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Establishing soil and surficial geologic habitat criteria for presumed gypsophiles — The example of *Eriogonum corymbosum* var. *nilesii*, Mojave Desert, U.S.A.

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ABSTRACT

Detailed soil and surficial geologic data are needed for ecological interpretations, yet are often absent or incomplete in published studies of arid land ecology or biogeography. Clear, edaphic habitat definitions are needed for gypsophilic plants including the Las Vegas buckwheat, *E. corymbosum* var. *nilesii* (LVB), a rare shrub endemic to the Mojave Desert. As a case study, we use soil profile data and high resolution (1:3000 scale) surficial geologic maps to identify likely edaphic controls of LVB habitat, potential habitat, and non-habitat distributions. We confirm gypsiferous substrates lacking hard, physical surface crusts as a boundary condition in most, but not all population clusters, but find that fine-grained, carbonate-rich soil lacking gypsum is also viable habitat, as is shallow (<1 m) sandy alluvium overlying gypsiferous sediments. Deep (>1 m), coarse-grained alluvium and/or surfaces with tightly interlocking desert pavement exclude LVB. Our results challenge the view of this target species as a true gypsophile, however, it remains unclear whether carbonate-rich habitats represent ideal conditions or refugia. This study underscores the important merits of surficial geologic mapping and soil morphological description for ecological research, conservation, restoration, and land management in arid environments, especially gypsum soils, worldwide.

1. Introduction

Soil geomorphic context is critical for interpretations of plant ecology in arid landscapes (Drohan and Merkler, 2009; Ellis et al., 2009; Hamerlynck et al., 2002; Monger and Bestelmeyer, 2006; The Nature Conservancy, 2007). Edaphic factors can largely define habitats for arid region flora, including gypsophiles, yet the exact range of soil, geologic, and geomorphic properties tolerated or required by a species of interest is often unknown or inadequately precise for effective species conservation or ecological restoration. Even for gypsophiles, where gypsum-rich parent materials and an arid to semi-arid environment are considered boundary conditions, it is not always clear how much gypsum is needed, nor why the mineral might control the distribution of a given species (Drohan and Merkler, 2009; Meyer, 1986; Palacio et al., 2007; Parsons, 1976). This information gap warrants concern because of the rare and/or threatened nature of gypsophilic plants in the U.S.A. (e.g., Morefield, 2004; USFWS, 2007), Spain (e.g., Pueyo et al., 2007), and other arid lands worldwide (Parsons, 1976).

Detailed soil profile descriptions, soil surveys, and/or surficial geologic maps from representative habitat areas are needed to: (1) define precise habitat criteria for individual, sensitive species, (2) evaluate the relative importance of soil, geologic, geomorphic, biotic, or other factors as habitat predictors, (3) compare soil–plant dynamics between disparate plant communities and environments, and (4) provide reference data for ecological restoration and land management. Plant communities are at least partially controlled by factors that may be taxon-specific and that may escape documentation without targeted study (e.g., Escudero et al., 2007). Because of the labor and complexity involved in characterizing the full range of habitat variability for one species, let alone an entire community, the acquisition of edaphic habitat data is sometimes best designed around only a few, or even just one, key species.

Perhaps due to cost, labor, logistics, and other factors, detailed geospatial data coverage is often lacking for gypsum habitats. In the western U.S.A., soil surveys and geologic maps for most areas of interest are commonly too coarse (1:24,000 to 1:250,000 scale) for the purposes of habitat definition, and most published scientific studies of gypsophile ecology unfortunately lack topographic, let alone soil or geologic maps. Well-intended attempts to correlate plant distributions based on substrate characteristics sometimes employ outdated map units that confuse bedrock lithology with soil type, geologic unit names, and/or

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landform type (e.g., The Nature Conservancy, 2007). These groups are not comparable because each indicates different concepts and scales of landscape classification.

Careful soil profile descriptions are needed to determine soil taxonomy and to interpret soil–plant relationships, and the omission of these data can limit the insights from ecological research. For instance, a range of studies on gypsum ecology in the Mojave Desert and neighboring regions have attempted to identify factors most important to the establishment, distribution, and survival of selective, gypsophilic flora including *Arctomecon humilis* Coville, *Arctomecon californica* Torrey and Frémont, and *Arctomecon merriami* Coville (Boettinger et al., 2010; Hickerson and Wolf, 1998; Nelson and Harper, 1991; Sheldon Thompson and Smith, 1997). Due to scope of work or other understandable constraints, most of these studies either entirely exclude soil characterization, or limit soil analysis to surface crusts or generalized mineralogical trends (i.e., to confirm gypsiferous, calcareous, or quartz-dominated substrates). Some researchers (Meyer, 1986; Meyer and García-Moya, 1989; Nelson and Harper, 1991; Sheldon Thompson and Smith, 1997) did analyze soils under the target species but sampled by depth rather than by genetic horizon without providing the morphological data needed to rule out potential mixing of two or more discrete soil horizons. Discrete horizons commonly have distinct mineralogy and/or chemistry and are likely to affect plant growth and development differently. Even when studies do specifically address genetic horizon characteristics in light of presumed gypsophily (e.g., Drohan and Merkler, 2009), they may lack detailed soil or surficial geologic maps to illustrate variability and spatial heterogeneity, or they may not define inhabited versus non-inhabited sites using natural soil-geomorphic unit boundaries or objective spatial definitions (e.g., a set radius from the species of interest).

The tasks of confirming gypsophily and identifying edaphic controls of plant distributions are further complicated by the variability of habitat characteristics between disparate areas, uncertain genetic relationships between distinct population clusters, and uncertainty regarding complex biotic controls on population distributions (e.g., dispersal, facilitation, allelopathy, predation, pollination, land disturbance, etc.). Nevertheless, without integrated soil, geomorphic, and/or surficial geologic data, it can be difficult to weigh the relative importance of edaphic vs. biotic factors in controlling species distributions.

Surficial geologic maps are interpretations of the genesis, history, and characteristics of geomorphic surfaces and landforms, including the soils formed therein. Their careful study can identify edaphic characteristics or surface processes indicative or definitive of a given habitat type. Because landform morphology, hydrology, sedimentation rate, and soil formation all engage in biogeomorphic feedbacks with plant communities (Monger and Bestelmeyer, 2006), high-resolution surficial geologic maps, in tandem with the digital topographic data often used as a base layer, can prove useful for predicting vegetation composition in areas not yet surveyed on foot. High-resolution topographic data also facilitate detection of potential microtopographic and microclimatic effects on insolation as well as water and soil-resource availability (e.g., Caldwell et al., 2008), particularly within the meter-scale islands of fertility that characterize arid ecosystems (e.g. Schlesinger et al., 1996). Similarly, small variations in the lithology of local geologic strata (e.g., gypsum vs. carbonate) may create important niche habitats that could be overlooked using coarse data sets.

Surficial geologic and geomorphic factors have been shown to influence gypsophile ecology around the world. Particularly important factors include: the nature of the (gypsum-bearing) parent material (Nettleton et al., 1982; Parsons, 1976), the influence of relative landform position and soil development on infiltration and water availability (e.g., Bochet et al., 2009; Hamerlynck et al., 2002; Pueyo et al., 2007; Smith et al., 1995), and slope angle and its effect on infiltration, physical crusts, and the flux of ions in soil solutions (e.g., Guerrero-Campo et al., 1999; Pueyo et al., 2007). Other key surface processes include dust flux and the dynamics of biological soil crusts (e.g., Williams et al., 2012), which can influence or facilitate seed establishment or emergence (e.g., Escudero et al., 2007; Pueyo et al., 2007). These factors should be addressed not only in terms of their influence on plant communities that inhabit gypsum substrates, but for their effects on individual species.

