# Species habitat model for Joshua Trees

# in Clark County, NV



Photo by Ken Nussear

Final report for 2013-SWECO-1460D – Submitted to Clark County Desert Conservation Program. March 2018 by Southwest Ecology LLC.



# Joshua tree (Yucca brevifolia brevifolia and Y. b. Jaegeriana)

#### **Species Overview:**

Joshua trees (Yucca brevifolia) are large tree-like succulent plants occupying midto upper-elevational zones of Mojave Desert shrubland communities (McKelvey 1938, Rowlands 1978, Cole et al. 2011). These slow-growing, long-lived vuccas (Comanor and Clark 2000, Gilliland et al. 2006, Esque et al. 2015) can take a long time to recover from disturbances such as fire – depending on post-disturbance environmental conditions (DeFalco et al. 2010). Taxonomically, two species of Joshua trees are gaining acceptance in the literature (Lenz 2007) – Yucca brevifolia and Y. Jaegeriana (see Distribution and Ecology section). Joshua trees are perhaps most famous for their symbiotic relationship with their small moth pollinators (Trelease 1893, Darwin 1874, Smith 2010). Each Joshua tree species requires its own species of *Tegeticula* moth for pollination (Pellmyr and Segreaves 2003), and the moths require the ripening seeds of the Joshua tree as sustenance for their developing larvae (Trelease 1893). Successful reproduction and growth to maturity of Joshua trees requires a remarkable coincidence of appropriate environmental and biological conditions (DeFalco et al. 2010). Joshua trees generally flower and seed unpredictably only every few years (Borchert and DeFalco 2016), a pattern called 'masting.' With sufficient precipitation, some seeds likely survive moth larvae predation, and develop in pithy fruits that do not open on their own (indehiscent), and require rodents or erosion to break up the fruit to free the seeds for dispersal (Waitman et al. 2012). Many of the seeds are consumed by seed-caching rodents and other granivores (Vander Wall et al. 2006). Caches that are forgotten or overlooked by rodents are perfectly placed for Joshua tree seed germination and establishment at about 2 cm deep in the soil (Waitman et al. 2012). Joshua tree seeds have very high germination rates when stored in dry conditions (e.g. >90 percent for several years), however, seeds in the ground deteriorate rapidly after about 18 months, thus there is not really a Joshua tree seed bank for future generations (Reynolds et al. 2012), meaning that the seeds that are present only occasionally are only good for a relatively short period of time. Seeds that germinate during summer rains have a better chance of survival than those germinating after spring rains (Reynolds et al. 2012), because the seedlings of summer germination avoid the harsh summer conditions for their first year of root and shoot development. Predation by herbivores can be as high as 50% in a single year for Joshua trees that are less than 1 m tall, and it may require 30 years for them to reach this stature (Esque et al. 2015). Small Joshua trees (e.g., <1 m tall) benefit by growing beneath other species of plants (e.g. white-bursage - Ambrosia dumosa, blackbrush - Coleogyne ramossisima) known as nurse plants (Brittingham and Walker 2000), and may be protected from herbivores in this way (Chameroy 2015). Joshua trees that are 1 m tall may flower, but it may take as long as 70 years for most Joshua trees to reach reproductive size (Esque et al. 2015). Mortality for adult Joshua trees is usually relatively low e.g., ~2-3% per year or less), but severe drought can cause increased mortality but is more severe on smaller Joshua trees (DeFalco et al. 2010). Drought can also increase herbivory and result in animals such as white-tailed antelope ground squirrels

(Ammospermophilus leucurus), jackrabbits (Lepus californicus), woodrats (Neotoma spp.), and pocket gophers (Thomomys bottae) – apparently as a last resort, and result in high levels of mortality among Joshua trees over large areas (DeFalco et al. 2010). Joshua trees are important to many wildlife species across the Mojave Desert (Miller and Stebbins 1964) and may be considered an umbrella species in this region. Besides the yucca moth, a whole community of may invertebrate species feed on the flowers, fruit, and stems of Joshua trees. The seeds also provide forage for many rodents (e.g. Merriam's kangaroo rats -Dipodomys merriami, white-footed mice Peromyscus leucopus, and woodrats -Neotoma spp.), and insects such as harvester ants (e.g., the rough harvester ant -Pogonomyrmex rugosus). Raptors such as red-tailed hawks (Buteo jamaicensis), great horned owls (Bubo virginianus) use Joshua trees for hunting perches and nesting platforms. Western screech owls (Otus kennicottii), and American kestrel (Falco sparverius) use them as hunting perches or nesting cavities. Burrowing owls (Athene cunicularia) also perch on Joshua trees, but use ground-based burrows for nesting. Northern and gilded flickers (*Colaptes auratus* and *C*. chrysoides; respectively), and ladder-backed woodpeckers (Picoides scalaris) find Joshua trees among the only species they can use to excavate cavities for nesting in the Mojave Desert. Small owls, ash-throated flycatchers (Myiarchis cinarescens), and feral honeybees, secondarily use cavities created by woodpeckers. Perching birds such as the western kingbird (Tyrannus verticalis), loggerhead shrike (Lanius ludovicianus), and cactus wren (Campylorhynchus brunneicappilus) all perch and nest among the Joshua tree branches. The shrike pierces prey species such as lizards, snakes and scorpions on the tips of the sharp Joshua tree leaves as a larder to remove bits of food to feed their young.

