Reframing *Fouquieria splendens* in its larger environmental and ecological context: Effect of topography and interspecific neighbors on ocotillo morphology and distribution

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Abstract--*Fouquieria splendens* is a stem-succulent native to the Chihuahuan, Mojave, and Sonoran Deserts that spans Mexico and the American Southwest. It is well-known for its variable morphology, the underlying reason for which remains incompletely understood. Here, we attempt to quantify the effect of topographic and interspecific factors on *F. splendens* morphology and distribution. To this end, we measured 27 ocotillos located in the Organ Pipe Cactus National Monument within the Sonoran Desert during June of 2019. We also quantified the spatial distribution of interspecific neighbors relative to *F. splendens* within two topographically different sites - a bajada gradient and a plain. Using ocotillo morphology, the distances to an ocotillo's nearest neighbors, and hydrographic data extracted from the National Hydrography Dataset, we demonstrate 1.) the effect of major, desert, interspecific neighbors, like shrubs and cacti, on ocotillo morphology; 2.) the effect of elevation on intraspecific spacing as individuals compete for limited space; and 3.) a trade-off between height and number of branches. This places *F. splendens* morphology in its larger environmental and ecological context, highlighting the importance of individual traits and associated trade-offs among traits affected by topography and interspecific neighbors. By examining the ocotillo in a multi-species community and diverse landscape, this study provides empirical insight into a wider range of factors contributing to the variation in *F. splendens* morphology and spacing.

Resumen--*Fouquieria splendens* es una planta suculenta nativa de los desiertos de Chihuahua y Sonora que se extienden por México y el suroeste de Estados Unidos. Es reconocida por su morfología variable, que continúa siendo no explicada del todo. Aquí intentamos cuantificar el efecto de factores topográficos y interespecíficas sobre la morfología y distribución de *F. splendens*. Para esto, medimos 27 ocotillos ubicados en el Monumento Nacional Organ Pipe Cactus dentro del Desierto de Sonora durante junio de 2019. También intentamos cuantificar la distribución espacial de los vecinos interespecíficas a *F. splendens* dentro de dos sitios topográficamente diferentes: una pendiente y una llanura. De acuerdo con la morfología del ocotillo, las distancias a los vecinos más cercanos de un ocotillo y los datos de la cuenca hidrográfica, extraídos del Conjunto de Datos Hidrográficos Nacionales, demostramos 1.) el efecto de los principales vecinos interespecíficas del desierto, como los arbustos y cactus, en la morfología del ocotillo; 2.) el efecto de la elevación en el espaciamiento entre vecinos de ocotillo más cercanos a medida que los individuos compiten por un espacio limitado; y 3.) una compensación entre la altura y el número de ramas. Esto se ajusta a la morfología de *F.*

splendens en un contexto ambiental y ecológico más amplio, lo que ayuda a entender la importancia de los atributos fenotípicos y compensaciones asociadas entre los atributos fenotípicos, afectados por las limitaciones de la topografía y los vecinos interespecíficas. Al examinar el ocotillo en una comunidad multiespecie y paisaje diverso, este estudio presenta una gama más amplia de causas que influyen en la variación en la morfología y el espaciamiento de *F. splendens*.

Fouquieria splendens (*F. spendens*) is a drought-deciduous stem-succulent endemic to the Chihuahuan, Mojave, and Sonoran Deserts and is known for its unusual and highly variable morphology (Killingbeck, 2017). *F. splendens* exhibits a stochastic production of segments, inflorescence, and branches (Darrow, 1943; Bowers, 2005; Killingbeck, 2017), which has made the ocotillo statistically and ecologically challenging to study. Past research has focused on the punctuated episodes of terminal segment production in ocotillos to better determine their growth patterns and causal effects (Darrow, 1943; Bowers, 2016; Killingbeck, 2016; Killingbeck, 2019). These episodes of segment growth are marked by visible, persistent seams which circumscribe the branch and are an attractive feature for dendroclimatic or desert ecology research (Kadmon, 1995; Bowers, 2005). However, conclusions on the effects on ocotillo morphology have been indeterminate as Killingbeck found that, in some ocotillos, no measurable stem elongation in new or extant stems occurred in 4-9 years (Killingbeck, 2017). As a result, despite the inclusion of detailed measurements on annual and seasonal rainfall, the variation in the morphology of ocotillos does not appear to be dominated by any singular or seasonal event. Thus, it is important to better understand ocotillo morphology in order to fully determine its ecological function in Southwest deserts and to test general ecological dynamics in multi-species desert communities.

As shown in past studies, the variable growth form of *F. splendens* leads to challenges in the field and during analyses. For instance, retrospective measurements on seasonal segment growth is currently not possible. Congruently, the production of new segments or elongation of extant stems shows high inter- and intra-plant variability (Bowers, 2005). Previous research on ocotillo inflorescence found that variation among branches on a single plant overwhelmed any differences between individuals (Bowers, 2005; Bowers, 2006; Killingbeck, 2009). Studies also indicate that segment growth produced during one year had little or no relation to the amount produced during the succeeding year (Darrow, 1943; Killingbeck, 2017). Furthermore, production of terminal segments increased in stochasticity with maturity, and growth ceased after branches attained a length of 10 to 15 feet (Darrow, 1943). In turn, the reasons behind this variability, whether genetic or environmental, remain inconclusive, and it is in our benefit to further explore which additional factors could be influencing or directing ocotillo growth.

Studying ocotillo growth in the Sonoran Desert is favorable because it is a multi-species desert with long mountain ranges and low-elevation valleys (Bowers and McLaughlin, 1982). Its topography makes it ideal to study ocotillo morphology near arroyos or along bajadas. Arroyos are characterized as washes that fill up seasonally with sufficient rain while bajadas are slopes that exhibit a gradient of water availability (McAuliffe, 1994; Stromberg, 2007). These geological features have allowed researchers

to study both diverse competition dynamics and topographic effects on the growth of various desert plant species in the field (Bowers and Lowe, 1986; Nobel and Zutta, 2007; Pierce, 2019); however these features have been overlooked in ocotillo studies. Wider studies on desert plant communities have investigated the interaction between morphology and competition. In particular, competition in desert communities is a likely candidate to influence plant form and spatial distribution. It has been assumed that deserts are unproductive and exhibit low competition because of their scarcity of water (Grime, 1973; Huston, 1979; Gaudet and Keddy, 1989). However, studies have revealed a diverse spatial distribution of desert plants, and have shown how competition among plants can vary in levels of intensity (Fonteyn and Mahall, 1978; Fowler, 1986; Kadmon, 1995; Ji et al., 2019). In particular, plant removal experiments in arid regions have suggested that interspecific competition is more intense than intraspecific competition (Fonteyn and Mahall, 1978) while experiments along productivity gradients revealed a positive relation between competition and plant density (Kadmon, 1995). Furthermore, Pielou's model provides evidence of nearest-neighbor distances increasing with plant size (Pielou, 1962), and Philips and MacMahon found that as dispersion patterns became more regular rather than random, plant size increased (Philips and MacMahon, 1981). Others have also defined specific, competition type interactions; Ji and colleagues (2019), who used remote sensing technology, found that shrub-shrub competition is most likely only active in locations where conditions have highly favored shrub establishment and survival. In turn, to a large extent, plant competition also drives patterns in plant density and size.