E. corymbosum Bentham var. *nilesii* (Reveal, 2004), commonly called the Las Vegas buckwheat (LVB), Niles' wild buckwheat, or “golden buckwheat”, is a Mojave Desert shrub long thought restricted to gypsum-rich soils in Clark County, Nevada. Because of its limited distribution as well as the vulnerability of its habitat to urban development, off-highway vehicle (OHV) use, mining operations, illegal dumping, and wildfire, LVB is considered a sensitive or special status species by the Bureau of Land Management (BLM) and it is a candidate species for federal protection (Morefield, 2004; USFWS, 2007).

Crucially, LVB exemplifies the broader challenges of inadequate habitat description and mapping for gypsophile ecology and conservation. Currently, it remains unclear whether this species is, indeed, a specialist best classified as a facultative gypsophile, an obligate gypsophile, or a gypsocline (Drohan and Merkler, 2009; Meyer, 1986; Mrowka, 2008; Parsons, 1976), or whether its current habitats might, instead, be best described as refugia (e.g., Meyer, 1986; Palacio et al., 2007). LVB habitat has been broadly defined as occurring on and/or near gypsum substrates on badlands surfaces or side slopes, or within thin, sandy alluvium over gypsum bedrock in washes (Drohan and Merkler, 2009; Morefield, 2004), however, these criteria are largely informal. The ecology of this species remains uncertain because existing soil-geomorphic data for most of the dozen or so known LVB habitat sites in Clark County (Ellis et al., 2009; Mrowka, 2008) are coarse in resolution or incomplete. Moreover, the fragmented distribution of LVB suggests that, for reasons not previously determined, not all gypsum-rich soils are suitable habitat.

Predictive habitat modeling and conservation of known sites require the ability to locate habitat areas via remote sensing and field mapping of surficial geology, soils, and/or landforms (e.g., Boettinger et al., 2010). Remote classification of gypsum substrates using ASTER satellite data has facilitated identification of previously unrecognized potential LVB habitat in Clark County (Clark County Desert Conservation Program, unpublished data, 2009), but surficial geologic mapping and soil profile data sets are still needed to refine these efforts (Ellis et al., 2009). In addition, habitat definitions established using surficial geologic maps provide important reference conditions for restoration of disturbed LVB areas near new developments or areas of OHV use. Better definitions may prove useful for (1) managing other species with partially overlapping geographic ranges (e.g., *Arctomecon californica*), and/or (2) comparing plant dynamics on gypsum soils between deserts in other regions or continents.

Finally, there is lingering uncertainty regarding the evolutionary history of LVB and the age of individual plants. Though recently clarified by the work of Ellis et al. (2009), any shared phylogenetic history between LVB and similar species or varieties found in Utah (Washington and Kane Counties) and Arizona (Mohave and Coconino Counties) has been obscured by extensive taxonomic revision and the possibility of hybridization (Ellis et al., 2009; Morefield, 2004; Mrowka, 2008; Reveal, 1967; USFWS, 2007; Utah Board of Water Resources, 2010). If *E. corymbosum* taxa were to be further revised, then distributions of LVB could prove to be even more restricted and more threatened than previously thought. This scenario is also relevant for other rare or threatened, but poorly understood, gypsophiles around the world. Projections for the coming decades regarding continued urban development and population growth as well as climate change all underscore the need to better understand the habitats and ecology of LVB before critical environmental thresholds are crossed.

This study was undertaken to identify geologic, geomorphic, or edaphic controls on the distribution and habitat definitions of LVB, and to provide much needed spatial data for conservation. The objectives of this study were: (1) to describe soil profiles and to develop high resolution surficial geologic maps in known LVB habitat areas, (2) to identify any patterns between LVB distributions and distinct surficial geologic deposits or soils and (3) to interpret, if possible, more precise soil geomorphic habitat criteria for LVB. With these objectives, we sought to test the hypotheses that (1) soil and surface characteristics are more important than the mere presence or absence of gypsum in controlling LVB habitats, and that (2) because of its effect on available water, solar insolation values would be a useful predictor of plant distributions. More broadly, insights from this study firmly underscore the relevance of targeted surficial geologic mapping and soil profile description for any attempt at modeling restricted species habitats, especially on the gypsum substrates of arid to semi-arid environments.

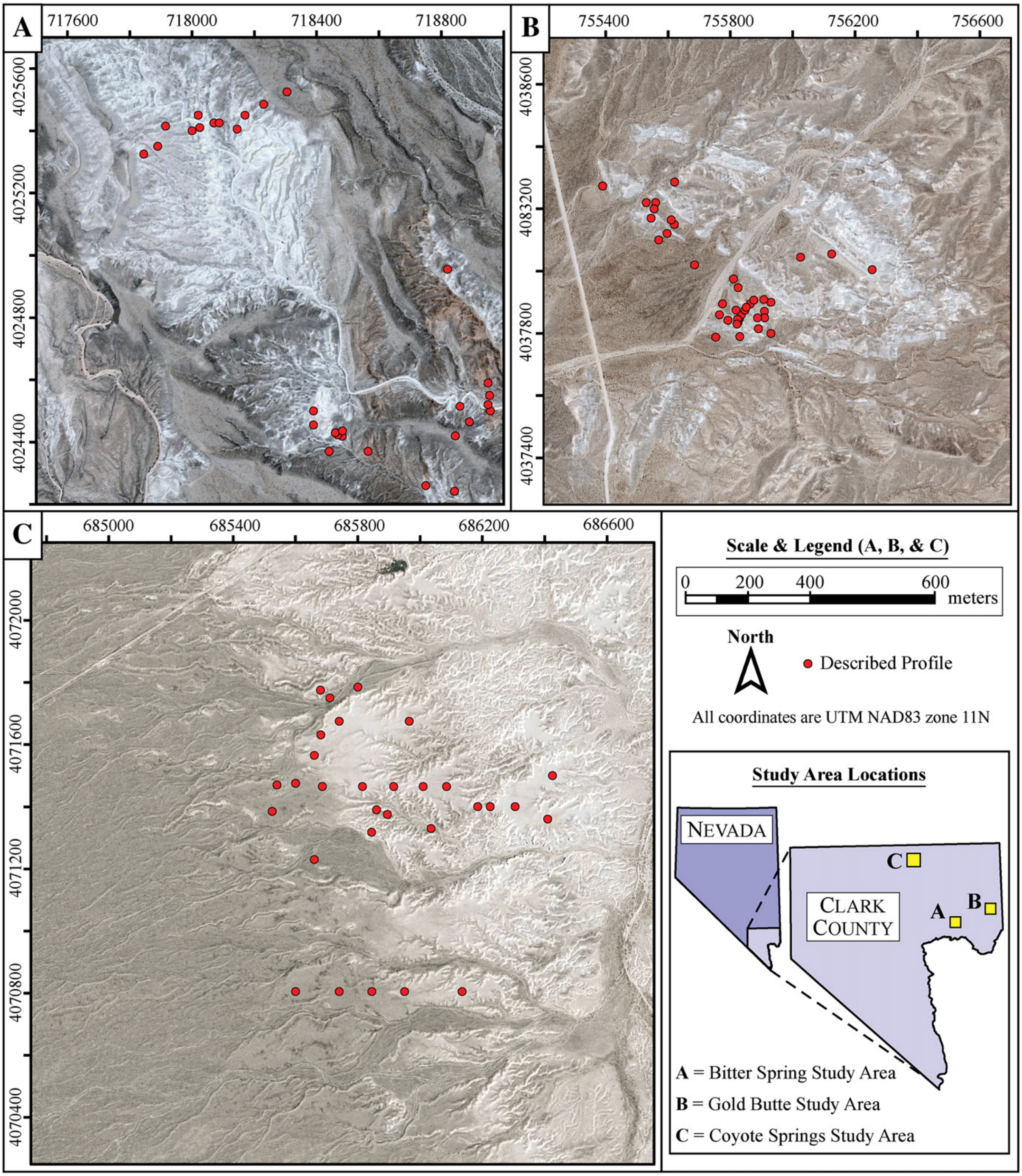

Fig. 1. Location of the three study areas in Clark County, Nevada, and the general distribution of studied soil profile sites in each area. Site coordinates are available in the data repository.

