Landscape Ecol (2021) 36:527–547
https://doi.org/10.1007/s10980-020-01149-8

RESEARCH ARTICLE

Geomorphic controls on shrub canopy volume and spacing of creosote bush in northern Mojave Desert, USA

James H. Gearon · Michael H. Young

Received: 30 June 2020 / Accepted: 27 October 2020 / Published online: 12 November 2020

Abstract
Context Studies on the role of geomorphology on vegetation structure at the basin scale are rarely available and less likely in the future due to access, funding, and potential health risks.
Objectives Our goal is to determine the primary abiotic controlling factor(s) on shrub canopy structure using a dataset of approximately 23 million individual shrubs, generated using remote sensing and ground-truthing by Young et al. (in Remote Sens 9(5):16, https://doi.org/10.3390/rs9050458, 2017). We posit that landscape position and local-scale geomorphic features in a desert alluvial fan environment will influence canopy volume and shrub spacing of creosote bush *Larrea tridentata*.
Methods We relate selected characteristics (canopy volume and spatial distribution) of identified *L. tridentata* to aspect and surface geomorphology at each shrub location. Statistical analyses included K-S testing, distribution fitting, and several generalized linear models (GLMs). The study was located in Eldorado Valley, Nevada, USA.
Results Aspect and surface age have demonstrable influences on both shrub canopy volume and shrub spacing for all 5 geomorphic surfaces studied, with the highest median canopy volumes on east-facing surface (0.758 m^3) almost 5 $\times$ larger than the lowest median volumes (0.152 m^3) on the WNW-facing surfaces; variability in shrub volume was also higher on east-facing than west-facing surfaces. Shrub spacing on alluvial flat and fan skirt surfaces (2.418 and 2.333 m, respectively) were larger than older alluvial fan, fan piedmont and fan remnant surfaces (1.776, 1.837 and 1.892 m, respectively).
Conclusions Results show a significant relationship between shrub spacing and canopy volume by aspect and geomorphic surface, indicating a threshold at which biotic effects on canopy structure from intra-species competition transition to abiotic effects governed by geomorphic and climatological factors.

Mojave Desert · Larrea tridentata · Geomorphology · Shrub characteristics · Soil structure

J. H. Gearon
Department of Geological Sciences, Jackson School of Geosciences, The University of Texas at Austin, Austin, TX 78705, USA

M. H. Young (✉)
Bureau of Economic Geology, Jackson School of Geosciences, The University of Texas at Austin, Austin, TX 78705, USA
e-mail: michael.young@beg.utexas.edu

Introduction

Background

Mapping and characterization of arid and semi-arid basins endemic to the American west has a storied history of field mapping by federal, state, and county soil agencies (Gardner 1998). The twenty-first century development of agronomic science and changes in federal and local funding priorities have limited soil mapping of land areas with little to no commercial or residential use. Prime examples of these un-mapped areas are the numerous desert basins found in the Basin and Range Physiographic Province in the American west. It is unclear whether the current limitation of in-field soil and landscape mapping will change in the near or distant future.

Growing interest in the linkages and relationships between surface geomorphology and canopy structure (size, shape and spacing) has led to a number of studies. Before 1990, only a handful of papers had addressed feedback systems between geomorphology and vegetation in arid environments: notably Huntington (1914), Bryan (1928) and White (1969) (from Wainwright 2009). Geomorphologists have since begun including ecological factors into experimental designs, and in turn biologists and ecologists have started considering the influence of surface and bedrock geology on the character and distribution of biota (Parsons and Abraham 2009; Wainwright 2009). Motivation for convergence between these fields may lie in the growth of interdisciplinary and collaborative research (Wainwright 2009). Creosote Bush (*Larrea tridentata*) is often studied as a desert shrub due to its widespread geographic distribution in much of the American southwest (Bedford et al. 2009), specifically in the Mojave Desert, where our study is located.

It is generally agreed that the prime influencer on *L. tridentata* size is the controlling effect of surface geomorphology on water storage and infiltration (McAuliffe 1994; Hamerlynck et al. 2002), while spacing of *L. tridentata* shrubs is controlled by interplant root-mediated allelopathy (Lunt et al. 1973) or competition (Clark and Evans 1954; Pielou 1962; Phillips and MacMahon 1981). However, the implications of these local processes at the regional scale and how they are impacted by surficial geology remains only partly understood. Many previous studies concerning the geomorphic influence on desert shrubs are constrained by the spatial extent at which desert geomorphic processes operate (Dunkerley and Brown 2002) and sample size resolution (Caylor et al. 2005). Those processes, like most Earth surface subsystems, operate on wide-ranging temporal and spatial scales (Parsons and Abraham 2009).

This study, while constrained in time, seeks to shed light on basin-scale ecogeomorphic connections ranging from sub-meter processes to regional trends. To do so, we use the dataset from Young et al. (2017), which indexed every identifiable *L. tridentata* shrub within a 35,000 hectare (86,500 acre) region of interest in a desert basin in southern Nevada. In total, 22,982,205 *L. tridentata* shrubs were identified, each with area and spatial location information estimated directly from the images; canopy volume and height calculated from relationships obtained through shrub-specific measurements; and, a suite of high-resolution land surface information.

The unprecedented nature of this dataset, the origin of which is described below in "Purpose of this study" section, allows for rigorous analyses of shrub canopy structure extending across a variety of spatially distinct geomorphic units, something previously unreachable due to sampling constraints. The secondary motivation for this research is studying the biogeological characteristics of the Boulder City Conservation Easement (BCCE) in the Mojave Desert region of Nevada and, by proxy, desert basins common to the Basin and Range province in the Western United States. This tract of land remains poorly characterized due to a lack of field studies in the area and, because of recently discovered naturally occurring asbestos in surface soils (Buck et al. 2013), further substantial soil characterization work in this area is unlikely. This means that future, systematic investigations of this critically important conservation area (O'Farrell 2009) and other remote desert valleys could be further constrained.

There are technical constraints on assessing geomorphologically-induced vegetation signals. Until recently, acquiring and storing large, fine-resolution, remotely-sensed data sets was prohibitively expensive or technologically implausible. Even with modern advances in cost-efficient remote data collection, resolving sub-meter data over large spatial extents (i.e., tens of thousands of hectares) is still time and cost intensive. Even with these hurdles, others have found intriguing connections between geomorphology and vegetation in semi-arid basins (Caylor et al. 2005; Monger and Bestelmeyer 2006; Saco et al. 2007; Corenblit and Steiger 2009; Yetemen et al. 2010). Caylor et al. (2005) examined links between drainage networks and soil water balance patterns that, along with soil processes, affect organization of vegetation (i.e., into distinct patterns) at the landscape scale. Their analysis used shrub characteristics data from Yang and Milne (1997) collected from 3 plots, each 30 m by 30 m, which is still fairly limited when considering basin scale. Corenblit and Steiger (2009) considered the intimate linkages and feedbacks between landform dynamics and biological evolution at the global scale and discussed the concept of evolutionary geomorphology, which is interesting by itself but difficult to apply at the basin or hectare scales. Monger and Bestelmeyer (2006) created an abiotic (soil-geomorphic) template to assess coupling to biotic (vegetation) response. Their templates show the connectivity of biotic and abiotic processes and suggest experimental work to further understand and apply their framework. Saco et al. (2007) reported the role of slope and translocation of resources from bare patches to vegetation patches at the scale of 100s meters, in some cases leading to banded vegetation patterns oriented perpendicular to surface runoff flow direction. Finally, Yetemen et al. (2010) investigated the associations between land surface properties and landscape morphology through a spatial analysis of elevation, geology, soils, and vegetation to better understand geomorphic response. In their case, the National Land Cover Database (NLCD) at 28.5 m resolution was used to study vegetation patterns, which was not sufficient to assess characteristics and spacing of individual shrubs. The limited scopes of these projects outline the difficulties in large-scale investigations of ecogeomorphology.

Purpose of this study

In this study, we use a suite of high-resolution, remotely-sensed data and image-derived geomorphic units to investigate the ecology and geomorphology of a large swath of arid lands and present results using vegetation characteristics of $\sim$ 23 million *L. tridentata* shrubs. We aim to provide insight on the complex geomorphologic, ecologic and hydrologic processes that dominate this region of southern Nevada. Specifically, our goal is to determine the primary abiotic controlling factor(s) on shrub canopy structure, and we hypothesize that landscape position and local-scale geomorphic features in a desert alluvial fan environment will influence and constrain canopy structure (e.g., canopy volume and shrub spacing) of *L. tridentata*.

