAM database (<https://maarjam.botany.ut.ee>), and sequences were assigned to VT when sequence similarity was  $\geq 97\%$ . Reads that did not match against the MaarjAM database were identified with BLAST using the NCBI database with a 97% identity threshold.

### *Constructing the Phylogenetic tree*

We constructed the bootstrap consensus tree using MEGA v7.0, by aligning representative OTU's with MUSCLE and then assembling those sequences into a neighbor-joining tree. One thousand rapid bootstrap replicates were built and used to apply a Maximum Composite Likelihood model for determining the evolutionary connections among the sequences (Tamura et al. 2004).

### *Statistical analysis*

We conducted simple linear regressions to evaluate relationships between elevation and soil characteristics. We then used generalized additive models (GAM) to describe the non-linear relationship between elevation and the % colonization of Joshua tree roots by AMF. GAMs are nonparametric extensions of linear models that allow the expected response to vary smoothly with a set of predictor variables (Yee and Mitchell 1991). We used the dry plant biomass of plants with or without AMF as a proxy to calculate the mycorrhizal growth response (MGR), and the effect of different AMF treatments on plant fitness (Johnson 2013). The MGR was calculated as the log response ratio,  $MGR = \log(\text{biomass treatment/biomass control})$  (Hoeksema et al. 2010). Positive values of MGR indicate that the plant biomass increased following inoculation, while negative values indicate a decrease in biomass in response to the fungi.

To examine the relationship between AMF taxa and elevation we carried out a principal component analysis (PCA) of the 11 sites based on the presence of

fungal taxa. The PCA of the 11 sites allows visualization of the data and demonstrates how the AMF are distributed among the sites and in relation to each other in a multivariate space. All calculations were performed using the R language for statistical computing with the following library packages: ggplot2, reshape2, plyr, ape, RColorBrewer, mgcv, broom, and tidyverse (The R Development Core Team 2018).

## **Results**

### *Weather conditions and soil properties along the elevation gradient*

Average summer temperature per site declined steadily with increasing elevation, with the warmest site at a daily average of 30.2°C and the coolest at 19.9°C ( $r^2=0.9$ ) (Table 1). Relative humidity generally increased with elevation ( $r^2=0.636$ ), as did the soil moisture at 10 cm ( $r^2=0.8$ ), increasing from 0.005 m<sup>3</sup>/m<sup>3</sup> to 0.14 m<sup>3</sup>/m<sup>3</sup>. Soil nutrients did not follow any noticeable trend with elevation, although pH declined from 8.06 to 6.63 with increasing elevation ( $r^2=0.827$ ).

### *Percent AMF colonization*

The percentage of root length colonized by AMF varied from 19 to 71% with an average of 46.7%, (SD=17.1). In the generalized additive models, mycorrhizal colonization decreased significantly with increasing elevation ( $r^2=0.48$ ;  $p=2.1 \times 10^{-4}$ ) (Fig.2).

### *Fungal community composition of inocula*

We identified 37 virtual taxa (VT) including sequences from 7 genera in the phylum Glomeromycota. The phylogenetic placement of the different AMF VT's were determined with a neighbor-joining tree, and shown with the relative abundance for each VT (Fig. 3). The most abundant taxa were in the families: Glomeraceae, followed by Gigasporaceae, Diversiporaceae, Paraglomeraceae, Claroidioglomeraceae, Ambisporaceae, and Acaulosporaceae (Fig. 4). We detected significant variation in AMF community composition at the genus level across the 11 sites. *Glomus* was the most abundant genus across all samples. *Paraglomus* and *Scutellospora* were only found in the lowest elevation sites (1,004–1,240 m and 1,004–1,290 m, respectfully). In contrast, *Ambispora* was distributed across the middle elevations, from 1,114 to 1,625 m. *Claroideoglomus* was found from mid to high elevations at 1,290 to 2,212 m, while *Diversispora* was located at the four highest elevation sites from 1,494 to 2,212. *Acaulospora* was only found at the two highest sites, 2,076 m and 2,212 m.

In the principal component analysis, PC1 explained 31% and PC2 explained 21% of the variation in fungal composition across sites (Fig. 5). The 11 sites show strong grouping of fungal taxa by elevation, with low (1004-1114m), mid (1240-1494), and high elevation sites (1625-2212) clustered together with similar AMF composition (hereafter referred to as low, mid or high elevation fungi).

*Scutellospora* and *Paraglomus* dominated at the low elevation sites, *Glomus sp.* and *Ambispora* at the mid elevations, and *Diversispora*, *Claroideoglomus*, and



*Acaulospora* at the high elevation. Only taxa with the 8 strongest loadings are shown (Fig. 5), as a plot of vector rank as a function of vector length drops off after the first 8 taxa (Fig. A2.1).

#### *Plant-mycorrhizal response*

The origin of fungal inoculum did not affect nutrient levels of seedlings inoculated with fungi after 1 month, but plant biomass increased significantly as a function of the fungal source (elevation) ( $p=2.53 \times 10^{-4}$ ) (Fig. 6). Plants inoculated with fungi from all elevations showed a positive trend at three months with respect to nitrogen absorption and plant biomass ( $p=1.73 \times 10^{-3}$ ;  $p=5.61 \times 10^{-6}$ ). Elevation of fungal source had no effect on nutrient absorption or plant biomass in seedlings 6 months after inoculation. The effect of the different fungal inoculum was significant for nitrogen and phosphorus levels in seedlings inoculated with fungi after 9 months ( $p=0.049$ ;  $p=3.9 \times 10^{-4}$ ). Plants inoculated with low-elevation fungi had higher average levels of nitrogen 9 months after germination, than plants grown with either the medium-or high-elevation AMF, or the control (Fig. 6). This same trend was observed at 9 months for phosphorus levels with plants inoculated with low-elevation fungi having higher levels than the mid-or, high-elevation fungi, or the control group. Potassium levels did not vary significantly with fungal treatment ( $p=0.13$ ).

The mycorrhizal growth response (MGR) of the seedlings varied with the different AMF inoculum treatments and across time (Fig. 7). For the first 3 months

most plants benefitted from their AMF associations, but fungi from the 3 lowest and warmest sites actually inhibited plant growth. Fungi from the low-elevation sites had a negative MGR at 1 month ( $-0.28 \pm 0.03$ ,  $n=9$ ), notably low when compared to the mid-elevation ( $0.97 \pm 0.08$ ,  $n=24$ ) or high-elevation fungi ( $0.16 \pm 0.08$ ,  $n=24$ ). However, after 6 months, even the lowland AMF provided a benefit to the plants, and by 9 months those same detrimental fungi produced the greatest benefits to their hosts, with the MGR of  $0.10 \pm 0.002$  surpassing both the mid- and high-elevation fungi ( $0.03 \pm 0.02$ , and  $0.05 \pm 0.02$ , respectfully). This demonstrates that the effects of particular AMF vary according to plant developmental stage.

## **Discussion**

### *Effect of elevation and soil properties on percent colonization*

Elevation gradients represent complex variations in environmental conditions that impact fungal communities and plant-mycorrhizal interactions. We found that the percentage of Joshua tree roots colonized by AMF decreased with an increase in elevation. These results agree with findings in other systems that demonstrated AMF colonization is restricted at higher elevations (Gai et al. 2012b, Horn et al. 2014), likely due to changes in soil moisture, nutrient availability, and pH. Other studies have pointed to the importance of changes in plant communities along elevational gradients, shifting from species that host AMF at the lower elevations, to those that host ectomycorrhizas and ericoid mycorrhizas at higher elevation, as a major factor driving AMF colonization rates (Bending and Read

1995). Along our 1200m elevation gradient, Joshua trees were replaced by ectomycorrhizal pines (*Pinus monophyla*) and manzanita (*Arctostaphylos glauca*) at the higher elevation sites, which suggests a changing community of mycorrhizal types that follows plant host abundance could explain some of the differences we see. Unfortunately, we were unable to assess colonization aggressiveness of the fungi from different elevation in greenhouse inoculated roots because all the plant material was required for nutrient analysis.

#### *Fungal community composition differs along an elevation gradient*

Patterns of change in AMF community composition were associated with elevation and soil pH. Consistent with other studies, we found that AMF community distribution patterns may be shaped by variation in climate or soil resources (Gai et al. 2012a, Geml et al. 2014, Egan et al. 2017). Climate and soil characteristics are common predictors of fungal symbiont distribution (Tedersoo et al. 2014) and may shape AMF distribution by affecting microbial processes such as decomposition or AMF functioning. For example, soil moisture and temperature affect AMF physiological responses such as hyphal growth rates, hyphal density, infection rates and spore propagation (van der Heijden et al. 1998a, Hawkes 2008). In controlled studies some AMF taxa proliferate under drought while others shrink in size (Klironomos, 2001). Many studies show pH can influence AMF distribution by changing soil nutrient bioavailability and metal sorption, or by directly impacting the physiology of AMF (Xu et al. 2017). AMF can also respond to changes in soil

nutrients such as phosphorus concentrations, resulting in different combinations of fungal communities for a plant species exposed to different phosphorus treatments (Gosling et al. 2013).

AMF spores are large (up to 640 $\mu$ m) and spore production is limited by moisture and nutrient availability (Augé 2001). They are often dispersal limited and are largely dispersed by animals across intermediate ranges (<2km), with some assistance from wind, and water, spores and hypha disperse over smaller distances (<10m) (Kivlin et al. 2011). Dispersal limitation can reinforce restricted ranges of fungi with different environment preferences.

Plant communities change with elevation and can exert a strong influence on local AMF assemblages. This could be due to different plant hosts giving preferential allocation of photosynthate to the best fungal symbionts. While typically considered generalists, some AMF have been shown to be more host specific than other (Helgason 2002, Smith and Read 2008, Öpik 2009, Majewska 2018) and different AMF taxa demonstrate various plant colonization strategies (Hart and Reader 2002). Preference for different plant communities could change the availability of the local fungal pool at each location along the Joshua tree elevation gradient and may contribute to some of the AMF taxa turnover that we see.

We found that AMF taxa were clustered phylogenetically by elevation, supporting a habitat filtering hypothesis. This finding supports our conceptual figure (Fig. 1), namely that fungal community composition changes with the elevation

gradient and in this case, resulted in a clear distinction of fungal communities for the three lowest sites, the five mid elevation sites and the 3 highest elevation sites (Figs. 3-5). It may be that changes in environmental conditions along the gradient act as filters that select for particular fungal traits. Such processes can result in phylogenetically structured communities that change with elevation (Horn et al. 2014). Specifically, AMF from the Acaulosporaceae family were found at the highest elevation sites, which were coolest, wettest, and had the lowest pH. Fungi from this family are commonly found in lower pH environments (Chagnon et al. 2013) or high elevation sites (Oehl et al. 2011), possibly a result of stress tolerance abilities (low pH, low nutrient soils, freezing temperatures). They sparingly use host carbon at these locations and tend towards low hyphal biomass production (both extra radical hyphae and internal root structures), instead producing diffuse hyphae (Hart and Reader 2002, Maherali and Klironomos 2007). This result is also congruent with our findings of low root colonization by AMF at high elevations, and is consistent with phylogenetic trait conservatism within the Glomeromycota (Hart and Reader 2002). As shown elsewhere (Kotlínek et al. 2017), Claridoglomaceae and Diversisporaceae were also more abundant at higher elevations, but less is known about their functional traits that may shape this distribution. AMF from Gigasporaceae (*Scutellospora*) were found at the lower elevation sites, which is typical for this family (Chagnon et al. 2013). These fungi require substantial carbon resources because they produce large extra-radical mycelial biomass, with robust, densely aggregated hyphae (Hart and Reader 2002).

The Glomeraceae were predictably distributed across all sites; this family comprises the most common AMF found in plant communities, and are the quickest and most thorough root colonizers, with the majority of fungal biomass occurring inside of the root (Hart and Reader 2002, Maherali and Klironomos 2007).

Furthermore, the principle component analysis based on OTU composition showed that the fungi at the low, mid and high elevations clustered together in distinct groups, indicating similarities in the AMF community composition at these locations. Our results reflect those of other studies that found fungi can experience strong habitat filtering, as evidenced by the loss or gain of taxa through taxon replacement, with increasing elevation (Gai et al. 2012a, Geml et al. 2014, Liu et al. 2015, Egan et al. 2017).

#### *Variations in plant response to mycorrhizal fungi*

Joshua tree response to AMF depended on the fungal community involved as well as the developmental stage of the plant. We expected that different fungal groups would produce different symbiotic outcomes for the plant (Fig. 1). Functional differences between AMF and how they colonize soil and roots can contribute to difference in host plant growth and nutrient accumulation (Maherali and Klironomos 2007). We also found that plant growth and nutrient accumulation also changed with plant developmental time (or time post inoculation). Plants inoculated with low-elevation AMF had higher levels of phosphorus and nitrogen at 9 months then did plants inoculated with mid-or high-elevation AMF (Fig. 6).

Additionally, the MGR of the Joshua tree seedlings inoculated with fungi from the three lowest elevations was first negative and then by 9 months had surpassed that of plants with other fungal treatments (Fig. 7). Low elevation fungi are costly for the plant to initiate symbiosis, but confer benefits over time. Fungal communities from the low elevation sites were unique in that they contained fungal taxa from the Gigasporaceae and Paraglomeraceae families. AMF from Gigasporaceae quickly and extensively colonize the soil providing a greater access to soil nutrients and water (Hart and Reader 2002), and a high rate of phosphorus transfer (Jansa et al. 2005, Avio et al. 2006). These fungi require significant carbon from the plant to build their extensive soil mycelial networks used in soil exploration and the solubilization of soil phosphorus (Hart and Reader 2002). This could explain why we see a reduction in plant mass from those treatments at earlier timepoints. An enhanced fungal network can absorb more nutrients and water leading to an increase in host photosynthetic rate (Wright et al. 1998). This could be particularly important for the survival of desert seedlings that must establish and survive through the stressful summer months (Reynolds et al. 2012), especially at the hottest and driest locations. The strong relationship between AMF community and MGR suggests that changes in the AMF community along the elevation gradient may have long term consequences for plant populations.

One inherent limitation in our study design is that this work only considers the nutrient accumulation of Joshua tree seedlings grown in greenhouse conditions that do not reflect desert climates. Greenhouse temperature was an average 17°C

throughout the seedling inoculation experiment. This temperature is similar to that found at the three highest elevation sites in September, which is one of the months that Joshua tree seeds began to ripen and germinate (Reynolds et al. 2012). There are multiple opportunities for seedling germination that depend on factors such as seed ripening, distribution from the indehiscent seed pods, and climate conditions (Esque et al. 2015), and are likely linked to El Niño pulse events (Reynolds et al. 2012). Future work that assesses plant-AMF response under field conditions or warmer greenhouse conditions would provide useful information on how Joshua tree seedlings respond to fungal symbiosis in current and future climate scenarios.

#### *Considering future climate induced range shifts*

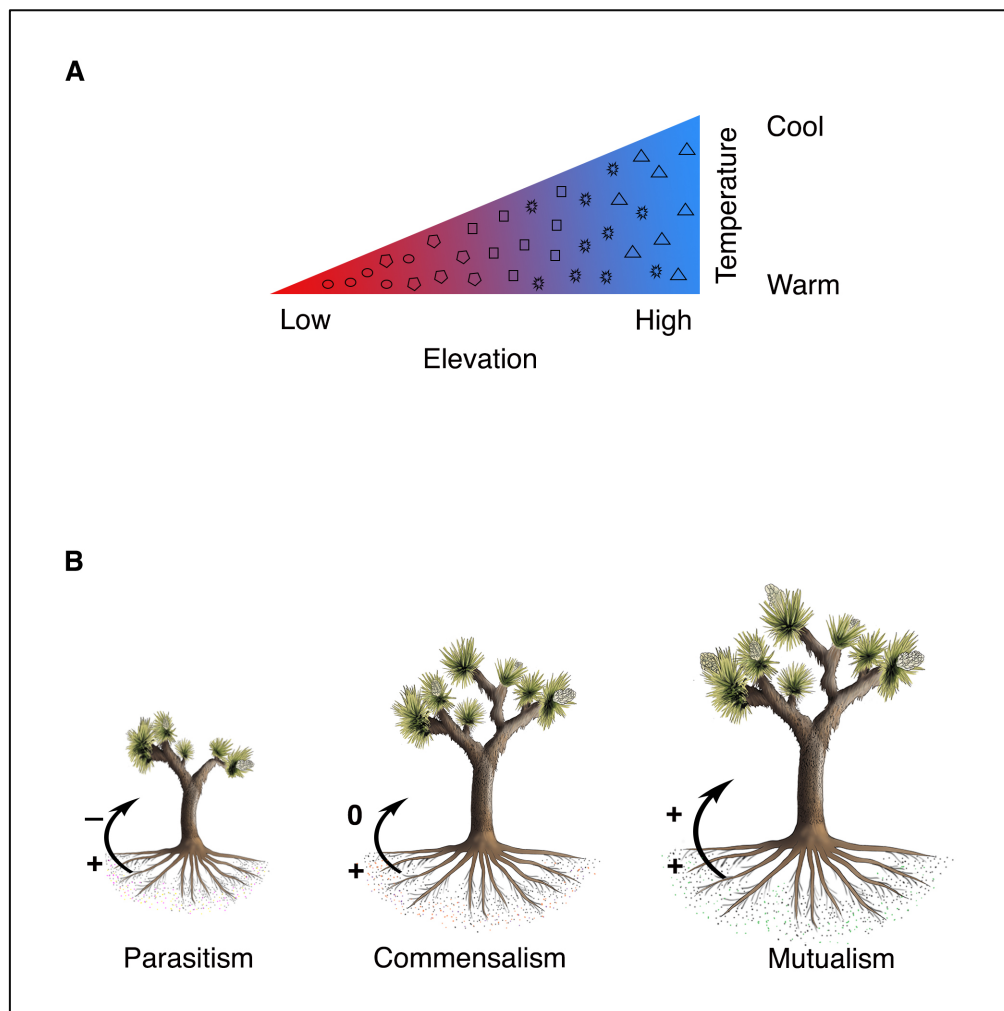
As Joshua tree populations shift due to the changing climate, they will encounter changing fungal partners, impacting tree function and likely seedling establishment. If Joshua trees continue an upslope migration with the changing climate (Barrows and Murphy-Mariscal, 2012) and lose access to lower elevation AMF communities, there could be an overall negative impact on seedling function. For example, current populations of plants with communities of Gigasporaceae and Glomeraceae at the low and mid elevations may have a higher competitive advantage. Controlled studies with other plant systems have found that these families of fungi provide complementary ecosystem functions that benefit plant hosts: Gigasporaceae provide a greater access to soil nutrients, while the extensive colonization by Glomeraceae confers reduced rates of infection by common soil