2. Methods

2.1. Study area and site locations

Three study areas (Fig. 1) were selected from among the known population clusters of LVB in Clark County, NV (Mrowka, 2008; USFWS, 2007). Study area boundaries were intended to encompass a representative range of locally expressed geomorphic surfaces and landforms, while maintaining similar study area sizes and comparable degrees of landscape complexity between locations. The three study areas were (1) Bitter Spring, located in the White Basin north of Lake Mead National Recreation Area, (2) Gold Butte, located approximately 10 km south of Whitney Pockets off New Gold Butte Road, and (3) Coyote Springs, located ~2 km southeast of the intersection of U.S. Hwy 93 and NV State Route 168. The Gold Butte and Coyote Springs study areas fall within Bureau of Land Management Areas of Critical Environmental Concern.

Approximately 30 sites were chosen within each of the three study areas (97 sites total) for targeted soil and surficial geologic classification. These sites were distributed to offer the best coverage of areas in which (1) LVB was present, (2) sites that looked similar to habitat sites but which did not contain any LVB, and (3) uninhabited areas that looked geomorphically or edaphically distinct from the habitat sites. Sites were arrayed in rough transects across key habitat areas, and supplemented with representative sites from unpopulated areas (Fig. 1).

2.2. Surficial geologic mapping

Surficial geologic mapping was performed between September 2009 and October 2012 in the field and remotely, using ESRI ArcGIS 10.2 software. Digital base data used to support our interpretations included 1.5 m resolution digital surface models (DSMs) derived from XYZ-only light detection and ranging (LiDAR) data collected by Airborne1 (El Segundo, CA) in November, 2009. National Agriculture Imagery Program (NAIP) data (USDA-FSA, 2006) and Quickbird data (made available through the Southern Nevada Public Lands Management Act Round 5 Conservation Initiative Program) also facilitated mapping. Surficial geology was mapped at 1:3,000 scale. We differentiated deposits, geomorphic surfaces, and landforms based on slope, aspect, elevation, morphostratigraphy, surface characteristics (including biological and physical crusts), sediment texture and lithology, soil profile characteristics, and vegetation. Structural geologic features were not mapped. Planar geomorphic surfaces and their side slopes were sometimes divided into separate map units because of the need to capture factors that could potentially influence habitat suitability, such as changes in hydrology and surface clast cover.

With the 1:3,000 map scale, we sought to maximize the ability of our data to explain differences between existing habitats and adjacent, similar soil-landforms that do not support LVB (i.e., potential habitat). Existing geologic map (1:100,000 or coarser) and NRCS soil survey (Order 3, 1:24,000 or coarser) coverage of the study areas was inadequate for these purposes (Buck et al., 2011; Soil Survey Staff, 2006) because these map units, by definition, incorporate a high degree surficial geologic and soil variability. Most relevant to the study of desert shrubs, the 1:3000 scale permits delineation of landforms as small as ~5 m^2, and linear features, such as rills or gullies, as narrow as 1.5 m. Such landforms may provide critical niche space for individual shrubs, but cannot be resolved at a coarser spatial scale.

2.3. Soil morphology and classification

Using shovels and a digging bar, 97 soil profiles (i.e., one per site) (Fig. 1) were excavated down to unaltered parent material or, in some cases, to an impenetrable hardpan (~10 to 100 cm depth). Thirty soil profiles were described at Bitter Spring and Coyote Springs, and 37 were described at Gold Butte. Morphological data were recorded following the methods of Schoeneberger et al. (2002) and Soil Survey Staff (2010), and soils were classified to the subgroup level using USDA NRCS soil taxonomy (Soil Survey Staff, 2010). Soil characteristics were used to help establish and to delineate surficial geologic map units.

Horizon suffixes used in this study for calcic and petrocalcic horizons follow the norms of Soil Survey Staff (2010), however, calcic and petrocalcic horizons are also described using the six-stage classification system of Gile et al. (1966) (stages I–IV) and Bachman and Machette (1977) (stages V & VI), recently summarized by Schoeneberger et al. (2012). Furthermore, we use “Av” to designate the presence of desert pavement underlain by a vesicular A horizon (Springer, 1958) even though this designation constitutes a departure from USDA Soil Taxonomy, in which the “v” horizon suffix designates the occurrence of plinthite (Soil Survey Staff, 2010). The geomorphic, pedogenic, hydrological, and ecological significance of vesicular horizons and desert pavements in arid environments is too great (Turk and Graham, 2011) not to explicitly recognize them as features distinct from other surface horizons in this study. Lacking a formally accepted, standardized nomenclature for these features, we use the “Av” designation of Springer (1958).

2.4. Morphometry and solar insolation

Slope angle, slope aspect, and elevation for each site were measured using the 1.5 m resolution LiDAR DSMs. However, available computing power was insufficient to use the LiDAR data sets for insolation mapping. Instead, we combined the high resolution LiDAR DSM from each study area with lower (10 m) resolution, less memory-intensive, USGS Digital Elevation Models (DEMs) (USGS, 2005) covering the viewshed. Pixel resolution of the LiDAR DSM was reduced from 1.5 m to 5 m, and resolution of the USGS DEM was artificially increased from 10 m to 5 m. Cells overlapping the study area were clipped out of the USGS DEM, and the LiDAR DSM was patched in to create one 5 m DEM for each study area and viewshed. This DEM could be analyzed on a personal computer, yet permitted more accurate insolation modeling of fine-scale topography within the study area, while also incorporating the shading effects of adjacent mountains. Insolation values for soil profile sites were calculated using the Points Solar Radiation tool in ArcGIS. For illustrative purposes, raster data showing insolation variability across the whole viewshed were also produced using the Area Solar Radiation tool. Clearly discernible artifacts (walls or cliffs) appear at the edge of each study area, however, these artifacts are not large enough to influence insolation calculations at any of the 97 individual study sites. All calculations were run for the whole year, assuming uniform sky, using a monthly interval, and a sky size of 200 cells. Separate analyses were also run for the summer and winter solstices, and for the equinoxes.

2.5. Habitat mapping

Observed relationships between LVB distributions, surficial geologic map units, soil morphology and taxonomy, and geomorphology were used to generate habitat classification maps. In ideal cases, soil profile sites and the map units in which they fall can be classified together on a purely objective, empirical, presence or absence basis: i.e., sites and map units are either known to contain one or more LVB individuals and are classified as habitat, or the species is not present and the unit is classified as non-habitat. This observation-based system works well where map unit polygons are small and plant distributions within habitat polygons are fairly uniform. However, this system fails when map units are larger, and polygons that cannot be subdivided based on any soil or surficial geologic criteria contain both large (0.5 to 1 ha) areas in which LVB is present, and similarly large areas in which it is absent. No single, objective, spatial definition for presence/absence could be found that worked for all three field areas.

Thus, in this study we employ a more interpretive, site-specific classification system that includes (1) “Habitat”, (2) “Non-habitat” and (3) “Potential Habitat” classes based on soil-geomorphic characteristics, spatial constraints, and LVB presence/absence. Designation of a site as “Non-habitat” means that either: the species was absent for the full spatial extent of the particular surficial geologic map unit polygon in which the site occurs, or that the buckwheat is absent for a distance of at least 50 m in all directions from the soil profile location within the map unit polygon. “Potential Habitat” sites are those in which LVB is similarly absent, but which bear close soil surface and/or geomorphic similarity to habitat characteristics and are thus considered likely to be able to support LVB. “Habitat” units were observed to support the species either across the full spatial extent of the surficial geologic map unit polygon in which the site occurs, or for a distance of at least 50 m in all directions from the map unit polygon's soil profile location.