Measuring desert plant, interspecies interactions can then help assess how plants survive or out-compete their potential competitors. Plant fitness has been well-studied and has led to recent novel observations regarding trade-offs between environmental context, competitor defences, plant growth, and plant reproduction on the population level (Lundgren and Marais, 2020; Pearse et al., 2020). All plants must balance the allocation of resources for growth, survival, and reproduction in order to maximize fitness within the constraints of competition. Ge and colleagues extend that concept to a three decade study of trait and competition relationships across 51 winter annual desert species (Ge et al., 2019). They found that trait trade-offs scaled to the entire community and were exhibited most by the dominant species (Ge et al, 2019). In turn, trait trade-offs can serve as an organizing principle for understanding plant population and community processes. Within the multi-species communities of the Sonoran Desert, we hypothesized our empirical approach to studying the ocotillo within its environmental context would help elucidate potential trait trade-offs.

This study examined how environmental and ecological factors such as elevation, intraspecific distances, and interspecific distances affected ocotillo morphology in order to better understand patterns in ocotillo growth form and its larger contribution to the spacing of plants in complex, desert plant communities. We measured the height, circumference, number of branches, and terminal segment lengths of ocotillos as well as the nearest intra- and interspecific neighbor distances; furthermore, we took measurements of elevation and cross-referenced distances to the nearest arroyo. Our study focused on major and minor nearby interspecific plants as well as shrub vs. cactus presence. By assessing the plant form of ocotillos as well as the spatial proximity of ocotillos and their interspecific neighbors across various elevations and sites, we modeled how interspecific and

topographic differences relate to and effect ocotillo growth form. Here we provide empirical insight on how to reframe the ocotillo in its larger environmental and ecological context, which has helped uncover novel patterns in ocotillo morphology and distribution. Results suggest that interspecific factors and topographic differences affect ocotillo morphology and spatial density, and they provide an important framework to reexamine this unique desert plant.

Materials and Methods--*Study Area*--The study area was located in the Sonoran Desert at Organ Pipe Cactus National Monument (31.94515°N, 112.81252°W), approximately 16 km north of the US/Mexico border in southern Arizona (Fig 1.). The plant community contains the most striking diversity out of the four main deserts in the American Southwest. Our focal species was the ocotillo, *Fouquieria splendens*, and we observed adjacent, interspecific species. These included *Carnegiea gigantea* (saguaro cactus), *Larrea tridentate* (creosote bush), *Stenocereus thurberi* (organ pipe cactus), *Ambrosia deltoidea* (triangle leaf bursage), *Cylindropuntia fulgida* (jumping cholla), *Jatropha cuneata* (limber bush), *Simmondsia chinensis* (jojoba), *Parkinsonia aculeate* (Mexican palo verde), and *Cylindropuntia leptocaulis* (pencil cholla).

We chose this study area for its uneven distribution of limiting resources across topographically distinct sites. We took measurements during June of 2019, focusing on two main sites: the upper section of a bajada (532 - 581 m) and the lower section of the bajada consisting of a relatively flat plain (501 - 506 m). In this study, we termed the upper and lower bajada as 'bajada' and 'plain' respectively for simplicity.

Data Collection--At each site, we selected ocotillos for measurement and marked their locations using a Garmin GPSMAP 64st. Using a tape measure, we took a series of morphological measurements to the nearest centimeter: height of the ocotillo, circumference at breast height (approximately 1.5 m from the ground), and segment lengths of 10 randomly selected branches as illustrated in Figure 2. We also counted the total number of branches. Interspecific spacing was quantified by measuring the distance from an ocotillo to the nearest major interspecific plant. We also recorded the major, interspecific plant's identity. A major interspecific neighbor was defined as the tallest and largest-bodied, interspecific individual greater than 1 m away and less than 10 m away from the observed ocotillo. We hypothesized that these plants dominated the local area's resources and could be a source of competition to other flora. Additionally, small interspecific plants up to 30 cm centimeters tall within a 1 m radius of the ocotillo were also identified and counted as minor, interspecific neighbors. Minor, interspecific neighbors were considered to have a small effect on the local area's resources, but could be taking advantage of the ocotillo for shade.

We measured 20 ocotillos on a bajada and 7 ocotillos on a plain. We traveled down from the peak of a south-facing bajada, selecting an ocotillo for measurement along an elevation contour every 10 m for a total of twenty ocotillos. Measurements on the bajada were taken over the course of three days. Over the following two days, seven ocotillos were measured

on a flat plain at an elevation similar to the bottom of the bajada gradient - two of those seven were measured within 10 meters of an arroyo.

Hydrographic Data-- Hydrographic data were accessed from the USDA Geospatial Data Gateway and collected from the National Hydrography Dataset (NDH). We cross-referenced the data from the NDH with our ocotillo data in ArcMap 10.7.1 (Esri, 1969) in order to determine the distance from each plant to the nearest arroyo.

Assumptions--Our data collection methods were based on several assumptions. Plant age was unknown; thus, at best, we can only use proxies of age such as the number of branches on an ocotillo (Darrow 1943). Past research defined mature ocotillos as individuals that are 2.5 to 4.5 meters in height and have 40 to 75 straight, slender branches (Darrow 1943). Based on that definition, none of our ocotillos would have been mature. In addition, we did not know the year in which each terminal branch was grown. Darrow found low correlation values for branches active in both consecutively-paired years, indicating that the segment growth during one year had little or no relation to the segment produced during the succeeding year (Darrow 1943). Thus, we assumed that segments were not necessarily produced in sequential years.

Morphology, Proximity, and Topography Analyses--We analyzed the relationships between ocotillos' morphology, site, elevation, the presence of major shrubs or cacti, proximity to the local arroyo, proximity to other ocotillos, and proximity to interspecific plants; we conducted these analyses using multivariate linear regressions in the program RStudio version 1.2.5033 (RStudio, 2009). We also ran *t*-tests for categorical variables, like site or major, nearby, interspecific plant group. All measurements followed log-normal distributions except for circumference and distance to the nearest arroyo, which were normally distributed. After log-transforming all response variables and centering all predictor variables, models constructed passed linear regression assumptions. Selection for the best fit model was based on Akaike information criterion (AIC) and an ANOVA test where $p > 0.05$ favored the simpler model (Supplementary Files).