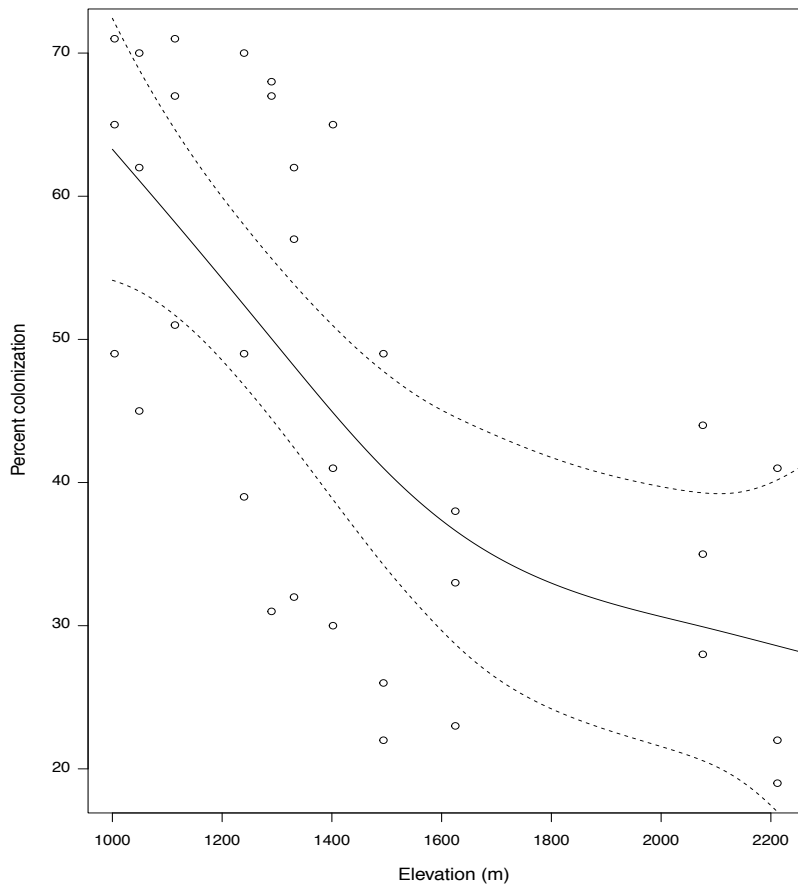
pathogens (Newsham et al. 1995, Maherali and Klironomos 2007). Future Joshua tree shifts into high elevation areas that lack Gigasporaceae could see fewer AMF benefits to the plants realized, resulting in reduced seedling establishment and a shrinking population. AMF have limited dispersal means but fungal communities will also likely shift as the climate continues to change (Van der Putten et al. 2010, Tedersoo et al. 2014). Further work testing these scenarios in the field would greatly benefit our understanding of Joshua tree and AMF symbiosis with fungal populations in future tree locations.

Assessing the outcomes of AMF functional groups and host response over both time and environmental space is necessary to predict and manage for target plant species under current and future climate scenarios. Recruitment of Joshua trees is influenced by temperature extremes (Loik et al. 2000, Dole et al. 2003, Claire and Hoines 2018, Harrower et al. 2018) and drought (DeFalco et al. 2010); both these factors can impact fungal community composition (Staddon et al. 2004). We have demonstrated in this study that there is a change in fungal community across an elevation gradient in JTNP and that it is associated with the change of the functional response in plants. We found that mycorrhizal impacts on Joshua trees can change from parasitic to mutualistic depending on the fungal community involved and the developmental stage of the plant. Appropriate matching of the Joshua tree fungal community with environmental conditions is an important consideration for Joshua tree restoration and assisted migration strategies.

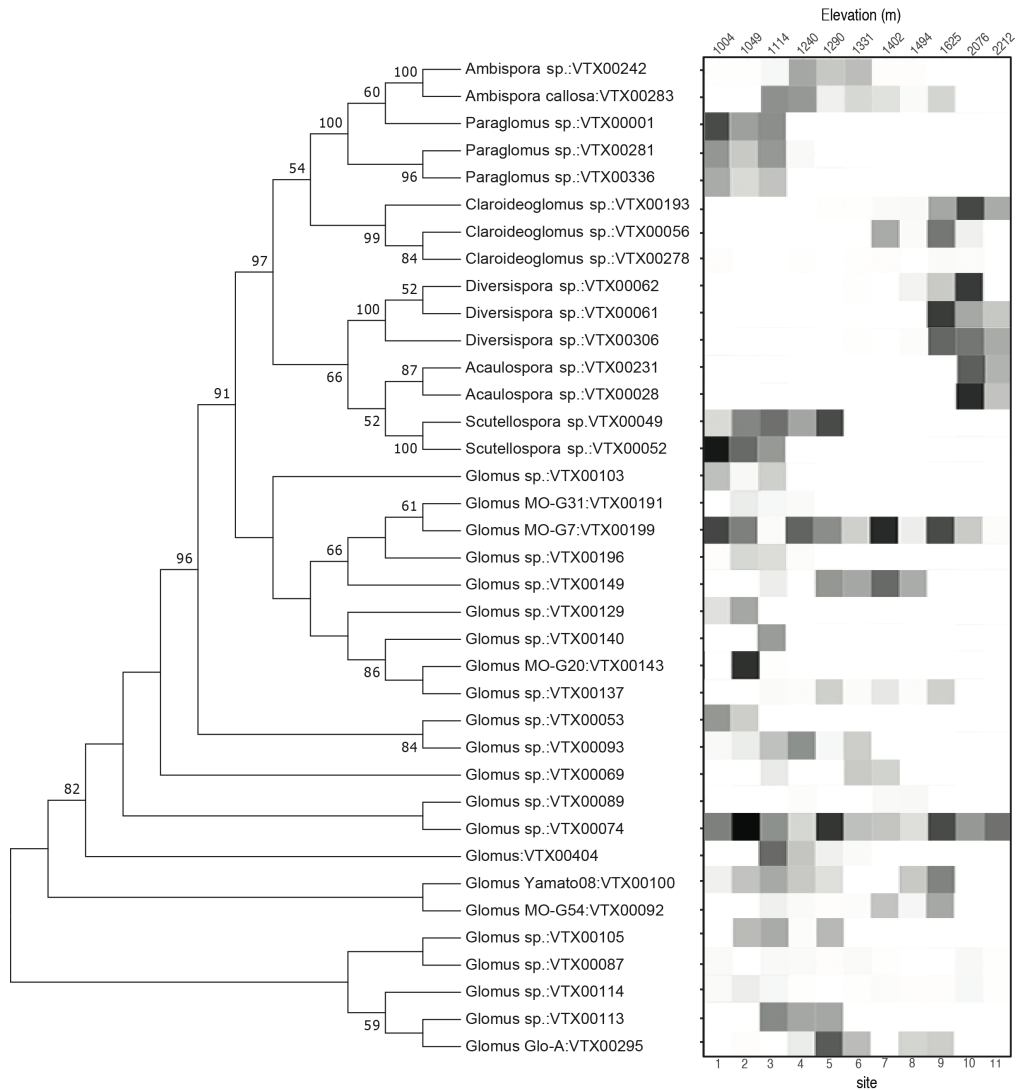
## Figures



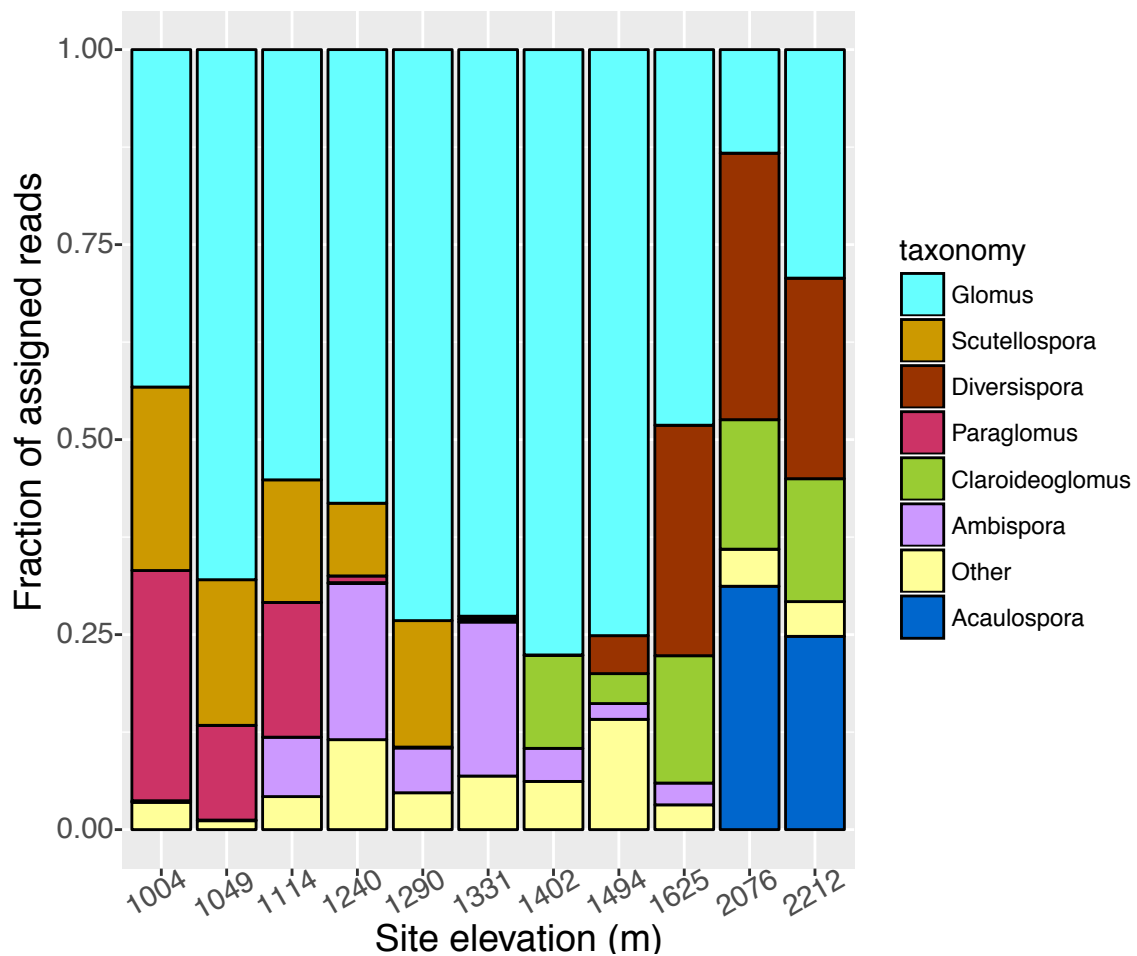
**Figure 2.1 Abiotic and biotic effects on plant-AMF mutualistic outcomes when inoculated with fungi from an elevation gradient.** A) Abiotic effects: AMF community composition in Joshua tree roots changes along an elevation gradient. Elevation gradient in the figure corresponds to a changing climate gradient with warmer temperatures at the lowest elevations and the coolest temperatures at high elevations. Changes in fungal communities are represented by the assorted changing black shapes. B) Biotic effects: Variation in the AMF community correspond to different symbiotic outcomes for Joshua trees. Outcomes can range from positive to negative with the arrow demonstrating fungal parasitism (+, -) of the tree, commensalism (+, 0) with the fungus benefitting but not damaging the tree, or mutualism (+, +) with both the tree and the fungi benefitting.



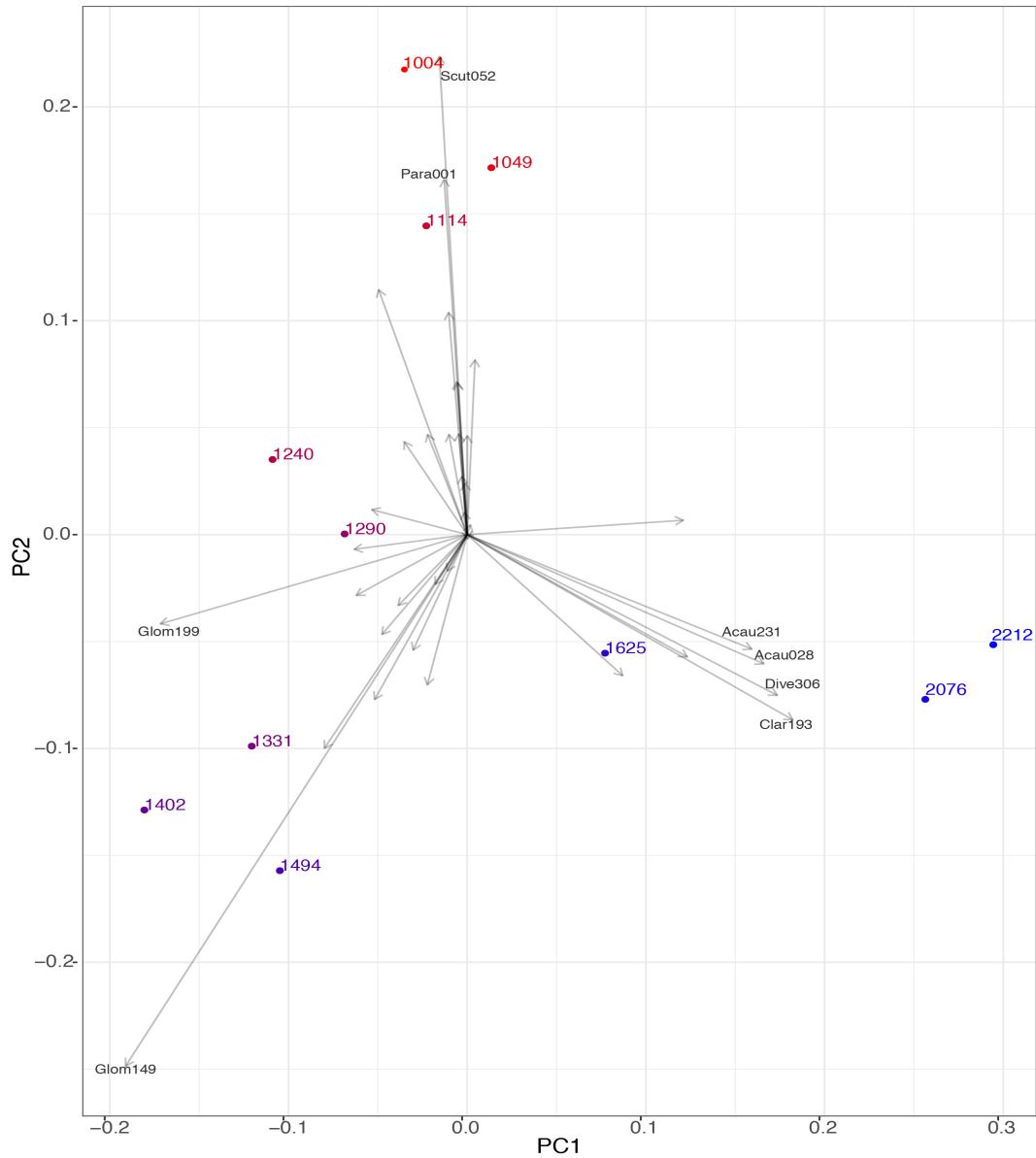
**Figure 2.2 Percent mycorrhizal colonization of Joshua tree roots measured as a function of elevation.** Solid line represents the fitted values from a generalized additive model that estimates the form of a relationship between the thirty-three root samples and elevation. Points show values for each of the three samples taken at a site. GAM fit indicates a greater degree of colonization for roots at lower elevations than higher elevations. Dotted lines represent 95% confidence intervals.



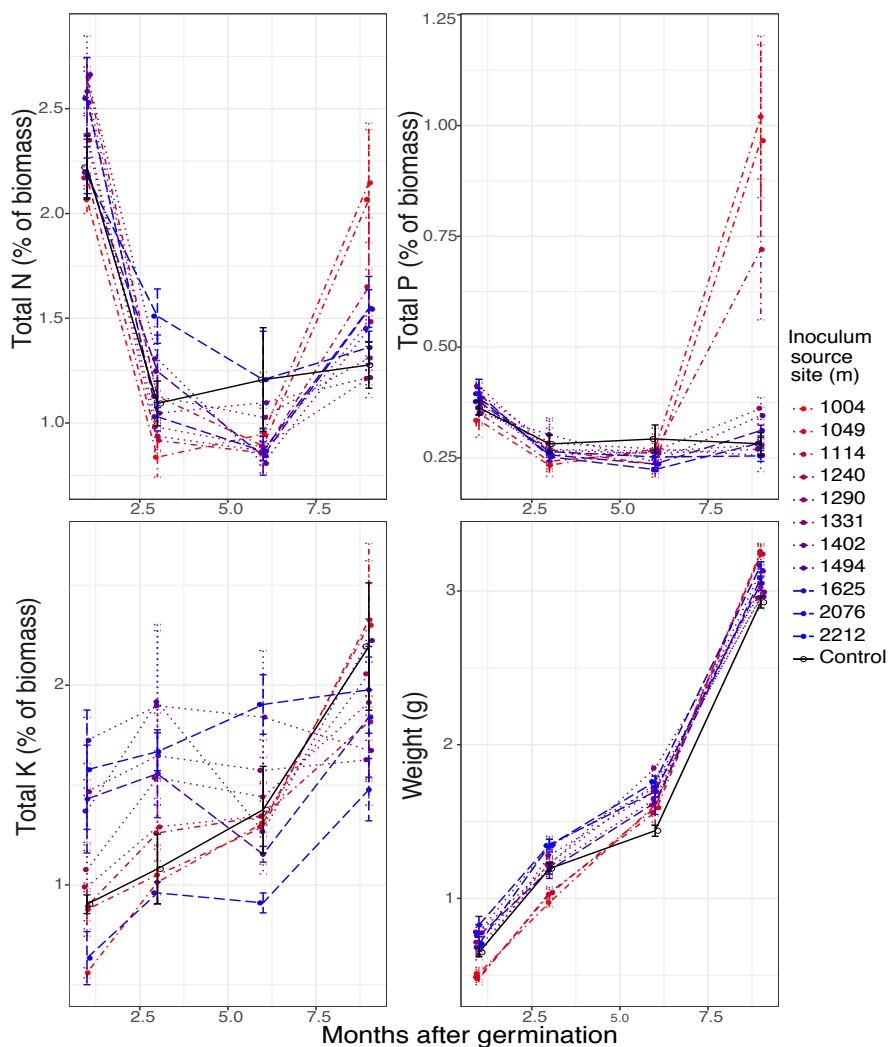
**Figure 2.3 Bootstrap consensus tree and heatmap of the relative abundances of each AMF virtual taxon (VT) across the elevation gradient in Joshua Tree National Park.** The tree was built using the Maximum Composite Likelihood method (Tamura et al. 2004) and evolutionary analysis conducted in MEGA7 (Kumar et al. 2016). Node numbers represent Bootstrap values with only those values above 50 displayed. Tips represent AMF species name and VT as they are listed in the MaarjAM database. For the heatmap, rows represent the presence of AMF and the darkness of square indicates the read abundance of each VT shown on the tree, at each elevation sampled.