3. Results

3.1. Surficial geology and soil morphology

Reduced-resolution surficial geologic and habitat classification maps are shown for each of the three study areas in Figs. 2, 3, and 4. Digital, 1:3000 scale maps can be accessed in the data repository, along with the detailed map unit descriptions and relative map unit age interpretations. Our surficial geologic map units, though tailored for floristic considerations, employ conventional nomenclature, with the first character of each unit name indicating general chronostratigraphic age: Q, Pleistocene or Holocene; T, Miocene; and the second character indicating the nature of the deposit and/or its degree of induration: a, alluvium; c, colluvium; ea, mixed eolian and alluvial sediments; p, playa; lv, eroded Las Vegas Formation; x, anthropogenically disturbed; rock, well-lithified sedimentary bedrock; ss, poorly lithified sedimentary rock; gyp, gypsum bedrock; tuff, tuffaceous (volcaniclastic) bedrock. Additional descriptive suffixes indicate age relationships (i.e., 1 is oldest, 2 younger, etc.) or landscape position (e.g., summit; or erode = side slope). Absolute geologic ages were not determined in this study, thus, our relative map unit ages are rough estimates only.

All three study areas are similarly comprised of a range of soil-geomorphic surfaces spanning the late Pleistocene through the present day, as well as outcrops of Miocene (Bitter Spring and Gold Butte) and late Pleistocene (Coyote Springs) bedrock. Surface ages for each map unit were estimated by comparing soil development and surface characteristics to similar features elsewhere in the region. This includes alluvial fans and spring deposits north and west of Las Vegas (Bell et al., 1998; Haynes, 1967; Page et al., 2005; Quade, 1986; Quade and Pratt, 1989; Springer et al., 2008), Ivanpah Valley (House et al., 2006, 2010), near the Nevada Test Site (Harden et al., 1991; Peterson et al., 1995; Taylor, 1986), and in the central Mojave Desert near Silver Lake and the Providence Mountains (Harden et al., 1991; McDonald et al., 2003; McFadden, 1988; Reheis et al., 1989; Wells et al., 1987). In the Bitter Spring and Gold Butte study areas, formation names and ages of bedrock units were based on field observations and on work by Beard et al. (2007). Relationships between map units and soil taxonomy are summarized briefly below, for each study area. Highly generalized soil profiles for habitat and non-habitat areas at each of the three study sites are illustrated in Fig. 5, and individual soil profile descriptions are available in the data repository. Comparisons of geomorphic parameters derived from the LiDAR data are illustrated for buckwheat habitats, by study area, in Fig. 6.

3.1.1. Results for Bitter Spring

Excluding small areas of human disturbance, the Bitter Spring study area is comprised of seven surficial geologic map units (Fig. 2), including four alluvial units, one colluvial unit, and two lithologically-defined

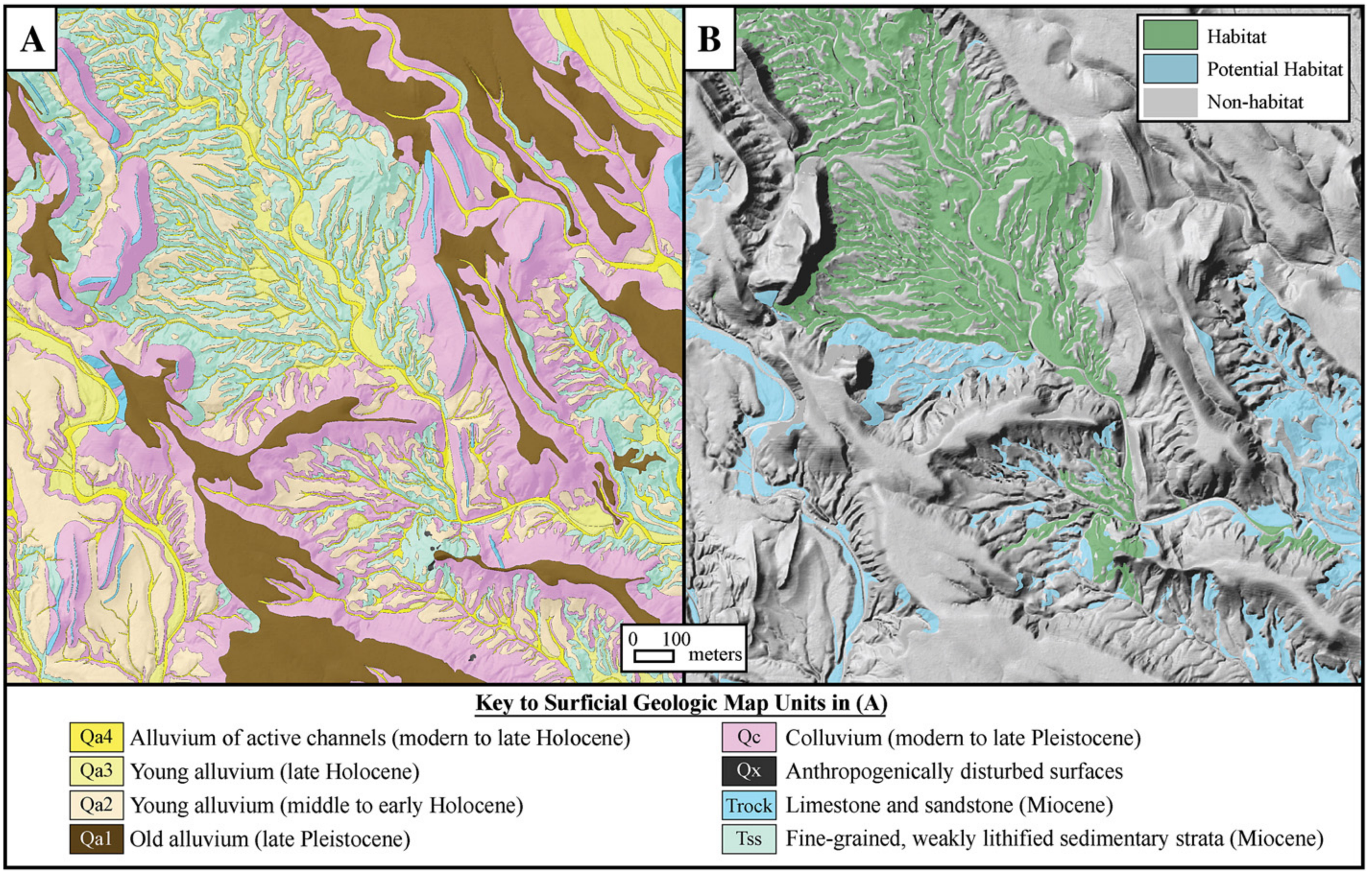

Fig. 2. (A) Surficial geologic map and (B) habitat map for the Bitter Spring study area.