# **Species Status**

Joshua trees were petitioned for listing under the Endangered Species Act (1973) by WildEarth Guardians in September 2015 citing five potential listing factors. These factors document a wide array of threats. e.g. habitat loss, climate change, overutilization, and the inadequacy of existing regulating mechanisms to protect populations now and in the future. The petition cites their relatively short dispersal distances and low germination rates (due to limited seed dispersers that impart a large reproductive cost) under a shifting and shrinking habitat as cause for protection. The USFWS still has this petition under consideration with determination expected in FY 2018.

U.S. Fish and Wildlife Service: Not Listed - currently under review/petition U.S. Bureau of Land Management (Nevada): None U.S. Forest Service (Region 4): None State of Nevada (NAC-527): None NV Natural Heritage Program: Sensitive List: Global Rank G4G5, State Rank SNR (Yucca brevifolia); G4G5T3T5, State Rank S4 (*Yucca jaegeriana*) IUCN Red List: Not listed CITES: Not listed

## Range

Joshua trees occur in the southern Mojave Desert of California, northwest Arizona, southwest Utah, and southern Nevada (Rowlands 1978, Cole 2011). Joshua trees are taxonomically subdivided into two distinct species (Lenz 2007), *Yucca brevifolia* – is found primarily in the western Mojave Desert of California; and Lincoln County, Nevada; Y. *jaegeriana* – primarily in Lincoln, Nye and Clark Counties, Nevada; Mohave County, Arizona; and Washington County, Utah. The two subspecies meet in a hybrid zone in Lincoln County, Nevada (Pellmyr and Segreaves 2003, Smith et al. 2010, Godsoe et al. 2009). *Yucca jaegeriana* is the only species known in Clark County, Nevada.

Joshua trees are abundant where they occur in many locations across the Mojave Desert (Cole et al. 2011), and including Clark County, Nevada. While population studies on Joshua trees are ongoing (Esque et al. 2010), there are currently no existing research projects of sufficient scale to determine the population status of either species of Joshua tree across Clark County, Nevada, or similar areas of this size. One previous 30-year demographic study quantified growth rates, but was of insufficient sample size to detect mortality or natality (Comanor and Clark 2000). However, there is concern that the species may be negatively affected by climate change (Cole et al. 2011, Barrows and Murphy-Mariscal 2012). For example, it has been demonstrated that Joshua tree stands in parts of Joshua Tree National Park are not reproducing rapidly enough to keep up with natural declines of the populations. Most concern is for Joshua tree stands occurring at lower elevations and most southerly latitudes. Generally, it has been predicted that species ranges may recede at the more southerly and low elevation trailing edges of their ranges in the northern hemisphere, and that formerly unavailable landscapes at the leading northern and higher elevation edges of their ranges are opened up (Svenning and Sander 2013). This prediction essentially describes how plant species have migrated in response to previous large scale climate change episodes (e.g., during multiple glacial periods). However, this hypothesis has not been demonstrated empirically for Joshua trees and more research is needed on this topic. It has also been hypothesized that as Joshua trees migrate to keep up with the pace of future climate change across the landscape that they will not be able to move fast enough and may perish (Cole et al. 2011). Thus, the current ecological discussion about Joshua trees is being debated vigorously.

#### **Species Habitat Model**

Joshua trees were modeled using three species distribution modeling algorithms, and an ensemble model was created to integrates these models into a single model less influenced by the shortcomings of any one of the methods. Similar patterns of predicted suitability were produced by the three modeling algorithms with a similar range for all three models, but with higher suitability scores predicted by the GAM model followed by the RF model, while the Maxent model tended to have lower predictive scores, but in the same general areas. The consensus model predicted areas of higher habitat suitability in western half of the county on upper bajada slopes and Gold Butte, and the upper Mormon Mesa area (Figure 1).

Performance was high in all models (where AUC scores were in the high 80's and 90's), with the highest overall for the Ensemble and Random Forest models. The Random Forest had the highest performance in all metrics but the Boyce Index, followed by MaxEnt and then GAM models (Table 1). AUC was highest in the RF and Ensemble models, but the Ensemble model had higher BI, than the others, and the second highest in all other scores (Table 1).

The Continuous Boyce Index [CBI] indicated good performance among all but the GAM model, where the rise in values for predicted values had a much lower peak (Figure 3). Standard Errors were generally low among the three modeling algorithms, with low to moderately low error in the Ensemble model throughout the predicted area. Approximated bins for the ensemble model based on the CBI were 0-0.5 unsuitable, 0.5-0.55 marginal, 0.5 to 0.7 suitable, and > 0.7 optimal habitat; with a suggested cutoff threshold near 0.55 (Figure 3), and the threshold value calculated from the AUC analysis for the ensemble model was 0.55 (Table 1).