Terminal Segment Length Analyses--Terminal segments refer to the last 5 segments on the ends of each of the 10 branches measured per ocotillo; they reflect the most recent growth in the plants and are the most distinct and easy to measure. We analyzed the terminal segment lengths using mixed-effect modeling to determine the effects of elevation, site, ocotillo morphology, and interspecific plant type as well as distance to the nearest arroyo, ocotillo neighbor, or interspecific neighbor (Supplementary Files). To account for pseudo-replication in the models, we designated ocotillo, segment, and branch number as random effects. We also calculated the terminal segment length interquartile range (IQR) for each ocotillo, and included it in all our analyses. Terminal segment length IQR represents terminal segment length variation where the larger the terminal segment length IQR, the more variation in terminal segment length the ocotillo has.

To further examine interspecific impact, we tested the effect of major, interspecific, plant type - either a shrub or cactus - on ocotillo terminal segment length. This was done using a

Kruskal-Wallis test because the data are non-normally distributed (Shapiro-Wilk's normality test $p<0.05$).

Principal Components Analysis--We carried out a principal components analysis (PCA) to describe the morphology of the individuals measured (Supplementary Files). We included five variables in this analysis: height, circumference, number of branches, median terminal segment length, and terminal segment length IQR. We scaled data such that each variable had the same variance (unit variance). This prevented variables with larger variances to dominate the PCA, and it was necessary because variables, such as height and segment length, had different magnitudes. After the analysis, we defined principal components (PCs) that accounted for sufficient variation as those with eigenvalues larger or equal than 1, meaning that such PCs capture more variation in the data than the original variables (Kaiser, 1960; Kaufman and Dunlap, 2000).

Results--*Site And Terminal Segment Length IQR Affect Height*--For ocotillos located along the bajada (n = 20), the best fit model was found to be the model only with terminal segment length IQR (β = 0.04, SE = 0.011, t = -3.94, P = 9.64e-04). However, for ocotillos across the bajada and plain (n = 27), the best fit for height included site and the terminal segment length IQR; both measurements were significant. We found that ocotillos with larger terminal segment length IQR, indicating higher variation in terminal segment lengths, were taller (β = 0.04, SE = 0.01, t = 3.64, P = 0.001). In addition, ocotillos growing on the plain (n = 7) reached greater heights on average than the ocotillos growing on the bajada ($\bar{x}_{plain}$ = 3.97 m; $\bar{x}_{bajada}$ = 2.85 m; $t(12)$ = -4.16, P = 0.001; Fig. 3c). Ocotillo height increased by an estimated 40% when the site changed from the bajada to the plain (β = 0.34, SE = 0.072, t = 4.67, P = 9.58e-05). Furthermore, although not in the best fit models, there was a weak negative effect of elevation with height (n = 27, β = -0.0037, SE = 0.0017, t = -2.22, P = 0.036; Fig. 3a) where for every 10 meter increase in elevation, the height of the ocotillo decreases by 3.63% .

Height, Site, and Minor Interspecific Group Affect Terminal Segment Lengths--The best fit, mixed-effect model of terminal segment length for all ocotillos (n = 1,349) included height and the number of cacti within 1 meter from the base of the ocotillo as well as the random effects of tree number and segment number. The minor, interspecific measurement was not significant in the best fit model, but height was significant. For every 1 meter increase in height, an ocotillo's terminal segments increase in length by an estimated 3.38 cm (β = 3.38, SE = 1.34, t = 2.53). On the other hand, for ocotillos along the bajada (n = 1,000), the best fit model had both height and the number of cacti within 1 meter as significant effects. For every 1 meter increase in height, an ocotillo's terminal segments increase in length by an estimated 8.37 cm (β = 8.37, SE = 1.34, t = 6.23). However, for every additional small cactus around an ocotillo's base, then its terminal segments decrease in length by 1.74 cm (β = -1.74, SE = 0.83, t = -2.11)

Similarly, from Kruskal-Wallis tests, we found a significant difference for terminal segment lengths between ocotillos whose nearest, major, interspecific neighbor was a shrub or cactus (n = 1,349, P = 0.023; Fig. 4). Ocotillos whose interspecific neighbor was a

shrub had more extreme terminal segment lengths than ocotillos whose interspecific neighbor was a cactus. There was also a significant difference for terminal segment lengths between ocotillos that grew on the bajada or plain (n = 1,349, P = 0.0024) where ocotillos on the bajada reached more extreme terminal segment lengths.

Number of Branches Affects Circumference--For ocotillos across the bajada and plain (n = 27), the best fit model for circumference included only branch number. Ocotillos with more branches had larger circumferences (β = 0.015, SE = 0.005, t = 2.88, P = 0.008; Fig. 5), and for every branch an ocotillo grows, the circumference (m) of the ocotillo grows by 1.54%. The same best fit model also best explained bajada-only ocotillos (n = 20). All other measurements were unrelated to circumference for all ocotillos and for ocotillos on the bajada.

Circumference, Major Interspecific Group, and Arroyo Distance Affect Number of Branches--For ocotillos along the bajada and plain (n = 27), the best fit model for the number of branches among ocotillos included interspecific distance, distance to the nearest arroyo, and the circumference of the ocotillo. This model received over two times more support than the second-ranked model, which included only circumference and arroyo distance. Individual ocotillos with a wider circumference (m) had more branches (β = 0.14 , SE = 0.045, t = 68.57, P = 3.76e-04). In addition, for every 10 meters an ocotillo grew away from its nearest arroyo, the number of branches decreased by 1.63% (Fig. 5). Major interspecific distance was only marginally significant in the model (β = 0.067 , SE = 0.036, t = 1.84, P = 0.079), but for every 1 meter closer an interspecific plant was to an ocotillo, the number of branches decreased by 6.89%. Furthermore, among ocotillos whose major interspecific neighbor was a shrub, the average number of branches was lower than ocotillos whose interspecific neighbor was a cactus (n_{cactus} = 11; n_{shrub} = 16; $\bar{x}_{cactus} \approx 21$ branches; $\bar{x}_{shrub}$ = 28 branches; t(19.1) = 2.5, P = 0.02, Fig. 5c).

Within ocotillos on the bajada (n = 20), the best fit model included the interspecific plant group as a sole predictor and the interaction term between circumference and the distance to the nearest neighboring ocotillo. This model received twice more the support as the second-ranked model, which included elevation. Within the best fit model, there was a significant positive effect of circumference (β = 0.12, SE = 0.037, t = 3.27, P = 0.005) where for every 1 m increase in circumference, the number of branches increased by approximately 12.7%. There was also a weak, negative, interaction effect between circumference and the distance to nearest ocotillo (β = -0.02, SE = 0.01, t = -2.25, P = 0.04) where ocotillos with wider circumferences that aggregated closer together exhibited fewer branches. No other effects were significant.