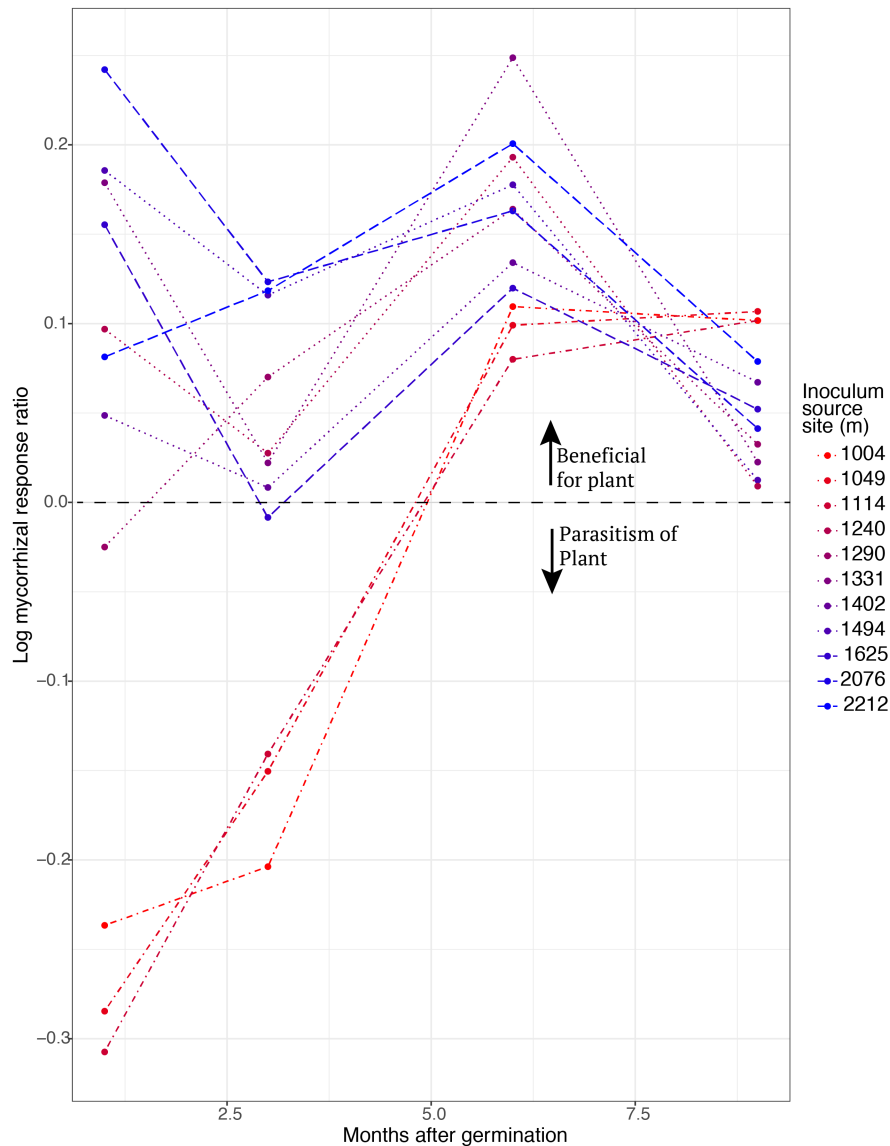
**Figure 2.4 Relative abundances of genera of AMF taxa colonizing Joshua tree roots harvested across an elevation gradient in Joshua Tree National Park.** Abundance is estimated as the proportion of assigned sequence reads within each site.



**Figure 2.5 Biplot of first two components (PC1 and PC2) of a Principal Component Analysis of eleven sites, based on the relative abundance of major fungal taxa.** Each point is labeled with the elevation in meters of one of the eleven sample sites, shown in color ranging from cool to warm depending on its position along the elevation gradient. The arrows represent the loadings for each AMF taxon across all sites. The 8 taxa with the strongest loadings are labeled using the first 4 letters in the genus name, and the last three numbers in the virtual tax ID, for example: *Scutellospora* sp.:VTX00052 = Scut052.



**Figure 2.6 Responses of Joshua tree seedlings to treatment with different fungal communities.** Joshua tree seedlings inoculated with fungal communities from one of the 11 elevation sites, or as no-AMF control, and were destructively harvested at 1, 3, 6, and 9 months (averaged in triplicate). Neither nutrient levels nor seedling weight varied by fungal communities from the medium and high elevation sites with respect to the control, however plants inoculated with low-elevation fungi had the lowest weights at 1 and 3 months, and the highest weights, nitrogen, and phosphorus levels at 9 months when compared to all other treatments or control. Colors correspond to AMF communities taken from field sites that range from warm to cool along an elevation gradient, or black for control, and points are jittered horizontally around value with error bars showing 1 SD. Line styles correspond to low-(dot-dash line), mid-(dotted line), and high-(dashed line) elevation fungal groups, or solid for the control.



**Figure 2.7 Mycorrhizal growth response for Joshua tree seedlings** (given as log mycorrhizal response ratio) at various monthly intervals following inoculation with whole fungal community inoculum from one of the eleven sites from across an elevation gradient. Log mycorrhizal response ratio is calculated as  $\log(\text{biomass treatment}/\text{biomass control})$ . Samples are shown in color ranging from cool to warm depending on their location along the elevation gradient. Line styles correspond to low (dot-dash line), mid (dotted line), and high (dashed line) elevation fungal groups. Those below the black dashed 0 line have a log mycorrhizal response ratio that suggests parasitism of the plant by AMF, while plant samples above the line are benefitting from the AMF symbiosis.



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## Chapter 3

### **Ecological Implications for Joshua Trees under the California Desert Protection and Recreation Act**

#### **Introduction**

The Natural Resources Management Act (NRMA), one of the most significant pieces of conservation legislation created in the 21<sup>st</sup> century, was signed into law on March 12, 2019. This public-lands act designates 1.3 million acres of new wilderness, expands several national parks, creates five new national monuments, and permanently reauthorizes the Land and Water Conservation Fund (LWCF) (S.47 – 116th Congress: Natural Resources Management Act of 2019). The bill was crafted over 25 years through the collaborative efforts of diverse stakeholders such as ranchers, off-road enthusiasts, the Bureau of Land Management, the Forest Service, and wilderness and conservation advocates. The final bill represented a compromise that preserved traditional land uses like ranching and off-road vehicle use, with the agreement to create huge parcels of wilderness and no new motorized routes.

More than half of the lands affected by NRMA are in the Southern California desert. The bill encompasses the long awaited for California Desert Protection and Recreation Act (CDPRA) championed by Sen. Dianne Feinstein and affects over 716,000 acres of Southern California desert. The Act creates eight new wilderness areas covering 280,000 acres and expands the Death Valley National Park and Wilderness, Joshua Tree National Park (JTNP), Anza-Borrego Desert State



Park, and San Geronio Wilderness. Protections would be expanded in Inyo and Imperial counties, and 77 miles of waterways established as Wild and Scenic Rivers. Over 200,000 acres of existing off-highway vehicle recreational land would also be permanently designated for off road vehicle use (S. 32 – 115th Congress: California Desert Protection and Recreation Act of 2018) (Fig. 3.1).

This new legislation followed closely a difficult period in national park history that involved a 35-day partial government shut down and resulted in national outrage over the destruction of JTNP resources by off-road vehicles and illegal campfires, Joshua trees being cut down, and campgrounds overflowing in waste. Following the widespread attention and public outpouring of support (Chiu, 2019; Stack, 2019), the arrival of the NRMA was widely well-received (Davenport, 2019), bringing more money and protection to our national lands.

JTNP will benefit directly from the CDPRA and gain approximately 4,518 acres (Fig. 3.2). These remnant parcels are contiguous or nearby the boundary of the park with the topography ranging from rugged granite mountains with pinyon pine juniper tree forests, Joshua tree woodland, flatlands, and seasonal washes. This landscape contains critical habitat for the threatened desert tortoise, burrowing owl and LeConte's thrasher and are recognized wildlife corridors for bobcats, desert bighorn sheep and other species. Permanently protecting these corridors is critical for the long-term health and survival of wildlife in the Joshua Tree National Park (S. 32 – 115th Congress: California Desert Protection and Recreation Act of 2018), however the CDPRA may ultimately do little to benefit current or future Joshua tree

populations in the local area. Here I first review the history of land preservation in the Mojave Desert and its relationship to JTNP. Next I introduce my ecological research on Joshua trees and their key interacting species in JTNP and describe how the CDPRA falls short on Joshua tree protection for current and future populations. Finally, I make recommendations for future research and argue that endangered species protection may be needed to regulate effective management of Joshua tree populations under the changing climate.

### *History of Desert Land Preservation*

The CDCRA is a continuation of over 25 years of legislation to establish and protect JTNP and the surrounding deserts from developmental sprawl, unregulated off-roading, and massive renewable energy development in the form of solar and wind farms. The original California Desert Protection Act (CDPA) in 1994 established the Death Valley and Joshua Tree National Parks and the Mojave National Preserve in the California desert when Congress determined that the federally owned desert lands constitute a public wildland resource of important value for current and future generations (S.16 – 103<sup>rd</sup> Congress: California Desert Protection Act of 1994). These lands were found to have unique scenic, historical, archeological, environmental, ecological, wildlife, cultural, scientific, educational, and recreational values, but have been threatened by development pressures and adverse activities.

Through these findings, Congress decided to enlarge and protect Joshua Tree National Monument, established in 1936, abolishing the monument and incorporating its lands into JTNP. Further expansions of the CDPA attempting to create new national monuments that link JTNP to the Mojave Preserve, as well as add additional lands to the park and guide renewable energy development died in committee and were not passed into law (S. 2921 – 111th: California Desert Protection Act of 2010). Following numerous revisions and lack of movement in the senate, President Obama utilized executive branch power through the 1906 Antiquities Act (S.54 – 59<sup>th</sup> Congress: Antiquities Act of 1906) to designate and protect the lands. Thus in February 2016, three new national monuments were created to protect a combined total of 1.8 million acres of California desert: Sand to Snow, Mojave Trails, and Castle Mountains (Presidential Proclamation, Barak Obama, 2016). These monuments link the landscapes of eastern California from the San Bernardino Mountains through JTNP, the Mojave Preserve, and reaching north into Death Valley. This designation effectively connects patchworked parcels and wilderness lands across the desert, providing a critical habitat linkage for many rare and endangered species.

Much of the impetus for the designation is driven by the quest for renewable energy (wind and solar farms) on lands now designated at National Monuments (Hamin, 2003). The vast landscape of what is now the Mojave Trails Preserve was acquired years earlier by the Wildlands Conservancy, and then transferred to the Bureau of Land Management for conservation. However, large-scale renewable

energy proposals to develop massive solar farms across those lands prompted pressure from the Wildlands Conservancy on politicians to protect the critical habitat from destructive industrial development (Wood, 2009). The debate over creating a monument encapsulates a rising tension between the goals of preserving wild lands and ambitious efforts to combat global warming. However studies and reports have repeatedly identified alternative locations for renewable energy development on private and degraded lands that will protect the desert landscape and allow California to meet its energy goals (Stoms et al, 2013; Hernandez et al, 2015). Large scale solar projects have damaging impacts on desert habitats and would greatly impact Joshua tree ecosystems through the damaging of fragile soil systems, disturbance of ancient (thousands of years old) deep rooted plant species, and ecosystem processes (Stoms et al, 2013).

This important designation helped to stop the conversion of biodiverse desert into industrial use through promoting habitat connectivity. This is an important move considering the increasing threats that deserts face from climate change and fragmentation from development (Archer and Predick, 2008; Dilts et al, 2016). However in April 2017 this designation was called into question by President Donald Trump who issued an executive order compelling the Secretary of the Interior to review the monuments for abolition, claiming to correct decades of undemocratic government overreach by returning public lands to the people (Beckett et al, 2017). Regardless of these setbacks, over 100 bills were combined

with broad partisan support and signed into law in May 2019. to become the Natural Resources Management Act, thus securing the preservation of these desert lands.

### *Joshua Tree Ecological Research*

To successfully manage species of concern, we must consider ecological research in the context of changing policies, and adaptive management strategies. In my ecological research I have studied the impact of climate change on Joshua tree populations and their key symbiotic partners across a climate gradient in JTNP that stretches up into the surrounding mountains (Fig. A1.1). This population of trees is threatened by the changing climate and may be locally extinct within a century (Cole et al, 2011) with few areas suitable for continued Joshua tree survival (Barrows and Murphy-Mariscal, 2012). Across the gradient, we found that Joshua tree death was greatest at the lowest elevations which are getting hotter and drier as the climate changes (Harrower and Gilbert, 2018). Additionally, populations of the trees are not reproducing sexually at their southern or northern local boundary limits. This is due to local climate impacts on the trees, and because the reproductive success of Joshua trees is tightly linked to its co-evolved yucca moth pollinator – a mutualist partner that is the only pollinator for the trees, and that also uses the seed pods as a nursery for her young, which feed entirely on Joshua tree seeds during their larval stage. A portion of the uneaten seeds then goes on to become the next generation of Joshua trees (Pellmyr, 2003). The abundance of moth and tree populations peak at approximately the same elevation (as do all measures

of tree vigor), however there are no moths at either elevation extremes of the trees' range. This helps to explain the lack of sexual reproduction of the Joshua trees in those areas. We found that climate change can act on the success of both species (tree and moth) distributions independently as well as on the outcome of the interaction itself; the outcomes of the mutualism (and benefit to Joshua trees) changes depending where it occurs on the elevation gradient. Taken together, these interactions between climate and reproductive success will impact the viability of current Joshua tree populations and the ability of future populations to track the changing climate.

When considering future outcomes for current Joshua tree stands, we found that the Joshua tree populations seem to be dying back at low elevations as predicted, but they do not seem to be moving successfully into higher elevations where their pollination mutualism is unsuccessful. Further, my results demonstrated that having robust, dense, flowering trees is important to support and attract enough moths for successful seed set, which is again linked to the elevation. It remains to be seen if Joshua tree vigor can improve at higher elevations and if it will be able to attract enough moths for successful reproduction. Joshua tree populations can survive for awhile without sexually reproducing because they can also reproduce clonally (Rowlands, 1978). However, without sexual reproduction and the genetic variation it generates, Joshua tree resilience to changing environmental conditions will likely be impeded and the ability to shift their range to follow geographic shifts in suitable conditions may be limited by a lack of seeds at the upper elevations.

Understanding how these different factors contribute to population dynamics is important as the climate changes and the phenology and range of the organisms shift. If symbiotic partners respond to environmental changes in different ways, these responses could result in changes of partner abundance, changes in the timing of key phenological events, extremes of costs or benefits, or decoupling of the symbiosis leading to ecosystem-wide consequences. In my research I found that the abundance of pollinating moths increases with tree density but is very low above a certain elevation (1500-1600 m). This elevation where trees thrive but moths do not could be an important transition zone for future work to focus on the Joshua tree-yucca moth climate mismatch. We will need to continue to monitor Joshua tree populations to see if they are reproducing and where, which will provide key information to understand if the Joshua tree populations are expanding or shrinking. However we do not yet have the species distribution models for the moths, needed to prompt future considerations for endangered species designation by the Department of Fish and Wildlife (DFW).

Underground, Joshua trees form important symbiotic interactions with a previously unknown community of arbuscular mycorrhizal fungi (AMF) (Chapter 3). In exchange for carbon, these fungi help plants to resist stress, disease, salinity and drought, and provide greater access to soil nutrients (Harrison, 1997). Using next-generation DNA sequencing technology, I profiled the unique fungal communities associated with Joshua tree roots across the climate gradient. I found that fungal communities in the Joshua tree roots change with elevation, resulting in

different functional outcomes for the Joshua tree seedlings. The outcomes of the symbiosis can change from parasitic to mutualistic depending on which fungal groups are associated with the trees and the stage of plant development (Chapter 3), which could have consequences for seedling establishment and distribution. Those fungal communities change along the climate gradient, and as the trees establish in new locations, they will encounter different partners which will have impacts on tree performance. Assessing the outcomes of fungal groups and host response over both time and environmental space is necessary to predict and manage for target plant species under current and future climate scenarios.