Performance	GAM	RF	Maxent	Ens	semble
AUC	0.87 0	.98	0.88	(	0.92
BI	0.89 0	.88	0.89	(	0.91
TSS	0.61 0	.88	0.64	(	0.74
Correlation	0.64 0	.86	0.67	(	0.74
Cut-off*	0.59 0	.55	0.42	(	0.55
rate) is highest	hich sum of sensitivity ( ntributions for input variabl			· · ·	
Term		GAM	RF	Max	Average
Winter min temperature		21.9	13.0	17.3	17.4
Summer precipitation		11.9	13.6	18.6	14.7
Summer max temperature		14.8	14.2	7.5	12.2
NDVI maximum		17.5	10.2	12.1	13.3
Temperature range		11.6	9.4	13.7	11.6
Surface texture (ATI)		3.1	9.5	4.9	5.8
Slope		<b>F</b> 0	7.3	7.6	6.9
		5.9	/.3	7.0	0.9
Roughness (T	RI)	0.0	7.7	10.8	6.2
Roughness (T Soil rockiness	,				
0 (	index	0.0	7.7	10.8	6.2
Soil rockiness Winter precip	index	0.0 3.2	7.7 6.1	10.8 7.5	6.2 5.6

Table 1. Model performance values for Joshua Tree models.

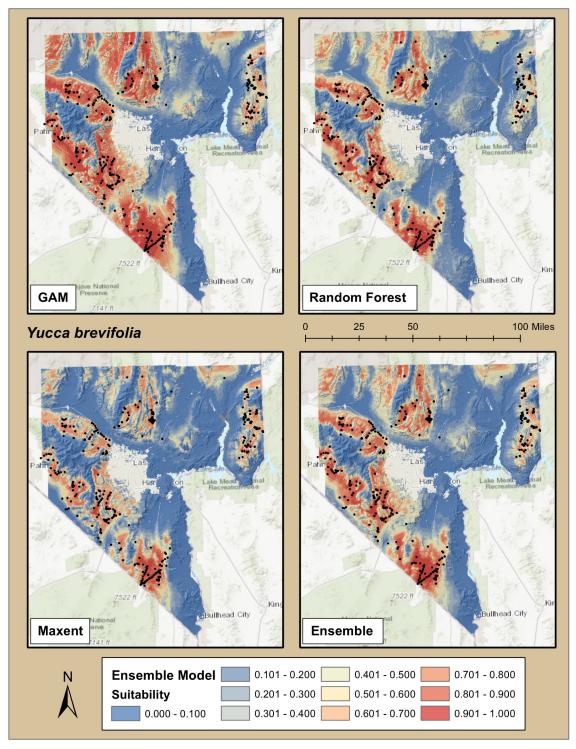


Figure 1. SDM maps for *Yucca brevifolia* for each of three modeling algorithms used (GAM - upper left, Random Forest - upper right, Maxent - lower left), and an ensemble model averaging the three (Lower Right).

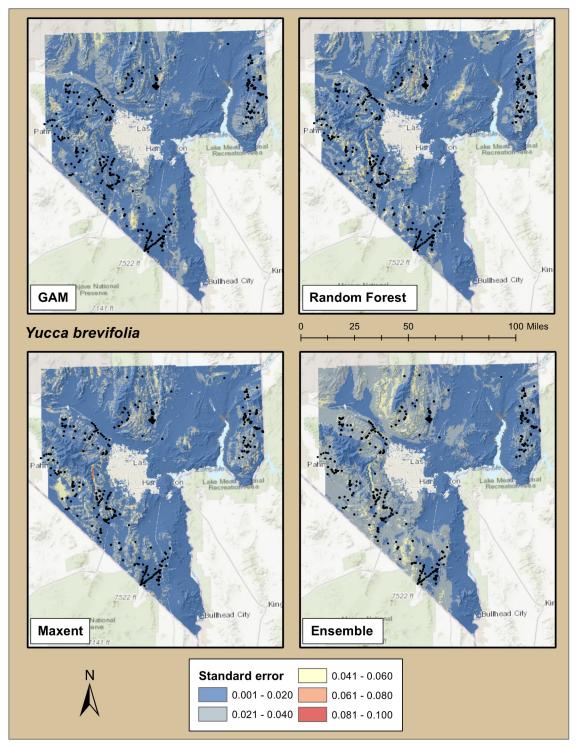


Figure 2. Standard error maps for *Yucca brevifolia* models for each of three modeling algorithms used (GAM - upper left, Random Forest - upper right, Maxent - lower left), and an Ensemble model averaging the previous three (Lower Right).