Elevation and Ocotillo Size Affect Nearest Ocotillo Distance--For ocotillos along the bajada and on the plain (n = 27), the best fit model of the distance to the nearest neighboring ocotillo included the height and circumference of the ocotillo as well as elevation. Individual ocotillos with wider circumferences and taller heights were farther away from neighboring ocotillos (β = 0.56, SE = 0.19, t = 2.99, P = 0.0069) where for every 1 m increase in circumference and height, the nearest neighboring ocotillo's distance

increased by an estimated 75%. Ocotillos at higher elevations and with wider circumferences were also farther from neighboring ocotillos, but the relationship was marginally significant ($\beta = 0.011$, $SE = 0.005$, $t = 2.03$, $P = 0.056$). For every 1 meter increase in circumference and elevation, the nearest neighboring ocotillo's distance increased by an estimated 1%.

For ocotillos along the bajada ($n = 20$), the best fit model for distance to the nearest neighboring ocotillo included branch number, elevation and distance to the nearest, major interspecific neighbor. Ocotillos higher up in elevation had closer neighboring ocotillos ($\beta = -0.02$, $SE = 0.007$, $t = -2.66$, $P = 0.018$; Fig. 6a). For every 10 meter increase in elevation, the nearest neighboring ocotillo decreased its distance by an estimated 18%. Individuals with more branches and with farther interspecific neighbors also had closer neighboring ocotillos ($\beta = -0.062$, $SE = 0.019$, $t = -3.26$, $P = 0.005$; Fig. 6b). All remaining predictors in the best fit model were not significant.

Arroyo Distance Affects Interspecific Distance --The best fit model of distance to the nearest interspecific neighbor among ocotillos includes only the distance to the nearest arroyo. This model received approximately twice as much support as the second-ranked model, which included elevation. Major interspecific neighbors that were close to an arroyo was farther from the ocotillo ($\beta = -0.0038$, $SE = 0.0019$, $t = -2.02$, $P = 0.054$), but this was marginally significant. However, among bajada ocotillos, the best fit model is the same as with all ocotillos, but the effect is significant and slightly stronger ($\beta = -0.0054$, $SE = 0.0023$, $t = -2.36$, $P = 0.030$) where for every 20 meters closer the interspecific plant is to an arroyo, its distance from the ocotillo increases by 10.25%.

Principal Component Analysis--We generated 5 principle components (PCs) in total. Of these, two (PC1 and PC2) were found to have eigenvalues above 1, and as such were considered to explain a sufficient proportion of variation to be included in our further analysis. Together, they capture 71.6% of variation between the individuals (Fig. 7).

PC1 captures 40.7% of variation within individuals. Main contributions to PC1 are the terminal segment IQR (40.6%), median terminal segment length (33.6%), and height (25.3%). PC2 captures 31.0% of variation, and contributions were mainly made by circumference (50.3%) and number of branches (47.9%).

Discussion--Our study aimed to reframe the ocotillo, a unique desert shrub, in its larger environmental and ecological context. We did so by modeling and determining the effect of topography and interspecific factors on *F. splendens* morphology and distribution. Past research has attempted to describe the causes and effects of an ocotillo's growth form, but did not test how potential competitors or topography relates to ocotillo morphology. Our approach integrated field data with existing theories of competition dynamics and desert landscape structure, which led to the discovery of novel morphological patterns in the ocotillo. These patterns are not only consistent with these theories, but they are also consistent across our analyses. By examining the ocotillo in this multi-species community and diverse landscape, we collected a wide range of field data and generated novel models

to describe *F. splendens* morphology among its nearby neighbors and within its local habitat.

In *F. splendens*, growth occurs either through the generation of new segments, the lengthening of extant segments, or by the production of new branches (Darrow, 1943; Killingbeck, 2016). We found height to be related to terminal segment length IQR where taller ocotillos exhibited greater terminal segment length variation and longer terminal segment lengths overall. This relationship was reinforced in the PCA because the main contributions to PC1 were height, median terminal segment length, and terminal segment length IQR. In addition, the PCA reinforced the positive relationship between circumference and the number of branches because the main contributions to PC2 were circumference and the number of branches. Furthermore, the PCA reinforced how the number of branches and the circumference were unrelated to ocotillo height and terminal segment length IQR in our models.

One possible explanation for this lack of relation between height and the number of branches could be the association of a potential trade-off where there is a choice between branch production and branch elongation. This choice could depend on the maximization of reproductive output. Stem growth is highly variable, but the production of flowers per stem is relatively consistent (Killingbeck, 2019). Since longer branches produce more flowers (Bowers, 2006), it would not be always advantageous to maximize branch number. It may be advantageous, under certain conditions, to lengthen extant branches to produce more flowers. However, stems can only get so high because of physical limitations (Ryan and Yoder, 1997); in those cases, growing a new branch would be more advantageous for reproduction. Then, the choice between the production and elegonation of branches would depend on maximizing reproductive output; however, further studies would need to quantify an ocotillo's flower production to its growth form by, for instance, counting shoots.

We also observed a consistent pattern where intraspecific distances and interspecific plant groups affected ocotillo morphology, specifically the number of branches and the terminal segment lengths. We found that ocotillos with major shrubs nearby had fewer branches, but then had longer terminal segment lengths. This suggested to us that there is a potential selective pressure, possibly due to competition, that an ocotillo undergoes in order to either produce or lengthen its branches. Local interspecific competition could be mediating this trade-off; a trait theory posited by Ge et al. (2019) shows how trait trade-offs are an indication of organization in an ecological community. In this study, an ocotillo's growth pattern between branch number and segment length could reveal community processes like competition. Congruently, we found that ocotillo size influenced the spatial distribution of other ocotillo neighbors. Larger ocotillos with wider circumference and taller heights had neighboring ocotillos that were farther away, which followed Pielou's model (Pielou, 1962). It is then possible that there is a relationship between competition and ocotillo plant density as suggested by Kadmon (1995), but our study did not reach this conclusion.

Site, elevation, and distance to the nearest arroyo also influenced ocotillo morphology and distribution. Ocotillos that grew on the plain, which is specifically the lower and flat-like portion of the bajada, were on average taller than their upper bajada counterparts. In addition, for ocotillos along the bajada, ocotillos were increasingly closer

to one another as elevation increased. In turn, intraspecific distances were modeled most strongly by limited spacing in higher elevation, leading to ocotillos with smaller plant forms. Finally, we observed that distance to the nearest arroyo affected interspecific distances and the number of branches on an ocotillo. The closer an interspecific neighbor was to an arroyo, its distance from the ocotillo increased. The closer an ocotillo was to an arroyo, its number of branches increased as well. Thus, these relationships indicate that the factors that relate to an ocotillo's branch number or segment length is not solely dependent on limited resources, such as water availability, that typically describe desert-communities. It seems to be a mix of local factors, including elevation, spatial availability, the proximity of neighbors, and the presence of particular desert plants like a shrub or cactus.