#### *Linking Research and Policy*

By investigating the complex interactions between climate change and multi-species responses in JTNP, I have identified some considerations and suggestions that could provide tools for conservation managers to better predict and manage Joshua tree populations. While the CDPRA designation protected lands important to regional Joshua tree habitat, there were no new additions or designations in the areas that would best protect the *future* populations of Joshua trees and their symbionts near JTNP. As my research suggests, climate change threatens much of the local populations of Joshua trees and their symbionts, and the long term survival of trees in the area will depend on land management at the northernmost locations of their distribution; this was not improved by the recent CDPRA policy. While our research has shown that Joshua trees at their highest



elevation range edge do not currently appear to be tracking the climate, this could change as the snow line starts to recede (Dole et al. 2003). The northern-most local range edge of Joshua trees sits between Big Horned Mountain Wilderness and San Bernardino National Forest (Fig. 3.3), areas that were established as part of the original CDPA (16 U.S.C. §§ 410aaa-83, 1994). Big Horned Mountain Wilderness is jointly managed by the BLM (Department of the Interior) and the Forest Service (Department of Agriculture) while the National Forest is solely managed by the Forest Service (Fig. 3.3). These two jurisdictions hold land that contains unique environments with many rare and endangered species and the northernmost local population of Joshua trees. Wilderness designation provides some of the strongest federal safeguards protecting the landscape from building roads, use of motorized vehicles, commercial development or industrial uses. However, the adjacent National Forest contains widespread off-road vehicle use, off-trail camp fires, and unregulated shooting and hunting (personal observation on numerous occasions) through this sensitive desert environment where future populations of Joshua tree seedlings will likely need to establish to survive warming climate conditions. This recreational use also extends into the adjacent wilderness lands, regardless of the changing management regulations.

As of April 3, 2019 Joshua trees are under review to be listed as endangered species – a process that has experienced countless setbacks due to lack of funding, political opposition, and the government shut down (personal communication with Department of Fish and Wildlife staff). Combining the complexities of inter-

jurisdictional agency management, and the implications presented by my work, the following research and management steps should be taken. First, we need better understanding of how Joshua trees and their symbionts will fair in future suitable locations as the climate changes. This will require observational and manipulative experimental approaches to better understand the outcomes of plant-fungal associations across space and time at future locations. Transplant studies and experimental warming field trails that use different Joshua tree seed genotypes from across its range, paired with the different soil fungal communities identified by my research, would provide more robust understanding of how the tree and fungal combinations might succeed in the future landscape. Incorporating my results on AMF species and plant functional responses could be useful towards developing an AMF planting protocol for managers in current post-fire Joshua tree restoration efforts and potential future assisted migration projects (Vitt et al, 2010). Now that we know which communities of fungi are distributed across elevations we can test seedling transplants inoculated with those different fungi in the field to determine which symbiotic outcomes best support tree survival in each location.

We lack species distribution models for yucca moths. With species distribution information, we can focus on the key variables and conditions that influence population numbers and promote favorable mutualistic outcomes, as well as quantify the health of the association in different locations and the potential for species to track the changing climate. Future work with species distribution modeling that predicts how moths may respond to the changing climate could help

us gauge if Joshua trees and their pollinators might overlap under future climate scenarios and how the local conditions may affect the outcomes of their mutualism. Results from my upcoming moth distributional modeling (a collaboration with DFW) will provide valuable data for understanding potential suitable locations for the release of reared moths or moth larvae to facilitate sexual reproduction of Joshua trees at range extremes. Moth populations should also be monitored at the northernmost distributions to determine if they are able to move into those areas of future Joshua tree range. We must also continue to monitor changes in reproductive success in Joshua tree populations. This will provide key information to understand if the Joshua tree populations are expanding or shrinking, which will be necessary to prompt future considerations for endangered species designation by the DFW.

Collaborative governance (Ansell and Gash, 2008) for protecting Joshua trees should begin with steps that are grounded in findings from the Conservation Agreement generated by the Species Assessment Report through the DFW's endangered species review, updated to include any new research. This would involve bringing stakeholders to the table to clarify local management expectations and procedures, the implications of privately owned land use on Joshua tree populations, individual goals and how they relate to the Conservation Agreement, as well as future management steps to be taken collectively and independently.

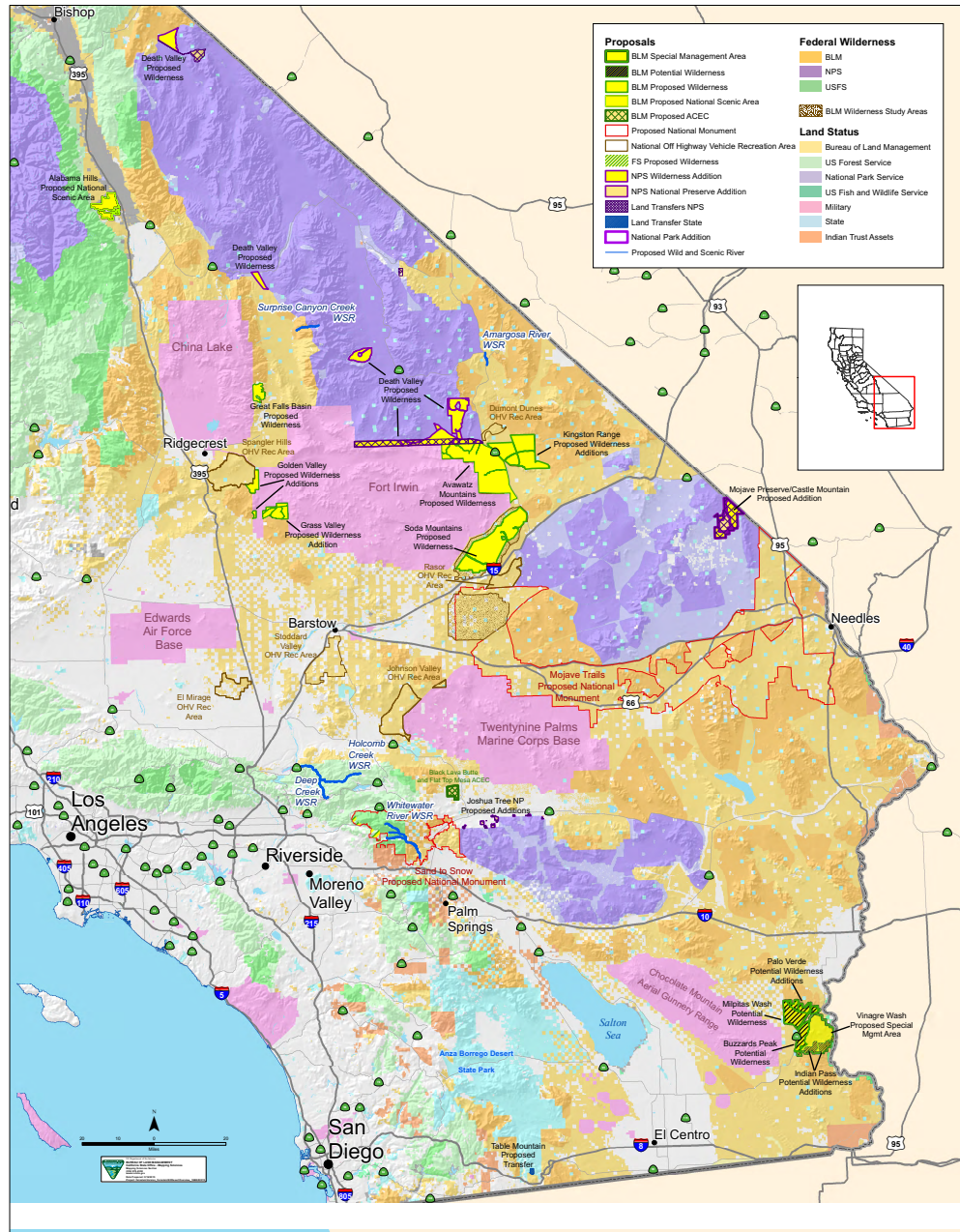
Considering that the most likely areas where Joshua trees can establish under future climate scenarios are in National Forests under the jurisdiction of the Forest Service, managers should begin to address the complex problem of how to navigate

and manage current off-road vehicle activity that crisscrosses the area and how that may impact future populations of Joshua trees that establish there. How to regulate desert lands from motorized vehicle use will be challenging when they are so far removed from administrative centers and infrastructure. By accessing local desert community culture and the strong local identity that is connected to Joshua tree iconography and species survival, there is potential for local buy-in regarding Joshua tree management efforts (Harrower et al., 2018). These efforts could result in stricter regulations for Joshua trees found on private land, changing recreational access in critical habitat, and remove off-roading from potential seedling establishment areas.

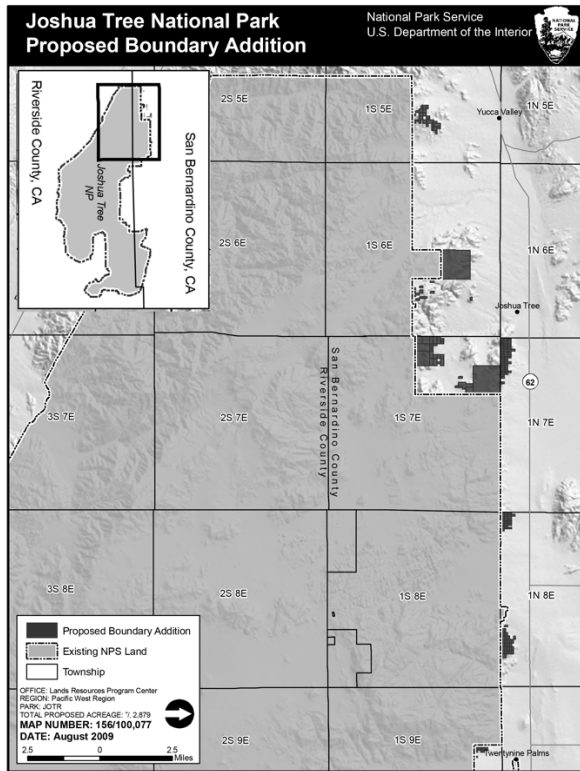
Successful Joshua tree management during rapid climate change requires understanding the key species interactions in the system and how they may change in relation to each other and the changing environment. This work must then be considered together with the needs of various stakeholders to develop equitable and effective policies that function across local and regional landscapes. If we are going to prioritize the local establishment and survival of this species in the Joshua tree area, then the previously mentioned efforts should be strongly considered. Likely, the most effective way to accomplish this will be to assign endangered species status to Joshua trees thus forcing regulation and management efforts by department officials, a strategy that has been found effective in other cases (Thomas, 2003; Duane and Guerico, 2010). Sharing these research efforts and others with key environmental groups, such as the Wild Earth Guardians (the group who originally

petitioned for Joshua tree review), the Mojave Desert Land Trust, and the Wildlands Conservancy, who maintain the legal power to leverage these and future research findings will be an effective way to prompt a future species assessment by the DFW.

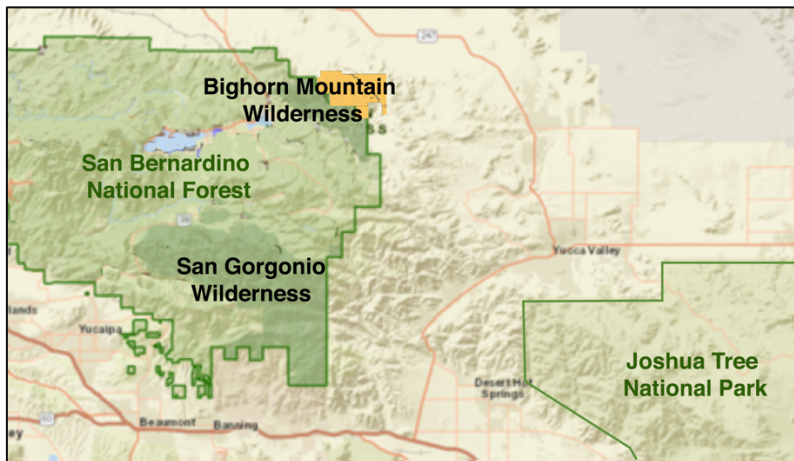
Figures



**Figure 3.1 Map detailing the new land acquisitions and managing agencies under the California Desert Conservation and Recreation Act. Image accessed Feb 25<sup>th</sup> 2019:**  
[https://www.feinstein.senate.gov/public/\\_cache/files/.feinsteininversion-feinsteinbilldesertoverview-16mar2015.pdf](https://www.feinstein.senate.gov/public/_cache/files/.feinsteininversion-feinsteinbilldesertoverview-16mar2015.pdf)



**Figure 3.2 Modified map of the Joshua Tree National Park proposed boundary addition under the California Protection and Recreation Act. Original image accessed Feb 25<sup>th</sup> 2019, <https://cook.house.gov/corca>**



**Figure 3.3 Modified USFS map of Bighorn Mountain Wilderness and San Gorgonio Wilderness with land designations. Bighorn Mountain Wilderness managed by the Forest Service (in green) and the Bureau of Land Management (in orange). Original image accessed on Feb. 25<sup>th</sup>, 2019: <https://www.fs.fed.us/ivm>**

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## Chapter 4

### **Staying with the Trouble: A Multispecies Collaboration with Joshua Trees**

#### **Introduction**

We are losing a great number of species at alarming rates because of the impact that our collective behaviors are having on the Earth's ecosystems (Ceballos and Ehrlich 2018). While numerous scientific studies bring attention to these damaging impacts ( Barlow et al. 2016, Pecl et al. 2017, Ceballos and Ehrlich 2018) we lack the magnitude of public response and behavioral shifts that are needed to address their underlying causes. Most of the destructive behaviors that contribute to accelerated species loss come from systemic socioeconomic and cultural causes (Díaz et al 2018). They are embedded within our social institutions, structures and the social relations within our society, and their solutions will require a range of disciplinary approaches (Van Dooren 2014, Demos 2016, Haraway 2016, Tsing et al. 2017). How can we more fully understand the complexity of species loss and reckon with the consequences of our actions on living beings to embrace behavioral changes that value the environment and social equity? Perhaps an emotional understanding of the issue is just as crucial as a scientific one. But how do we arrive at that? In my work, I engage with artmaking and arts theory from a deep human desire to create art, but also driven from my frustration for the inability of science alone to motivate the magnitude of societal response that we need. Art can play a transformative role by initiating the behavioral shifts and inciting demand for

environmental policy to move towards more sustainable and equitable societies (Miller 2014, Curtis 2017, Tsing et al. 2017, Harrower et al. 2018).

Narrative driven art is a powerful way to establish environmental consciousness, which is realized as an intellectual and emotional understanding of our impact on ecological systems (Van Dooren et al. 2016). Through the art of storytelling, science information can be distilled and also given emotional significance which is critical for effective science communication (ElShafie 2018). In my work, I am interested in multispecies storytelling through art and science. My art studio is both a place where I physically make art but also includes the field and laboratory where I collect data that I use to form narrative and understand the world. I believe that narrative (especially when grounded in an artist's personal connection to place) is the key to transforming public attention for and understanding of the profound challenges we face.

In my work, the Joshua tree becomes a symbol of the nature-culture divide and an iconic representation that I use to focus attention on the impact that our actions have on the environment. By nature-culture divide I refer to a tension inherent to the dualism and Western categorization of “nature” and “culture” as things existing separate from one another, but also to the method of questioning their separate functioning as two entities versus a continuous engagement in biotic feedback (Latour 2012).

The powerful symbology of the Joshua tree became even more clear to me when considering the public response to the news that Joshua trees were destroyed

during the 2019 Government shut down at Joshua Tree National Park (Stack 2019). Public outrage was immense at the loss of the two Joshua trees and they became a symbol of the damage that President Trump's actions were having on our public resources (Associated Press 2019). But with climate change, we are poised to lose all of our Joshua trees, and that is an ax that we are collectively wielding (Dole et al. 2003, Cole et al. 2011, Barrows and Murphy-Mariscal 2012, Harrower and Gilbert 2018).

Joshua trees are threatened by the changing climate, and may be locally extinct from their namesake park within a century (Cole et al. 2011). The trees form obligate symbiotic relationships with a yucca moth pollinator who purposefully pollinates the trees' flowers in exchange for room and board for her developing moth larvae. This relationship is arguably one of the most well know examples of coevolution in ecology (Pellmyr 2003). The trees also form important relationships with underground communities of mycorrhizal fungi, enhancing seedlings' abilities to gather nutrients and water (Chapter 3). These multispecies lives and relationships are embedded in ecological, social, and cultural relationships that can nourish or harm them. My ecological research explores the symbiotic interactions of Joshua trees with their moth and fungal partners, and how the outcomes of those relationships could shift with the changing climate, impacting Joshua tree populations (Harrower and Gilbert 2018). Drawing from my deeply personal connection to desert landscapes and by bridging art and science disciplines, I bring a

unique perspective to these ecological issues and provide opportunities to connect with these challenges in novel ways.

Through my art practice, I shift my focus from the interactions of species under climate change at the molecular and microscopic level to the larger societal level, seeking to understand how art that is connected to an ecological practice can impact social change. Through this work I endeavor to understand species and environmental entanglements: those between Joshua trees and fungi, the trees and moths, my own relationship to these trees and to desert culture, the responses of people to the trees and their potential loss, as well as our human impact on the environment which in turn impacts the biological systems we are embedded within.

In my interdisciplinary work I utilize both art and science methodologies, aiming to bring ethnographer Anna Tsing's "arts of noticing", a practice guided by a passionate immersion in the lives of the non-humans studied (Tsing 2010). I expand this practice to Thom Van Dooren's call for an "art of attentiveness", which requires developing the multidisciplinary skills to both pay attention to others and meaningfully respond (Van Dooren et al. 2016). However, in my work I have found that the art of attentiveness is best actualized when focused on local issues or organisms and a meaningful connection to a place (Harrower et al. 2018). Here I refer to engaging a community in the local impact of a global issue. For example, Joshua tree loss due to climate change which is linked to my personal narrative of being raised in the Joshua tree community and then returning for my dissertation research. These artful practices help to focus and guide my work in ecological as

well as the social systems. Working as a social practice artist by uniting my ecological and artistic practice to understand Joshua tree systems in Joshua Tree National Park (JTNP), I bring the arts of attentiveness to the ecological systems that I study. I utilize a variety of science tools and arts media to communicate the complexity and ecological importance of species interactions, also endeavoring to co-create meaning and understanding of these concepts with diverse communities of artists and scientists, as well as the local Joshua tree community and the greater community of people concerned about Joshua tree loss. As an artist and scientist, I bring attention to the Joshua tree ecosystem's form, content, and symbols. I utilize concepts and theories that inform and resonate with the public, and I point to the role that the artist plays in the evolving relationship between society and nature.