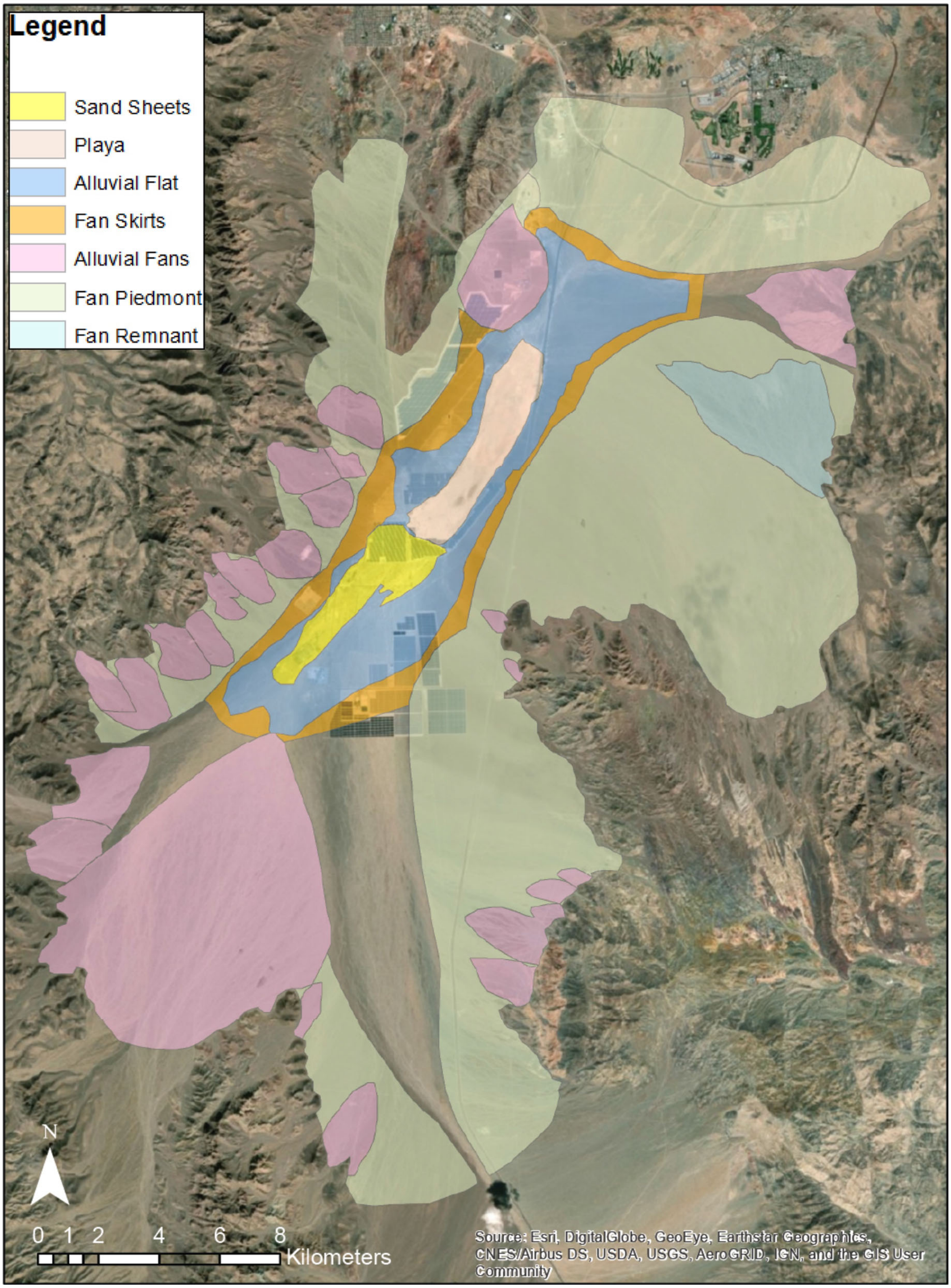
To our knowledge, no study to date has reported on the use of such a comprehensive data set of desert shrub characteristics obtained from high-resolution images at the basin scale. The benefit of conducting a high-resolution, basin-scale study, in this case in a conservation easement, is that local climate, precipitation, soil properties, and floral variability are all naturally controlled and (mostly) preserved from anthropogenic disturbance. Isolating variables such as small-scale changes in surficial geology to assess causal relationships at the basin scale becomes substantially easier due to the relative spatial and temporal uniformity of the area of interest. Additionally, the availability of high-resolution data allows for less error and more precision in the search for these relationships.

Materials and methods

Site description

The study area for this research is within the Boulder City Conservation Easement in Eldorado Valley, Nevada (35° 56.15 N, 114° 53.93 W) (Fig. 1). The BCCE (35,000 ha in area) was created in 1994 to preserve, protect, and enhance the flora and fauna of the area, specifically the Desert Tortoise (*Gopherus agassizi*) a once endangered (now threatened) species indigenous to the southwestern United States (O'Farrell 2009). The time period for this easement was originally set at 50 years.

The BCCE is a large desert drainage basin. Like nearly all desert basins common to the American Southwest, the BCCE is within the Basin and Range Physiographic Province, which is defined by north–south trending faults manifesting as alternating narrow mountains and wide basins. With the increase in relief, weathering processes began transporting alluvium basin-ward. This explains the common geomorphic trend of fan piedmont and fan apron creation in American desert basins, where alluvial material fines basin-ward along gentle slopes and segregates several


Legend
Sand Sheets
Playa
Alluvial Flat
Fan Skirts
Alluvial Fans
Fan Piedmont
Fan Remnant
N
0 1 2 4 6 8 Kilometers
Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

◀**Fig. 1** Boulder City conservation easement located in Eldorado Valley, Nevada, USA with demarcated outline of geomorphic units within the BCCE following the schema developed by (Peterson 1981)

geomorphologic regimes in a basin. This leads to a succession of disparate channels next to the mountain front which, moving basin-ward, coalesce into fan aprons (bajadas). The center of the basin is typically defined by a flat playa where the finest weathered alluvial material collects. The BCCE follows this evolution, with surface runoff flowing toward Eldorado Dry Lake, a dry lakebed in the center of the easement (Clark County 2019).

Geographically, the BCCE extends south-southwest from just south of Boulder City, Nevada, for approximately 35 km. The elevation of the study area ranges from 521 m in Eldorado Dry Lake to 2152 m on McCullough Mountain (Young et al. 2017). From 1931 to 2004, mean annual precipitation in Boulder City, NV was 138 mm (Station 261071, Western Regional Climate Center, Reno, Nevada). Temperature ranges from 0.5 °C in January (mean minimum temperature) to 32.5 °C in July (mean maximum temperature). The mean annual temperature is 19.6 °C. The topography of the BCCE is a flat, level alluvial plain that extends radially upward toward the surrounding mountain ranges—The Eldorado Mountains and Opal Mountains to the east, the McCullough Range to the west, and the River Mountains to the north (Clark County 2019). The soil of the BCCE is generally igneous- and sedimentary-derived, young alluvial deposits, consisting of a coarse, gravelly sand mixture (Clark County 2019). The soils contain low organic matter and low carbon/nitrogen ratios. Carbonates in the shallow subsurface likely contributed to the creation of petrocalcic horizons (O'Farrell 2019).

Data collection

The parent study to this work (Young et al. 2017) led to the development of a dataset to assess the location and geomorphology of Desert Tortoise (*Gopherus agassizii*) burrow locations in the Boulder City Conservation Easement (BCCE), northern Mojave Desert, NV. In that study, both LiDAR (point density: 5–8 points/m^2) and multispectral airborne photography (4 bands, 15.24 cm/pixel) were collected to characterize the BCCE. The multispectral images were more effective in characterizing canopy structure than LiDAR, which was used mainly for creating DEMs and other topographic surface derivatives. Shrubs were identified and characterized by a search algorithm that iteratively categorized pixels as either shrubs or bare ground, using threshold values for the Normalized Difference Vegetation Index (NDVI) and Average Reflectance (AVGr) of a given pixel. Shrubs were identified when 5 or more pixels fell within the accepted thresholds and exceeded an area of approximately 34 cm^2. Differential shrub area and threshold values allowed for accurate estimates of shrub species as well as structure (especially canopy area). A comparison of shrub canopy area obtained from direct field measurements and calculated by the algorithm showed high correlation ($R^2 = 0.928$; n = 199).

Canopy structure

We assessed several *L. tridentata* shrub characteristics and their variability across the BCCE. Shrub height was calculated using a power law function that relates shrub area to height ($R^2 = 0.683$; n = 199), and canopy volume was calculated as the frustum of an inverted, right circular cone (see Hamerlynck et al. 2002). The power law approach for shrub height is more effective than LiDAR returns, which Young et al. (2017) found underestimated *L. tridentata* canopy height by $\sim$ 40% (Others have reported the same limitation of using lidar on sparse open canopies (e.g., Glenn et al. 2011)). The full methodology for the large-scale characterization of shrub canopy location and structure can be found in Young et al. (2017), and the dataset is available for download (Andrews et al. to be submitted). With the *L. tridentata*-specific location and volume data available, shrub spacing was determined accordingly and then assigned to geomorphic surface and/or other landscape descriptors (as described below). These shrub spacing calculations were conducted by determining planar distance to the nearest feature centroid for every shrub in the field of interest (Near Tool, ArcGIS, v15.1, ESRI 2016). Data were stored in ArcGIS shapefiles (.shp) and ArcGIS geodatabases (.gdb). Analyses and manipulations were carried out using ArcGIS tools and Python, including libraries SciPy, a scientific computing Python package (Virtanen et al. 2020); Pandas, a high-performance data structure and analytics package for Python (McKinney 2010); and Matplotlib and Seaborn for data visualization (Hunter 2007).

Geomorphic surface designation

General desert geomorphic zones were mapped using aerial photography and descriptions from Peterson (1981), who denoted two major physiographic parts of desert basins—piedmont slope and basin floor—based on slope, presence of depositional versus erosional landforms, and alluvial provenance. The piedmont slope is defined by a range of slope gradients greater than 1% and up to 30% near the bounding mountain front (Peterson 1981). Alluvial provenance for fan alluvium is a narrow range of directly upslope mountain valleys. Piedmont slopes are also characterized by distinguishable major landforms, notably mountain-valley fans, ballenas, alluvial fans, fan piedmonts, and fan skirts (Peterson 1981).

The second major physiographic part identified by Peterson (1981) is the basin floor, demarcated by slope gradients less than 1% and by a change in sediment routing direction from orthogonal to the bounding mountain front, to parallel with the long axis of the desert basin. Basin floors (also called bolson floors) are characterized by constituent major landforms: alluvial flats—both relict and recent, sand sheets, beach plains, alluvial plains, lake plains, and playas. These major landforms are in turn composed of component landforms of which one is considered: The fan remnant; a part of the fan piedmont major landform. One of these fan remnants is easily identified via aerial photograph (Fig. 1). Other than one fan remnant geomorphic surface, this study will focus at the major landform scale, as more specific mapping via aerial imagery is difficult without ground truthing, which would be somewhat counter to the goals of studied remote basins. Here, we study five major landforms and one component landform from the piedmont slope and basin floor major physiographic parts, though we note that these designations are general and that overlap in age of certain component landforms or landform elements is likely. Also, playa and sand sheets surfaces (Fig. 1) were discarded from analysis; data coverage of the playa in the original dataset was negligible, and sand sheets are patchy and hard to discern accurately from aerial photography. Additionally, sand sheets are often only identifiable by large numbers of closely-packed shrubs, and identifying geomorphic features using vegetation violates the independent nature of the study of their relationship. A further complication exists within the alluvial flat major landform. Alluvial flats can be relict or recent, with the latter generally mantling the former in areas. We designated recent alluvial flat for this study based on observations that the majority of mantled, drainage-laden deposits correspond to alluvial flat locations, with only a few barren relict deposits interpreted as appearing beneath. All surfaces used in analysis and their corresponding definitions are available in Table 1.

Relative surface age for all identified geomorphic surfaces was determined using Peterson (1981) and the NCSS Handbook Glossary of Landform and Geologic Tools (Table 1), as well as geomorphic and stratigraphic first principles (e.g., surficial aeolian deposits are younger than underlying developed fan piedmonts) (Schoeneberger and Wysocki 2017). Relative age was assigned as follows (from youngest to oldest): (1) Alluvial Flats, (2) Fan Skirts, (3) Alluvial Fan, (4) Fan Piedmont, (5) Fan Remnants. This designation also generally corresponds to the distance of surfaces from the basin center.