However, there are limitations to our study. The very underlying mechanism for this posited trait trade-off is unknown and our models do not help in elucidating how interspecific spacing occurs. For instance, we found that major interspecific distance was negatively related to distance to the nearest arroyo, suggesting that overall interspecific spacing was mainly mediated by limited resources, but no water availability measurements were taken. Our cross-reference with the hydrographic data from the NDH would not be enough to fully explain desert interspecific neighbor spacing. Similarly, although ocotillos higher on the bajada had closer neighboring ocotillos, leading to more aggregation under limited space, the causality of this aggregation is still uncertain. Others have suggested it could be a mix of increasing soil particle size as elevation increases and root morphology (Yeaton & Cody, 1976). Since the ocotillo's root system is shallow, reaching a depth of only 3-6in (USDA Index of Species), it could be in competition with species with deep taproots, as it has been observed before (Cody, 1985). With limited spacing in the upper bajada to spread roots, there could be greater chances of competition among ocotillos and its nearby cacti neighbors.

Age and high intra-plant variability also continued to be problematic factors while analyzing our data, especially with terminal segment length. This is no new problem as it has been shown that variation among branches on a single ocotillo overwhelmed any differences between individual ocotillos (Bowers, 2005). Our mixed effect models were sufficient but unable to fully describe the existing relationships between terminal segment length and nearby interspecific neighbors. Nonparametric tests and nonparametric factors such as the terminal segment IQR made it possible to observe those relationships. However, future research will need to use factors that decrease variation within the ocotillo but increase interpretive and descriptive power in order to better understand ocotillo morphology and growth. In addition, if larger sample sizes were used and more ocotillos on topographically different sites were measured, we would expect our principal components to better reflect our linear models.

Ultimately, the indication of a trade-off between branch number and terminal segment length, and their modeled relationships between ocotillo morphology, interspecific and intraspecific distances, and topography opens paths to further explore their causal effects. Our trade-off indication may help explain previous observations on the irregularity of *F. splendens* terminal segment formation (Killingbeck, 2017) by revealing novel factors impacting ocotillo morphology. However, we encourage further testing of ocotillo growth patterns along various topographically different sites. In addition, tests on the fitness and genetic basis of ocotillo growth are clearly needed to definitively assess our

interpretations. Accurate predictions of ocotillo growth and spacing will likely rely on models that incorporate both individual traits and extrinsic environmental factors. Overall, our approach and results can better help frame desert species within their environmental and ecosystem dynamics and can be used to better understand the role and impact of ocotillos in desert communities.

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Fig. 1--Organ Pipe National Monument Site (OPNM) Map. Top left corner shows the outline of the OPNM. Waypoints for ocotillos on the bajada, arroyo, and plain are represented by circular points. Bounding box on the right zooms into the ocotillos on the bajada. Hydrographic data were retrieved from the National Hydrography Dataset, symbolized by the blue line, and the topographic basemap was imported from ESRI. The distance from each ocotillo to the arroyo is represented by a color ramp from blue to red corresponding to increasing distance. Additional details such as campground and trail location are included for reference.

Fig. 2--*Fouquieria splendens* morphology measurements. Five different types of measurements were taken in the field per ocotillo using measuring tape: 1) circumference (*Circ)* taken at breast height (H_c = 1.5*m*), 2) the full height of the ocotillo (H_m), 3) number of branches, 4) number of segments per 10 branches chosen above breast height, and 5) each of the 10 branches' segment lengths (T_n where n = 1, 2, 3, …*)*.

Fig. 3--Ocotillo height related by site, elevation, and terminal segment length interquartile range (IQR). Data points are coded by landform types where orange circles represent ocotillos on the plain and red triangles represent ocotillos on the bajada. The dashed linear regression lines indicate a significant association ($P < 0.05$); the shaded bands indicate 95% confidence intervals. (a) Elevation is negatively related to height (β = -0.004, SE = 0.002, t = -2.22). (b) Terminal segment length IQR is positively related to height (β = 0.041, SE = 0.015, t = 2.77). (c) There was a significant effect of site where ocotillos on the plain exhibited higher heights on average compared to ocotillos on the bajada ($\bar{x}_{plain}$ = 3.97 m; $\bar{x}_{bajada}$ = 2.85 m; $t(12)$ = -4.16, P = 0.001).

Fig. 4--Terminal segment length skewness and nonparametric interspecific plant group effects. (a) Histogram of terminal length showing a long right tail. (b) Violin plot of terminal segment lengths among ocotillos whose nearest, major, interspecific neighbor was either a cactus or shrub.

Fig. 5--Number of branches related by circumference, distance to the nearest arroyo, and interspecific plant group (e.g. shrub or cactus). The dashed linear regression lines indicate a significant association ($P < 0.05$) except for the regression line between the circumference and number of branches among ocotillos with cacti nearby. (a)-(b) Data points are coded by interspecific plant groups where circles represent ocotillos with major interspecific neighbors that were shrubs and triangles represent ocotillos with major interspecific neighbors that were cacti. (c) There was a significant effect of interspecific plant group where ocotillos with a cactus exhibited more branches on average compared to ocotillos with a shrub ($\bar{x}_{cactus}$ = 28.7 m; $\bar{x}_{shrub}$ = 20.4 m; $t(19.1)$ = 2.47, P = 0.02).

Fig. 6--Regressions of distance to the nearest neighboring ocotillo with (a) elevation (n = 20, β = -0.02, SE = 0.007, t = -2.59) and (b) number of branches (n = 20, β = 0.033, SE = 0.013, t = 2.49) for only ocotillos measured on the bajada.

Fig. 7-- Principle component analysis plot of *F. splendens* morphology. Principle component 1 accounts for 40.7% of all variation and is mainly contributed to by height, terminal segment IQR, and median terminal segment length. Principle component 2 accounts for 31.0% of all variation and is mainly contributed to by circumference and branch number.