Art is a powerful tool for social change, both as an inquiry-based practice as well as a platform to share complex environmental issues with a diverse public (Curtis et al. 2014, Curtis 2017). Narrative techniques through art can connect people to complex concepts at an emotional level, increasing public understanding and empathetic response to our role in the crisis of species loss (Harrison and Harrison 1993, Jacobson et al. 2007, Ballengée 2015, A'Bear et al. 2017, Curtis 2017). Art has the potential to influence values, beliefs, knowledge and the development of societies (Belfiore and Bennett 2006) which are some of the same factors that contribute to the environmental behavior of citizens (Jackson 2005). The process of creating or experiencing art can facilitate a space for dialogue around important issues, and harness the power of narrative and imagery to deliver

educational messages inspiring aesthetic appreciation and emotional response (Carlson 2000, Curtis et al. 2014). The art-making process also focuses attention on the subject being studied, often building an emotional connection, which can generate empathy and understanding around science concepts, organisms, and ecological systems (Kay 2000, Curtis et al. 2014, Ballengée 2015). By engaging with the arts we can better navigate the nature-culture divide and reckon with our responsibilities as caretakers on this planet.

Critical theorist Donna Haraway argues that to caretake effectively, we must reframe the dominant narrative of our human exceptionalism as something operating outside of nature, and instead recognize that we are entangled within a sympoetic system – collectively producing systems that do not have self-defined spatial or temporal boundaries, but that information and control are distributed throughout with great potential for change (Haraway 2016). With this framing, the distinctions between nature and culture fall apart, and enhance our recognition and responsibility for our contributions and impacts within the system and change our personal responsibilities to the participants. She calls upon us to commit to doing the best we can with what we have, while expressly seeking solutions that value above all equity and sustainable practices – or as she calls it, “staying with the trouble” (ibid). My art and science practice are my cumulative attempt to engage the multilayers of species and cultural entanglements, and to stay with the trouble for Joshua trees.

In conversation with my interdisciplinary ecological work, I critically engage in an art practice aimed at troubling the nature-culture divide. Through a



multiyear, science-artist residency at JTNP, I have done quantitative ecological research and engaged in social practice art to understand and share complex species interactions. This includes an experimental painting practice that incorporates material elements of my study organisms and research data into the artworks, two stop motion animations that interrogate themes of climate change, species loss, and motherhood, as well as a participatory art and mock online dating site where you can interact with the trees from my field sites.

The questions guiding my work are: how can art-science-integrated research build understanding of interspecies connections for Joshua tree communities (e.g. trees, fungi, moths and culture)? How might this approach provide an enhanced platform with which to capture a diverse public interest, building understanding and motivating sustainable behaviors more effectively than either discipline on its own? Through this work I aim to better understand the form and function of the organisms that I study as well as to share with others the hidden beauty of these threatened species interactions.

In this paper, I will first contextualize my work within the ecological and social practice art fields. Next, I will situate my practice utilizing a multispecies studies lens and discuss how it informs my interdisciplinary practice and understanding of the nature/culture divide. I will then describe the multimedia projects that comprise *Staying With the Trouble for Joshua Trees*, and reflect how they contribute to artistic and critical conversations, connect to each other and back

to my ecological research. Finally, I will discuss the themes that emerge from the work as a whole and how that relates back to my conceptual framing.

### ***Art Practice Context for Staying with the Trouble for Joshua Trees***

*Staying with the Trouble for Joshua Trees* exists in conversation with intersecting histories across environmental, ecological and social practice art. Artists have long engaged with the critical issues of their generation to create profound works of art and to define new cultural movements. This includes the iconic spiritual representations during the Renaissance period, the use of 19<sup>th</sup> century realism seeking social justice, the abstraction of form in revolutionary Russia and in response to momentous science concepts such as relativity, documentary photography as a social justice tool in the twentieth century, and current environmental artists responding to the Anthropocene/Capitolocene era (Janson et al. 1997, Miller 2014, Demos 2016). While some critics state that the avant-garde art movement (experimental or unorthodox art in response to art, culture, or society) is dead (Kramer 2013, Bunzl 2014) scholars argue that the new avant-guard is alive and well, repositioned and working strategically between nature and science about the posthuman future of social and environmental responsibility (Cassidy 2017).

Ecological and social practice artists make provocative work that engages and challenges the nature-culture divide (Gablik 1991, Miller 2014, Demos 2016, Harrower et al. 2018). In the 19<sup>th</sup> century, environmental artists were among the first to record the visual beauty of the American West, drawing visitors to the national

parks with the narrative that our shared resources serve purposes much greater than extraction based uses, and ultimately generating support for their protection and preservation (Winfrey and Dunaway 2011). Critical theorists Suzi Gablik's writings and critiques were transformative for artists in that she challenged the idea of what art was and the role of the artist, creating a new social and environmental context for making art that still resonates today. She challenged artists to engage with social frameworks and issues in a way that is meaningful and with outcomes that reconstruct culture and challenge people's understanding of sustainable existence. She argues that we must respond to our planet's needs with complex interdisciplinary works that demonstrate interaction. Art that is grounded in interconnectedness and community, results in work that is more accessible and powerful to the public that it was intended for (Gablik 1992). Ecological art is a political, environmental, and social art practice that began by shifting away from the elite art world to become a tool of democratic values (Efland 1990). In this respect, it is a method of analyzing social conditions and values. Inherent to this practice is the belief that art education and art practice should serve as an agent for social change. Its practitioners stress interdisciplinarity; art that is taught or practiced across disciplines is better able to create understanding about the social, cultural, and political values in which it is situated (Eisner 1988). They seek art as a process and form of research that moves away from traditional aesthetics and monetary valuation of a finished product towards a means of analyzing institutionalized power structures and seeking more equitable and sustainable societies (Freedman 1994,

Stuhr 1994). The artist aims for critical awareness and a deeper inquiry into the current issues and how we can address them and becomes an instrument to conduct inquiry (Eisner 1988, Springgay et al. 2005, Irwin et al. 2018).

Similarly, social practice art promotes dialogue and collaborations with communities to engage socio-political and environmental issues. Pioneered by Suzanne Lacy, this art form utilizes community organizing strategies and interventions with a diverse group of participants to create cross-disciplinary discursive space (Lacy et al. 1995). This practice values diversity and equity and can provide access to groups often excluded from public processes (Schupbach and Ball 2016). Promoting diverse inclusion in relationships to natural environments is important to demonstrate the interconnectedness between nature and society, and to develop equitable and sustainable solutions (Giesecking et al. 2014). This is increasingly important as we respond to the effects of demographic shifts, social inequity and climate change.

Contemporary ecological artists and social practice artists continue to respond to issues of environmental crisis utilizing symbols and narratives of the nature-culture interface that actively engage the public to reckon with current social and environmental issues (Gablik 1991, Novacek 2008). These artists work across multiple disciplines to engage different cultures of practice through research, dialogue, and exhibition. By engaging across disciplines and beyond the commercialized role of art within society, the artist finds new means of social

engagement functioning as both a reflection of society and a tool to transform it (Gablik 1991).

### ***Examples of Ecological and Social Practice Artists***

#### *Early Foundational Artists*

*Staying with the Trouble for Joshua Trees* draws on ecological and social practice art, inspired by and learning from historical and contemporary artists and interdisciplinary scholars. One of the formative eco-art practitioners, Joseph Beuys, used art as a forum for his environmental and political beliefs, collaborating with organisms in his art practice. In his work entitled “7,000 Oaks” he planted over 7,000 oak trees across Germany, each accompanied by a basalt stone. The oaks were used as a symbolic representation of time and sculpture, with meaning rooted in Druid symbolism as they used oaks to define their holy places (Druid means oak). As a symbol of bringing the sacred to a public space, next to each tree he placed a large basalt column as a marker, with the hopes to inspire society to awaken to the great spiritual and environmental importance within the urban environment (Beuys 1982). In another influential performance, “Coyote: I Like America and America Likes Me”(1974), he spent a week alone living with a wild coyote in a New York City art gallery. The coyote symbolized the spiritual world and the sacred status to Native Americans, before the coming of European settlers at which point both groups become pest to be exterminated (Beuys 1974). The debasement of the coyote was a symbol of what white colonizers have done to North American culture and

land, and he believed that performance art could evoke a deep emotional response from the audience and potential for social change. However, critics argue that by mystifying nature and misappropriating indigenous religious traditions, Beuys effectively enlisted the coyote in a “social sculpture”, thus reinforcing the idea that humans are dominant over other beings and systems (Gandy 1997). Like Beuys work, I draw on the power of iconic symbology, working with the Joshua tree to bring attention to the impacts that our actions are having on species, and that those species are exquisitely connected to a larger system. In *Staying with the Trouble for Joshua Trees*, I appropriate popular culture tools to draw attention to the environmentally unsustainable behaviors and practices of societies and create opportunities for reflection and knowledge production towards sustainable and equitable nature/culture practices.

One of the first artworks to focus on climate change and draw attention to the issue as well as explore the system itself was Newton and Helen Harrison’s “San Diego as the Center of the World” (1974), leading to “The Lagoon Cycle” thus beginning a decade of projects centered on food production after sea level rise with climate change (Harrison and Harrison 1985). In this work, they did not explicitly deal with the human practices driving climate change, but engaged with the human responses that follow – specifically how socioeconomic class might translate into survival, posing the question: “will you feed me, when...” This research-based arts practice grew into an advisory group, The Harrison Studio, which works with many kinds of organizations to consider how overarching metaphors in landscape scale

planning can best build sustainable societies. They describe the universe as a giant conversation taking place simultaneously among all life forms, and that we need a greater understanding of how our resource use and habitat destruction disrupts living systems and species interactions. They posit that the notion that technological solutions to save a rapidly expanding population together with an infinitely growing economy is contradictory, and that to make socially transformative art requires cross discipline collaborations that engage the public (Harrison and Harrison 1993).

Continuing on the theme of environmental survival, they have become increasingly interested in climate change and species migrations. Their most recent project “Future Garden for the Central Coast of California” (2019) is a collaboration with artists and scientists to create trial gardens within climate controlled geodesic domes. Native plant species are subjected to increasing temperatures and water conditions that reflect future weather patterns to determine plant resiliency for future restoration and management projects. Like many of the Harrison’s ecological projects, *Staying with the Trouble for Joshua Trees* is grounded in systems thinking and uses an interdisciplinary approach to understand how we can manage our resources and better co-exist with other organisms on our rapidly changing planet.

#### *Contemporary Ecological and Social Practice Artists*

Other contemporary artists are facilitating ways to consider how our livelihoods intersect with science and are entangled within multispecies assemblages through bio art, sonic art, information art, environmental art, and social

practice art. These artists generate multimedia installations and performative interventions that engage with multispecies questions and environmental context, often providing speculative worlds for what could be (Kirksey 2014, Demos 2016). These ideas have been carried forward and are represented (and merged with other disciplines) in the practice of multispecies ethnographies. This approach for considering culture culminates in multidisciplinary collaborations and works, and is well exemplified in the works of artist/writer/curator/and scholar Eben Kirksey's "Multispecies Salon" (2014) (Kirksey 2014). This art project and rich ethnography seeks to illuminate how diverse organisms are entangled in political, economic, and cultural systems, creating new biological and cultural research trajectories.

Of particular influence on my own thinking about the gestures of an art practice in relation to science research, has been the work of Natalie Jeremijenko. An artist, scientist, and experimental designer intent on disrupting toxic human behaviors in playful and educational ways, she creates opportunities for participation and the production of knowledge. Her work spans a range of media, but she is most noted for the creation of "The Environmental Health Clinic" (2007). This participatory art and social experiment develops and prescribes locally targeted, fun strategies to remediate environmental systems. Building on the premise that when people are ill they schedule an appointment with the doctor to determine the next appropriate steps, Jeremijenko utilizes this model to prescribe people actions for their local environmental issues. "Impatients" (individuals seeking guidance but who are tired of waiting for legislative action) visit the clinic or attend



a discussion to discuss an array of concerns with her, such as contaminated land, polluted air, and storm-water runoff. One prescription to address storm-water runoff which can cause sewers to flood and increase river pollution, involved putting in small plots of greenery (often with plants to attract local pollinators) in no-parking zones around the city. Like “The Environmental Health Clinic”, *Staying with the Trouble for Joshua Trees* attempts to make both art and politics more thoughtful, locally focused and fun, operating between popular culture, art and science. While the socio-geographic contexts in which my work is situated differs from Jeremijenko’s, as my work largely operates in rural and protected desert landscapes, there are similarities in that we focus on current environmental issues that are important to the people living within the affected areas. We seek to empower community members by providing opportunities for learning about and participating in research and actions to address the problem. Furthermore, by creating these opportunities for shared experiences around key issues, *Staying with the Trouble for Joshua Trees* assimilates the ideas and concerns of the participants which will help to guide future projects direction.

As an art practice and an installation, *Staying with the Trouble for Joshua Trees* is in dialogue with the history of works that represent the finality of species loss. Ann Hamilton’s exhibition, “The Common SENSE” (2011), was a product of her research in the Burke Museum of Natural History. She covered the walls with photographs of the specimens stacked many deep and viewers were invited to remove the images and take them home, eventually leaving blank walls. Through

this she intended to address the feeling of loss from species extinctions due to unsustainable human lifestyles (Hamilton 2011). Artist Brandon Ballengée illustrates loss by cutting extinct species out of the original John James Audubon drawings in a “Framework for Absence” (2007). His work therefor beacons the viewer to reflect not only on the loss of the species, but the loss of a one-of-a-kind work of art. Like Hamilton and Ballengée, *Staying with the Trouble for Joshua Trees* uses provocative ways, such as printmaking with carvings made in the image of threatened Joshua trees from the National Park, to engage viewers to consider species loss. The Joshua tree ink print functions as a memento of Joshua tree loss, and a reminder to visit the online site to contribute a writing to the tree of the same print that they took home. By creating exhibits that give the public a chance to conceptualize extinction and biodiversity loss, artists create moments for introspection and, hopefully, motivate personal responsibility and environmental stewardship.

### ***Theoretical Context for Staying with the Trouble for Joshua Trees***

*Staying with the Trouble for Joshua Trees* engages with scholarship that considers how multispecies interactions function in the context of environmental destruction. All organisms are situated in deeply entangled histories and futures. To understand these entanglements, my art-science practice and scholarly work is situated across interdisciplinary fields that include symbiotic species theory and multispecies studies. This interdisciplinary middle ground between the arts and

science references back to a time before the academic solidification of the “two cultures” (Snow 2012). Referencing multidisciplinary scholars from within and between these fields, I will contextualize my interdisciplinary practice. Next, I will draw on these disciplines to explore how themes of art as research and meaning making contribute to my practice, as well as how narrative through art can convey complex concepts and inspire emotional response, promoting equity and diversity in ecological and cultural systems.

### *Grounding Multispecies Theory in Science*

Ecological theories are a central process to my artistic practice. Symbiosis is not unique to the Joshua tree system, and is largely responsible for the myriad of ordinary and extraordinary organisms and systems starting with the original creation of eukaryotic cells from bacterial symbiosis (Margulis and Sagan 2002). Ever more complex life forms and stories are the result of more multidirectional associations with other species which form together to create the holobiont – an organism and its microbiota. These symbiotic assemblages are more than a reduction into competitive versus cooperative outcomes, but relate within a dynamic complex system with other organisms and environmental processes at play, and involve a dizzying array of possibilities with which to understand it (ibid). Research of holobionts is gathering momentum with help from the rapidly expanding fields of “omics” fields, genomics, transcriptomics, and proteomics (Joly and Faure 2015). I am interested in holobiont functioning and adaptation under future climate change

scenarios. I draw on the works of Nancy Johnson to consider the range of outcomes for Joshua trees and their mycorrhizal fungi as one component of the holobiont system. Johnson's important work furthered the idea that plant-fungal mutualisms can result in a continuum of outcomes from parasitic to mutualistic that depend on the local environment where they occur (Johnson 1997). In a similar frame, I consider the obligatory interactions between Joshua trees and their moths through Judith Bronstein's theories of context-dependency – that mutualistic outcomes depend on the identities of the partners involved as well as the local environment of where that interaction is occurring (Bronstein 1994). The overarching theme in my ecological work is to consider these symbiotic interactions of the Joshua tree holobiont system within the range of possibilities that will change as the environment changes.

### *Multispecies Studies across Disciplines*

I connect these ecological theories to my arts practice by drawing on research from multispecies scholars. This interdisciplinary scholarship (largely existing across the humanities and social sciences) pays careful and critical attention to the interactions occurring between species and within the environment particularly during the era of climate change. It aims to problematize and work across the nature-culture divide without collapsing these categories into each other, while bringing attention to the differences at all levels (Kirksey and Helmreich 2010, Smith 2013, Haraway 2016, Van Dooren et al. 2016). This field of study

considers social justice, ethics concerning the wellbeing of entities, and environmental ethics concerned with the health of ecosystems and species. It draws on histories in feminist science and technology studies and philosophy, and does not suppose easy or final answers (Latour 2004).

Multispecies study demands an art of attentiveness, both for paying close observant attention to others and for learning methods of response with mutually beneficial ends, thus crafting better possibilities for multispecies coexistence with its requisite entanglements (Van Dooren et al. 2016). This form of immersive research and way of approaching the world becomes a way of knowing and being with others that brings careful attention to them (Tsing 2012). The research processes that support ways of knowing and understanding have profound consequences and shape our world. Through this understanding of the construction and assembly by diverse agents we have a greater grasp on the shaping of outcomes. This work draws scholars from across disciplines into the conversation to better frame ways multispecies attentiveness. By paying careful attention to multispecies we develop a new understanding and appreciation of our human experience.