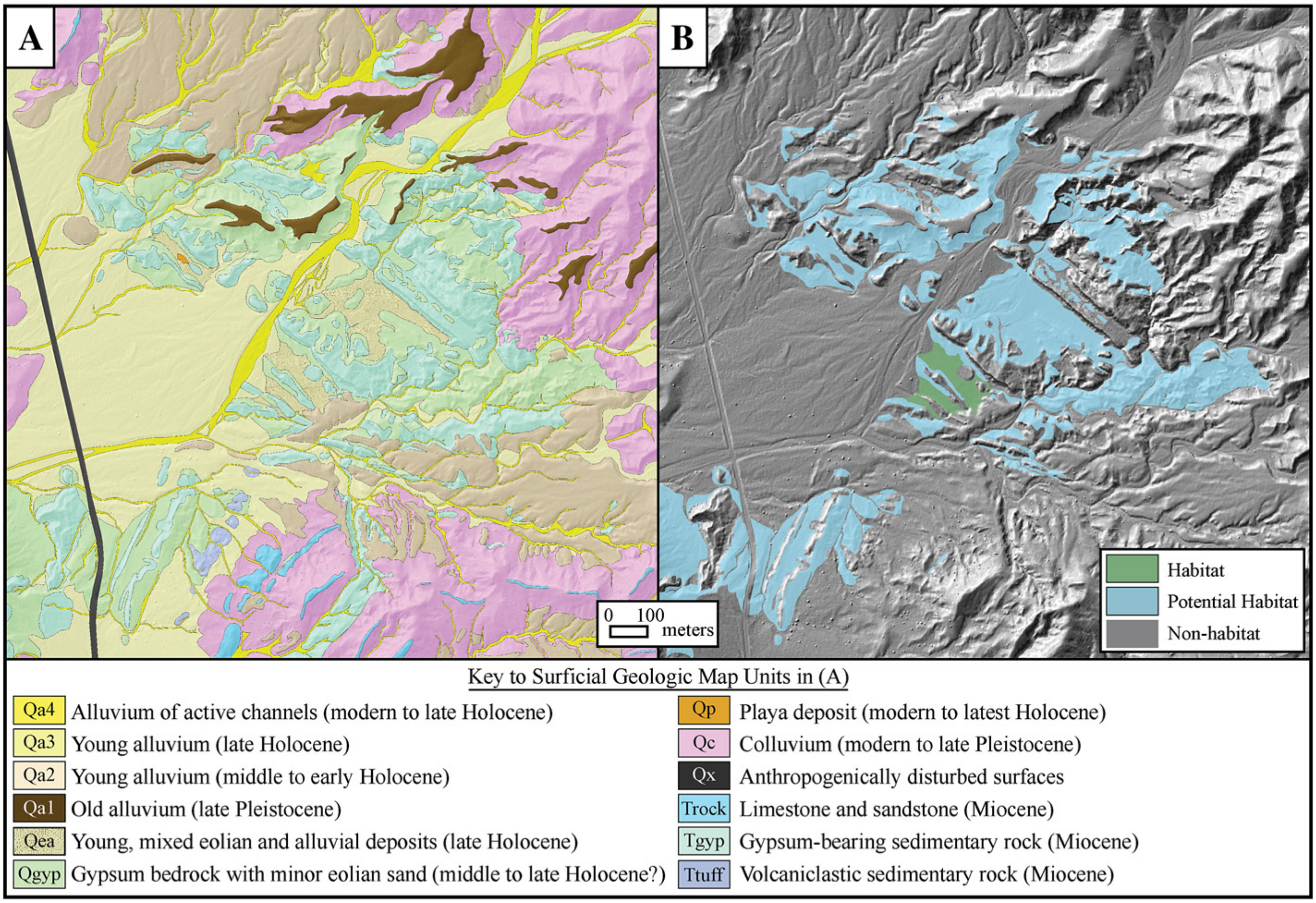

Fig. 3. (A) Surficial geologic map and (B) habitat map for the Gold Butte study area.

units. Overall, the Bitter Spring study area is characterized by deeply incised, inset, late Pleistocene to early Holocene alluvial fan remnants mapped as Qa1 and Qa2, respectively. These gravelly sediments lie unconformably on top of middle-Miocene units Tss and Trock, which are markedly (~15 to 30°) dipping, gypsum-rich sedimentary strata of the Horse Springs Formation, collectively mapped as "Thl" by Beard et al. (2007). These strata are widely exposed in badlands side slopes throughout the study area, except where capped by the gravelly alluvial fan remnants or by thin wedges or sheets of gravelly colluvium (Qcg). Rills and gullies as well as broad (3–30 m) active channels (Qa4) are common throughout the study area, with scattered bars of slightly older young alluvium (Qa3) that sit 0.5 to 1 m higher than the active washes.

Soil morphology and taxonomy at Bitter Spring vary due to meter-scale lithological changes in the stratigraphic units exposed across the White Basin, and due to the variable thickness of alluvium or colluvium across the study area. Calcic Petrocalcids characterize the Qa1 map unit, exhibiting both a well-developed, tightly interlocking desert pavement and a prominent, stage III petrocalcic horizon (Gile et al., 1966; Schoeneberger et al., 2012) at 20–50 cm depth that is exposed in eroding side slopes of the fan surface. Soils developed within unit Qa2 are comprised of Lithic Torriorthents, Leptic Haplogypsids, and Typic Haplocalcids. These bear a pronounced vesicular A (Av) horizon (Springer, 1958) with interlocking surface clasts (desert pavement) composed of Paleozoic carbonates from the mountains to the north and east. Overall, these gravelly, sand-dominated soils contain no or < 1% crystalline gypsum masses or "snowballs" (e.g. Buck and Van Hoesen, 2002) and exhibit stage I calcic horizons (Gile et al., 1966; Schoeneberger et al., 2012). Owing to variable substrate lithology, all three of the comparatively simpler Qa3 profiles observed were different, yielding a Lithic Haplogypsid, a Typic Torriorthent, and a Typic Calcigypsid. In the erosional and bedrock-dominated areas, colluvial unit Qcg was observed to contain one Leptic Haplogypsid and a Typic Calcigypsid, while unit Tgyp typically consisted of either Leptic Haplogypsids, or Typic and Lithic Torriorthents, depending on the nature of the underlying strata (non-cemented marl or mudstone vs. indurated, rigid, siltstone).

At Bitter Spring, map units Tss and Qa3 were found to support apparently thriving LVB populations, and are mapped as "Habitat" wherever field observations confirmed the presence of the species (Fig. 2). Although Qa3 is an alluvial unit, its thickness is highly variable, and it is possible that the depth to buried Tss strata is shallow where LVB occur. Thus, instances of both Tss and Qa3 adjacent to Tss in which LVB do not grow are classified as "Potential Habitat". Map units Qa1, Qa2, Qa4, Trock (indurated limestone or siltstone), and Qc were not found to support any LVB and are considered "Non-habitat".

3.1.2. Results for Gold Butte

Surficial geologic units at Gold Butte (Fig. 3) did not greatly differ from Bitter Spring, however, folding and faulting of the more gypsiferous bedrock appear to have prevented formation of the badlands that characterize the White Basin. The center of the Gold Butte area is dominated by northeast-dipping (30°) outcrops of rock gypsum or gypsum-cemented strata (Tgyp). These exposed strata best match the middle Miocene Thumb member (gypsum facies) of the Horse Spring Formation (Beard et al., 2007) and form high (2–7 m tall) resistant ridges that weathering and runoff have veneered with rigid, physical gypsum crusts. Side slopes and swales between these resistant