Aspect calculation

Surface aspect (direction of surface inclination) was calculated as a continuous measurement (0°–360°) using a 1 m^2 cell-size DEM and the Aspect Tool (ArcGIS, v15.1, ESRI 2016), which identifies the maximum downslope change between a cell and its neighbors. To constrain any aspect relationship between shrub canopy size or spacing, numeric aspect values were categorized into 16 bins, each representing 22.5° on a circle, with East representing 90° and North representing 0°. These bins are narrower than other studies that examine similar relationships (e.g., Istanbulluoglu et al. 2008; Marston 2010). Herein, we binned each shrub contained in an identified surface accordingly and determined the strength of association of shrub volume across the full range of aspects (0°–360°).

Competition analysis

A positive linear relationship between plant size (canopy volume) and spacing in arid environments has been interpreted to indicate a biotically

Table 1 Explanation of geomorphic descriptor data: information from the NCSS handbook: glossary of landform and geologic terms (Schoeneberger and Wysocki 2017; Peterson 1981)

(Piedmont slope) Fan Piedmont	The most extensive landform on piedmont slopes, formed by the lateral, downslope, coalescence of mountain-front alluvial fans into one generally smooth slope with or without the transverse undulations of the semi-conical alluvial fans, and accretion of fan aprons. Also recognized and used as a landscape term
(Piedmont slope, Fan Piedmont) Fan Remnant	A general term for landforms that are the remaining parts of older, nonactive, fan-landforms, such as alluvial fans, fan aprons, inset fans, and fan skirts, that either have been dissected (erosional fan-remnants) or partially buried (non-buried fan-remnants). A fan remnant must retain a relatively flat summit that is a relict fan-surface (> 50% intact). A non-buried fan-remnant is a relict surface in its entirety
(Piedmont slope) Fan Skirt	The zone of smooth, laterally-coalescing, small alluvial fans that issue from gullies cut into the fan piedmont of a basin or that are coalescing extensions of the inset fans of the fan piedmont, and that merge with the basin floor at their toe-slopes. These are generally younger fans that onlap older fan surfaces
(Piedmont slope) Alluvial Fan	A low, outspread mass of loose materials and/or rock material, commonly with gentle slopes. It is shaped like an open fan or a segment of a cone. The material was deposited by a stream at the place where it issues from a narrow mountain valley or upland valley or where a tributary stream is near or at its junction with the main stream. The fan is steepest near its apex, which points upstream, and slopes gently and convexly outward (downstream) with a gradual decrease in gradient
(Basin floor) Alluvial Flats	(colloquial: western United States) A nearly level, graded, alluvial surface in bolsons and semi-bolsons that lacks distinct channels, terraces, or flood plain levels

competitive regime (Clark and Evans 1954; Pielou 1962; Yeaton et al. 1977; Fowler 1986). Median shrub canopy volume and shrub spacing values thus were computed groupwise for aspect and geomorphology levels. These medians were then investigated for correlative power. The analysis was chosen to be run on median group values for computational efficiency and visualization efficacy. Each group has over one million datapoints, making the median value a powerful, robust and accurate descriptor of the data.

Data analysis

Full-scale statistical exploration and preliminary analyses of this large dataset were found to be computationally untenable and therefore down-sampling was performed on the dataset. The dataset was sampled at 5% of the original $\sim$ 23 million datapoints using stratified random sampling to preserve proportions of data groups. Kolmogorov–Smirnov tests were performed for each response variable between the sample and full dataset to quantify representability (D = 0.00, p-value = 0.29 for shrub canopy volume and D = 0.00, p-value = 0.70 for shrub spacing). Volume of and spacing between individual shrubs were analyzed separately as continuous response variables of differing distributions. Shrub canopy volume data exhibited a heavy-tailed, right-skewed distribution. Shrub spacing data was distributed more symmetrically, with a positive offset and a larger tail. Both response variables were fit to a suite of distributions to predict the probabilities of the magnitude of shrub canopy volume and inter-shrub spacing values. Distribution fitting was done with the SciPy Python Package (Virtanen et al. 2020) and the "fitdistrplus" and "GAMLSS" packages in R (Rigby and Stasinopoulos 2005; Delignette-Muller and Dutang 2015). Firstly, histograms and Cullen-Frey graphs were produced for both response variables to identify candidate distributions. Shrub spacing and canopy volume were then iteratively fit to a suite of distributions. AIC values, log-likelihood, and visual inspection allowed for the selection of the best-fit distributions for both response variables. Shrub spacing values were best fit to a Gamma distribution, parameterized with shape k and scale θ that has a probability density function (Eq. 1; Virtanen et al. 2020):

$$f(x,k,\theta) = \frac{x^{k-1}e^{-\frac{x}{\theta}}}{\theta^k\Gamma(k)} for\, x > 0\, and\, k,\theta > 0 \quad (1)$$

Shrub canopy volume data were best fit to a generalized half normal distribution (GHN). parameterized with shape β, location μ, and scale α that has a probability density function (Eq. 2; Cooray and Ananda 2008):

$$f(x,\beta) = \frac{\beta}{\Gamma(\frac{1}{\beta})}\exp\left(-|x|^{\beta}\right) for\, x > 0 \quad (2)$$

The GHN distribution is identical to an exponential distribution when $\beta = 1$ and is identical to a half normal distribution when $\beta = 2$.

To model both response variables as a function of covariates, data exploration was conducted on a variety of explanatory variables, both continuous and categorical (see Young et al. (2017) for more information). From those, two categorical explanatory variables were selected for further study: geomorphic designation and binned aspect, which demonstrated first order predictive power based on graphical exploration. A Generalized Linear Model (GLM) was constructed for both response variables (R Core Team 2020). Shrub spacing was modeled with a Gamma GLM with an identity link function (R^2 = 0.1). Shrub canopy volume was modeled with a Gamma GLM with an inverse link function (R^2 = 0.3). Both GLMs utilized the Gamma family parameter due to the positive continuous nature of shrub volume and spacing values. Both GLMs utilized the same fixed covariates: geomorphic surface (categorical with 5 levels) and direction (binned aspect: categorical with 16 levels). The interaction terms are *GeomorphicSurface* × *Direction*. The R^2 values for both GLMs are used as a measure of explanatory power, not fit. Physical implications of the modelled relationships will be addressed in the "Discussion" section.

Regarding p-values and statistical significance, a massive dataset tends toward significance, largely due to the disconnect between the initial purpose of inferential statistical models (e.g., ANOVAs) and their current widespread applications. As sample size increases, small variations become statistically significant, which in turn can obfuscate the underlying physical reality. In fact, the American Statistical Association cautions against using the term "statistical significance" because it is prone to misinterpretation (Wasserstein and Lazar 2016). While p-values will be reported for transparency, other measures of and justifications for physical effects will be reported and discussed with the aim to move beyond "a $\alpha < 0.05$ world."