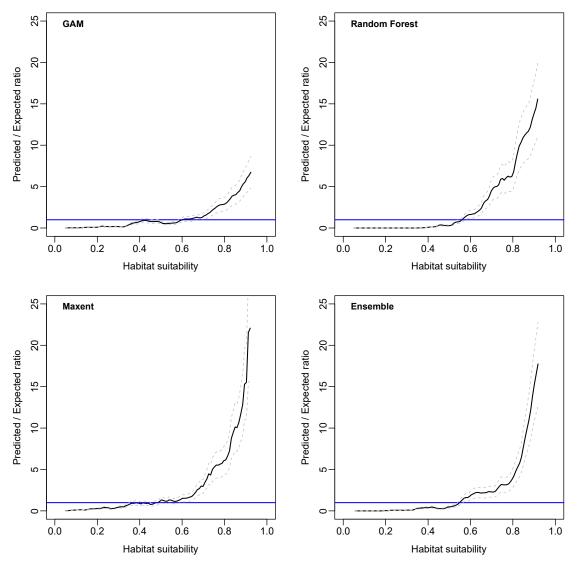


Figure 3. Graphs of Continuous Boyce Indices [CBI] for *Yucca brevifolia* models for each of three modeling algorithms used (GAM - upper left, Random Forest - upper right, Maxent - lower left), and an ensemble model averaging the three (Lower Right).

### GAM Model

Six variables contributed 10% or more from the GAM model ensemble totaling 88% of model contribution (Table 2). Winter minimum temperature was the strongest contributor with 21% model contribution, and peaked relationship, where habitat suitability was higher in areas that had relatively warmer minimum temperatures (0-3 °C),but decreasing above 4 °C (Figure 4). NDVI maximum (17.5%) was also a peaked response with highest habitat values at just above the average for the study area. (Figure 4). Habitat suitability was predicted to be higher in areas with lower Summer maximum temperature (12%) with predictions becoming negative above 37 °C (Figure 4). Summer precipitation and temperature range (~ 12% contribution near the mean values for the study area (Figure 4). The terrain wetness index (10%), which indicates topographic position – indicated higher suitability in areas with higher values – which correspond to lower areas that have the potential for greater runoff in the watershed (Figure 4).

The GAM model predicted the largest extent of highly suitable habitat for this species (Figure 1). Highest habitat predictions were in western half of the county on upper bajadas surrounding the Spring, western McCullough and Sheep mountain ranges. Additional habitat was predicted in Gold Butte – where there were many localities, and in the northwestern corner of the county – where very few localities were available for confirmation (Figure 1). Standard Error was estimated to be generally low throughout the county for this model, with very small areas of moderate error near Coyote Springs, and near the Lucy Gray mountains (Figure 2).

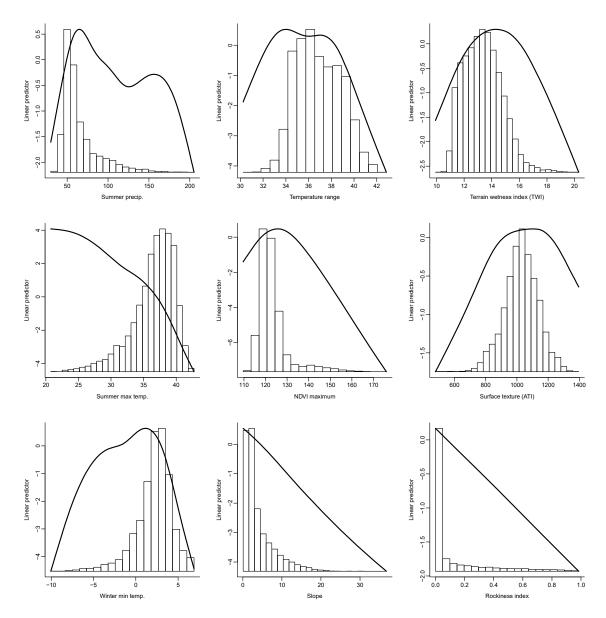


Figure 4. GAM partial response curves for the *Yucca brevifolia* model overlaid over distribution of environmental variable inputs in the study area.

#### Maxent Model

The Maxent model had five variables contributing more than 10% each, and four of these were top variables as the GAM model (Table 2). The collective contribution of the top 5 variables was 72%. Summer precipitation (18.6) and winter minimum temperature (17.3) were the top 2 contributors. Habitat suitability was predicted to be higher in areas with greater summer precipitation, and winter minimum temperature had a peaked suitability response between 0 °C and 4 °C falling sharply above that range (Figure 5). Temperature range was also a peaked response, and largely followed the range within the study area. NDVI maximum had a peaked response at lower values, but slightly above the study

area average. Surface roughness contributed 10.8%, and had a peaked response at lower values, and was also generally similar to the roughness distribution within the study area (Figure 5).

Habitat prediction for this model was concordant with the point locations for the species, and tended to remain tightly around them (Figure 2). Exceptions were the upper Mormon Mesa, western slopes of the Sheep range, and the northwestern corner of the county, where habitat was predicted, but few localities were available. However, predicted habitat was in similar areas relative to the other models overall (Figure 2).

Standard Error was low (0.02 - 0.04) overall, with some pockets of moderately low error in the Pahrump valley, and with higher error (0.08 - 0.01) near the western edge of the Red Rock area (Figure 2).