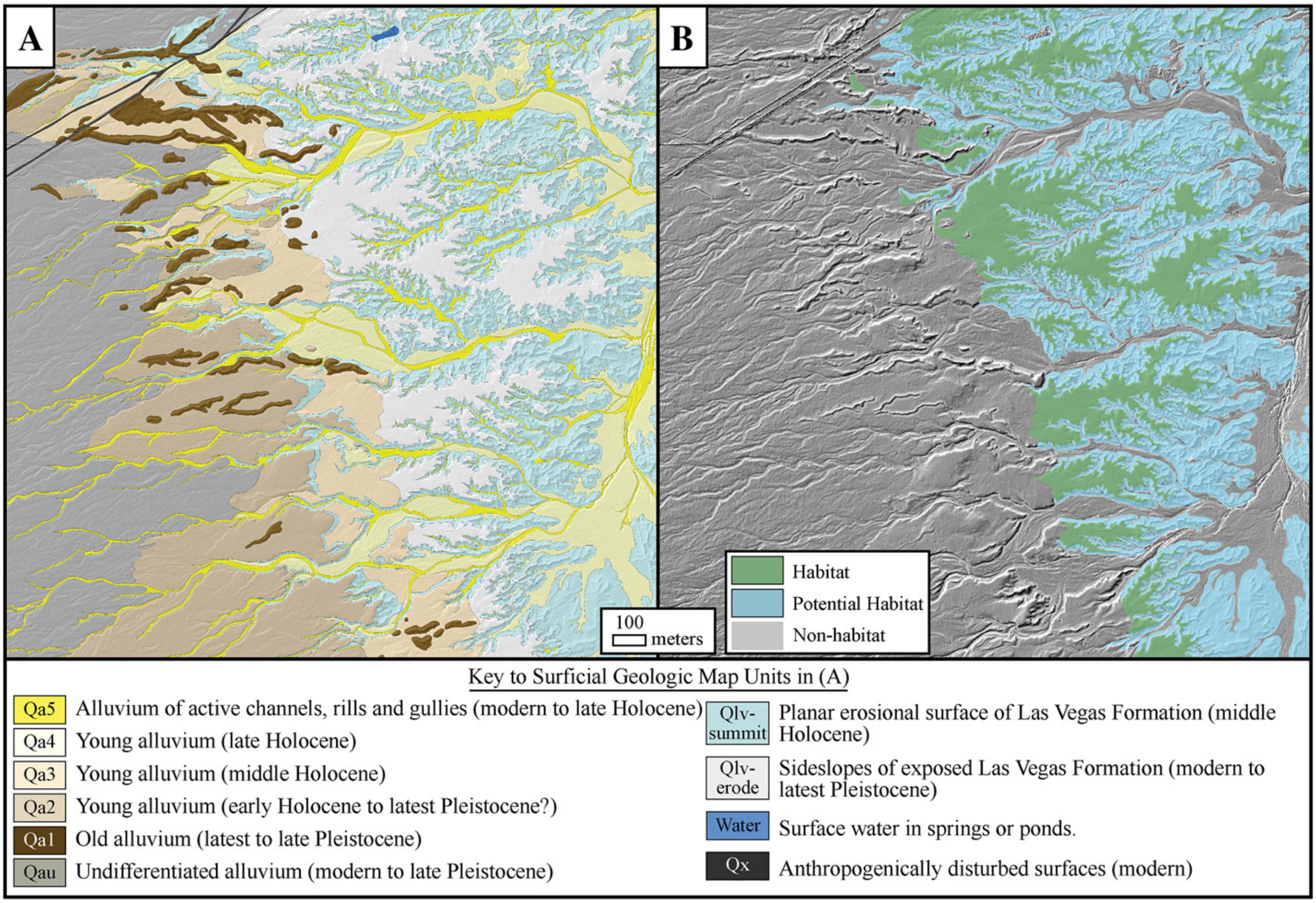

Fig. 4. (A) Surficial geologic map and (B) habitat map for the Coyote Springs study area.

outcrops are underlain by softer, gypsiferous mudrocks (shale, siltstone, and claystone) and are almost completely covered by pinnacle-building biological soil crusts (Fig. 5). These swales act as traps for eolian dust, and grade laterally into sandier, gravelly alluvium (unit Qa3). They are also locally incised as much as 0.5 m by rills, gullies, and small, narrow (≤2 m wide) active washes (Qa4). Highlands and unstable foothills to the east and northeast are veneered with unconsolidated, gravelly colluvium (Qcg), and high-standing alluvial fan remnants (unit Qa2, 2–3

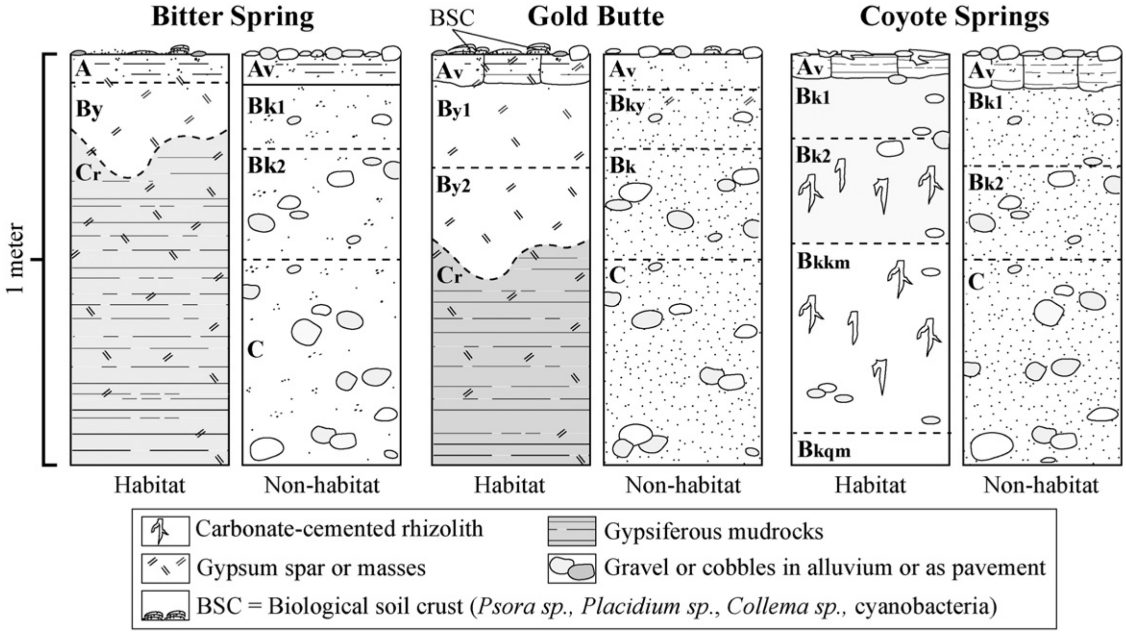

Fig. 5. Schematic profiles illustrative of habitat and non-habitat soil morphology at each of the three study areas.

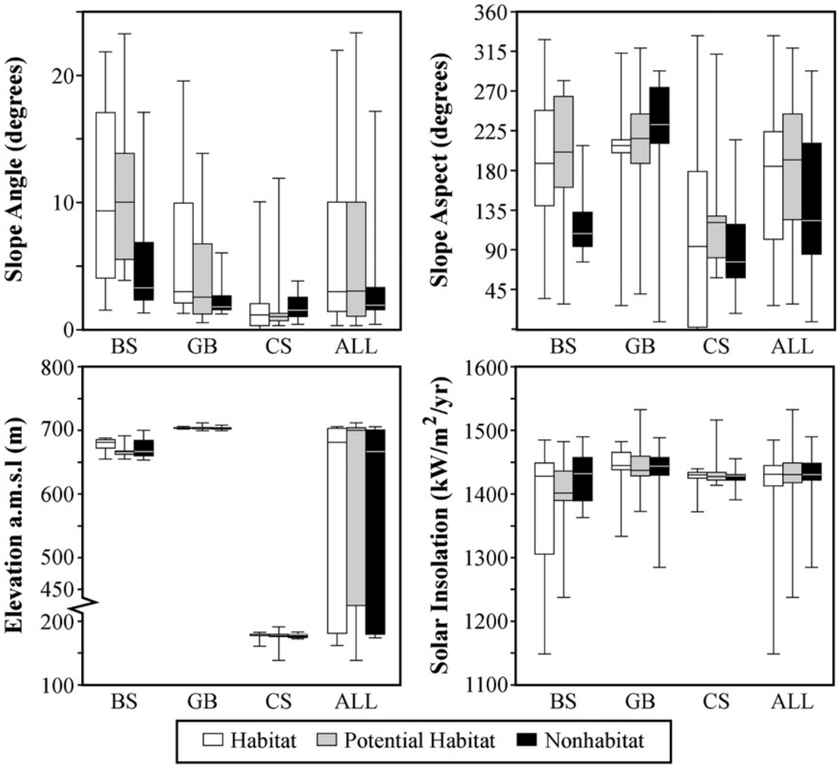

Fig. 6. Boxplot representations of DSM-derived landscape data, showing minimum, maximum, 1st quartile, 3rd quartile, and median (2nd quartile) values of slope, aspect, elevation, and insolation, by study area and by Las Vegas buckwheat habitat class. BS = Bitter Spring; GB = Gold Butte; CS = Coyote Springs, ALL = data from all three study areas combined.

m high, and unit Qa1, ~10 m high) are analogous to those observed in Bitter Spring. One small (~300 m^2) playa deposit (Qp) was recognized at Gold Butte and mapped separately because of surface characteristics indicative of intermittent ponding.