### *Connecting Multispecies Studies and Staying with the Trouble for Joshua Trees*

In my practice as a multispecies storyteller, cultivating the art of attentiveness, I act as an agent of change by advocating for communities and organisms not represented by economic interests or political parties, and through developing new ways to communicate the complex nature-culture divide. I do that

by investigating these organisms and interactions utilizing a toolkit of interdisciplinary tools, going beyond an anthropocentric view (organisms as symbols or resources for human use), to better provide a “thick” accounting of the complications of multispecies existence under rapid environmental change - “thick” referring to the method which directs interpretive attention to material practices and the nuances and complexity that accompany them (Geertz 1973). This work also requires a way of engaging with other beings that entails an interest in what happens to another, rather than considering one’s own position against them (Rose 2007). Sociologist Bruno Latour argues that we should look beyond the false divisions of nature and culture, wilderness and civilization, but that we need to recognize our deep affiliation with nature, and that non-human entities are integrated into our systems of valuation for their existence as beyond resources to be consumed (Latour 2012).

Through *Staying with the Trouble for Joshua Trees*, I consider Joshua trees, their fungi and pollinators, with Haraway’s frame for coexistence. She proposes that holobionts or “companion species” – species that are impacted historically, socially, and culturally and that are in conversation with many other species – should be respected within their own right, outside of the colonialist framing of the organism as resource or in relation to the being in power (Haraway 2003). We are not individuals but are each a multispecies assemblage of diverse forms of life that that “become” together (Haraway 2003). Broadening these “becoming-with” ontologies, we are all embedded within a lived physical and societal experience that is

dependent on many varying entanglements. With their entangled histories that stretch into the millions-of-years ago, I bring attention to the Joshua tree holobiont's relationships and investigate how those partnerships will continue - or not - into the quickly changing future. This framing is a useful reminder that where we draw the boundaries of organism matters, that the respect and "person-hood" status we give to other species matters, and ultimately that the "stories we use to tell other stories with matters" (Haraway 2016).

To develop strong connections across the nature-culture divide will requires a multitude of interdisciplinary approaches and, as Anna Tsing calls for, "a passionate immersion in the lives of the non-human being studied" (Tsing 2010). Through studying multispecies relationships and their environmental context, I become attentive to the diverse ways of life co-created through these entangled worlds. Relationships emerge from these shared co-evolutionary histories that involve exchange, and bring about new meanings and understandings of ecosystems and our interconnectedness. Through this passionate immersion in my study system, I use science methodologies to mechanistically detangle holobiont networks that I find through molecular analysis of tree and fungal DNA, and through controlled studies of functional responses. I further engage from the micro to the macro as I zoom out to consider how these science discoveries can inform my art practice and my engagement within sociocultural systems.

This shifting of perspectives in my research is important for considering species within ecological and cultural systems. There is an entire network of

feedback interrelationships between organisms and environment. Organisms and environment are engaged in mutual transformations and in conversation with each other, which is impacted by ever greater systems, local ecosystem, landscape, weather, societies, until you encounter the super organism (Margulis and Sagan 2002). Through *Staying with the Trouble for Joshua Trees* I shift my focal lens, moving between science and art practices and between the micro and the macro scale, to provide an artistic narrative intending to make multispecies connections tangible and relatable. From that understanding can blossom empathy, connection, and responsibility.

I have found numerous benefits to approaching ecological research as both a scientist and an artist. As Latour critiques, the way that scientists build up artifacts, conduct studies and reference each other's papers to establish authority and celebrate advancements is not built from truth in nature but an interpretation of it that need not be the dominant form of knowing or unequivocal truth in the world (Latour 2012). Science tends to privilege specific ways of knowing, whereas art has given me permission to explore and engage my study system with open-ended inquiry. As an artist, I am free to develop unique and flexible ways of paying close attention to the organisms that I work with. That deep appreciation and attention to my study species in turn drives my science – the art and science become muses for each other giving me a greater appreciation for my work than I had when working within a single discipline. I have also found unexpected benefits to my science research from the process of paying attention through art. Sketching Joshua tree



flowers at the warmest locations of my field sites to use in one of my art projects, I realized there were no moth pollinators yet it was the middle of pollination season. Thus, I began an entirely new branch of my dissertation and discovered mechanisms that link the lack of moths to lack of Joshua tree sexual reproduction at the warmest areas of their distribution (Chapter 1). The process of making art reinforced my science, led to new discoveries and becomes another way of knowing and truth seeking in the natural world.

Through my art practice I benefit from different ways of knowing my system, similar to cultural anthropologist Andrew Mathews who uses drawings to weave together natural and oral histories through landscape walks, archival research, and interviews (Mathews 2018). With these techniques he can weave together the complex histories of landscape change using line drawings to gesture towards what mattered at different moments between organisms within their environment, and how those multispecies entanglements structure forms across our changing planet.

With my multidisciplinary lens I then translate those discoveries and ways of knowing into a narrative tailored to my different art projects. Narrative driven art can communicate complex concepts and inspire emotional response (Springgay et al. 2005). The narrative techniques embedded within *Staying with the Trouble for Joshua Trees*, are another way that I share my story of entanglement with Joshua trees hoping to encourage other people to pay attention to these systems. This approach provides an in-road for connectivity thinking for myself and others while

remaining open for other interpretations and experiences. By engaging with the other through the visual and narrative format, I provide scaffolding that allows participants to build connections to the research and its implications, and to reckon with the selfishness, negligence, and systems of oppression that have resulted in much turning away as opposed to engaging with the work that needs to be done. This form of storytelling is an important form of witness and an engagement with the multitudes of species embedded within ecological systems, a celebration of their important diversity, and a way to draw other people into new relationships and accountabilities (Van Dooren et al. 2016). Through better understanding of our connections to species and the environment we can become accountable for the overwhelming species losses in which we are complicit.

I leverage the Joshua tree as an iconic image in my narrative to engage others in the emotional impacts of species loss. An ‘icon’ refers to a tangible entity that a viewer can relate to and is unique in that it can overcome language barriers and directly communicate meaning. Iconic imagery has been shown to be a powerful tool for shaping public conversation, empathy and eco-literacy (Gustafsson et al. 2015). Deeper exploring of public engagement with icons involves understanding how symbols gain meaning and how those meanings are rooted in culture and experience (Sassoon and Caur 1997). Some work has identified the importance of icon proximity – that is the distance from where that icon resides to that of the target public – as key for generating public impact, and found a greater emotive response to iconography that was localized to the

participants home area (O'Neill et al. 1991). In my research, I have found from a mixed-methods analysis of three case studies, a strong emotional response from participants who engaged with my research when they had local ties to the organism and icon used (Harrower 2018). This suggests that the ability to ignite public response lies in selecting imagery that has a close proximity to the public you are looking to engage. Utilizing symbols that are already linked to the local personal narrative can enhance the building of eco-literacy and empathy through methods of constructivist learning. While the artful techniques that I describe could be used to approach non-iconic species representation, to generate a strong audience connection to the work would require a clear narrative connecting an emotional story to the work.

In *Staying with the Trouble for Joshua Trees*, I create multiple channels for diverse participants to engage emotionally with the Joshua tree system while constructing knowledge. In this way the participant is not a passive recipient of knowledge but rather constructing it on an individual level (Fosnot 1996). I generate this form of knowledge both through the collaborative interdisciplinary art creation process, as well as through the power of local iconography and interacting with the audience during an exhibition. As knowledge is the construct of the learner, by providing multiple points of access via online engagement, in person participation, and multimedia art making, people can build their own connections and theories and develop greater levels of understanding and interspecies empathy. These multiple interactive components throughout the art making and viewing process have been

shown to be crucial for stimulating constructivist learning (Flexer 1984, Ramey-Gassert 1994, Novtz 2001). This constructivist approach gets at concept development and deep understanding as the focus rather than learning of facts, behaviors or skills (Fosnot 1996, Chaille 2003) which can support community wide behavioral shifts (Trent 2000).

By engaging others with a multispecies and interdisciplinary lens I find pathways for how art can contribute to meaning making and support better understanding of the complexities of Joshua tree species interactions and the human role of species loss. I further expand this to explore how narrative driven art that is informed by a science practice can affect empathy and provide useful ways to understand the complexity of these interactions and our shared entanglements.

### ***Project Overview of Staying with the Trouble for Joshua Trees***

*Staying with the Trouble for Joshua Trees* is a social practice artwork of alternative communication and meaning seeking, offering new possibilities through interdisciplinary and liminal spaces to understand ecosystems and generate connection. It is a provocation to pay attention to and care for the Joshua tree system. As Haraway notes, “Caring means becoming subject to the unsettling obligation of curiosity, which requires knowing more at the end of the day than at the beginning.” (Haraway 2013). I have a unique ability to pay attention to and care for my system through interdisciplinary means, with a long professional history working within and between both art and science disciplines. As a scientist and an

artist I bring these skills forward to advocate for communication and opportunities between the art and science fields.

As a scientist I am interested in the deep history that produces living form and requisite species interactions, as well as the human history that both cares for and ravages our planets resources. In many ways, my art practice is a response to the reductionist nature of science which attempts objective observation aimed at understanding how everything comes together. As a scientist, I follow the rigorous framework of my discipline to remove myself and as many factors as possible to focus on the various mechanistic elements of the system so I can hypothesize the key functions of Joshua tree existence, quantify and define scientific fact, and hopefully arrive at some management guidelines and a greater understanding of the system then we had before. The art I make in reaction to and collaboration with my science functions in part as a way to insert myself back into the process; to reflect and reckon with the fact that we are deeply connected and embedded within these systems (Soule and Lease 1995). This work thus communicates an experience combining a visceral and intellectual understanding of the system. It provides a way to reflect on my otherness as a being deeply engaged in my own symbiotic processes from the microbiomes that co-exists throughout my body to the social communities I engage in and the ecosystems that I value and depend on.

*Staying with the Trouble for Joshua Trees* is an integrated artistic, communicative, participatory and educational social practice work - an attempt to develop new understandings for the Joshua tree nature-culture system, rather than

reorganizing existing knowledge. It is an invitation to participate in Joshua tree *knowing*, through an interdisciplinary fusion that takes place across three core projects. The first of these projects *Soil Symbiosis*, is a conceptually driven and medium-pushing painting experiment to explore the tension existing in Joshua tree and fungal symbiosis. Drawing on materials gathered from my study organisms and incorporating my ecological data into the composition, this work is a window into the beauty and complexity of symbiosis. Paintings from this work go on to become the backdrops in the second project, *A Joshua Tree Love Story*. This collaborative stop-motion animation draws on my experiences doing research in Joshua Tree National Park to demystify the science process, while providing an emotional narrative to engage viewers on themes of climate change, species loss, and mothering. Finally, I will discuss *Hey Jtree*, a mock online dating site and curatorial art project where participants can interact with the Joshua trees from my field sites through science, art, and play.

### ***Soil Symbiosis***

Through the experimental painting process of *Soil Symbiosis*, I explore the relationships between aesthetic and ecological systems. I do this by immersing myself in the morphology and science findings of the Joshua tree and fungal symbiosis and then creating systems of aesthetics that drive the art creation process, encoding the data into the work. This process influences my understanding of the system through these explorations by providing a different lens with which to

consider it - the artwork thus functions as both a mirror and a looking glass. The process of creating these systems of aesthetics to describe the symbiosis provides another conceptual tool and way for me to understand the complexity of these symbiotic interactions. This assists in my ability to form a narrative which further informs my science discussions and analysis, also leading to new ideas and future directions. In these ways, the outcomes of *Soil Symbiosis* have had both intended and surprising outcomes. While aiming to communicate the complexity and beauty of Joshua tree fungal symbiosis to others, I also discovered the unexpected benefit of an improved ability to find connections and an enhanced capacity to form my results into a science narrative (e.g. by identifying the key messages and story within my work I was able to distill complex amounts of information and target the most important components to highlight). The act of creating the work also functions as a meditational tool for me to process the emotional weight of environmental work.

With *Soil Symbiosis*, I am interested in experimenting with materials and techniques, as well as the deep content and narrative that contributes to the story driving the work. Like Georgia O'Keefe, I find an interplay between realism and abstraction of the subjects in my work, which reference small and large forms. By highlighting landscape elements, underground worlds, and microscopic imagery, I draw attention to the unique outcomes of these symbioses, provoking emotional and psychological responses from the viewer.

I create and employ rule-based methodologies that code my science discoveries into the artwork creation and include elements of my study organisms into the process, such as Joshua tree fibers, Joshua tree seed oil, and the spines as painting tools (Fig 4.1). I work to match the colors and shapes in the paintings to data on soil nutrients, temperatures, fungal species and tree distributions that I discover through my ecological research (Table 4.1). For example, paintings representing species interactions at the lowest elevation sites have warmer tones than high elevation sites. High pH soil is represented with the addition of blues, while for low pH I use red based tones. I tear into and re-stitch the canvas using Joshua tree fibers to create symbolic representations of the tension inherent to symbiotic species interactions, also evoking the tensions between ecosystems and humanity (Fig 4.2). The use of strings also references Haraway's "string figures" - weaving stories with the looping of threads that create patterns on our vulnerable and wounded earth, a bringing together of multispecies stories that relay connections and tell multispecies stories that contribute to our multispecies worlding (Haraway 2016). The numbers of tears created in the canvas, colors used, and stitching patterns of the interactions change in response to the varying densities and identities of fungal species associating with Joshua trees across the landscape (Table 4.1). These fungal associations exist on a spectrum from beneficial to parasitic depending on the species involved and the environmental conditions where it occurs which is represented through patterns of stitching on the canvas.



My painting process is also highly technical and experimental. I manipulate the properties of paint using fluid dynamics through changing paint density and with novel application techniques. I extract seed oil from Joshua tree seeds using a press, and mix very small amounts of that into different colors of paint which are then applied to the canvas in varying amounts that correspond to abiotic conditions from my field sites. I thin the paint using acrylic mediums and water (all in precise amounts for each pigment that is based on detailed methodologies that I have fine-tuned) and then layer with higher density pigments on the top. By swiping across this layered painting with different tools (Joshua tree spines, acetate, fabric) the layers of paint move across and into each other, creating the organic rolling effects and cellular structures that are reminiscent of topography in Joshua tree soils and the patterned branching of mycelial and root structures (Video of technique accessible at: <https://www.juniperharrower.com/symbiosis>). These forms also recall microscopic views of plant morphology and mycorrhizal fungal structures within plant cells (Fig 4.3).

This scientific painting process requires detailed note taking to recreate the desired textures and effects. By choosing to encode my science findings into stories that are represented in the work across the climate gradient, I am forced to closely consider the many different interacting components and their relationships to each other. Referencing the works of conceptual artist Charles Gaines' systems approach to painting which creates aesthetic, rule based works that attempt to move beyond the artist's personal subjectivity (Shaked 2017), my data translation becomes

another graphical tool for conveying information that allows for greater understanding and interpretation of the data by a more diverse audience.

Once the complexity of the symbiosis has been described, many of the paintings then have Joshua tree forests composed and painted into the foreground, inspired by actual trees from my fields sites (Fig 4.4). Tree sizes and densities represent demographic data that corresponds to their location on the climate gradient. I draw on the iconic imagery of the Joshua tree to bring attention to the issues Joshua trees face with the changing climate, and also for their unique and striking form. While diverse in appearance and approach, these works share conceptual threads critical to the work of Anselm Kiefer. Like Kiefer I utilize iconography to focus attention on the issues facing Joshua trees, but also to ask the viewer to consider the use of iconic symbolism. Does losing an organism matter less if it does not have the cultural significance that an organism the Joshua tree does? Why are some lives valued more or less than others? Similar to Anselm, I incorporate unconventional natural materials into my paintings, working to create a balance between spontaneity and meticulous planning to achieve the finished works, however my work differs from Anselm in that I use my own science research findings to guide aesthetic decisions.

There are also important unplanned aesthetic moments where new textures and unintended qualities appear in the work, thus becoming a collaboration with nature, the environment, and the current moment. This responsiveness references how organisms relate to one another within their environments, giving rise to form

and function. In these ways I co-create with the Joshua tree, using the materials from my study organisms as symbolic impact. Through these poetics of space and juxtapositions of controlled chaos, I find an interplay between realism and abstraction, parasitism and mutualism, until I reach a final resolution on the canvas.

I have been experimentally evolving this artform since early 2016. In an art exhibition on October 10<sup>th</sup>, 2018, 15 paintings of various sizes were exhibited at Joshua Tree Living Arts, arranged along a climate gradient within the gallery. I accompanied the artwork with a 20 minute research talk describing the science that informs the compositions and shared my art making process. Reproductions of paintings were also included in a visual library used by interpretive rangers at Joshua Tree National Park as part of my artist-scientist residency through iSWOOP (interpreters and scientists working on our parks), a program dedicated to connecting the public to research that is happening in the national parks through innovative visual tools. The inclusion of the paintings provided another tool for the rangers to use to engage the public. Paintings from *Soil Symbiosis* also go on to become back drops in my second project *A Joshua Tree Love Story*.

### ***A Joshua Tree Love Story***

*A Joshua Tree Love Story* (2019) is a stop motion animation addressing the loss of Joshua trees and their symbionts in Joshua Tree National Park (film accessible at: <https://www.juniperharrower.com/joshua-tree-stop-motion-story>). This animation utilizes aesthetic imagery and music based on a narrative that is

informed by ecological research and place-based connection. With this work I hoped to demystify the research process and what scientists look like – in this case a young mother with her baby doing field research. I intended to provide a narrative driven story that connects the emotional impact of species loss to science research and introduces possible solutions along with their complexities and potential issues. While the project sought to foster an understanding of the desert ecosystems ecologically important participants, it also attempts to be non-didactic by using an emotional musical score, thus allowing viewers to construct their own response to the narrative driven imagery and build a personal connection to the work.

To generate an emotional connection to the impact of species loss, the film portrays Joshua tree loss using illustrated and animated imagery and follows the character of a scientist and mother doing field research with her young son (based on the real life story of me and my son). The narrative follows me and my baby on a research expedition across my field sites in JTNP to investigate if the rapidly changing climate is having an impact on tree survival, and to explore the intricacies of the species interactions that the tree depends on. Tiny yucca moths (as large stop motion puppets) appear in magnified detail (Fig 4.5). Viewers experience the moths stuffing pollen gathered from one blossom into the ovary of another flower and then laying their eggs inside – an important ecological behavior that is very difficult to witness in the field. Belowground, the microscopic web of fungal interactions in the Joshua tree root system comes alive with clay and glass beads, symbolizing nutrient transfer from the soil via the fungi to the plant, in exchange for plant sugars.