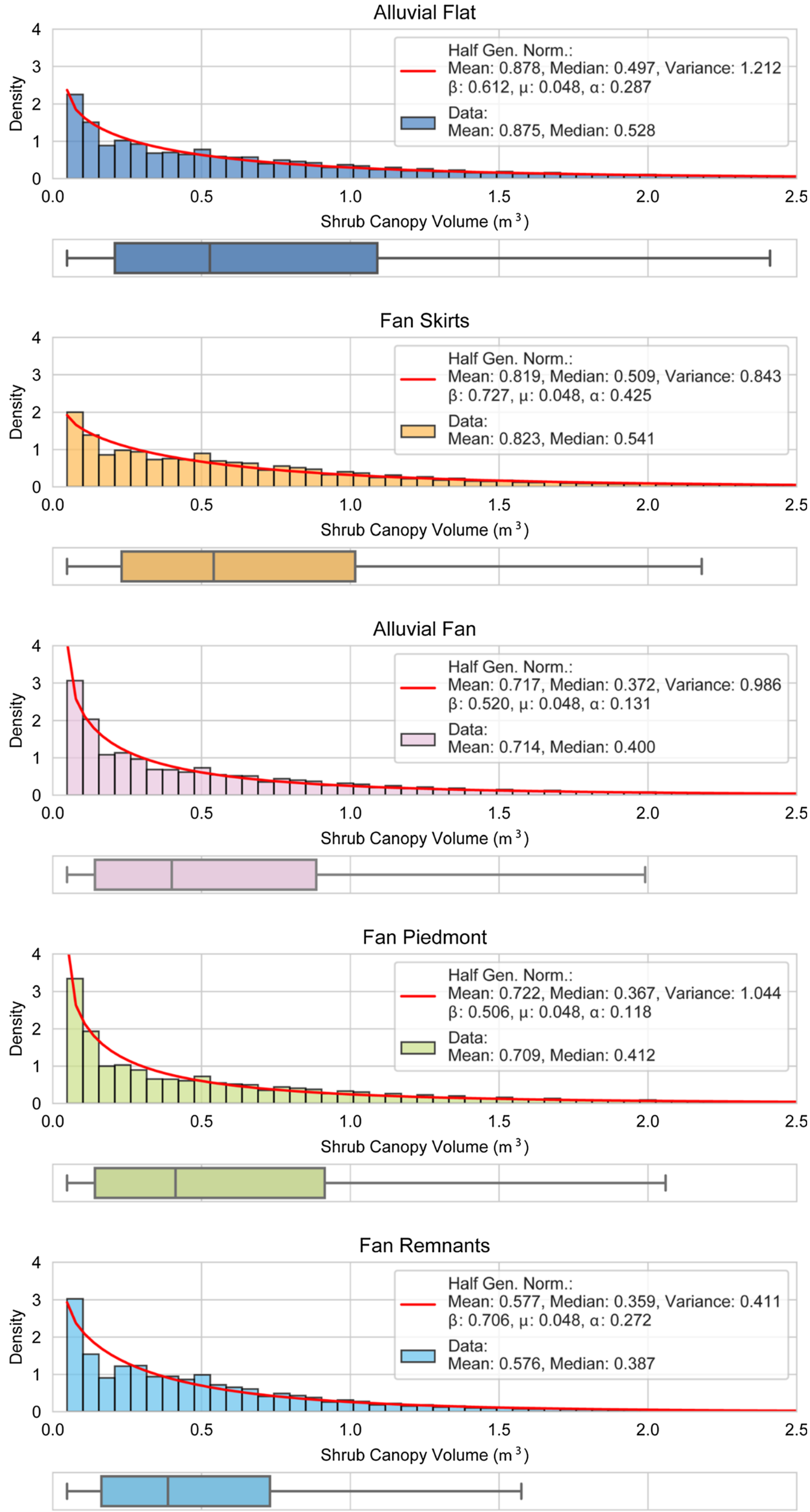
Results

Shrub canopy volume

Shrub canopy volume and geomorphology

Results indicate that *L. tridentata* shrub canopy volume varies with geomorphic surface. Specifically, canopy volume is negatively correlated with geomorphic age and generally distance from the center of the basin (Fig. 2). All five categories follow the GHN distribution—heavy-tailed with higher mean than median values. This observed distribution can be explained by (1) the physical limitation that outliers of shrub volume and spacing cannot be negative, and (2) the mis-identification of closely packed shrubs (shrub islands) or Catclaw Acacia trees (*Senegalia greggii*) as one large shrub. The Fan-Remnants (FR) has a median value of 0.387 m^3—the lowest of any category. The median shrub canopy volumes in the Fan Piedmont (FP) and Alluvial Fan (AF) category are similar at 0.412 and 0.400 m^3. Median canopy volumes of remaining categories Fan Skirts (FS) and Alluvial Flats (AFl) are appreciably higher than previous categories; 0.541 m^3 and 0.528 m^3 respectively. The range in volumes of shrubs found on AFl surface is the highest of any surface (variance = 1.212). The similarity of medians between FP and AF categories can be possibly explained by the spatial co-location of these two geomorphic surfaces, with Fan Piedmonts typically being the downslope-evolving amalgam of discrete alluvial fans, as well as the relative hardiness of *L. tridentata*, which can grow successfully on older, structured soils. There does appear to be a visual distinction in canopy volumes between the FR, FP, and AF categories versus the FS and AFl categories, where variability from the fitted distributions in the form of larger boxplot IQR ranges and variance moment values are observed on the younger surfaces. This difference (addressed further below) provides evidence for geomorphic influences on *L. tridentata*

Fig. 2 Density histograms for shrub canopy volume, fitted to a half generalized normal probability density function for each geomorphic surface. Box plots are plotted on the same x-axis. Surfaces are arranged in increasing relative age from top to bottom. Relevant statistics and parameters are reported



canopy volume. Here, median values, IQR, variance, and full data ranges with a "flatter" distribution (FS & AFl) may indicate surfaces with more active recruitment.

Aspect–volume relationship

Irrespective of geomorphology, aspect and shrub canopy volume were investigated for correlative power using 16 density histograms with fitted GHN PDFs, 16 corresponding box-and-whisker plots for each direction category and each geomorphic surface. The resultant plots (Figs. 3, 4) were generated using the entire dataset (23 million data points). The results indicate a strong preference for shrubs to establish on east-southeast facing soil surfaces.

Results show shrub canopy volume distribution for every binned aspect category (Fig. 3), and the goodness-of-fit between the plotted data and the GHN distribution. For both the full dataset and the fitted

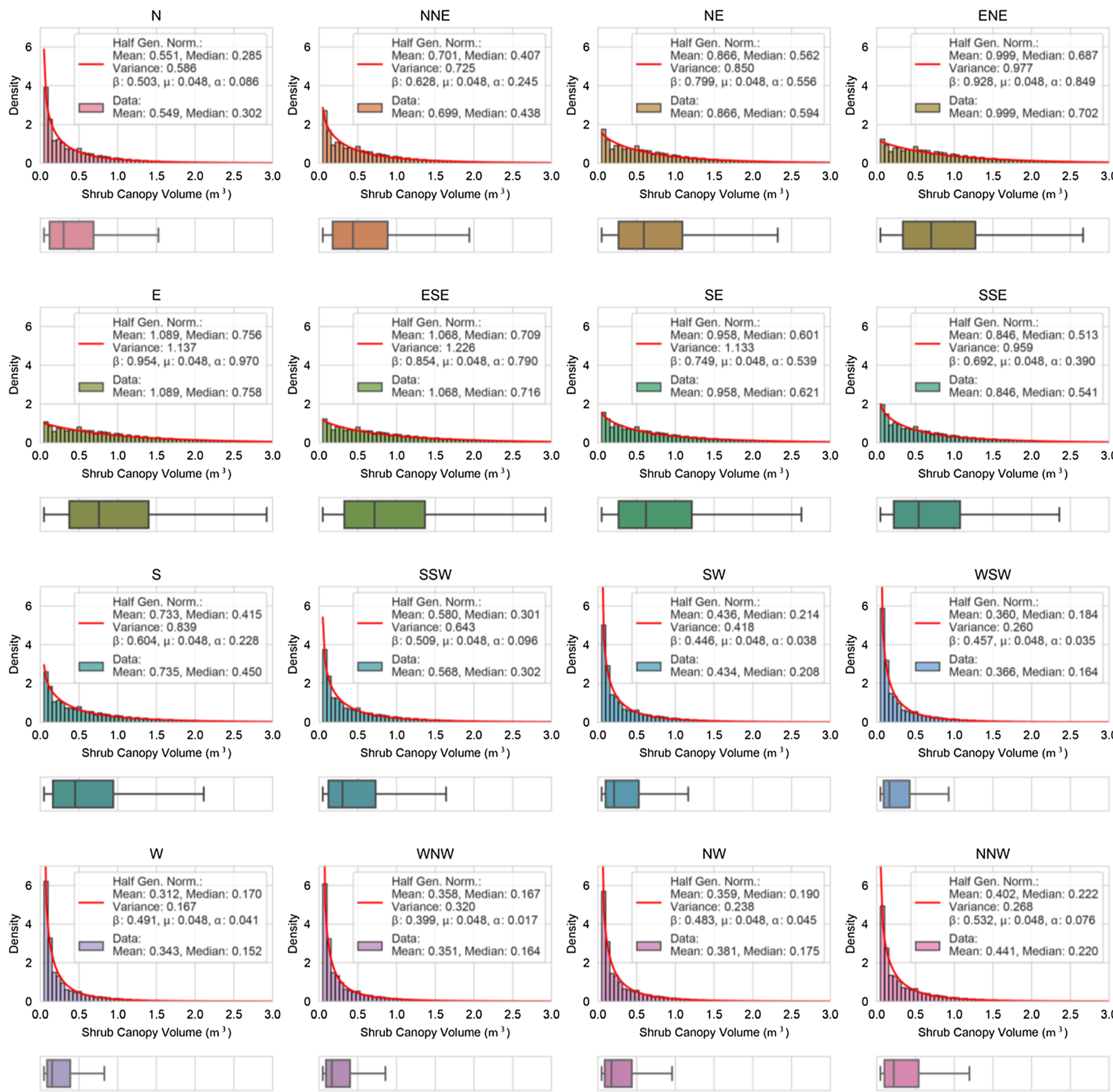


Fig. 3 Density histograms for shrub canopy volume, fitted to a half generalized normal probability density function for each of 16 binned aspect categories. Box plots are plotted on the same x-axis. Relevant statistics and parameters are reported

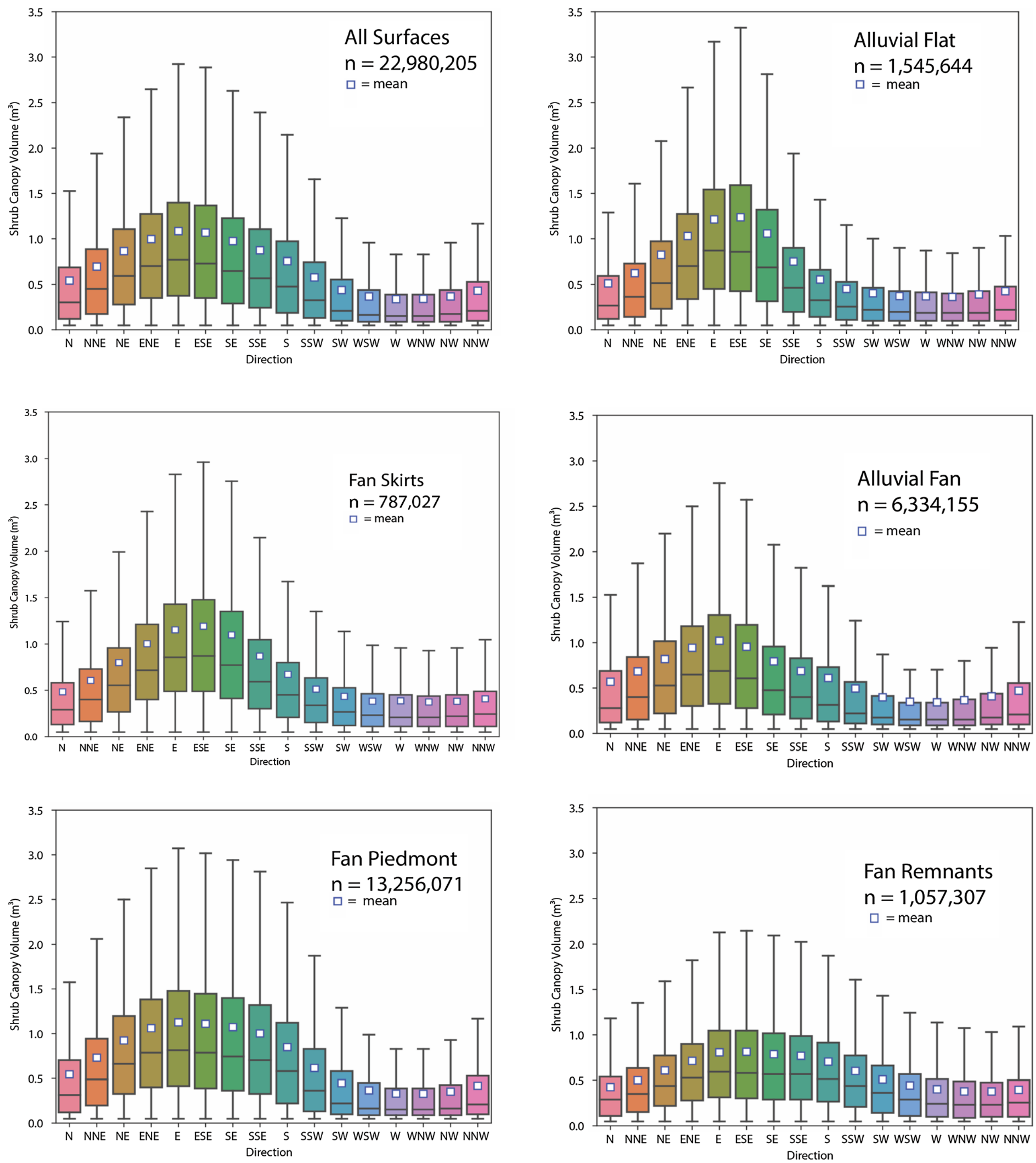


Fig. 4 Shrub canopy volume plotted against 16 directions (22.5 deg./category) for every geomorphic surface. Results show the relationship between canopy volume and E facing aspects holds for every observed surface

PDFs, the highest median (0.758 and 0.756, respectively) and mean canopy volumes (1.089 for both) were observed on east-facing surfaces, the lowest median (0.152 and 0.170, respectively) and mean volumes (0.343 and 0.312, respectively) were observed on west-facing surfaces. The reported distribution parameters—especially shape (β) and scale (α)—are also largest on east-facing surfaces and smallest on west-facing surfaces (WNW specifically), demonstrating physical significance of the distribution parameters when describing shrub canopy volumes by aspect. These findings can and should inform modelling of *L. tridentata* canopy structure and distribution.

