

# Niches of common bryophytes in a semi-arid landscape

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**ABSTRACT.** The Santa Monica Mountains, adjacent to the Pacific Ocean just west of Los Angeles, California, have low elevation, high relief and a Mediterranean climate. To date 122 species of bryophytes have been found, especially in the moist drainages. Species that were common (about half of the 122) were compared in terms of microhabitat variables (substrate softness, moisture, slope and shadiness) and in how they distinguished mesosites (varying vascular vegetation types, elevation, parent rock type, distance to the coast and insolation). This constitutes a descriptive comparison of the ecologies of the species in the flora. Acrocarpous mosses, pleurocarpous mosses and liverworts tended as groups to differ in some habitat preferences. Only a few bryophyte species were strong indicators of vascular vegetation type. The diversity of sampled mesosites was to a great extent explicable as a scaling-up of the variety of microsites that each contained, thereby allowing for a diversity of bryophytes in a biome that might generally be characterized as inhospitable.

**KEYWORDS.** Bryophyte, floristic habitat sampling, microsite, mesosite, niche axes, Santa Monica Mountains, California.



Many floras include notes on species' habitats, such as "often in calcareous seeps" or "on rocks and occasionally on bark." It is also possible to compare species to one another. For example, one could assert that *Hedwigia detonsa* tends to be on shadier sides of rocks than *Grimmia laevigata*. If one takes that step of comparing one species to the next, it is natural to take the additional step of arraying all the species in a community from the one that is most characteristic of sunny spots to the one that is the most shade-loving. Another popular descriptive approach is to carry out a gradient analysis as an ordination. This can be done by presenting the diversity of sites in the area based on species associations or the variety of species based on tendencies of coöccurrence (Kershaw & Looney 1985, McGarigal et al. 2000).

Such results can increase one's knowledge of how species sort themselves out in a community, results that are intimately tied to the scale and topographic position of sites that one has sampled (Silvertown et al. 2006; Virtanen et al. 2001). Here we bring together the approach of comparing the habitat of each species to every other species and the approach of ordinating sites and comparing the species by which the sites differ. This combination allows us to compare species in terms of habitat differences that are manifest at two scales.

The work was done in the Santa Monica Mountains (SMM) of southern California, just west of Los Angeles. The SMM are a low elevation, high relief, coastal range with a Mediterranean climate (Rundel & Gustafson 2005). Winters are short, wet

and mild; summers are long, dry and hot. Rainfall varies annually and topographically but with a mean of 48 cm per year. Often no rain falls from June through September. Ours is the first description of bryophyte niches from a climate as arid as that of the SMM. The SMM are geologically young, steep and deeply incised by creeks. The bottoms of the drainages are dominated by stands of oak (*Quercus agrifolia*), sycamore (*Platanus racemosa*), willow (*Salix* spp.) and bay (*Umbellularia californica*), while the drier slopes are covered with ceanothus (*Ceanothus* spp.) or chamise (*Adenostoma fasciculatum*) chaparral, coastal sage scrub (*Salvia* spp.), patches of grassland and exposed rock outcrops with spike-moss (*Selaginella bigelovii*). The geology is a mosaic of andesitic volcanics of low pH and uplifted marine sandstones of high pH.

“Mesosites” in a landscape represent habitats in which an assemblage of bryophytes lives. A mesosite could be a place at the bottom of a drainage with a dense tree canopy, or a north-facing slope covered by coastal sage scrub. Within mesosites, there are a variety of “microsites,” distinguished by the kind of substrate, how long it stays moist after a rain, the steepness of the incline and the amount of shade. Vitt and Belland (1997) defined microhabitats as habitat patches ranging in size from millimeters to centimeters. In the SMM, some species, such as *Porella cordaeana*, appear to need a characteristic habitat on the scale of a meter<sup>2</sup>, while many other species need only a cm<sup>2</sup>. A crack on the side of a boulder may be all that *Grimmia lisae* needs, and a small indentation on the ground is often enough for *Tortula atrovirens*. Sampling both micro- and mesosites allows us to ask how much of the species richness comes from the variety of microhabitats within mesosites as opposed to the variety of mesohabitats sampled in the landscape?