Viewers see the Joshua trees across the set wither and die, following the predictions that the trees will be locally extinct from their namesake park within 100 years (Barrows and Murphy-Mariscal 2012). The impact of the loss is heightened by the parallel aging of the baby into an old man, to emphasize that species loss can occur within a human lifetime.

This project began with an intention to show the animated micro worlds and make the science processes more accessible to a broader audience. After workshopping the idea with the team at iSWOOP through my artist residency, I decided to ground the narrative by connecting the aging of my son to the dying of the trees. In this way I leverage an emotional connection to the child, and we are reminded of the loss that they will see in their lifetime, becoming another tool to evoke empathy and promote understanding. The role of the child goes beyond the mother-son researcher narrative, but further symbolizes our future generations and the importance of promoting a nature connection for our children. Haraway calls upon us to “Make kin, not babies” (Haraway 2016) to remind us that forming empathetic and caring connections to other people and species outside of our tight genealogical circles of kinship, is crucial towards evolving our capacity for more equitable and sustainable societies. Through the child symbology and the researcher-tree relationship, I invite the viewers to consider the future of our shared kin – my child becomes our children, my kinship with the trees signals our need to build relationships with the natural world.

Mid-way through the animation the researcher falls asleep and we get to experience the dream with her. The sci-fi-esque nightmare scape with tarantula robots (evoking artist Marnia Johnston *Paranoia Bugs*, 2005) roaming the desert with Joshua trees on their backs is a nod towards technoscience speculation and commentary on the tendency for societies to look to science to fix things (as exemplified in geo-engineering or biotechnology) as opposed to addressing the underlying issue (limit carbon and restructure industrialized agriculture) (Klein 2015). This nightmare of mobile trees, inspires the researcher to move the trees and their fungal and moth symbionts from the climate change threatened locations up into the nearby surrounding mountains to cooler locations. The dream scene points to how dream logic and metaphor can inspire and lead to epiphanies and references both the creative and science process, in the case here, an epiphany to move the trees. This scene thus introduces the current practice and discussion in ecology of assisted species migrations as a solution to manage climate change induced species loss (McLachlan et al. 2007). This also has important ecological (and in some cases ethical) considerations to address. Namely, that by so directly managing and intervening in ecosystem design we are making choices to value some species over others, which also may result in unintended consequences (parasitism and/or species invasions) in the future locations. Many interdisciplinary scholars argue for the need to consider this as a feasible strategy, as there are no landscapes untouched by human impact and we must embrace the roles of caretaker and designer to promote the kinds of ecosystems that we want to support (Harrison and Harrison 2007).

Which species gets chosen, who does the deciding, and which landscapes, other species, or people are disenfranchised to accomplish those goals all connect back to the importance and need for diverse and equitable policy creation and management strategies (McLachlan et al. 2007).

After moving the trees, the animation flashes forward 90 years later. The trees at the original sites are gone, the mother is gone, and the child is now an old man wistfully reviewing the changed landscape and reminiscing of times past. He makes the journey back to the high elevation where they had moved the trees, to find that the trees and moths are there and thriving. The scene reaches a crescendo as the old man sits against a Joshua tree and moths rise up out of the soils around him signifying that the symbiosis is alive and well. I intended for a variety of interpretations on this ending. One intention was to provide a possibility of hopefulness for the Joshua tree story, a respite from the onslaught of depressing information, which may or may not contribute to “environmental melancholia” and inaction. Psychosocial researcher Renee Lertzman describes environmental melancholia as the collective global ambivalence and grief caused by widespread habitat loss and environmental destruction (Lertzman 2015). I share the story of my research, my connection to desert organisms, my science process, and seek to empower the viewers with a message of hope, inspiring a collective call to action to deal with species loss.

But there is also an undeniable religious quality to the last scene. The purposefully epic and happy moment to celebrate - the trees have survived! The

moths are good, we did it! - over simplifies the difficulties of species management, and also has a “white savior” connotation (suffused with self-righteous and god granted purposes (Cammarota 2011)). It is here that I break scene for the first time and you see the box that contains the animated world, and the hint of the “other”, referencing the afterlife. I do this to prompt the viewer to consider the bigger question of should we be doing this? Who has the right and power to make these kinds of decisions? Where are our priorities and what happens when we manage these landscapes? A growing number of species survival is only possible because of purposeful human attention, maintenance, and care (Rose et al. 2017). I am explicitly drawing attention to this form of nature curating, which means to select and assemble, but which also means to care for, and the decisions we make regarding which organisms will be cared for.

*A Joshua Tree Love Story* involved collaborations with a team of artists to create all of the needed characters, sets, and props. I created a series of photographs for different emotional states for my son and I which were then used to create 20 changeable masks from paper clay, which was sanded and then watercolor painted (Fig 4.6). The dolls were constructed from wire armature, clay, and cloth, and the clothing was replicated from outfits that we wear while doing field research (Fig 4.7). We created 7 sets for the animation that were built in the style of natural history museum dioramas to reference that history of science communication, and also to use in future exhibitions. Backdrops of the underground scenes were created using my experimental painting techniques described in *Soil Symbiosis*. The large



scale moth puppet and Joshua tree flower were built out of wire, fabric, feathers, paint, glue, tape, and clay (Fig 4.5).

*A Joshua Tree Love Story* is animated through a combination of object, puppet, and digital animation techniques combined to reference my research experiences, where inanimate is given meaning through motion. I chose foremost the medium of stop motion to utilize the tangibility and relatability in my animation to real objects. In this way I can also explore the relationship between animation and its potential to evoke audience empathy to better understand how we relate to this form of moving image. Different from 2d animation, stop motion utilizes recognizable materials and objects, and exists within a physical space (Buchan 2013). While not a mirror to lived reality, it is not complete fabrication, but provides metaphorical meaning and scaffolding for understanding. This creates a higher potential for relatability and a new experience of connection. An example of the impact of metaphor through animation is found in the Quay brothers' classic animation, "Street of Crocodiles" (1986). The protagonist puppet wanders aimlessly in search of more and more decaying and repurposed items – the puppet is a figure of the dehumanized world. Masters of imbuing the everyday object with life, they create multiple meanings by putting recognizable objects in motion and in reference to each other. In *A Joshua Tree Love Story* I utilize similar techniques. I rely on viewers understanding of the Joshua tree as both an endangered organism that is being studied by the researcher, but also as the iconic Joshua tree, as symbol of the nature/culture disconnect. It relates to nature in that it exists and we associate it with

wildness, but we also ascribe cultural significance to this plant above others even though it is not a “usable” resource other than aesthetic or spiritual one.

With this work I intended to form an empathetic connection to the audience. Here I am relying on the imagination of the viewer to conceive of the characters as beings with relatable traits (Buchan 2007; Buchan 2014). It is through the implied narrative and the animation of objects that the viewer may integrate the animation through their role as active audience participants – thus generating empathy (Papapetros 2012). I additionally accomplished this connection to the audience through crafting detailed facial expressions on each interchangeable mask. The more the viewer can relate to the metaphorical narrative, the stronger the potential impact of the work. Thus the outcome depends on the viewer to complete the illusion and engage with an aesthetic to generate an emotional experience (Buchan 2014). If the perceived animation is constructed as belonging to a relatable world, then the viewer will generate a proximal experience (Grodal 2009). The audience can engage with the moment of suspended disbelief and partake as active emotional participants in the viewing process.

Through thoughtful use of animation theory and techniques, *A Joshua Tree Love Story* brings a unique voice to the issue of climate change and species loss. By triggering an exterior hypothetical world that relates to the personal interior world, I have provided a powerful way for the audience to connect with the narrative of Joshua tree species loss.

An early version of *A Joshua tree love story* was screened at SymbioArtlab (Oakland, CA), following a science talk about the same research to 45 people. During the event, I collected feedback via an anonymous survey (10 questions, close-ended, and 1 open ended question) to gather data that would influence the future direction of the project. With this feedback we learned that art can connect with people emotionally, and that the animation was most effective when paired with a science talk (Harrower et al. 2018). This led to the creation of a second shorter and complementary stop motion animation *Can You Imagine Joshua Tree National Park Without Any Joshua Trees?* (2018) (accessible at: <https://www.juniperharrower.com/stop-motion-research>) that relies less on metaphor, and instead has a strong science narrative to guide learning. The two animations will be shown together as part of the iSWOOP visual library at Joshua Tree National Park, screened at the park visitor center and the Indian Cove Amphitheatre. With the help of Marjie McGraw, I have also developed a Common Core ecology and art lesson plan for educators to use in conjunction with this animation (Available online at: <https://www.juniperharrower.com/joshua-tree-stop-motion-story>).

### ***Hey Jtree***

*Hey Jtree* is an interdisciplinary social practice and curatorial art project presented in three media: a mock “online dating” website to meet Joshua trees, collaborative art created for individual trees, and a series of site specific interactions

with the trees. *Hey Jtree* invites people to fall in love with Joshua trees from my long-term ecological research sites and is a response to *Soil Symbiosis* and *A Joshua Tree Love Story* intended to create participatory art that facilitates widespread public engagement. Building on 6 years of research in JTNP, the interactive website [www.HeyJtree.com](http://www.HeyJtree.com) features anthropomorphized profile descriptions for 16 charismatic trees from my field sites, and curated selections of multimedia art from invited artists (Fig 4.8). The ecological findings are displayed for each tree, including directions for a scavenger hunt to visit the tree accompanied by a portable audio ritual experience guiding the encounter. Encouraging widespread public engagement, people can send love letters to their favorite tree through the website, participate in targeted eco-actions and eco-data collection through Instagram (@HeyJtree #HeyJtree) and iNaturalist (project name HeyJtree).

As a curatorial art project and an installation, *Hey Jtree* is in dialogue with the history of works that incorporate nature based imagery, social practice and place based art, and art addressing issues of species loss due to climate change. Like Kirksey's *Multispecies Salon*, and Jeremijenko's *Environmental Health Clinic*, I am interested in finding innovative and interdisciplinary tools to disrupt the damaging ways that we connect with the environment, and to create opportunities for diverse participation and the development of new knowledge. Through the participatory framework of *Hey Jtree*, I invite participants to reconstruct their connection to nature through the playful reframing of a dating site. The dating site functions as an in-road and invitation for meaning making to create an open and accessible artwork.

By inviting the audience to co-create the work, I activate the potential of art to contribute to paradigm shifts through constructing new metaphors and personal connections. We construct many of our understandings metaphorically (Lakoff and Johnson 1980), thus artistic metaphors are powerful for embodying and communicating important issues, and give a shared collective power for social construction (Dissanayake 1988).

With *Hey Jtree* I invite people to care for and explicitly participate in the Joshua tree system, utilizing the frameworks from creative placemaking. Creative placemaking is an arts-based community development tool to connect stakeholders through issues that impact local livelihoods, building community identity and belonging (Giesecking 2014; DeLaPena 2017). Artists engage in creative placemaking by utilizing symbols and narratives of the nature/culture interface to actively engage the public on current social and environmental issues. This practice values diversity and equity and can provide access to groups often excluded from public processes (Jackson 2011). Promoting diverse inclusion and relationships to natural environments within a community is important to demonstrate the interconnectedness between nature and society, and for developing equitable and sustainable solutions (DeLaPena 2017). This is increasingly important as we respond to the effects of demographic shifts and social inequity under climate change.

*Hey Jtree* is an innovative approach to content and form that functions in part by creating networks of influence. This is achieved through highlighting

ecological and social connectivity by utilizing internet technology. Through accessing tech and social trends to broaden social engagement and deepen empathy, I am co-opting the tools that so often divide us from our environments. This transmedia artwork unfolds over time, inviting audience/participants to express their collective love for Joshua trees through social media and on-site experiences, while also providing a space to grieve current and future tree loss. The hands-on workshops provide unique site-specific discourse while eco-actions facilitate public environmental responsibility for caretaking our natural resources.

By empowering the public to consider what is happening to Joshua trees and express their love individually and collectively for the trees, I provide a way for meaningful engagement with ecological research. By including the audience in the process of developing the knowledge, the audience is not a passive viewer but engages with the art process and can become changed by the work. This process of engagement became significant to this work, and echoes cultural studies scholar Alexander Wilson in that humans and nature construct one another (Wilson 1991). These contributions add to my interpretation of the ecological system to inspire and motivate other connections and interpretations and new ways of knowing.

My target audiences are the diverse publics visiting our parks, the local communities of Joshua tree, and art/science scholarly communities. National Parks have low rates of visitation by minority groups, with limited initiatives to address this gap. *Hey Jtree* engages diverse groups of people, highlighting contributions by ethnic minorities and LGBTQ artists. Promoting diverse

inclusion and relationships to natural environments across communities is important to demonstrate the interconnectedness between nature and society and to develop equitable and sustainable solutions.

As of March 2019, *Hey Jtree* is shared as part of the interpretive nature talks at JTNP. I share this work through online platforms, public art events and lectures (Fig 4.9), and through guided place-based art events at my field sites (Fig 4.10) to promote and encourage widespread participation in this work. This work was featured on KCET artbound as part of the Warhol funded Mojave Project (<http://mojaveproject.org/dispatches-item/the-joshua-tree-myth-mutualism-and-survival/>) and exhibited at the 2018 Joshua Tree Music and Art Festival, in the rural desert community of Joshua Tree, to educate the public about Joshua tree ecology and climate change. This included an educational and ritualized “meeting of the trees” that I led for 65 people that utilized props to “become a Joshua tree” and explain the trees’ symbiotic interactions and how they may change with climate. Using guided imagery and performance art, I led an audience to become Joshua trees and introduced them to Joshua tree ecology through the act of physically embodying a tree and learning about its functions. I created a “moth mask” to act out pollination between audience members pretending to be trees and utilized a large “fungal web” prop to connect participants and demonstrate the complexities of the underground tree and fungal symbiosis. Participants then made ink prints from hand-carved silhouettes of the Joshua trees (created by invited artists) that they could take home and reference to find their tree on the

*Hey Jtree* website and learn more, as well as submit a love letter to their tree (Fig 4.11). Feedback collected from surveys and a focus group from this project suggested that art based on ecological work can have emotional and behavioral impacts especially when focused on local issues (Harrower et al. 2018). Generating a local connection to local issues through art is a powerful way to activate feelings of responsibility and kinship (Jokela 2007; Lippard 1998; Harrower et al. 2018). By connecting complex concepts to locally important organisms we activate previous knowledge and empathy, with a high chance for behavioral changes or paradigm shifts (Lippard 1998; Anderson and Guyas 2012).

The project was also shared as part of my artist residency at JTNP and through the Every Kid Outdoors Act – legislation created so that every 4<sup>th</sup> grader in the US has free access to our National Parks with a participatory art or science component. Prior to meeting with the school group, the students watched my stop motion animations and used a modified version of my Joshua tree curriculum to prepare for the field trip. In February 2019, I led a group of 4<sup>th</sup> graders from Morongo Valley Elementary school to meet Joshua trees from my field sites, participate in the educational ritual “meeting of the trees” described previously, create drawings, and develop names and personalities for their trees (Fig 4.12). Working with them at their classroom, we created stencils that were used to print a Joshua tree class forest (Fig 4.13). This work was a modification on the *Hey Jtree* project, framing the work as a “pen-pal” site as opposed to a dating site to



make it accessible for the young students. I felt that it was critical to bring this work to the students living here so they could learn about and engage with the organisms, histories and cultures that form their local ecosystems.

The ritual guided tree meeting that came out of these two participatory experiences become a component of how I work with artists at my field sites who create the writings and music for the different trees. By creating a ceremony space I focus attention and create a new possibility for learning or paradigm shifts to occur (Grimes 1995; Pryer 2002). Ceremonies can transcend the individual and resonate beyond the human realm as an act of reverence that brings meaning and effect to the present moment (Trinh Minh-ha 2005). This technique encourages pause from the frantically paced world into a state of enhanced consciousness where participants can learn science and interact differently with the Joshua tree. Participants reported feeling a new connection to the trees and an enhanced ability to make more meaningful art (Harrower et al. 2018) (An inquiry process that generates new insights and paradigm shifts is most effective at generating insights when it induces an emotional response (Milton 2002)). Through these different opportunities for engagement, I activate multiple senses – the visual, aesthetic, intellectual and auditory – to create a playful, place-based and emotional experience that facilitates new ways for considering and engaging with the trees.

Site-specific artworks encourage processes and outcomes marked by social engagements that change conventional relationships between artists, artwork and audiences (Doherty et al. 2004). The artists contributing to *Hey Jtree* visit and engage with the trees as a site-specific artwork. Participants can bring a recording of the tree ritual and the musical soundtrack to meet and engage with the trees at each tree's location in the national park and then share a picture or response with their tree through an online platform. Rather than simply interpreting or viewing the art, the audience becomes active participants and engaged in a large-scale community artwork connecting to each other and nature in new ways (Bourriaud 2004). The different ways that we connect to each other and back to nature matter and have great implications and consequences for the entire system (Tsing 2015). These consequences are realized in our histories, politics, and colonizations, which consequently shape the world we exist in.

### ***Conclusions***

By approaching my study system through art and science, I have developed a deeper understanding of the form and function of the Joshua tree system that I am able to share with others. *Staying With the Trouble for Joshua Trees* is one way that I respond to the issues of species loss and provide a bridge to the ecology which informs my practice. This is also how I invite others to participate and share their concern and support for Joshua trees, and move the scope of my practice from the micro to the macro. This work was communicated across multiple platforms reaching a diverse audience with the help of numerous collaborators.

I will continue to build on these projects and seek opportunities to share with the public. I am in conversation with galleries and educational facilities and this will likely be shown at the Institute of Contemporary Art in San Jose, the Randall Museum of Science Nature and the Arts in San Francisco, and to launch the new opening of the gallery and visitors center at Joshua Tree National Park. *A Joshua Tree Love Story* will be screened at the Museum of Art and History in November 2019, and at future locations as we are just beginning to submit to film festivals. One of the main diorama sets from this film will be exhibited at the MOXI – the Wolf Museum of Exploration and Innovation in Santa Barbara along with another animation that I have created inspired by algae in desert soils.