The box-and-whisker plots for shrub canopy volume as a function of aspect (Fig. 4: All Surfaces) across the entire field site (i.e., all surfaces binned together) give insight into the importance of surface direction. Median canopy volumes ranged from 0.758 m^3 for surfaces facing east to 0.152 m^3 for surfaces facing in the west direction. The range of shrub canopy volumes and group median values are substantially higher toward east-facing slopes and become distinctly lower across west-facing slopes. Data within every directional bin are expectedly skewed toward higher volumes, as Q1 necessarily tends toward zero. Results indicate larger IQR (Q3–Q2) ranges, associated with larger median values, as well as Q4 (upper quartile–upper whisker) values in the east-facing slopes, indicating a higher number of large shrubs and a larger variability within those directional categories. The results demonstrate that east-facing shrubs are typically larger in volume, but more variable in size, than shrubs found soils facing the west. The difference in ranges may be due to more active recruitment of shrubs on east-facing slopes, and/or that a small number of individual shrubs located in shrub islands are interpreted as single (larger) shrubs, highlighting the limits to our analytical capability.

It is appropriate to consider the relative importance of geomorphic surface and aspect on shrub volume. Here, we represent shrub volume as a function of both, subdivided by geomorphically-defined surfaces (Fig. 4). It is clear that the patterns of aspect-volume for each geomorphic surface considered separately is similar to the basin-wide aspect graph shown (Fig. 4: All Surfaces) with larger medians and ranges of shrubs facing east directions versus those facing west directions. There is observable variability between each graph; shrubs located on the FR surface have the lowest median, range and IQR of any category and every direction. Shrubs found on the AFl surface have larger medians and ranges, as well as far more variability across every direction. The effect of aspect on shrub volume appears more influential on younger geomorphic surfaces, although present regardless of surface age or designation.

Shrub spacing

Geomorphology–spacing relationship

Shrub spacing analysis (Fig. 5) indicates that shrub spacing of *L. tridentata* is modulated by geomorphic surface (and therefore surface age). This points to a fundamental relationship between geomorphology and spacing when using major landform scale geomorphic surfaces. All surfaces are well fit by the Gamma distribution as seen by the visual similarity of fit as well as numerical similarity between mean and median values. Visual fits of the Gamma distribution are better on the AFL and FS categories compared to the older three categories. Median shrub spacing on younger surfaces (AFL and FS) are clearly larger than older surfaces (AF, FP and FR). That the oldest geomorphic surface has the third-highest spacing value is initially surprising but may be related to end-stage competitive processes—namely dispersion—that have been documented in arid and semiarid settings (Fowler 1986). The AFL category has the largest range of shrub spacing, the same relationship observed with volume in Fig. 2.

Aspect–spacing relationship

Results show a meaningful relationship between aspect and shrub spacing, if not as obvious as the aspect-volume relationship. Mean and median shrub spacing values (and fitted Gamma values) maximize on east-facing slopes (Fig. 6). The largest median shrub spacing value is 2.186 m (E), while the smallest spacing value is 1.591 m (WSW). Similarly, distribution variance increases toward east-facing slopes indicating differential shrub growth typical of active recruitment surfaces. To further investigate the interconnected effects of geomorphology and aspect on shrub spacing, all 16 aspect categories were plotted for each geomorphic surface (Fig. 8). Results demonstrate the complex interaction between aspect and geomorphology. Median spacing increases on east-facing surfaces for every geomorphic category. Values are slightly right skewed. For geomorphic-defined surfaces, specifically on the AFL and FS surfaces, larger spacings were observed on east-facing slopes,

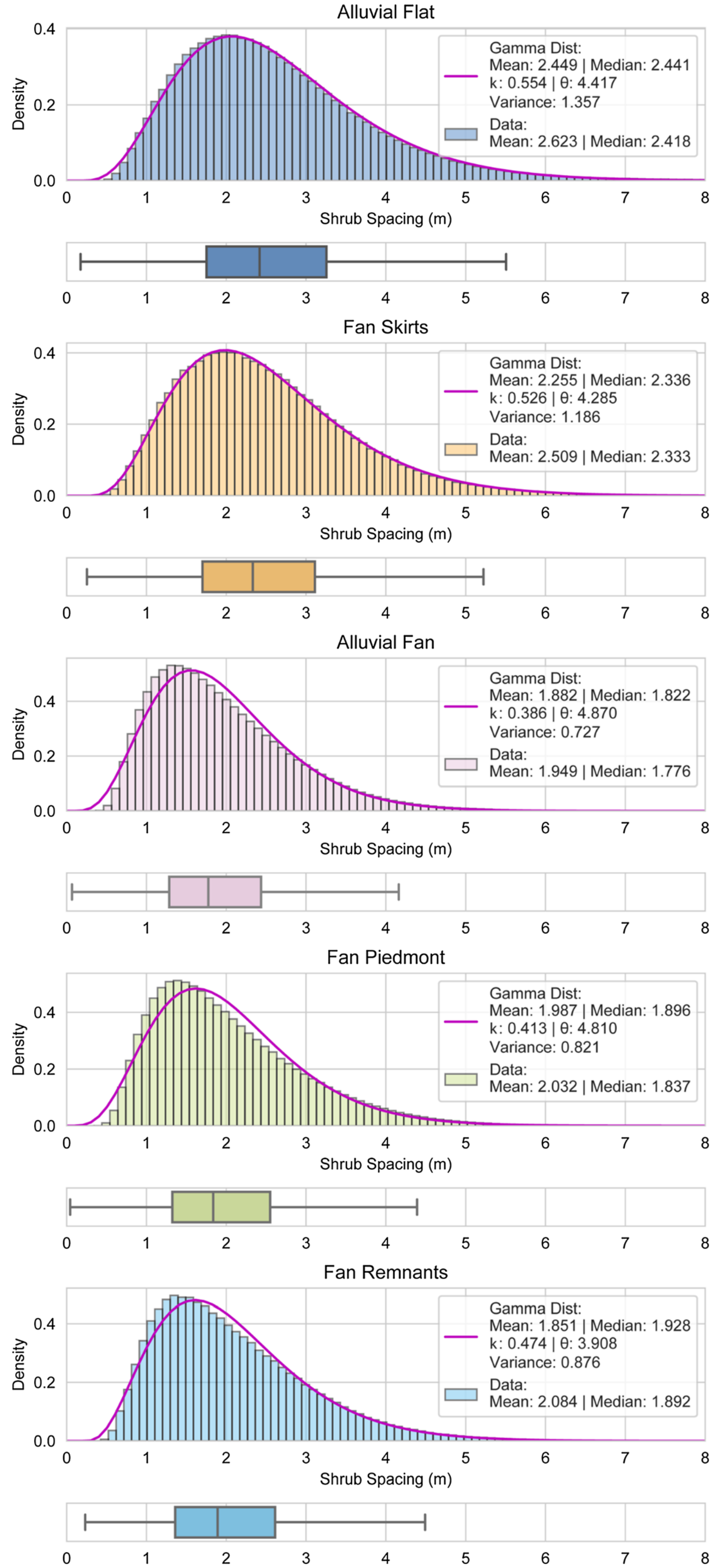


Fig. 5 Density histograms for shrub spacing, fitted to a gamma probability density function for each geomorphic surface. Box plots are plotted on the same x-axis. Surfaces are arranged in increasing relative age from top to bottom. Relevant statistics and parameters are reported

indicating larger shrub spacing variability, possibly indicating active surface recruitment. The FR category has the weakest aspect-spacing signal of any geomorphic surface. This may be explained by the growth tendencies of *L. tridentata*, which often recruits in former plant spaces leading to dispersion (sensu McAuliffe and McDonald 2006).

Discussion

Geomorphic influences on *L. tridentata* canopy volume

Larrea tridentata canopy volume is negatively correlated with geomorphic surface age, which have been shown by others to be caused by increased argillic (B_{tk}) horizon development (e.g., McFadden et al. 1987). The observed trends in the canopy volume of *L.*