#### METHODS

Early in our studies, an attempt was made to survey bryophytes in all vascular vegetation types in the SMM. To date, this has resulted in a list of 122 species (Sagar 2007). Taxonomic nomenclature follows Norris and Shevock (2004) and Doyle and Stotler (2006). After we knew how to recognize many species, a mesosite-based study was undertaken

during the wet seasons of 2005 and 2006. One hundred and three mesosites that promised to have unusual bryophytes or numerous species of bryophytes were selected (Fig. 1). These mesosites were not representative of the landscape as a whole. There was an under-representation of exposed south-facing slopes and dry ridges, which are extremely poor in bryophyte cover and diversity within a mesosite. The census method used was derived from floristic habitat sampling (Newmaster et al. 2005; Vitt et al. 2003). At each mesosite all microhabitats within a mesosite were searched for bryophyte species and how well the species was doing on the various microhabitats was compared.

The mesosites were as large as a hectare each, although they were not measured plots. Instead they were locations such as a rock outcrop and surroundings or a section of ravine with fairly uniform vascular vegetation. The goal was to keep in the observer’s mind all the observations within a mesosite while at that mesosite. At the next mesosite the observer would start over without considering the patterns of occurrences in previous mesosites. This approach ensured that all microsites at a mesosite were assessed.

At each mesosite, a list was made of all the bryophyte species. Then, the softness of each species’ substrate was categorized into four classes—hard rock, soft rock, compact soil and loose soil. Each species was given “abundance points” based on how well it was doing in each substrate softness class relative to other examples of that kind of bryophyte in the experience of the senior author, who scored all the abundances. Our scoring system consisted of giving 3 points when a species was doing very well, 2 when doing okay, 1 when a species was doing poorly although found in several patches or doing well in one patch, 0.6 when seen only twice with neither patch being luxuriant and 0.3 points were given when the species was seen once in a small patch. Abundance points and substrate softness categories are admittedly subjective and crude measures. However, the analyses to be done were in essence averages of many replicate comparisons, so according to the law of averages, as the number of observations increased, the importance of accuracy must have decreased. Next, the moisture preferences were

