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A hierarchical analysis of vegetation on a Mojave Desert landscape, USA

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ABSTRACT

To examine four elements of the hierarchical structure of desert communities, we analyzed plant species composition and 13 environmental variables at 126 sites within a 755 000-ha Mojave Desert landscape, southwestern USA. By a coarse, six-group level (out of 17 groups) in cluster analysis, four generalized community types emerged: widespread, low-elevation communities with *Larrea tridentata* or *Ambrosia dumosa*; communities on unique soils (e.g., gypsum) indicated by *Atriplex* spp.; higher elevation/rugged terrain communities including *Coleogyne ramosissima*; and disturbance-associated communities such as *Bebbia juncea-Hymenoclea salsola*. Based on indicator species analysis (ISA), there was no clear level of the community classification that optimized discriminating among communities, because each of four measures of ISA peaked at different hierarchical levels. Three general types of indicator species were identified based on whether their value for discriminating among communities peaked at coarse (e.g., *L. tridentata*), intermediate (*Atriplex hymenelytra*), or fine (*Krameria grayi*) levels of the community hierarchy. Environmental variables differed in their relationships to the hierarchy, with some (e.g., pH) not differing among communities at any level and others, such as rooting depth, differing among communities at multiple levels. Hierarchical analytical techniques can help identify structural patterns within arid land plant communities, species distributions, and vegetation–environment relationships.

1. Introduction

Biological communities are increasingly viewed as hierarchical systems where finer scale units are nested within broader units (O'Neill et al., 1986; Schneider, 2001; Englund and Cooper, 2003). A central tenet of hierarchy theory, when applied to landscapes, is that broad-scale environmental factors and communities constrain the development of finer scale nested communities (Allen and Starr, 1982). In northern Minnesota, for instance, Palik et al. (2003) found that fine-scale wetland communities were six times more likely to be nested within glacial moraines than within glacial lake plains. Their analysis provided a framework for identifying environmental variables associated with plant distributions at different hierarchical levels and for identifying probable locations of fine-scale communities of conservation priority.

Considering arid lands, past reviews of Mojave Desert vegetation studies in the southwestern USA, for example, highlighted the single-scale focus of most community studies (Vasek and Barbour, 1977; Rowlands et al., 1982). Hierarchical analyses may help enrich our understanding of community and species patterns of desert vegetation (El-Ghonemy et al., 1980). Components of a hierarchical landscape analysis could include exploring: (1) hierarchical patterning of plant communities, (2) identification of characteristic species for different levels of the hierarchy and hierarchical levels at which communities and species are maximally distinguished in their distributions, (3) environmental variables associated with community distributions at different hierarchical levels, and (4) how a hierarchical perspective may help identify unique, fine-scale communities or assist with other practical applications such as mapping vegetation at different scales.

Indicator species analysis (ISA; Dufrêne and Legendre (1997)) is one of the statistical tools for hierarchical community analysis and has been widely used for identifying species that discriminate among hierarchically classified communities. An application proposed for ISA is to identify optimal levels of clustering (i.e. number of groups) in hierarchical community analyses (Dufrêne and Legendre, 1997; Aho et al., 2008). For example, when clustering beetle communities in Belgium, Dufrêne and Legendre (1997) found that the strength of indicator species had different peaks between two and 10 groups but was optimized at a three-group level. Using a vegetation data set from western Montana, USA, McCune and Grace (2002) reported that a mean *P*-value criterion for indicator species optimized at four groups,

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whereas the number of significant indicators was high between three and eight groups and was zero after 12 groups. These studies, combined with others (e.g., Perrin et al., 2006), suggest that there can be considerable variability in the results of this technique among communities, which have seldom included desert vegetation, but communities at intermediate hierarchical levels are typically best discriminated through ISA. Similarly, hierarchical ISA can help identify species distribution patterns among communities at different levels of a hierarchy (Dufrêne and Legendre, 1997). Some species can be associated with broad-level groupings, while others are indicative of finer scale, nested communities.

Environmental variation is a major factor structuring the distributions of species and communities, but the relationships of different environmental variables with biota can change at different scales (Miller and Franklin, 2006). Previous studies in North American deserts have highlighted the correlation of variables such as elevation (Ezcurra et al., 1987), slope aspect (Evens, 2003), soil texture and rooting depth (McAuliffe, 1994), and soil chemistry (Drohan and Merkler, 2009) with plant distributions. In the northern Sonoran Desert, for example, Parker (1991) found that the distributions of columnar cacti perennial communities were strongly associated with elevation and slope aspect, and secondarily by a soil parent material gradient related to differences in texture and pH varying with granitically or volcanically derived soils. This study also illustrated the potential for hierarchical influences, as relationships of vegetation to the environmental variables could change if finer scale variation within these soil types was assessed. Analyzing such hierarchical structure could help determine if maximal differences among community types defined by species composition coincides with maximal environmental variation among communities. This congruence could result if variation in environmental factors is most strongly correlated with species distributions at a particular hierarchical level.