Soil morphology and taxonomy at Gold Butte chiefly reflect the depth to bedrock (or sedimentary strata), local lithology (degree of induration) of the parent material, and/or the age and thickness of overlying alluvium. Consequently, soil taxonomy between map units Tgyp, Qgyp, and Qea form a toposequence with transitions between Lithic Torriorthents on Tgyp summits and steep side slopes, to Lithic Torriorthents and Leptic or Lithic Haplogypsids on gentler Qgyp slopes, to predominantly Leptic Haplogypsids in swales (Qea). Data coverage in the alluvial units was sparse, however, Qa3 was observed to exhibit young, simple Aridisols with incipient development of calcic and/or gypsic horizons; these soils are Typic Haplocambids or Typic Torripsamments (though the latter was not directly observed in any profile). Qa2 soils are best classified as Typic Haplocambids, however, only two pits were excavated in map unit Qa2, and one of those was considered transitional to Qea.

At Gold Butte (Fig. 3), LVB were found most commonly within unit Qea, however, the fringes of unit Qgyp within ~ 1 m elevation of Qea were found to support several of the plants. Additionally, one large individual was found growing on an eroding side slope of Qa2 immediately adjacent to Qea, and, again, no more than one vertical meter above the Qea surface. Both Qea and Qgyp are considered potential LVB habitat. Unit Tgyp, except where local microtopography has trapped sediment and formed an area of Qgyp too small to map, appears not to support LVB.

3.1.3. Results for Coyote Springs

Alluvial fan gravels and sands comprise much of the Coyote Springs study area (Fig. 4), and are divided into six units. Unit Qa1 occurs as narrow (5–10 m wide) ballenas that stand 2 to 3 m above a slightly younger alluvial surface mapped as Qa2, and both of these units were observed to have extremely well-developed desert pavements with tightly interlocking clasts of Paleozoic or Precambrian limestone, dolomite, and quartzite eroded from the adjacent mountains. Rills and gullies as well as broad (3–50 m) active channels (Qa5) continue to erode the Coyote Springs study area, with bars of slightly older young alluvium (Qa4) that sit 0.5 to 1 m higher than the active channels (equivalent to Qa3 at the other study areas). An intermediate surface mapped as Qa3 grades laterally into flat-lying strata of the Pleistocene Las Vegas Formation (Haynes, 1967; Quade, 1986; Quade and Pratt, 1989; Springer et al., 2008). The Las Vegas Formation, a carbonate-rich sequence of white, pink, and brown palustrine or marshland silts, is exposed at Coyote Springs as either spatially extensive (1.5 to 17.5 hectare) planar surfaces (Qlv-summit) bearing an erosional lag and/or a pavement of calcareous siltstone or rhizolith fragments, or as actively eroding side slopes (unit Qlv-erode). Many of the geomorphic surfaces observed in the field area merge together upslope, near the western end of the study area where bar and swale topography dominate. Because of both the merging of geomorphic surfaces as well as distance from habitat sites, this area has been left on the map as undifferentiated alluvium (Qau).

Soils in Coyote Springs alluvial units 1–5 reflect a chronosequence of Typic Haplocalcids, with the most tightly interlocking desert pavement, thickest vesicular horizon, and greatest (strong stage I to stage II) calcic horizon development (Gile et al., 1966; Schoeneberger et al., 2012) observed in unit Qa1. At the other extreme, soils in Qa5 are characterized by poorly interlocking pavement or no pavement at all, and extremely incipient stage I carbonate horizons (Gile et al., 1966; Schoeneberger et al., 2012). Soils in the Qlv-summit and eroded side slope (Qlv-erode) unit are polygenetic, overprinting either (1) exhumed and/or relict Petronodic Haplocalcids with extremely well-indurated, but relict carbonate root traces, or (2) Calcic Petrocalcids (stage III petrocalcic horizons). Bearing this polygenesis in mind, the modern soils best classify as Typic Haplocalcids or Calcic Petrocalcids. Rarely, soils in the Qlv-summit surface may have 0–5 % gypsum as fine masses but, besides this very low gypsum content, horizons bearing these masses are typically too thin to qualify as gypsic. Similarly, amorphous silica coats were observed in several instances, but these horizons did not resist slaking and therefore do not meet the criteria for a duripan (Soil Survey Staff, 2010).

At Coyote Springs, LVB grew almost exclusively within Qlv-summit (Fig. 4), and this map unit is uniformly designated as "Habitat." However, within the Qlv-summit unit, many areas 100 m or greater in diameter were completely barren of vegetation. These areas are especially common along the eastern edge of the study area. In addition to Qlv-summit, two small LVB individuals were also found in areas mapped as Qlv-erode. We therefore consider Qlv-erode to be "Potential Habitat" when adjacent to Qlv-summit, but recognize that this unit is generally too steep and too unstable to support vegetation. Except for the extreme margin of Qa3 immediately adjacent to Qlv-summit, none of the alluvial units (Qa1, Qa2, Qa3, Qa4, Qa5, and Qau) at Coyote Springs were found to support LVB. Therefore, these units are considered "Non-Habitat".

3.2. Insolation and other data

Slope, aspect, elevation, and solar insolation did vary between study areas (Fig. 6), but not in a consistent manner. Both t-tests and also Chi-square tests for independence (with Yates Continuity Correction) were used to evaluate these data, however, the only significant association found ($p = 0.006$) was that between the occurrence of LVB habitat sites and the Qlv-summit map unit at Coyote Springs, where 90.9% of all habitat sites fall within Qlv-summit. No other map units or morphometric measures returned significant relationships, at any individual study area, nor for all areas combined, nor for the results of solar insolation calculations for solstice and equinox days. Results at the other study areas reflect necessarily small sample sizes, as well as the occurrence of LVB in just two map units at Bitter Spring, and three at Gold Butte (Qea, Qgyp, and one on the fringe of Qa2). Lack of significant results may indicate that some edaphic factor (e.g., surface characteristics, soil texture, etc.) outweighs the importance of insolation in determining habitat suitability.

4. Discussion and interpretation

Surficial geologic maps and soil profile data from the three separate LVB population clusters mapped in this study corroborate previously suggested habitat criteria, but also add new detail and, further, strongly suggest that factors more complex than mere gypsophily control the distributions of LVB. While surficial geology and soil morphology, alone, clearly do not entirely control LVB distributions, our comparison of map units and soil characteristics to observed distributions of LVB at the three study areas does offer some important insights. In particular, LVB habitat includes: (1) fine-grained gypsum-rich substrates that lack strong physical crusts, (2) fine-grained carbonate rich, low gypsum parent materials formed from springs and paleowetlands, and (3) young, inactive, alluvial or mixed alluvial and eolian siliciclastic deposits with variable secondary gypsum and/or carbonate. Additionally, LVB habitat is strongly affected by the degree of desert pavement development and the thickness and grain size of siliciclastic sediments: areas with tightly interlocking desert pavement or deep (>1 m) coarse-grained alluvium are not suitable for LVB.

4.1. Gypsum and carbonate

Our surficial geologic maps indicate that gypsum-rich bedrock and soft sediments are found exposed at the surface and actively eroding, or at shallow depths under eolian veneers, alluvium, and/or colluvium throughout much of the Bitter Spring and Gold Butte study areas. Generally, LVB at Bitter Spring and Gold Butte occurred in the poorly lithified strata only, or in thin (<1 m), younger, Holocene sediments unconformably overlying these strata. Outcrops of rock gypsum with hard physical surface crusts did not support LVB. Thus there is no doubt that gypsum substrates should remain a prominent part of LVB habitat criteria, and the lack of habitation in some gypsum-rich areas may, in part, be explained by physical surface crusts, the degree of lithification, or other factors discussed below.