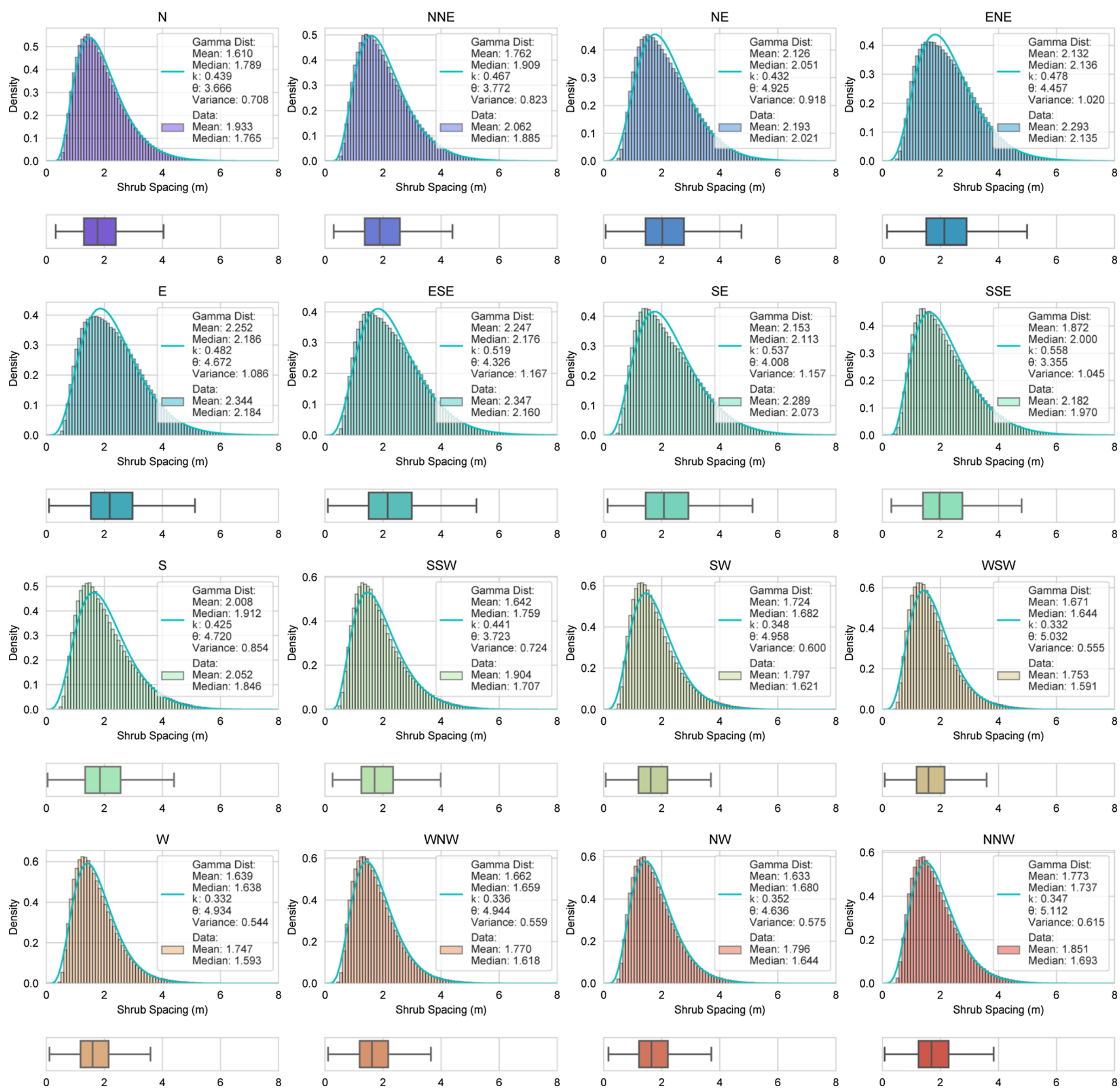


Fig. 6 Density histograms for shrub spacing, fitted to a gamma probability density function for each of 16 binned aspect categories. Box plots are plotted on the same x-axis. Relevant statistics and parameters are reported

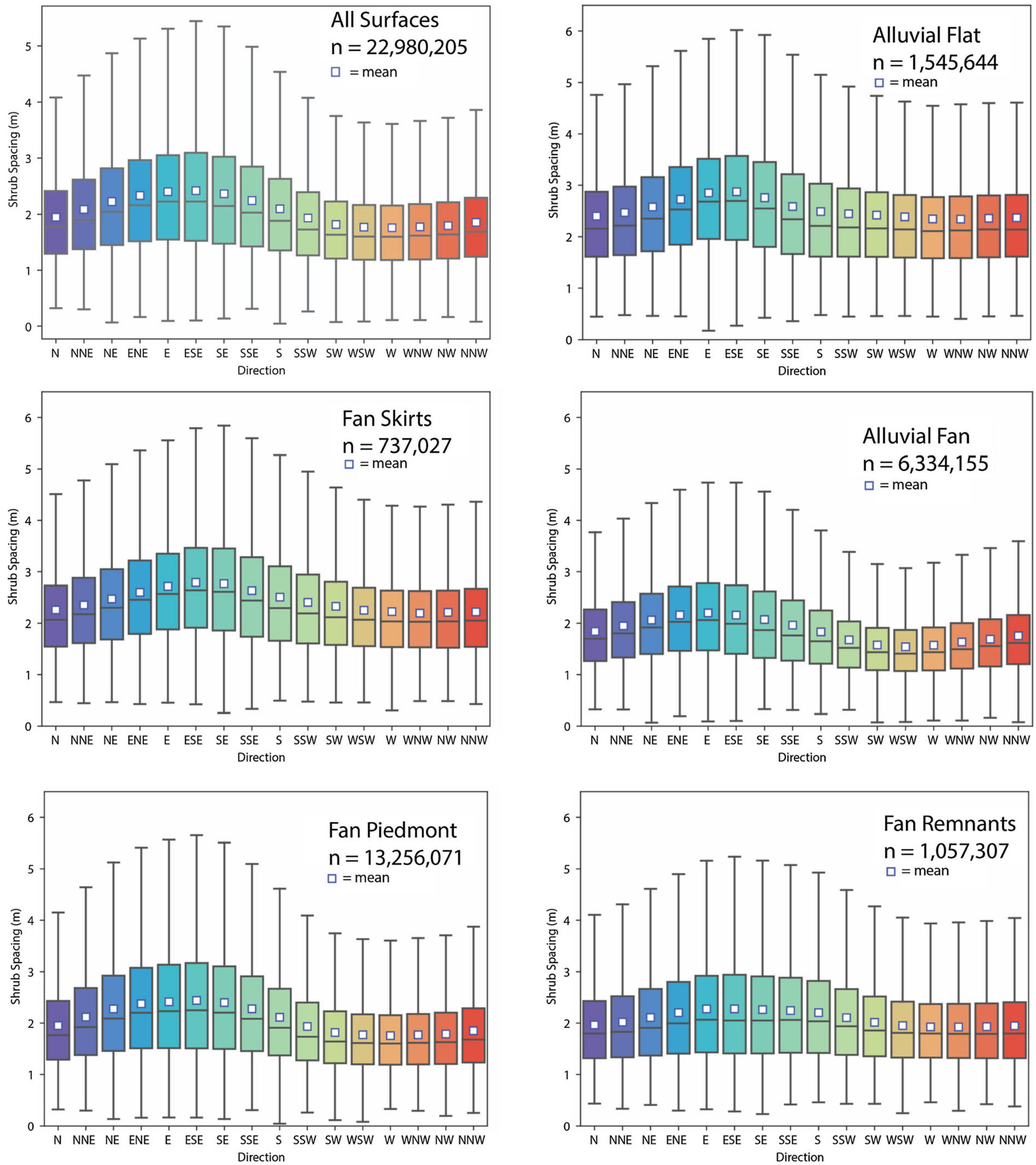


Fig. 7 Shrub spacing binned in 16 directions (22.5 deg./category) for every geomorphic surface

tridentata follow previously defined reports of shrub–soil–water interactions. Depending on soil surface stability, proximity to sources of dust, and other factors, these developed horizons can be—though not always—mantled by desert pavements consisting of closely packed, angular gravel that form dark, hardened surfaces (McFadden et al. 1987). These soils consist of A_v and (sometimes) B_{tk} horizons, with argillic material as well as calcium carbonate. The presence of these three pedogenic characteristics has

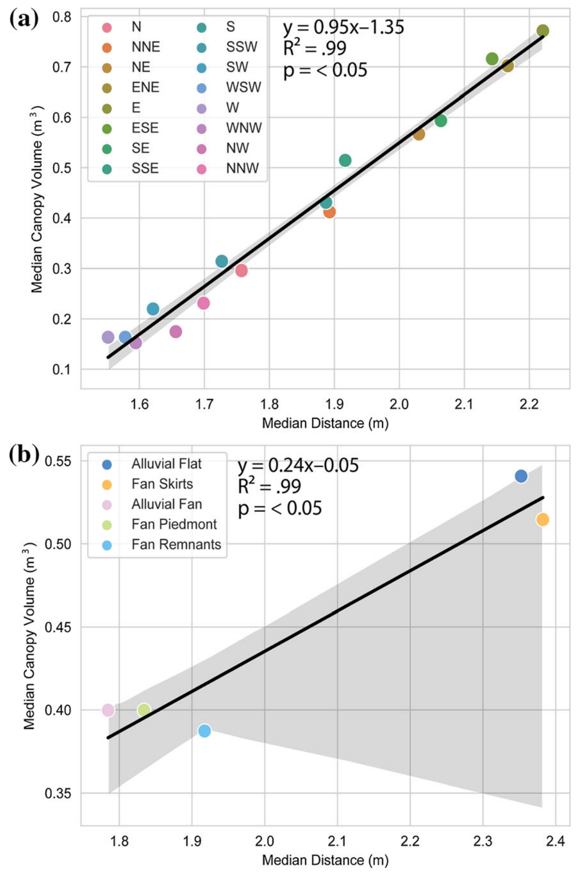


Fig. 8 Group medians for shrub spacing and canopy volume—(**a**) using aspect as co-variate and (**b**) using geomorphic surface as covariate. Gray areas indicate 95% confidence intervals on regression

been shown to restrict surface infiltration and subsurface percolation of precipitation throughout the rooting zone of *L. tridentata* shrubs (Gile et al. 1998; McAuliffe and McDonald 2006). Shallow infiltration or surface ponding of water from these restrictive developed soils leads to larger soil evaporative losses (as a fraction of precipitation) and less water available for root uptake (Young et al. 2004, 2009). This limiting factor of clay-rich horizon development and petrocalcic development both reduce deep percolation of water, thereby negatively affecting *L. tridentata* shrub growth (Shreve and Mallery 1933; Gile et al. 1998; Hamerlynck et al. 2002), leading to smaller shrubs. The Fan Remnants (FR) category typifies a well-developed soil, leading to reduced shrub canopy volume. These soil attributes are inferred based on previous findings in arid desert basins of the United States southwest; they show that *L. tridentata* shrub size can be correlated to basin-wide trends of soil morphology.