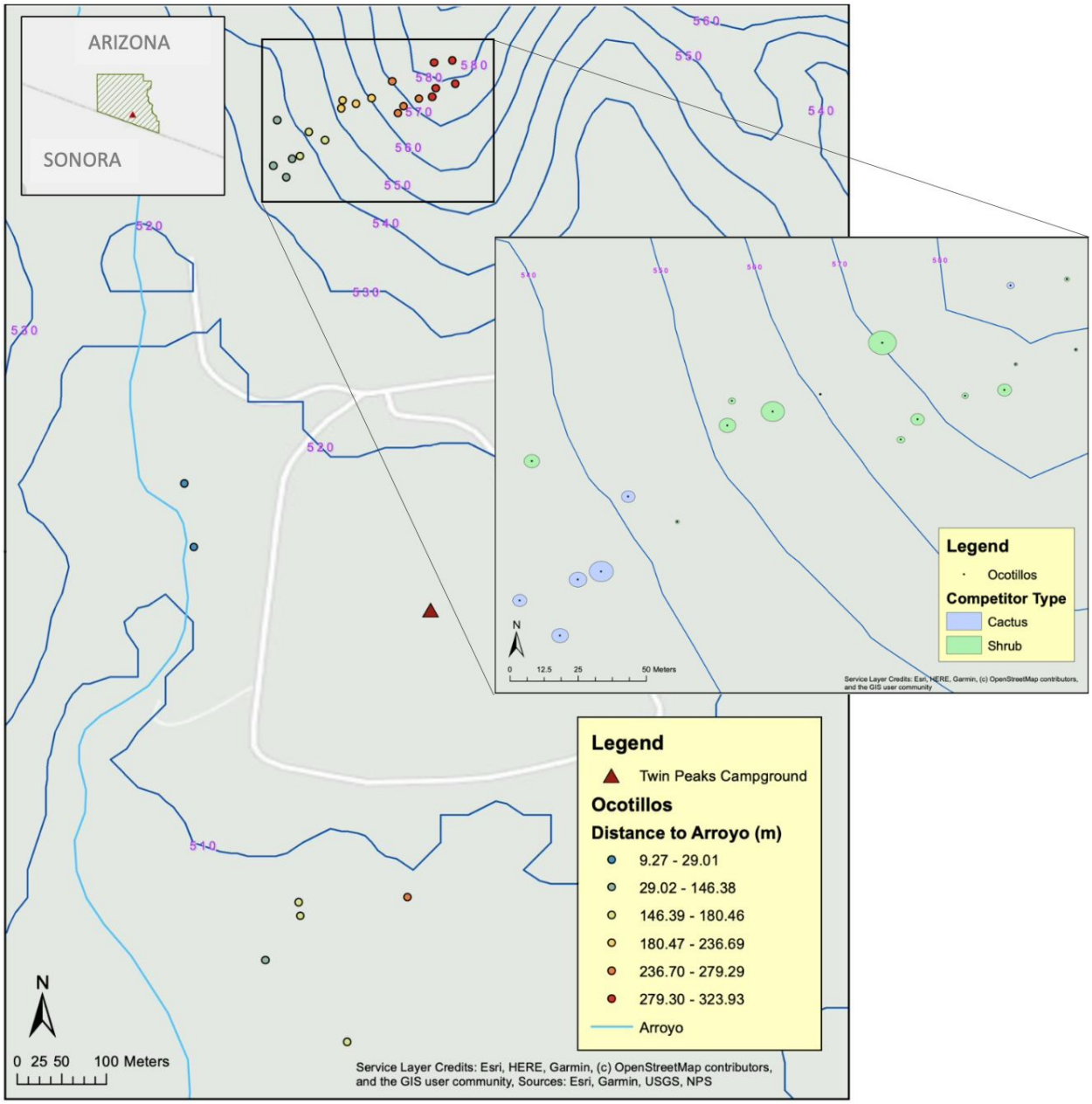
ARIZONA
SONORA
Legend
Ocotillos
Competitor Type
Cactus
Shrub
N
0 12.5 25 50 Meters
Legend
Twin Peaks Campground
Ocotillos
Distance to Arroyo (m)
9.27 - 29.01
29.02 - 146.38
146.39 - 180.46
180.47 - 236.69
236.70 - 279.29
279.30 - 323.93
Arroyo
N
0 25 50 100 Meters
Service Layer Credits: Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community, Sources: Esri, Garmin, USGS, NPS