Nevertheless, our study suggests that LVB may not require gypsum. LVB at Coyote Springs occurs exclusively within the Las Vegas Formation, and offers habitat insights similar to those of Drohan and Merkler (2009). It is also important to note that gypsum-poor carbonate parent materials are also common as thin strata in Bitter Spring (units Trock and Tss) and Gold Butte (units Tgyp and Trock), and, when not well-lithified, appear to support LVB. Thus, the range of LVB habitat criteria should be expanded to include fine-grained, calcareous, gypsum-poor to non-gypsiferous deposits of springs or paleowetlands as well as soft sediments of the Horse Springs Formation.

4.2. Siliclastic units

Sediment thickness, grain size, and, perhaps to a lesser degree, surface age, appear to be factors determining whether alluvial substrates will or will not support LVB. We observed that LVB was absent in older soils with tightly interlocking desert pavements, higher gravel content, and/or thicker alluvium. Thus, coarse-grained late Pleistocene as well as early to middle Holocene geomorphic surfaces can be excluded from possible habitat considerations. In fact, surfaces of any age that are composed of thick (>1 m), coarse-grained sediment are unlikely to be suitable habitat for LVB, and active washes are also unlikely to sustain LVB because of active channel flow and erosion. The trend of buckwheat being excluded from old, gravelly, higher elevation geomorphic surfaces matches influences of relative soil age and landform position on water availability and infiltration rate (Hamerlynck et al., 2002; Smith et al., 1995) and is also supported by observations of LVB habitat made by Drohan and Merkler (2009). Tightly interlocking pavements promote runoff and reduce infiltration (Hamerlynck et al., 2002; Smith et al., 1995). Pavements may also adversely influence seed establishment or germination, however, more research is needed to determine whether this is true for LVB. Similarly, gravelly soils and pavements in the Qa1 and other alluvial units may cause low water-holding capacities or rapid infiltration rates that exclude LVB. If not controlled by biotic factors, this study demonstrates that some sites which upon cursory observation appear to be viable areas for LVB (e.g. potential habitat) but do not contain LVB will, upon closer inspection, likely be found to have deeper alluvium, more closely interlocking surface clasts, less carbonate or gypsum, or more strongly indurated bedrock than habitat sites.

Sediment thickness, grain size, and surface age also bear consideration for areas influenced by fine-grained, mixed eolian and alluvial processes and biological soil crusts. One of the best examples is the Qea unit at Gold Butte. Biological soil crusts 0.1 to 3 cm thick actively trap eolian dust, stabilize the surface, and create a 1 to 6 cm thick vesicular A horizon (Williams et al., 2012) atop shallow alluvium that in turn mantles gypsiferous sediments. This important LVB habitat does not have the strong physical surface crusts which can be common on gypsum-rich sediments, nor interlocking surface clasts (e.g. desert pavement), yet at least some secondary, pedogenic gypsum is typically present. More research is needed, but Qea and similar deposits appear to be highly suitable LVB habitat. The comparable surface horizons of unit Qgyp are less ideal as habitat, because they directly veneer hard, indurated gyprock rather than thin, fine-grained, soft alluvium.

Grain size appears to be more important than geomorphic age as a habitat characteristic based on the close relationship between units Qea and Qa3 at Gold Butte, and given the absence of LVB in unit Qa3. As mentioned previously, fine-grained, carbonate-rich sediments of mixed alluvial, spring, and/or palustrine origins are also habitat regardless of their geomorphic age.

4.3. Morphometry and other factors

Slope angle does not appear to be a controlling factor for LVB habitat, however, surfaces with the lowest slope angles at Bitter Spring and Gold

Butte also tended to be those with the most tightly interlocking desert pavements. Surficial geologic characteristics including the mineralogy, texture, degree of lithification, and presence of surface crusts or desert pavement outweighed slope angle and the other morphometric parameters as habitat predictors. Solar insolation (Fig. 6, and data repository maps) did not vary significantly between habitat classes at the 5 m resolution permitted by our data set, and is discounted as a variable controlling LVB habitat. We nevertheless recommend microclimate and/or very-high resolution (~0.1 to 0.5 m) solar insolation studies because of their potential to identify important soil–water relationships that were not resolved even at the 1:3,000 surficial geologic map scale nor the 5 m pixel size insolation analysis used in this study. More detailed, experimental analysis of water holding capacity and other hydrological considerations also merit consideration for future research.

Much additional work is needed on the physiology and ecology of LVB, its relationship with biological soil crusts, and on its potential competition with other plants. We especially note the potential importance of shrub age uncertainty and an inevitable temporal bias to interpretations of modern habitat patterns: data collected in this study represent a short time-slice only, and we cannot discount the possibility that LVB may once have flourished in areas in which it is absent today.

5. Conclusions

Soil profile description and surficial geologic mapping are critical steps in the characterization of selective habitat species distributions, and the use of a representative, spatially disparate sampling of habitats for study is extremely important. Detailed landscape divisions would prove advantageous for the study design of ecological research in other, analogous environments around the world. Surficial geologic maps can save time and increase efficiency especially when conducting site characterization, or when deciding where and how to sample for soil chemical analyses.

We find that soil profile description and 1:3000 scale surficial geologic mapping permit new, more detailed habitat modeling of a rare and potentially threatened Mojave Desert gypsophile than was previously possible. Our results show that soil and surface characteristics outweigh the mineralogy as habitat determinants, and refute the hypothesis that morphometric parameters including insolation exert any dominant control on LVB distributions. Besides offering a more cohesive definition of habitats for the LVB, the new insights gained from surficial geologic and soil profile data also provide reference conditions for ecological restoration of LVB habitat (and that of species with overlapping habitat ranges) in disturbed areas, and raise new hydrological, soil chemical, and ecological questions.

Our results suggest that the following criteria, in addition to gypsum-rich substrates, should be considered when modeling LVB habitats. LVB favors: (1) fine-grained, gypsum rich substrates that lack physical surface crusts and that are not indurated. Secondly, (2) fine-grained calcareous soils or strata that lack tightly interlocking desert pavements are viable habitats commonly associated with the Las Vegas and Horse Springs formations. It remains unclear whether the Las Vegas Formation is an optimal habitat for LVB or, instead, a case of LVB merely surviving in an otherwise harsh environment due to reduced competition. Nevertheless, the occurrence of LVB in gypsum-poor, calcareous substrates appears to challenge prior assumptions of gypsophily. (3) Sediment depth and grain size are important habitat controls. LVB are extremely unlikely to thrive in areas of thick (>1 m) gravelly alluvium and/or tightly interlocking desert pavement, however, LVB can be found in fine-grained alluvium, particularly those with an eolian component that forms a thin (<1 m) cover over gypsum bedrock. In this study, these habitats were commonly associated with well-developed biological crusts. Finally, (4) geomorphic surface age appears less important than mineralogy (e.g. gypsiferous or calcareous), grain size, and sediment thickness. However, because older geomorphic surfaces tend to have tighter desert pavements and thicker coarse-grained alluvium, most can be excluded as LVB habitat, and active arroyos are also unsuitable.

Individual deposits, soils, and landforms which support LVB or other gypsophilic desert shrubs may be quite small, thus, use of large-scale maps and/or high-resolution satellite data are recommended for any attempt at habitat modeling, especially if the geological parent material is a suspected control of plant distribution. While there is no direct translation between map scale and raster resolution, the ability to identify landforms only moderately larger than individual shrubs was an asset in this study. It is hoped that the increasing availability of LiDAR data will promote more frequent inclusion of detailed soil geomorphic mapping in future habitat studies for gypsophiles and other desert flora. Surficial geologic mapping and analysis of soil profile morphology and, ideally, soil profile chemistry, are vital considerations for studies of vegetation dynamics, nutrient requirements, plant biogeography, and habitat management, particularly within the Mojave Desert and other arid ecosystems.

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Appendix A. Supplementary data

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