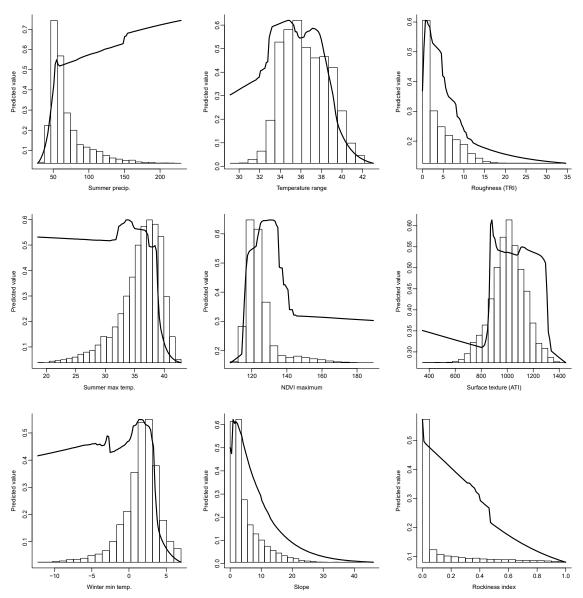


Figure 5. Response surfaces for the top environmental variables included in the Maxent ensemble model for *Yucca brevifolia*.

#### Random Forest Model

The Random Forest models had four environmental variables contributing  $\sim 10\%$  or more collectively accounting for 51% of the total model influence, with six additional variables contributing lesser, but not minimal amounts (Table 2). Four of these top five variables were consistent with the Maxent and GAM model selections. Summer maximum temperature was the highest contributing variable (14.2%), and the response curves indicated a thresholded response, favoring cooler areas, with habitat suitability falling sharply in areas above 37 °C (Figure 6). Summer precipitation also contributed strongly (13.6%) where predicted habitat suitability was very low in areas with below 60mm, and increased sharply above that level. Winter minimum temperature was also an important contributor (13%), and had a similar thresholded response to summer precipitation, with

predicted suitability rising sharply in areas receiving more than 100m winter precipitation. NDVI maximum contributed 10.2%, and suitability tended to occur in areas that were slightly above the average for the study area (Figure 6).

Standard error maps for this model indicated low (0.02 to 0.04) error rates generally surrounding areas of predicted habitat (Figure 2, Figure 1). There were a few small areas of higher standard error (0.06 - 1.0) in Hidden valley west of Apex, in the mountains East of Apex, and on the western side of the Red Rock area (Figure 2).

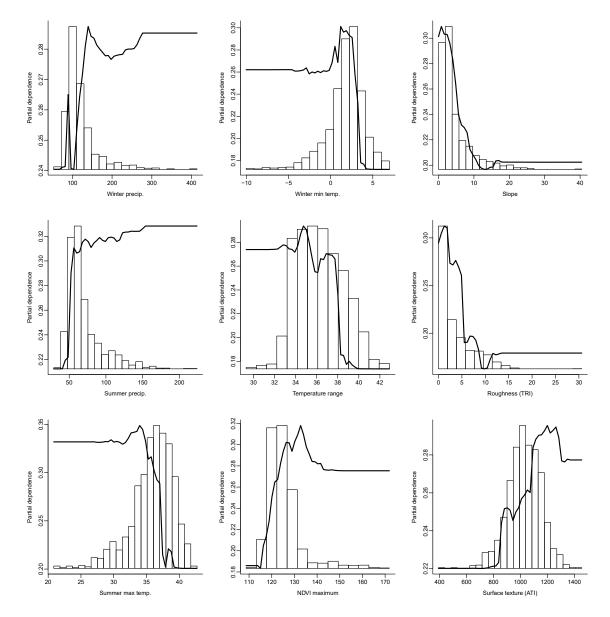


Figure 6. Partial response surfaces for the environmental variables included in the Random Forest ensemble model for *Yucca brevifolia*. Histograms represent the range of each environmental variable across the x-axis, and predicted dependence relative to habitat suitability values are on the y-axis.

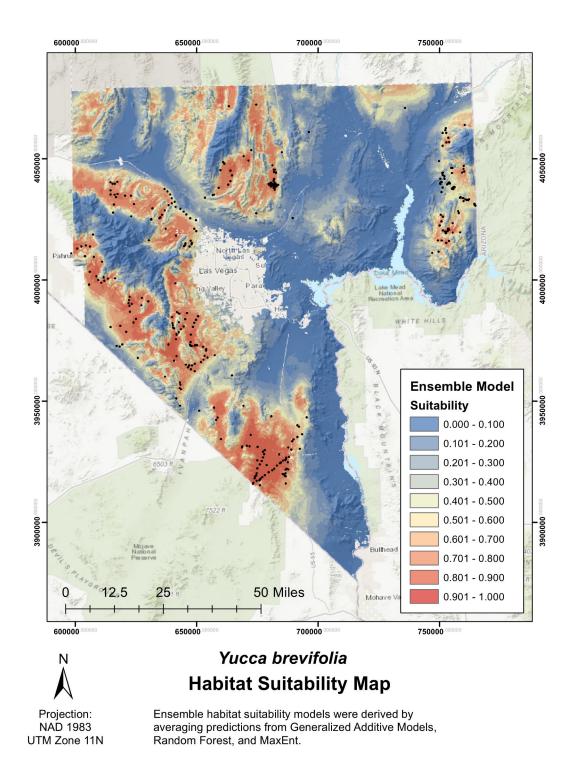


Figure 7. SDM map for Yucca brevifolia Ensemble model.