I will continue to develop *Soil Symbiosis*, expanding the canvas size and also complicating the composition by including images of the moth, tree, and seed pods in representative proportions that correspond to data from my research climate gradient. I am also experimenting with making paint from ground soils as opposed to using acrylic, and discovering how to get the textures that replicate my previous acrylic experiments representing soilscares.

I will continue to share *Hey JTree* at science and art conferences, host public printmaking events, exhibit with cultural spaces, run outreach at public schools, collaborate with park rangers and local organizations. I will continue to engage artist responses to the Joshua tree narrative and will generate momentum through Instagram and iNaturalist platforms which allows widespread contributions to this project and enlists the public as witnesses and citizen science/artists helping to

collect ecological and artistic data. Through this I hope to create socially relevant art, build interdisciplinary art/science theory, and positively impact social and ecological systems.

Through *Staying With the Trouble for Joshua Trees*, I share my work and traverse scales of belonging, from local to global levels to foster greater ecological awareness of our multispecies entanglements. By elevating public awareness about Joshua tree ecology through inspired artworks I have found that I can increase public knowledge and the desire for involvement with conservation issues which will hopefully lead to more environmentally supportive policies and personal behavior shifts.

I have found recurring themes through my interdisciplinary work, namely that an arts practice is both a form of inquiry-based research and a tool for meaning making from ecological research. My work has demonstrated that narrative through art can convey complex concepts and inspire emotional response, promoting equity and diversity in ecological and cultural systems. Artists can act as agents of change by advocating for communities and organisms not represented by economic interests or political parties and through developing new ways to communicate the complex nature-culture relationship.

Connecting my research to art has given me a powerful way to process my ecological research, provided me with continued inspiration across the disciplines I work in, and greatly assisted with my ability to impact change as an ecologist. Through empowering myself and others by engaging with this work, I foster a sense

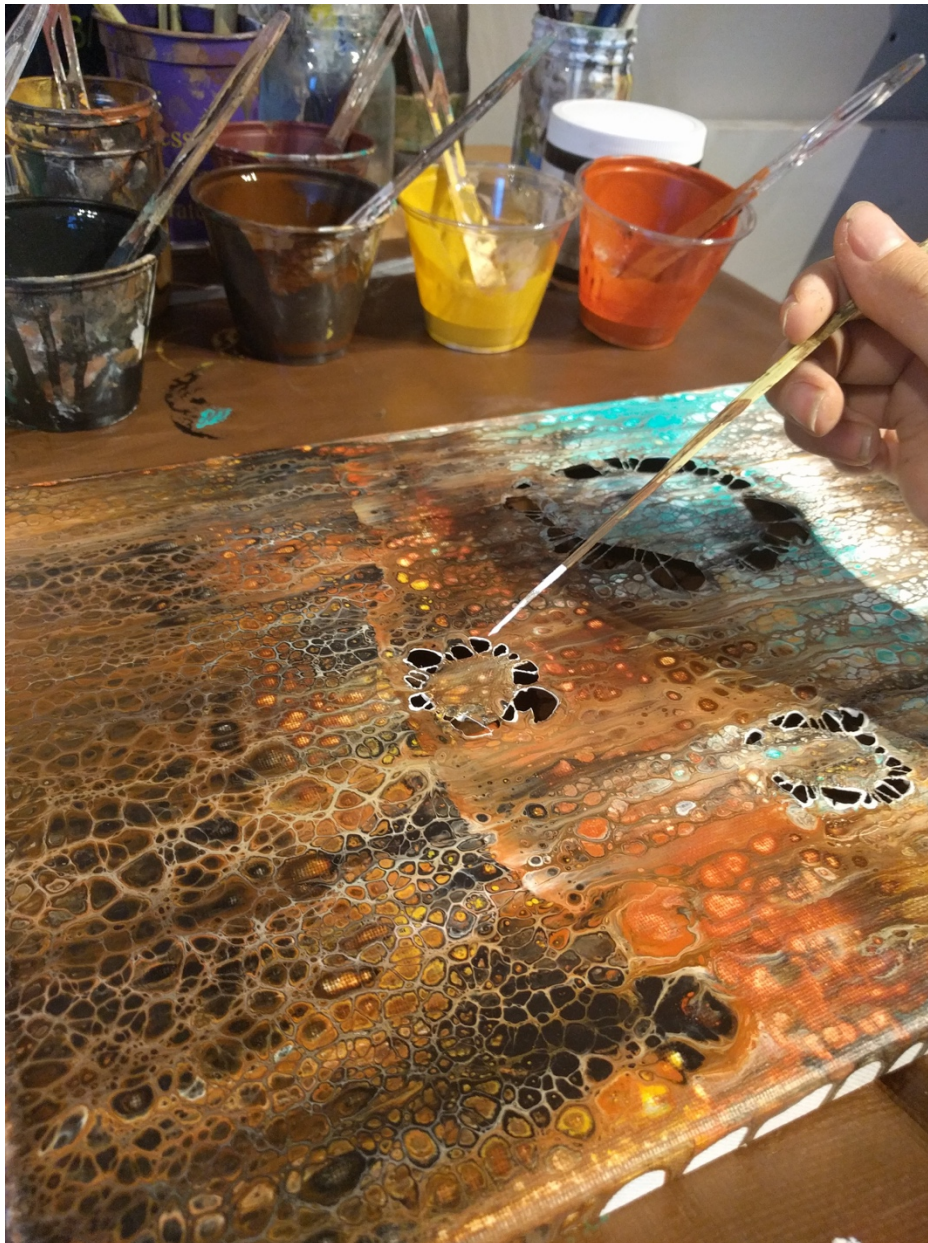
of agency for advancing multispecies justice. With the increased impacts humans are having on our resources and planet, we need diverse thinkers who can communicate across disciplines and seek equitable solutions to effectively meet the challenges of a complex social-ecological system.

## Tables

**Table 4.1 Ecological data translated into instructions for *Soil Symbiosis* paintings.**

<b>Elevation</b>	<b>Low (1004-1114m)</b>	<b>Med (1240-1494m)</b>	<b>High (1625-2212m)</b>
<b>Canvas tearing by AMF colonization</b>	High AMF colonization, 5-6 tears signifying interaction	Med AMF colonization, 4 tears signifying interaction	Low colonization, 2-3 tears signifying interaction
<b>pH</b>	High pH (basic) - use blues in small quantity	Medium pH - use green	Low pH (acidic) - use reds in small quantity
<b>Weather and colored ground</b>	Warm and dry - warmest colored ground	Moderate temp - yellow orange colored ground	Cold and wet- blue colored ground
<b>Tree distribution</b>	Low numbers of trees, short	Lots of trees, many tall	Low numbers of trees, many short
<b>Moths</b>	No moths, no pods (to few as you move up in elevation), few flowers.	Many moths and pods and flowers	No moths, no pods (few as you move down in elevation), few flowers
<b>Seeds</b>	High numbers of white seeds, less black seeds eaten	High number of black seeds, more black seeds eaten	High number of white seeds, less black seeds eaten
<b>Key Fungal Species</b>	Gigasporaceae - large extraradical biomass, robust densely aggregate fungi. Lots of white fungal structures done with swiping. Stitching is away from symbiotic tear (circle in middle). Can also paint microscopic images onto paper that goes behind tears to symbolize the diff AMF in each.	Glomeraceae - most thorough colonizers, majority of fungal mass inside the roots - moderate amount of white swiping. Stitching is extensive within the symbiotic tear. Circle offset.	Aculosporaceae - low hyphal biomass (intra and extra cellular), diffuse delicate hyphae - Low amount of white swiping. Very delicate and thin string for the stitching. No circle within.
<b>Symbiosis over time</b>	Early parasitizing, then better than the others resulting in largest, and most nutrients in plant tissue at 9 months - show early images with small seedlings, lots of roots, eventually with the biggest seedlings and biggest roots.	Better than control, early images have medium seedlings medium roots.	Better than control, early images have medium seedlings medium roots.

## Figures



**Figure 4.1 Conceptual experimental painting.** This work is created by coding Joshua tree ecological research data (pH, nutrients, temperature, soil moisture, tree density and fungal species) as well as the study organisms into the process, such as Joshua tree fibers, Joshua tree seed oil, and the spines as painting tools.



**Figure 4.2** Symbolic painted representations of the tension inherent to symbiotic species interactions in the Joshua tree/fungal symbiosis. This tension can exist on a spectrum from mutualism to parasitism with impacts on Joshua tree functioning. This painting from the collection *Soil Symbiosis*, corresponds to data from the low elevation sampling sites, and contains warm colors, high mycorrhizal fungal species density, and a high level of extra-radicle hyphae.

Title: Low Elevation Mycorrhizal Fungi

Medium: Acrylic paint, Joshua tree fibers, Joshua tree oil, soap and alcohol.

24"x36"





**Figure 4.3 *Soil Symbiosis* painting representing mid elevation soil and extra-radicle hyphae.** Textures also evoke microscopic imagery and plant xylem/phloem.  
Title: Mid Elevation Soil Fungi  
Medium: Acrylic paint, Joshua tree oil, soap and alcohol.  
18"x24"



**Figure 4.4 Conceptual soil/fungal painting from *Soil Symbiosis* with Joshua tree forests inspired by actual trees from the mid elevation sites.** Tree sizes are relative and densities represent demographic data that corresponds to their location on the climate gradient.  
Title: Mid Elevation Soil Fungi with Trees  
Medium: Acrylic paint, Joshua tree oil, soap and alcohol.



**Figure 4.5 Yucca moth and Joshua tree flower stop-motion puppets from *Joshua Tree Love Story*.**

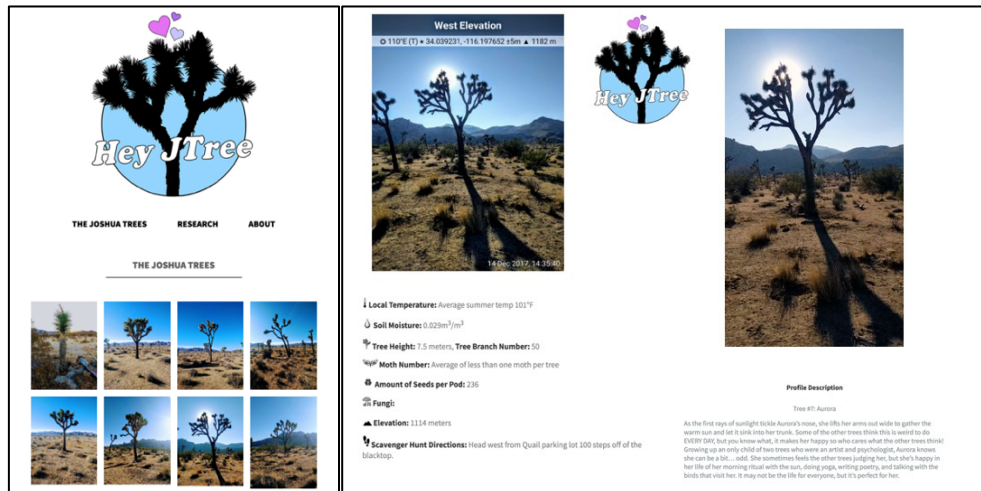
Medium: Upcycled foam, wire, cloth, felt, feathers, hot glue and acrylic paint.



**Figure 4.6 Paper clay masks based on photos for *Joshua Tree Love Story*.**  
Materials: Paper clay, watercolor, ribbon



**Figure 4.7 Animation set and dolls from *Joshua Tree Love Story*.** This set was built to replicate a field research site in Joshua Tree National Park, and shown here with a doll representation of my character (doing research in the park with my son Jack).  
Materials: Upcycled wine crate, paper, sand, rocks, wire armature, clay, cloth, paint, marker and props



**Figure 4.8** *Hey Jtree* is a social practice and curatorial art project designed as a mock-online dating site to meet Joshua trees from my field sites in Joshua Tree National Park. The interactive website [www.HeyJtree.com](http://www.HeyJtree.com) features anthropomorphized profile descriptions, ecological data, and a scavenger hunt for 16 charismatic trees from her field sites, including curated selections of multimedia art from invited artists. To encourage widespread public engagement, people can send love letters to their favorite tree through the website, participate in targeted eco-actions and eco-data collection through Instagram (@HeyJtree #HeyJtree) and iNaturalist (project name HeyJtree).



**Figure 4.9** *Hey Jtree* community education and participatory art session in Joshua Tree, CA, during the event “This Land is Your Land”. There I shared Joshua tree ecology with a group of participants, followed by a printmaking session.



**Figure 4.10 Place-based experimental art-science as part of the *Hey Jtree* project.** Here I explain the ecology of Joshua tree symbiosis to local participating artists, which was featured on KCET and the Mojave Project.



**Figure 4.11 *Hey Jtree* printmaking during the Joshua Tree Musical Festival.** After participating in a performance art piece to “become a Joshua tree” participants made prints of their favorite tree to take home, and as motivation to go online and contribute a love letter to their tree on the website [www.heyjtree.com](http://www.heyjtree.com).



**Figure 4.12** *Hey Jtree* participatory art with 4<sup>th</sup> grade students through the “Every Kid Outdoors Act”. In this case the project is framed as a “Pen-Pal” site to meet Joshua trees. Students accompanied me to my field sites where I gave them a lesson in Joshua tree ecology and field illustration. Students then drew their favorite Joshua tree and created a story and name for their tree.



**Figure 4.13** Creating Joshua tree stencils and a class forest with 4<sup>th</sup> grade students after their field visit to Joshua Tree National Park, as part of the *Hey Jtree* project.

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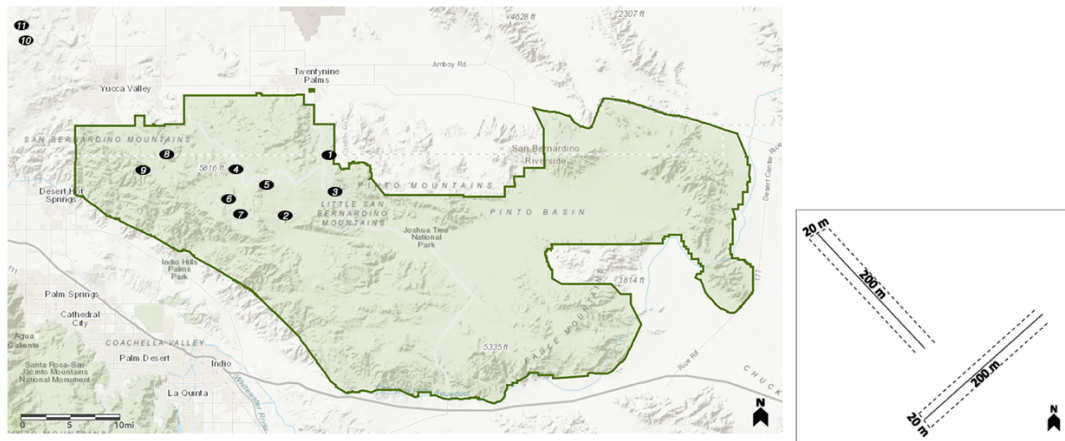


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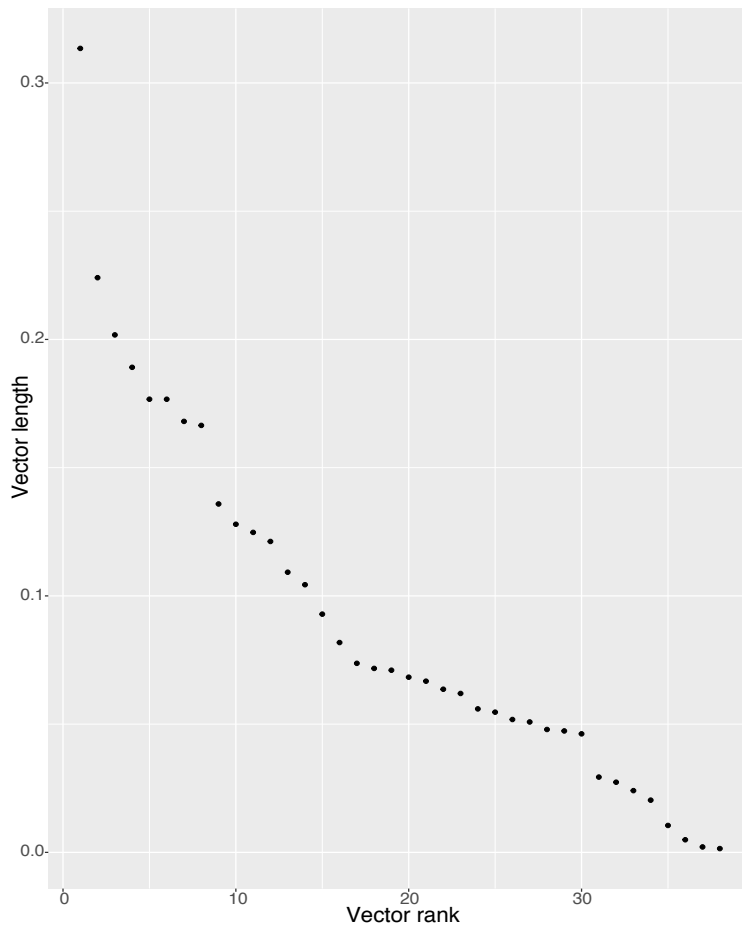
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## Appendices

### Figures



**Figure A1.1** The location of field sites and transect layout at each site that was used in this study. The 11 field sites were located along a 1,200-m elevation gradient (ranging from 1,004 to 2,212 m) in Joshua Tree National Park, in southwestern California, USA (located at 33.8734° N, 115.9010° W), with two additional sites located north west of JTNP to include the northern most point of the local Joshua tree distribution. At each site, we sampled two 20x200-m belt transects randomly positioned and separated by 50 m, and running from south-west to north-east.



**Figure A2.1** Plot of vector rank as a function of vector length used in the Principal Component Analysis of eleven sites, based on the relative abundance of major fungal taxa.