Fig. 1

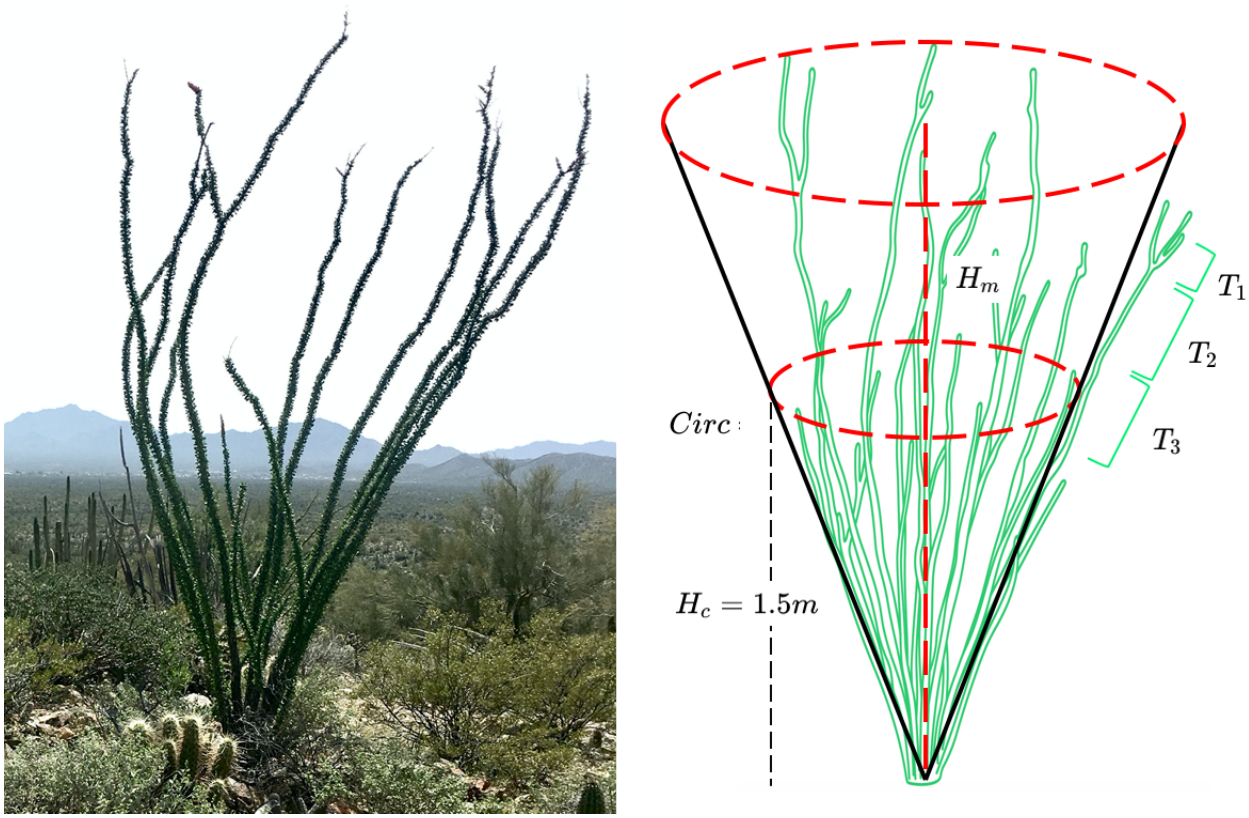

Fig. 2

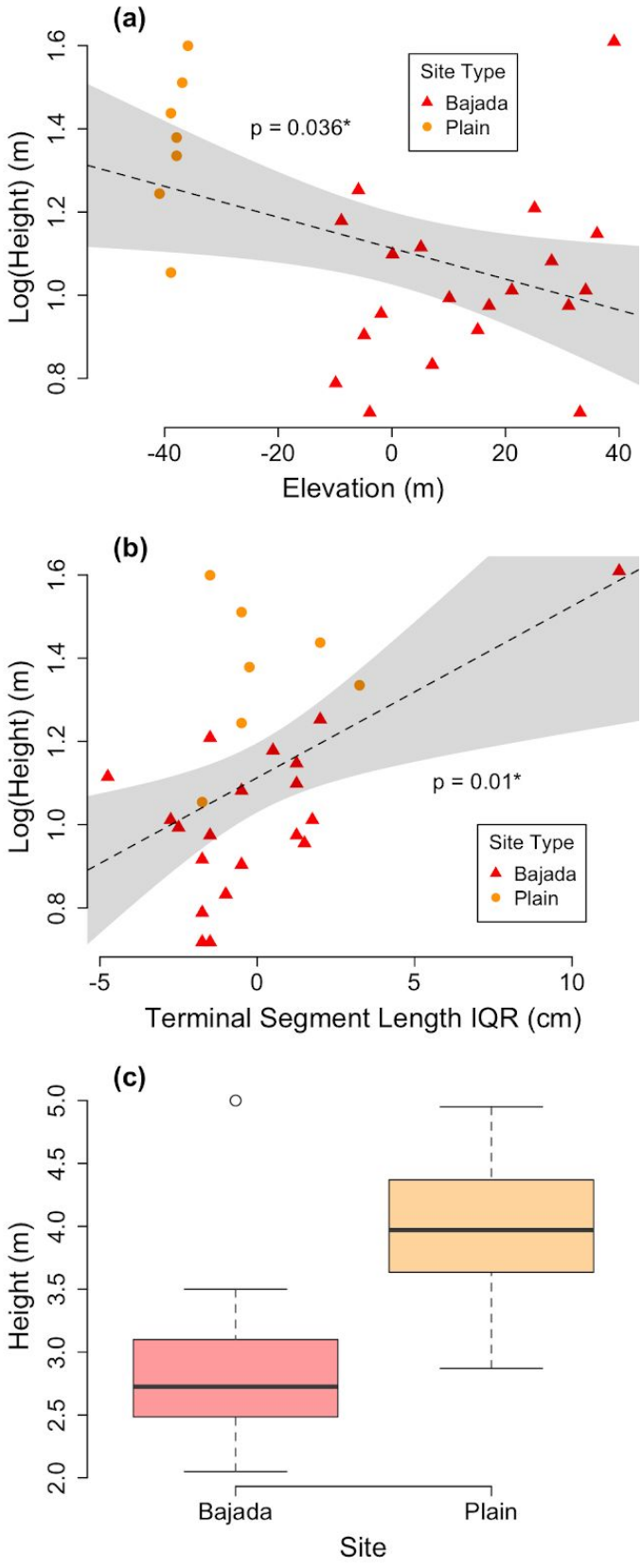
(a)
Log(Height) (m)
0.8
1.0
1.2
1.4
1.6
p = 0.036*
Site Type
Bajada
Plain
-40
-20
0
20
40
Elevation (m)
(b)
Log(Height) (m)
0.8
1.0
1.2
1.4
1.6
p = 0.01*
Site Type
Bajada
Plain
-5
0
5
10
Terminal Segment Length IQR (cm)
(c)
Height (m)
2.0
2.5
3.0
3.5
4.0
4.5
5.0
Bajada
Plain
Site

Fig. 3

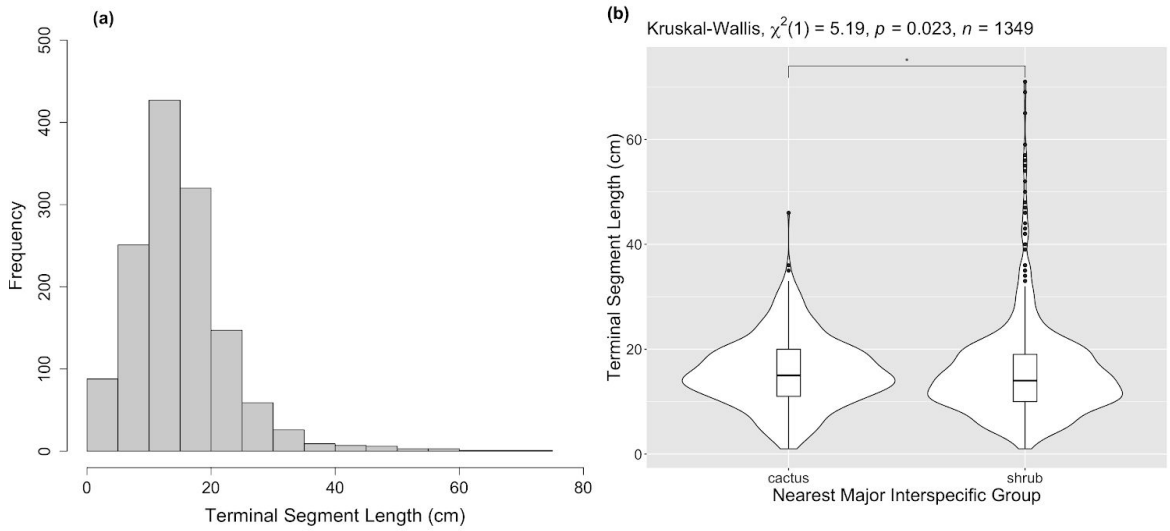
(a)
Frequency
0
100
200
300
400
500
0
20
40
60
80
Terminal Segment Length (cm)
(b)
Kruskal-Wallis, $\chi^2(1) = 5.19$, $p = 0.023$, $n = 1349$
Terminal Segment Length (cm)
0
20
40
60
cactus
shrub
Nearest Major Interspecific Group