The ecophysiological responses of *L. tridentata* to reduced permeability horizon development (argillic or petrocalcic horizons) are represented well by the large range of shrub volumes when binned by geomorphic surface. We found that argillic soil horizonation and general structural soil trends on older surfaces provide (at least in part) a causal explanation for differential shrub growth, though we note that argillic content in arid soils has different effects on shrub growth depending on the magnitude and extent of horizonation. For example, argillic horizon development (*structured*) restricts water movement, but *unstructured* argillaceous soil of similar clay content allows for higher water retention (O'Geen 2013). This phenomenon may explain the highest shrub canopy volumes and spacings on the AF surface—an undeveloped geomorphic surface which operates as a sink for eolian and alluvial fines (Young et al. 2004). Indeed, soil profiles generated by the National Cooperative Soil Survey (NCSS) in their Soil Survey Geographic Database (SSURGO) (Soil Survey Staff, accessed 04 Oct 2019) for the BCCE indicate a clay content of 20–30% for soils co-located in the alluvial flat portion of the basin—Tipnat soil type (SSURGO). Therefore, younger soils with appreciable clay content—such as alluvial flats—serve as favorable growth regimes for *L. tridentata.*

Aspect–volume relationship

Results presented in "Aspect–spacing relationship" section provide a strong case for predictably large shrub canopy size on east-facing slopes. Considering causal mechanisms for this distribution, we assess the two main ingredients for plant productivity: solar radiation and access to water. In addressing the first, numerous studies documenting various photosynthetic strategies of *L. tridentata* have been conducted. Previous workers have shown that most carbon gain and maximum net photosynthesis occurs in *L. tridentata* before noon (Oechel et al. 1972; Meinzer et al. 1986; Ogle and Reynolds 2002), when soil water potentials are higher (less negative) and leaf temperatures are lower than in the afternoon. Harsher environmental conditions in the afternoon decrease water-use efficiency and soil–water availability

(Neufeld et al. 1988). Thus, *L. tridentata* shrubs have developed growth patterns that reflect a preference for morning sunlight, with shrub canopies often oriented with their branches facing toward the SE. (Neufeld et al. 1988) Findings in Neufeld et al. (1988) showed several sampled populations of *L. tridentata* shrubs with longer branches in the NE section of the plant canopy and shorter branches in the SE. These branches were inclined on average anywhere from 30° to 70° from horizontal and were situated with the maximal leaf-surface area exposed to the E-SE (Neufeld et al. 1988). This preferential growth orientation minimizes branch self-shading in the morning hours when photosynthetic conditions are optimal and maximizes self-shading during the middle of the day and early afternoon, when solar radiation is more direct and temperatures are highest. Additionally, the aperture angle of individual folioles (compound leaves) has been found to be highest in the morning and lowest in the afternoon, reducing direct radiation interception by 24% in water-stressed shrubs (Ezcurra et al. 1992). This is another stratagem that minimizes transpiratory water loss during the hottest times of the day.

These strategies all take advantage of the early to mid-morning window when photosynthetic conditions are optimal. Previous findings support the suggestion of an E-SE preference in canopy branching to maximize irradiated leaf surface area during this critical time. Though the approach used in this study (remotely sensed images versus shrub-by-shrub analyses) did not allow us to directly observe individual shrub branch orientations, our results support the hypothesis that *L. tridentata* shrubs growing on E-SE facing slopes have preferentially larger canopy volumes because they are topographically situated to receive the most sunlight during the critical photosynthetic window: morning hours when temperatures are low, relative humidities are high, and soil water is more available.

The aspect effect is exaggerated on the younger surfaces (AFl & FS) but is present on all assigned geomorphologic surfaces (Fig. 4), following the results of the geomorphic surface graphs from "Shrub canopy volume" section. The AFl surface is distinct in every geomorphic surface relationship. This appears to agree with the presented conceptual model and further highlights the nuanced interplay between abiotic forcings on shrub canopy structure in desert basins. The muted effect of aspect on shrub canopy volume for the oldest surface (FR) demonstrates that pedogenic structure becomes the major governing influence on shrub size at a certain arbitrary point in surface development. The converse to this is the heightened effect of surface aspect on younger surfaces, where water availability is more evenly dispersed throughout the soil column.

Geomorphic influences on *L. tridentata* spacing

The implications of shrub spacing (particularly *L. tridentata*) in desert environments have been discussed for the better part of a half-century. Ecologists have long used the spatial distribution of *L. tridentata* to develop theories of both intra- and inter-species competition in semi-arid and arid environments. One metric used in arid environment botany is the relationship between plant spacing and size in a confined area. A positive correlation between *L. tridentata* shrub canopy size and spacing can indicate biotic competition in arid environments (Clark and Evans 1954; Pielou 1962; Yeaton et al. 1977; Fonteyn and Mahall 1981; Fowler 1986), with the fundamental assumption being that shrubs compete for limited resources, especially water.

Closely spaced shrubs will therefore compete for a comparatively smaller pool of resources, leading to smaller canopy volumes and higher mortality rates. As some shrubs die off, leaving irregularly shaped open spaces, root systems from neighboring live shrubs would tend to grow there, whether by compensatory or non-compensatory processes (Brisson and Reynolds 1994, 1997), while still avoiding other live root systems (i.e., by root communication (e.g., Callaway and Mahall 1991)). This phenomenon can be observed in the disparity between shrub canopy size and spacing on the older geomorphic surface, Fan Remnants (FR). The FR category has the 3rd largest median shrub spacing value and the lowest median shrub canopy volume for any surface (1.892 m and 0.387 m^3, respectively) as seen in the distance of the FR datapoint from the line of best-fit (Fig. 8). The important caveat to this argument is that the absence of a positive correlation between shrub size and proximity to other shrubs does not imply no competition.

Median shrub canopy size is linearly correlated with median spacing between shrubs (Fig. 8, $R^2 = 0.99$) for any defined group (aspect and geomorphology), and it decreases with geomorphic age and west-facing aspects. Previous work assessing competition in *L. tridentata* through size-spacing relationships addresses abiotic influences on competition in the form of mineral, nutrient, and water availability (Fowler 1986) but does not link temporal changes in competitive behavior to geomorphologic development or hillslope position.

The classical ideal of shrub competitive behavior (positive correlation of shrub size and spacing) does consider how differences in soil composition can affect plant health and by extension, group competition. There are constraints within this competition metric including inherent scale and sample-size dependent issues (Fowler 1986). Therefore, we propose a more nuanced model of desert shrub competition: subtle differences in surface character of desert soils (surface age and aspect) have a substantial effect on shrub canopy structure (size and spacing) and by proxy, competitive behavior. On undeveloped surfaces, *L. tridentata* size and spacing increases, allowing for increased competition between shrubs. As soil surfaces age (and therefore pedogenic structure increases), root-available water decreases, especially in interspaces (Caldwell et al. 2008). As this occurs, shrubs reach a spacing arrangement that eventually mitigates negative intraspecies interactions. On older, more developed surfaces, shrubs may demonstrate "less competitive" behavior in the form of shrub dispersion (smaller volumes with larger spacing). In other words, each shrub or shrub island becomes a monopoly unto itself.

Aspect–spacing relationship

Following the above-mentioned relationship between shrub canopy and shrub spacing for competitive shrub regimes, it makes functional sense that shrubs that grow larger because of an east-facing topographic advantage would also have larger shrub spacing. However, when comparing Figs. 4 and 7, *L. tridentata* shrubs sometimes grow larger on east-facing slopes without also being spaced further apart. This finding demonstrates that aspect can influence *L. tridentata* canopy volumes more than shrub spacing as soil development proceeds. The weak influence of aspect for the FR category (Fig. 7) further demonstrates pedogenic control on shrub growth; Caldwell et al. (2012) also reported on the influence of the temporally-slower pedogenic processes as a driver for shrub growth in the Mojave Desert. Results suggest that shrub recruitment locations on old surfaces with likely A_v and B_{tk} horizon development (such as the FR surface), are governed almost entirely by zones of suitability—less Av or Btk horizon development, or possibly plant scars from former *L. tridentata* locations (McAuliffe and McDonald 2006). Aspect may provide more solar radiation during optimal growth windows to these shrubs, but if the shrubs are too water-limited by pedogenic processes, the aspect signal is limited.

Conclusion and conceptual model

This study aimed to investigate abiotic influences on shrub canopy volume and spacing in a desert basin using remotely designated geomorphology and elevation-derived aspect. Aspect and surface age (as a proxy for structure) have demonstrable influences on both shrub canopy volume and shrub spacing. The magnitude of shrub volume and spacing is controlled by aspect, with the largest canopy volumes and spacing on east-facing surfaces and the lowest on west-facing surfaces. This is largely due to the favorable photosynthetic conditions inherent to east-facing shrubs, which receive more sunlight during the cooler and more humid pre-noon hours. Aspect effects are apparent on every identified geomorphologic surface, especially younger, actively recruiting surfaces denoted by larger shrub canopy volume variability (AFl and FS). Aspect appears to diminish in effect (but not disappear) on older, pedogenically developed surfaces (FR).

Results suggest a conceptual model in which pedogenic development in the form of clay-rich horizon development (and perhaps desert pavement formation in some areas) modulates root water availability and controls the bounds of aspect effect on size and spacing of *L. tridentata* shrubs. Young surfaces with less horizon development allow more water entry into the soil column and hence enhanced competitive behavior among shrubs (biotic effect), manifesting in identifiable shrub canopy structure (larger and further spaced shrubs) that is apparently modulated by aspect effects. With increased time and at some pedogenic (abiotic) "threshold," soil development—and identified barriers to water availability—becomes the higher-order control on shrub canopy structure, muting the effects of hillslope aspect and reducing median values and variability in canopy volume and spacing. When this threshold occurs in the development of basin-scale, arid landscapes is likely influenced by a number of geomorphic and climatological factors.

Finally, we recognize that shrub canopy structure in these arid basins is a reflection of 100s to 1000s years of soil development and higher frequency meteorological events. Thus, a significant, multi-year drought decades earlier could mute the influences of aspect on shrubs, or amplify them, leading to nuanced and site-specific interactions between soil, geomorphology, and biota. We hope that these results inform future basin-scale models of shrub structure, which will be increasingly important in areas undergoing increased aridity and desertification due to climate change.

Acknowledgements This study was sponsored by the Clark County Desert Conservation Program, Las Vegas, Nevada, under contracts CBE 603383-14 and CBE 604014-16. We gratefully acknowledge Doug Merkler for numerous conversations and his insight into Eldorado Valley, Erik Hamerlynck for his thoughts about shrub death, John Andrews for his analytical work, and Evan Stein for his statistical advice.

References

Bedford DR, Miller DM, Schmidt KM, Phelps GA (2009) Landscape-scale relationships between surficial geology, soil texture, topography, and creosote bush size and density in the eastern Mojave Desert of California. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM (eds) The Mojave Desert: ecosystem processes and sustainability. University of Nevada Press, Reno, pp 252–277

Brisson J, Reynolds JF (1994) The effect of neighbors on root distribution in a Creosotebush (*Larrea tridentata*) Population. Ecology 75(6):1693–1702.

Brisson J, Reynolds JF (1997) Effects of compensatory growth on population processes: a simulation study. Ecology 78(8):2378–2384

Bryan K (1928) Historic evidence on changes in the channel of Rio Puerco, a tributary of the Rio Grande in New Mexico. J Geol 36(3):265–282.

Buck BJ, Goossens D, Metcalf RV, McLaurin B, Ren M, Freudenberger F (2013) Naturally occurring asbestos: potential for human exposure, southern Nevada USA. Soil Sci Soc Am J 77:2192–2204.