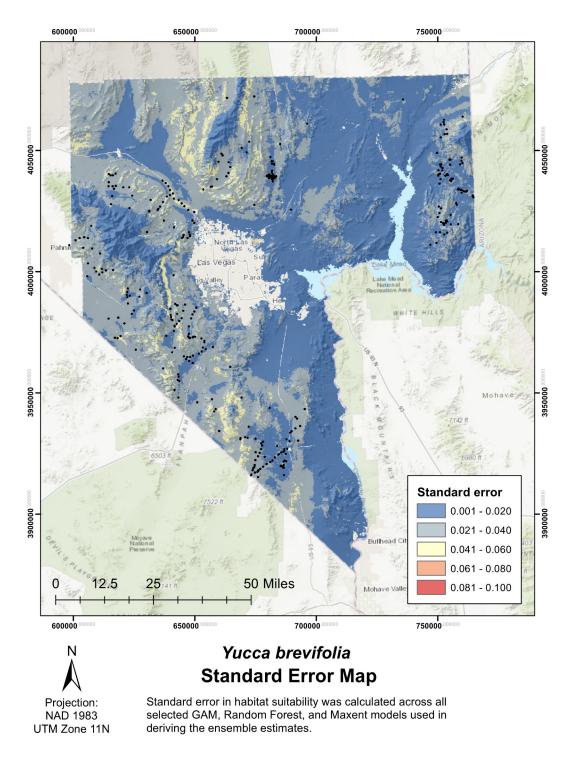


Figure 8. Standard Error map for Yucca brevifolia Ensemble model.

#### Model Discussion

*Distribution of Localities* – Localities (N= 363 unique presence points at 250 m2 grid intervals – and 313 after geographic thinning) for *Yucca brevifolia* are distributed throughout Clark County especially on upper portions bajadas surrounding the McCullough, Spring, and Sheep ranges in the western half of the county, and in the mountainous areas of Gold Butte – which tend to be lower in elevation. There are several areas of predicted habitat that lack locality information (e.g. Upper Mormon mesa north of I-15) but on visual inspection using aerial imagery do indeed have Joshua Trees (Figure 7). However other areas, such as the northeastern extent of the county near Beatty, and on the Nevada National Test Site do not have imagery of sufficient quality for inspection.

Standard Error – There is generally low Standard error throughout the study area, but a few areas of moderate Standard Error (0.04 - 0.06) are indicated in Figure 8 near the Sheep Range, on the western extent of the Red Rock area, and sporadically in the western McCollough range (Figure 8). The western extent of the Red Rock area has a sharp transitional habitat with steep slopes, and thus the zone for this species may be narrow there, and indeed absent in many areas.

### Distribution and Habitat Use within Clark County

Joshua trees are widespread in Clark County, Nevada. Geomorphically Joshua trees occupy some higher elevation valley bottoms, bajadas, and lower mountain slopes. They are found in all types of soil origins including: granite, volcanic, sandstone, and various limestone species including dolomite. They generally do not occur in very fine soil textures of playas in lower valley bottoms.

Joshua tree stands occur around the western base of the Virgin Mountains and other areas of similar elevation in the Gold Butte National Monument. There are also stands further to the north on the Mormon Mesa in shallow sandy hollows on top of mudstones. The valleys, bajadas, and lower mountain slopes between the Arrow Canyon Range and the Desert Range have extensive Joshua tree habitat of high quality – although some large portions of those areas were damaged by wildfire during the past 15 years. There are also extensive stands on the west side of the Desert Range and in some of the valleys currently occupied by the Nellis Bombing Range. Much of the desert habitats on the north side of the Spring Range and south of State Highway 95 are occupied by sparse to moderately Joshua tree stands. Joshua tree stands almost entirely encompass the Spring Range, Mt. Potosi (except for areas burned multiple times), and the State Line Mountains, except for a small area that was developed on the east side. However, the most extensive and robust Joshua tree populations occur along State Highway 93 to the north and south of Searchlight, and westward to the California state line from there. This area includes Clark County's very scenic Joshua Tree Highway. This population extends across low passes in the McCollough Mountains and into the next valley over to Sheep Mountain. Habitat modeling indicated that the highest areas predicted to be highly suitable were located within Mojave desert scrub and Blackbrush ecosystems, indicative of mid and upper bajadas (Table 3).

Moderate suitability habitat was predicted to be within the same habitat, with inclusion of Pinyon Juniper ecosystems, and potentially some salt desert scrub, although this seems uncharacteristic for this species, and may reflect some inaccuracy in the ecosystem designation, or the model prediction (Table 3).