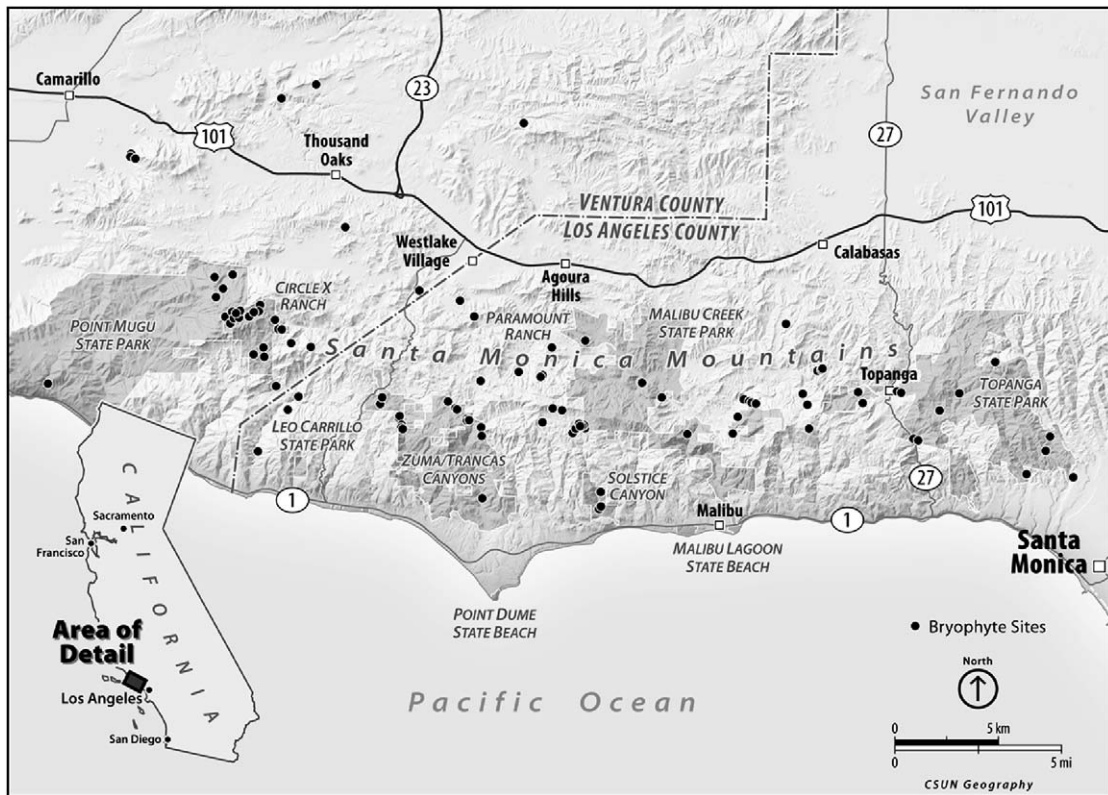


Figure 1. Map of the Santa Monica Mountains with mesosite sampling locations indicated by black dots.

considered in four classes—dry spots with high runoff, substrate that would hold moisture, places that after a rain would be saturated for some time and places that receive water from seepages or streams for much of the year. Again points were given for each moisture class. The slope of the substrate was scored in three classes— $0-20^\circ$ ,  $>20^\circ$  but less than  $90^\circ$  and  $>90^\circ$ . And shadiness was scored in four classes—sunny all day, less than  $\frac{1}{4}$  shade,  $\frac{1}{4}-\frac{3}{4}$  shade and fully shaded all day. The scoring for all four niche variables was repeated for all species. When two species occupied similar microhabitats, special attention was given to assigning points so as to differentiate the microsite preferences of ecologically similar species. At the end of scoring a mesosite, we counted the number of “occurrences” of each species, counting occurrences as separate if they were at least 1 m apart.

For each mesosite, location and elevation were recorded with a GPS or from a USGS 7.5' map. Notes were taken on topography, classifying the mesosite as a slope, ridge, ravine or outcrop. Dominant

vegetation was recorded, which was later classified into the following vascular vegetation types: oak-sycamore/willow, oak-bay, oak, *Ceanothus*, chamise, coastal sage scrub/*Selaginella*. Parent rock type was scored as volcanic or sandstone. Solar insolation for each mesosite was obtained from a 30 m Digital Elevation Model (Goldstein 2000): solar insolation is the amount of sun a mesosite would receive on the equinox, taking into account the path of the sun and the obstruction of the surrounding macrotopography. Finally, distance from the coast was measured from a digital aerial map.

#### ANALYSES AND RESULTS

**Numbers of species.** We found 61 species at three or more mesosites. The three most common were *Didymodon vinealis* (75 mesosites), *Timmiella anomala* (74 mesosites) and *Grimmia lisae* (72 mesosites). *Asterella californica* and *Fissidens sublimbatus* occurred at 60 mesosites each. There were 11 species that occurred only at two mesosites, and 18 more that occurred at only one mesosite.

Some of the species found infrequently are of a small stature that could have been overlooked at some additional mesosites (e.g., *Microbryum davallianum* and *M. starckeanum*) or ephemeral species that could have been missed because conditions were not favorable for them to have appeared when the mesosite was visited (e.g., *Phascum cuspidatum*, *Pleuridium subulatum* and *Sphaerocarpos texanus*). Acrocarpous mosses dominate the SMM bryoflora, with 35 species found at three or more mesosites. There were 17 pleurocarpous mosses occurring at three or more mesosites. There were nine liverworts that occurred at three or more mesosites.