We conducted an integrated set of analyses using multivariate classification methods, ISA (Dufrêne and Legendre, 1997), and environmental analysis to explore four components of the hierarchical structure of plant communities on an eastern Mojave Desert landscape. First, we assessed the community structure of the landscape to identify broad-scale and nested community types using hierarchical cluster analysis. Second, with ISA, we evaluated which level of the community classification hierarchy optimized discrimination among communities. Based on suggestions in the literature, we expected that some intermediate level of the hierarchy would provide the most distinctive separation of communities (McCune and Grace, 2002). Third, we determined the distributions of species among hierarchical communities, anticipating that widespread species would characterize broad-scale communities and rarer species finer scale communities. Fourth, we determined which hierarchical levels displayed the greatest discrimination in environmental variables. We expected that the importance of environmental variables would be hierarchy-specific and that the same levels maximally distinguished by ISA would correspond to maximal environmental variation among communities. In addition to augmenting knowledge on the theoretical understanding of desert plant communities, results may have practical implications for identifying nested, fine-scale communities, mapping desert vegetation, and developing community-specific management strategies at relevant scales.

2. Materials and methods

2.1. Study area

This study occurred within the 449 000-ha (land area excluding full-pool areas of Lakes Mead and Mohave) Lake Mead National Recreation Area managed by the National Park Service and 306 000 ha of surrounding Bureau of Land Management lands, in the eastern Mojave Desert of southern Nevada and northwestern Arizona, USA (Figs. 1-2). The study area receives approximately 70% of its precipitation as fall/winter (September–April inclusive) rains, and much of the remainder as summer (July and August) monsoonal storms (WRCC, 2010). Near the center of the area at an elevation of 768 m, the Boulder City, Nevada, weather station has reported the following averages from 1931 to 2004 records: 4 °C January daily minimum temperature, 39 °C July daily high temperature, and 14 cm/yr of precipitation (WRCC, 2010). Major landforms include low mountain ranges, bajadas (coalesced alluvial fans), relatively flat plains, washes serving as intermittent drainageways, and playas (dry lakes). Livestock grazing is not authorized in the study area; major herbivores include exotic *Equus asinus* (wild burro) and native *Ovis canadensis nelsoni* (bighorn sheep), *Lepus californicus* (jackrabbit), and a variety of other animals.

2.2. Data collection

The Clark County, Nevada (Lato, 2006), and Central Mohave County, Arizona (Strait, 2006), soil surveys covered the study area. Soils were mapped following standard U.S. Natural Resources Conservation Service protocols (Soil Survey Division Staff, 1993) in an order 3 survey (minimum mapping unit = 4 ha) for Clark County and an order 2-3 survey (minimum mapping unit = 16 ha) for Mohave County. We used the soil surveys as a framework for this study, by sampling points where soil pedons were fully described, including type localities for soil series and field notes for characterizing the series and inclusions within mapping units to capture variability (Lato, 2006; Strait, 2006). We sampled all of these sites (n = 126) for which we had access to geographic coordinates of their locations. Springs, which support small areas of moist-affinity vegetation in the study area, were not included in the soil survey, but washes meeting minimum mapping criteria were included. The sampling sites provided extensive coverage of the landscape (Fig. 1) and included 17 soil great groups (U.S. soil classification system) and two orders (Aridisols and Entisols). While exhaustively inventorying all possible plant communities on the landscape was not a goal of our study, sampling encompassed a variety of plant communities across a range of soil types. The finest scale communities included in our study would likely be equivalent to the alliance or association level of the U.S. National Vegetation Classification (Jennings et al., 2009) and are similar in resolution to the finest levels of some recent Mojave Desert community classification studies (Ostler et al., 1999; Thomas et al., 2004; Keeler-Wolf, 2007).

At each of the 126 sites, we delineated a 30 m × 30 m (0.09 ha) plot containing a 10 m × 10 m subplot at the southwestern corner. This subplot contained 1 m × 1 m quadrats centered at 0.5, 5, and 9.5 m along the southern and northern boundaries of the subplot (n = 6 quadrats). We visually categorized the areal percent cover of each perennial plant species rooted in each quadrat using the following cover categories from Peet et al. (1998): 1 = trace (assigned 0.1%), 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = > 95%. The remainder of the subplot and whole plot was surveyed for species not already recorded in quadrats for a complete census of species on plots, using the same cover categories as for the quadrats. Cover was represented as the average cover (in %) from quadrats and as the subplot and whole plot cover (%, from the midpoints of cover classes) from species not in quadrats. Nomenclature followed NRCS (2010).

Elevation (measured with a GPS), slope aspect (compass), and slope gradient (clinometer) were recorded from the centers of