Modeled Habitat suitability in the county is highest in the western McCullough range in a large area extending to the border, and northward to the Lucy Gray Mountains (Figure 7). Modeled habitat for is low or absent in the I-15 corridor, but picks up again north of I-15 near the Goodsprings and Blue Diamond area, and continues on the upper bajadas - occurring on all sides of the Spring Range. (Figure 7). Habitat is predicted in the upper bajadas north of US Highway 95 from Beatty, eastward to the Sheep Range, and in the valleys north of Las Vegas along US Highway 93, Upper Mormon Mesa, and throughout Gold Butte (Figure 7).

Ecosystem	Low	Medium	High
Alpine	124	0	0
Blackbrush	49078	131500	234060
Bristlecone Pine	7564	0	0
Desert Riparian	10712	0	0
Mesquite Acacia	13049	2294	4358
Mixed Conifer	26917	419	0
Mojave Desert Scrub	811609	275515	192295
Pinyon Juniper	86682	22606	6452
Sagebrush	1601	1333	1762
Salt Desert Scrub	44544	27529	6546

Table 3. Ecosystems within Clark County, and the area (Ha) of Low Medium and High predicted suitability within each ecosystem.

## **Ecosystem Level Threats**

Joshua trees occur throughout the Blackbrush, Mesquite/Acacia, middle to upper Mojave Desert Scrub, lower Pinyon-Juniper, and lower Sagebrush Ecosystems of the Desert Conservation Plan area. Primary ecosystem threats to the Joshua tree are development, and wildfire associated with red brome (*Bromus madritensis*) invasions. Development is most evidently a threat to Joshua tree populations on the west side of the Las Vegas Valley. Perhaps an even greater threat to Joshua tree stands is wildfire fueled by invasive plant species. There are many old fire scars that have reduced Joshua tree populations around the base of the Spring Mountains, and a few around the McCollough Mountains. These older burned areas likely resulted from previous forest fires that dropped down from forests and woodlands into desert shrublands. More recently low elevation desert shrubland has burned as a result of red brome grass invasions during the past 15 years. During that period massive fires occurred in the Desert Range and Arrow Canyon area, as well as northern Mormon Mesa, and the new Gold Butte National Monument. Some of these areas will likely benefit from restoration programs that are ongoing with Federal, State and County agencies.

# **Threats to Species**

Threats to this species within Clark County are reflected in the increased fire risk and incursion of development in to Joshua tree habitat. The landscape scale wildland fires that occurred in the Southern Nevada Fire Complex in 2005 are illustrative of the fire danger, as large expanses of desert habitat burned within Clark County, much of in Joshua tree habitat (e.g. in Hidden Valley, near Coyote Springs, and in Gold Butte). Increased presence of invasive grasses increases the inter-shrub fuels that increase fire risk (Van Linn et al. 2013). Loss of habitat due to urbanization, and expansion of anthropogenic infrastructure continues within the county, and while much of the predicted Joshua Tree habitat is within conserved areas, it is also the case that additional habitat loss and fragmentation will continue (table 4). Habitat fragmentation also leads to increased incursion of invasive grasses, and provides the potential for increased ignition sources, thereby increasing fire risk (Van Linn et al. 2013).

Table 4. Categorized modeled habitat values (High, Medium, and Low) and the average area (Hectares) predicted in the potential impact areas, conservation areas, already disturbed areas, and overall area

Habit Level	Impact	Conserved	Disturbed	Area (Hectares)
High	13583	141478	2072	446847
Med	26287	144207	10269	462322
Low	82806	227143	27504	1065037

# **Summary of Direct Impacts**

Direct impacts to this species include fire, destruction due to vandalism and removal during development, and rodent damage to trees during drought. Habitat area within Clark County likely to be impacted includes 136 km<sup>2</sup> of high, and 263 km<sup>2</sup> of medium quality habitat (Table 4). Low suitability habitat was the largest amount of habitat located within conserved areas, with  $\sim$  140 km<sup>2</sup> each of high and medium suitability habitat located within conserved areas. Most of the areas that are categorized as already disturbed were within low and moderate habitat for this species (Table 4).

## **Existing Conservation Areas/Management Actions**

Among the largest stands of protected Joshua trees are in the Gold Butte National Monument, and wilderness areas therein. Secondarily, Lake Mead National Recreation Area provides protection for some smaller areas of Joshua tree habitat in Clark County, but their most extensive habitats are in Arizona. Redrock National Conservation Area similarly provides conservation areas for Joshua trees existing there. The Desert National Wildlife Refuge also provides conservation lands for Joshua trees, especially around the lower elevation edges of the refuge area. BLM's Wee Thump Wilderness that is east of Searchlight provides protection to the most robust Joshua tree stands in the county.

There are some preliminary active restoration projects that include outplantings of young Joshua trees and the distribution of Joshua tree seed along with other experimental treatments. That work is sponsored by Las Vegas BLM, with research and monitoring provided by USGS – Western Ecology Research Center.