Callaway RM, Mahall BE (1991) Root communication among desert shrubs. Proc Natl Acad Sci 88:874–876

Caldwell TG, Young MH, Zhu JT, McDonald EV (2008) Spatial structure of hydraulic properties from canopy to interspace in the Mojave Desert. Geophys Res Lett 35(19):6.

Caldwell TG, Young MH, McDonald EV, Zhu J (2012) Soil heterogeneity in Mojave Desert shrublands: biotic and abiotic processes. Water Resour Res 48:W09551.

Caylor KK, Manfreda S, Rodriguez-Iturbe I (2005) On the coupled geomorphological and ecohydrological organization of river basins. Adv Water Resour 28(1):69–86.

Clark County (2019) Clark County Desert conservation program Boulder city conservation easement management plan. Ver. 3.4. plus appendices, p 44

Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35(4):445–453

Cooray K, Ananda MM (2008) A generalization of the half-normal distribution with applications to lifetime data. Commun Stat Theory Method 37(9):1323–1337

Corenblit D, Steiger J (2009) Vegetation as a major conductor of geomorphic changes on the Earth surface: toward evolutionary geomorphology. Earth Surf Process Landforms 34:891–896.

Delignette-Muller ML, Dutang C (2015) fitdistrplus: an R package for fitting distributions. J Stat Softw 64(4):1–34

Dunkerley DL, Brown KJ (2002) Oblique vegetation banding in the Australian arid zone: implications for theories of pattern evolution and maintenance. J Arid Environ 51(2):163–181.

ESRI (2016) ArcGIS desktop (version 15.1). Environmental Systems Research Institute, Redlands

Ezcurra E, Arizaga S, Valverde PL, Mourelle C, Floresmartinez A (1992) Foliole movement and canopy architecture of Larrea-Tridentata in Mexican Deserts. Oecologia 92(1):83–89.

Fonteyn PJ, Mahall BE (1981) An experimental-analysis of structure in a desert plant community. J Ecol 69(3):883–896.

Fowler N (1986) The role of competition in plant-communities in arid and semiarid regions. Annu Rev Ecol Syst 17:89–110.

Gardner DR (1998) The national cooperative soil survey of the United States (No 7). US Department of Agriculture, Natural Resources Conservation Service, Resource Economics and Social Sciences Division, Washington, DC

Gile LH, Gibbens RP, Lenz JM (1998) Soil-induced variability in root systems of creosotebush (*Larrea tridentata*) and tarbush (*Flourensia cernua*). J Arid Environ 39(1):57–78.

Glenn NF, Spaete LP, Sankey TT, Derryberry DR, Hardegree SP, Mitchell JJ (2011) Errors in LiDAR-derived shrub height and crown area on sloped terrain. J Arid Environ 75:377–382

Hamerlynck EP, McAuliffe JR, McDonald EV, Smith SD (2002) Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. Ecology 83(3):768–779

Hunter JD (2007) Matplotlib: a 2D graphics environment. Comput Sci Eng 9:90–95.

Huntington E (1914) The climatic factor as illustrated in Arid America. Geogr J 46(4):308–310

Istanbulluoglu E, Yetemen O, Vivoni ER, Gutiérrez-Jurado HA, Bras RL (2008) Ecogeomorphicimplications of hillslope aspect: inferences from analysis of landscape morphology in central New Mexico. Geophys Res Lett 35:L14403. https://doi.org/10.1029/2008GL034477

Lunt OR, Letey J, Clark SB (1973) Oxygen requirements for root growth in 3 species of desert shrubs. Ecology 54(6):1356–1362.

Marston RA (2010) Geomorphology and vegetation on hillslopes: interactions, dependencies, and feedback loops. Geomorphology 116(3–4):206–217

McAuliffe JR (1994) Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. Ecol Monogr 64(2):111–148.

McAuliffe JR, McDonald EV (2006) Holocene environmental change and vegetation contraction in the Sonoran Desert. Quatern Res 65(02):204–215

McFadden LD, Wells SG, Jercinovich MJ (1987) Influences of eolian and pedogenic processes on the origin and evolution of desert pavements. Geology 15(6):504–508.

McKinney W (2010) Data structures for statistical computing in Python. In: Proceedings of the 9th Python in science conference. pp 51–56

Meinzer FC, Rundel PW, Sharifi MR, Nilsen ET (1986) Turgor and osmotic relations of the desert shrub *Larrea tridentata*. Plant Cell Environ 9(6):467–475.

Monger HC, Bestelmeyer BT (2006) The soil-geomorphic template and biotic change in arid and semi-arid ecosystems. J Arid Environ 65(2):207–218

Neufeld HS, Meinzer FC, Wisdom CS, Sharifi MR, Rundel PW, Neufeld MS, Goldring Y, Cunningham GL (1988) Canopy architecture of Larrea-Tridentata (dc) cov, a desert shrub—foliage orientation and direct beam radiation interception. Oecologia 75(1):54–60. https://doi.org/10.1007/bf00378813

O'Farrell T (2009) Management action plan for the Boulder City conservation easement. Las Vegas, NV; June 2020.

O'Geen AT (2013) Soil water dynamics. Nat Educ Knowl 4(5):9

Oechel WC, Odening WR, Strain BR (1972) Photosynthetic rates of a desert shrub, *Larrea-Divaricata cav*, under field conditions. Photosynthetica 6(2):183

Ogle K, Reynolds JF (2002) Desert dogma revisited: coupling of stomatal conductance and photosynthesis in the desert shrub, *Larrea tridentata*. Plant Cell Environ 25(7):909–921.

Parsons AJ, Abrahams AD (2009) Geomorphology of desert environments. In: Geomorphology of desert environments. Springer, Dordrecht, pp 3–7

Peterson FF (1981) Landforms of the basin & range province: defined for soil survey, technical bulletin 28. Max C. Fleishmann College of Agriculture, Nevada

Phillips DL, MacMahon JA (1981) Competition and spacing patterns in desert shrubs. J Ecol 69(1):97–115.

Pielou EC (1962) The use of plant-to-neighbour distances for the detection of competition. J Ecol 50(2):357–367.

R Core Team (2020) R: a language and environment for statistical computing. In: R foundation for statistical computing, Vienna, Austria. https://www.R-project.org/. Accessed 20 June 2020

Rigby RA, Stasinopoulos DM (2005) Generalized additive models for location, scale and shape (with discussion). Appl Stat 54:507–554

Saco PM, Willgoose GR, Hancock GR (2007) Eco-geomorphology of banded vegetation patterns in arid and semi-arid regions. Hydrol Earth Syst Sci 11(6):1717–1730.

Schoeneberger PJ, Wysocki DA (2017) Geomorphic description system, Version 5.0. Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE

Shreve F, Mallery TD (1933) The relation of caliche to desert plants. Soil Sci 35(2):99–113.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Soil survey geographic (SSURGO) database. https://sdmdataaccess.sc.egov.usda.gov. Accessed 04 Oct 2019

Virtanen P, Gommers R, Oliphant, T, Haberland M, Reddy T, Cournapeau D, Burovski E, Peterson P, Weckesser W, Bright J, van der Walt S, Brett M, Wilson J, Millman K, Mayorov N, Nelson A, Jones E, Kern R, Larson E, Carey C, Polat I, Feng Y, Moore E, VanderPlas J, Laxalde D, Perktold J, Cimrman R, Henriksen I, Quintero E, Harris C, Archibald A, Ribeiro A, Pedregosa F, zan Mulbregt P, Vijaykumar A, Bardelli A, Rothberg A, Hilboll A, Kloeckner A, Scopatz A, Lee A, Rokem A, Woods C, Fulton C, Masson C, Häggström C, Fitzgerald C, Nicholson D, Hagen D, Pasechnik D, Olivetti E, Martin E, Wieser E, Silva F, Lenders F, Wilhelm F, Young G, Price G, Ingold G, Allen G, Lee G, Audren H, Probst I, Dietrich J, Silterra J, Webber J, Slavič J, Nothman J, Buchner J, Kulick J, Schönberger J, de Miranda Cardoso J, Reimer J, Harrington J, Rodríguez J, Nunez-Iglesias J, Kuczynski J, Tritz K, Thoma M, Newville M, Kümmerer M, Bolingbroke M, Tartre M, Pak M, Smith N, Nowaczyk N, Shebanov N, Pavlyk O, Brodtkorb Per P, Lee P, McGibbon R, Feldbauer R, Lewis S, Tygier S, Sievert S, Vigna S, Peterson S, More S, Pudlik T, Oshima T, Pingel T, Robitaille T, Spura T, Jones T, Cera T, Leslie T, Zito T, Krauss T, Upadhyay U, Halchenko Yaroslav O, Vázquez-Baeza Y (2020) SciPy 1.0: fundamental algorithms for scientific computing in Python. Nat Methods 17(3), 261–272.

Wainwright J (2009) Desert ecogeomorphology. In: Parsons AJ, Abrahams AD (eds) Geomorphology of desert environments. Springer, Dordrecht, pp 21–66

Wasserstein RL, Lazar NA (2016) The ASA statement on p-values: context, process, and purpose. Am Stat 70:2

White LP (1969) Vegetation arcs in Jordan. Journal Ecol 461–464.

Yang Y, Milne B (1997) Water balance modeling project vegetation plots data, Sevilleta LTER database. https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.81.185474. Accessed 21 Mar 2019

Yeaton RI, Travis J, Gilinsky E (1977) Competition and spacing in plant communities—Arizona-upland-association. J Ecol 65(2):587–595.

Yetemen O, Istanbulluoglu E, Vivoni ER (2010) The implications of geology, soils, and vegetation on landscape morphology: inferences from semi-arid basins with complex vegetation patterns in Central New Mexico, USA. Geomorphology 116(3–4):246–263.

Young MH, McDonald EV, Caldwell TC, Benner SG, Meadows DG (2004) Hydraulic properties of a desert soil chronosequence in the Mojave Desert, USA. Vadose Zone J 3:956–963

Young MH, Caldwell TG, Meadows DG, Fenstermaker LF (2009) Variability of soil physical and hydraulic properties at the Mojave Global Change Facility, Nevada:

implications for water budget and evapotranspiration. J Arid Environ. https://doi.org/10.1016/j.jaridenv.2009.01.015
Young MH, Andrews JH, Caldwell TG, Saylam K (2017) Airborne LiDAR and aerial imagery to assess potential burrow locations for the desert tortoise (*Gopherus agassizii*). Remote Sens 9(5):16.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.