Fig. 4

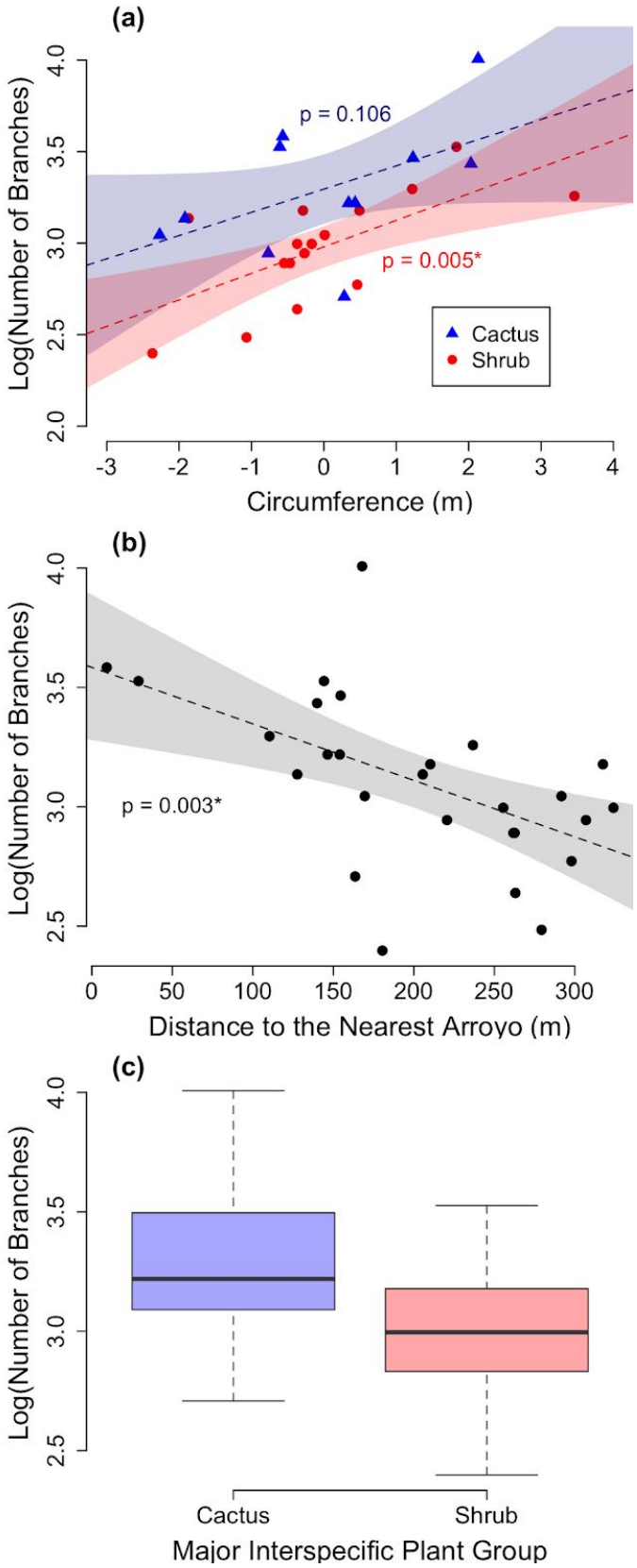
(a)
Log(Number of Branches)
p = 0.106
p = 0.005*
Cactus
Shrub
Circumference (m)
(b)
Log(Number of Branches)
p = 0.003*
Distance to the Nearest Arroyo (m)
(c)
Log(Number of Branches)
Cactus
Shrub
Major Interspecific Plant Group

Fig. 5

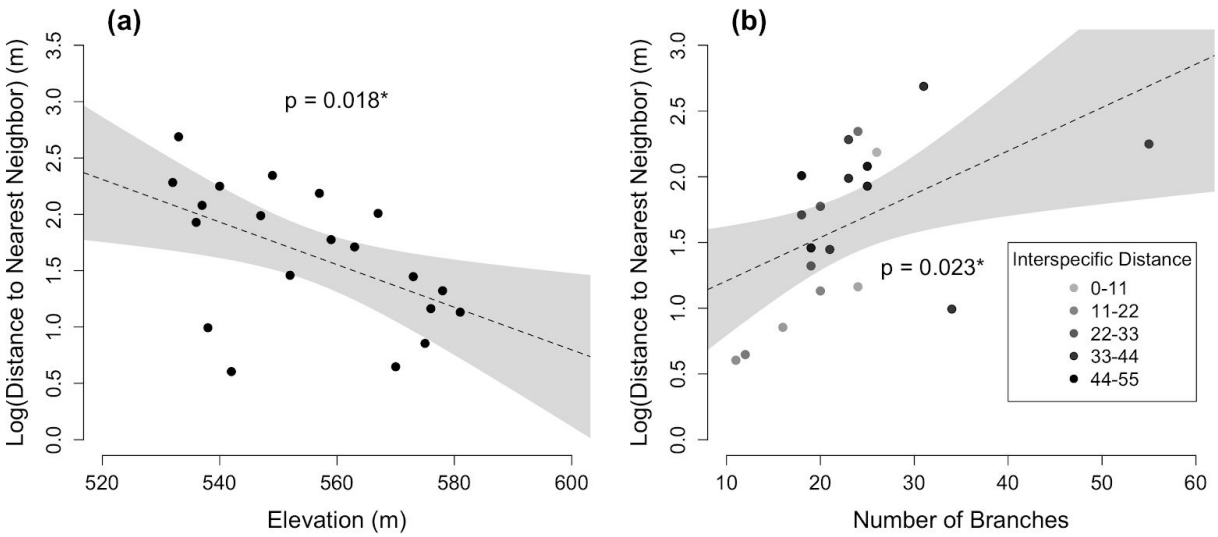
(a)
p = 0.018*
Log(Distance to Nearest Neighbor) (m)
Elevation (m)
(b)
p = 0.023*
Log(Distance to Nearest Neighbor) (m)
Number of Branches
Interspecific Distance
0-11
11-22
22-33
33-44
44-55

Fig. 6

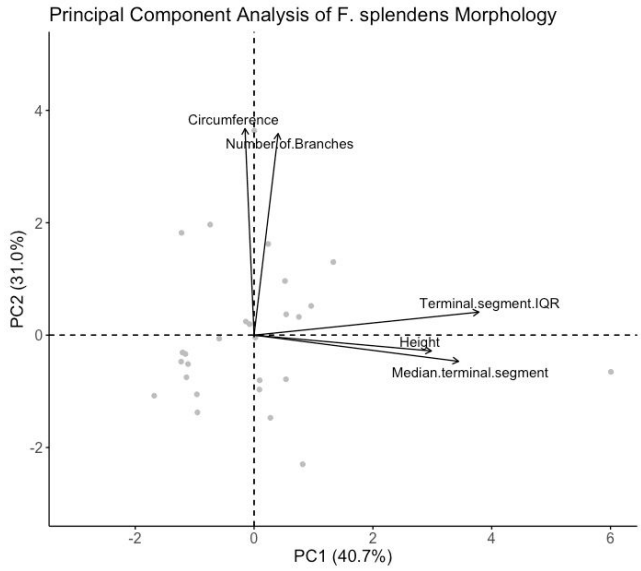
Principal Component Analysis of F. splendens Morphology
Circumference
Number.of.Branches
Terminal.segment.IQR
Height
Median.terminal.segment
PC2 (31.0%)
PC1 (40.7%)
4
2
0
-2
-2
0
2
4
6

Fig. 7