## References

- Barrows, C.W., and M.L. Murphy-Mariscal. 2012. Modeling impacts of climate change on Joshua trees at their southern boundary: How scale impacts predictions. Biological Conservation 152:29-36.
- Borchert, M.I., and L.A. DeFalco. 2016. Yucca brevifolia fruit production, predispersal seed predation, and fruit removal by rodents during two years of contrasting reproduction. American Journal of Botany 103:830-836.
- Brittingham, S., and L.R. Walker. 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. Western North American Naturalist 60:374–383.
- Cole, K.L., K. Ironside, J. Eischeid, G. Garfin, P.B. Duffy, and C. Toney. 2011. Past and ongoing shifts in Joshua tree support future modeled range contraction. Ecological Applications 21:137–149.
- Chameroy, E. 2015. Nurse plant relationships between *Yucca brevifolia Jaegeriana* and *Grayia spinosa*. Master's Thesis. University of Nevada, Las Vegas.
- Comanor, P.L., and W.H. Clark. 2000. Preliminary growth rates and a proposed ageform classification for the Joshua tree, *Yucca brevifolia* (Agavaceae). Haseltonia 7: 37–46.
- Darwin, C. 1874 Letter to J. D. Hooker, April 7, 1874. In A Calendar of the Correspondence of Charles Darwin, 1821-1882. F. Burkhardt, S. Smith, Eds. Cambridge University Press. Cambridge. Accessed 25 Jan 2018 at: https://cudl.lib.cam.ac.uk/view/MS-DAR-00095-00321/1.
- DeFalco, L.A., T.C. Esque, S.J. Scoles-Sciulla, and J. Rodgers. 2010. Desert wildfire and severe drought diminish survivorship of the long-lived Joshua tree (Yucca brevifolia; Agavaceae). American Journal of Botany 97:243–250.
- Esque, T.C., P.A. Medica, D.F. Shryock, L.A. DeFalco, R.H. Webb, and R.B. Hunter. 2015. Direct and indirect effects of environmental variability on growth and survivorship on pre-reproductive Joshua trees, *Yucca brevifolia* Engelm. (Agavaceae). American Journal of Botany 102:85-91.
- Esque, T.C., B. Reynolds, L.A. DeFalco, and B.A. Waitman. 2010. Demographic studies of Joshua trees in Mojave Desert National Parks: Demography with emphasis on germination and recruitment. Mojave National Preserve Science Newsletter 1:9-12.

- Gilliland, K.D., N.J. Huntly, and J.E. Anderson. 2006. Age and population structure of Joshua trees (*Yucca brevifolia*) in the northwestern Mojave Desert. Western North American Naturalist 66:202–208.
- Godsoe, W., E. Strand, C.I. Smith, J.B. Yoder, T.C. Esque, and O. Pellmyr. 2009. Divergence in an obligate mutualism is not explained by divergent climatic factors. New Phytologist 183:589–599. doi: 10.1111/j.1469-8137.2009.02942.x
- Lenz, L. W. 2007. Reassessment of *Y. brevifolia* and recognition of *Y. Jaegeriana* as a distinct species. Aliso 24:97-104.
- McKelvey, S. D. 1938. Yuccas of the Southwestern United States. Arnold Arboretum, Harvard University, Jamaica Plain, MA
- Miller, A. H., and R.C. Stebbins. 1964. The lives of desert animals in Joshua Tree National Monument. University of California Press.
- Pellmyr, O., and K.A. Segraves. 2003. Pollinator divergence within an obligate mutualism: two yucca moth species (Lepidoptera; Prodoxidae: *Tegeticula*) on the Joshua Tree (*Yucca brevifolia*; Agavaceae). Annals of the Entomological Society of America 96:716-722.
- Reynolds, M.B.J., L.A. DeFalco, and T.C. Esque. 2012. Infrequent pulse events drive germination and establishment of Joshua tree (Yucca brevifolia) in the northeast Mojave Desert. American Journal of Botany 99:1647–1654.
- Rowlands, P.G. 1978. The vegetation dynamics of the Joshua tree (*Yucca brevifolia*) in the southwestern United States of America. University of California, Riverside, California, USA.
- Smith, C.I. 2010. Coevolution of Joshua trees and their Pollinators: A Short Review. Mojave National Preserve Science Newsletter. Number 1: 4-8.
- Svenning, J.C., and B. Sandel. 2013. Disequilibrium vegetation dynamics under future climate change. American Journal of Botany 100:1266–1286.
- Trelease, W. 1893. Further studies of yuccas and their pollinators. Annual Reports of the Missouri Botanical Garden 4:181-226.
- Vander Wall, S.B., T.C. Esque, B.A. Waitman, D.F. Haines, and M.G. Garnett. 2006 . Joshua tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. Ecoscience 13:539–543.
- Van Linn, P. F., K. E. Nussear, T. C. Esque, L. A. Defalco, R. D. Inman, and S. R. Abella. 2013. Estimating wildfire risk on a Mojave Desert landscape using remote sensing and field sampling. International Journal of Wildland Fire 22:770–779. doi: 10.1071/WF12158.
- Waitman, B.A., S.B. Vander Wall, and T.C. Esque. 2012. Seed dispersal and seed fate in Joshua tree (*Yucca brevifolia*). Journal of Arid Environments 81:1–8.
- Wildearth Guardians. 2015. Petition to list the Joshua tree (*Yucca brevifolia*) under the endangered species act.