A few of the uncommon species are at the edge of their range in the SMM. *Dendroalsia abietina*, a species which in northern California is abundant on oak and sometimes on adjacent rocks, was found at only two mesosites, both on nearly vertical north-facing volcanic rock in shaded oak-bay woodlands. *Antitrichia californica*, another species abundant to the north, was found at five mesosites, but it was scant at all five locations. *Tortula californica*, *T. guepinii* and *T. inermis* are relatively more common to the south and southeast (Flowers 1973; Sharp et al. 1994), while *Tortula systylia* tends to prefer higher elevation habitats and cooler climates (Norris & Shevock 2004). Although it was not a surprise to find these four pottiads, they were encountered more rarely than their congeners *T. atrovirens* and *T. muralis*.

Although the SMM have some perennial streams, truly aquatic species (e.g., *Fontinalis*) are missing. Similarly, species of certain special microhabitats such as rotten logs are missing as a result of frequent fires. Species specialized on limestone are also missing, although limestone does occur as a few small lenses in the SMM. Many of the drainages with considerable fog drip have substantial stands of oaks and willows with rough bark that could be expected to host many more bryophytes, yet in the SMM there are very few epiphytes.

**Niches within mesosites.** Species were arrayed from the one that did best on the hardest of substrates to the one that did best on the softest of substrates. The abundance points were converted to a continuous index by taking a weighted average across the four substrate classes. For example, at Upper

Sycamore Canyon, *Fissidens sublimbatus* had 0 points for hard rock, 1 point for soft rock, 3 for compact soil, and 2 points for loose soil, so its softness index was:

$$\frac{0 \times 1 + 1 \times 2 + 3 \times 3 + 2 \times 4}{(0 + 1 + 3 + 2) \times 4} = 0.7917$$

Within a mesosite each species was compared to every other species that was found at that mesosite by calculating pairwise differences in their index values. At Upper Sycamore Canyon, the difference between *Fissidens sublimbatus* and *Scleropodium obtusifolium* was 0.7917-0.2500, i.e., 0.5417.

Species that occurred in fewer than three mesosites were not included in this analysis. There were 6,728 differences between pairs of species within mesosites. A program was written in Visual Basic to collapse all these differences onto a single number line, "the softness niche axis," via three steps. (1) The 61 species that occurred in three or more mesosites were put on a number line in an arbitrary order. A "cophenetic correlation" between the empirical differences and the made-up distances was calculated as Pearson's *r*, which at first was very close to 0. Then, the program swapped the positions on the number line of every species with every other species. Whenever swapping increased the cophenetic correlation, the new order was retained; otherwise the old arrangement was left in place. The program was allowed to run through several iterations of swapping all the species pairs until the cophenetic correlation stopped changing, signaling that it had arrived at a ranking of the species from the one that lived most consistently on hard substrates (*Grimmia laevigata*) to the one that lived most consistently on loose soil (*Cryptomitrium tenerum*). (2) The program adjusted the positions along the number line by adding and subtracting decimal 10<sup>th</sup>s +.9, +.8, ...-.8, -.9 one species at a time, using the positions that maximized the cophenetic correlation. The program was allowed to loop through all the species five times, adding and subtracting 10<sup>th</sup>s. After five loops, there were only tiny changes in cophenetic correlations. (3) The program adjusted the decimal hundredths of each species, again looping through all the species five times. The final position along the number line was dubbed the species' "niche preference" for substrate softness. This was done for all four niche axes.

The final cophenetic correlations for the niche axes were  $r = 0.7607$  for substrate softness,  $r = 0.7732$  for moisture,  $r = 0.5144$  for steepness of slope and  $r = 0.6059$  for shadiness. Cophenetic correlations are an indication of how easily the data could be collapsed onto the number line; a value of 1.0 would mean the data were perfectly linear.

**Figure 2** shows the species arrayed along the four axes. Panel **A** shows the placement of the species based on their preferences for substrate softness and moisture, and Panel **B** shows their relative preferences for the microsite's shade and slope.

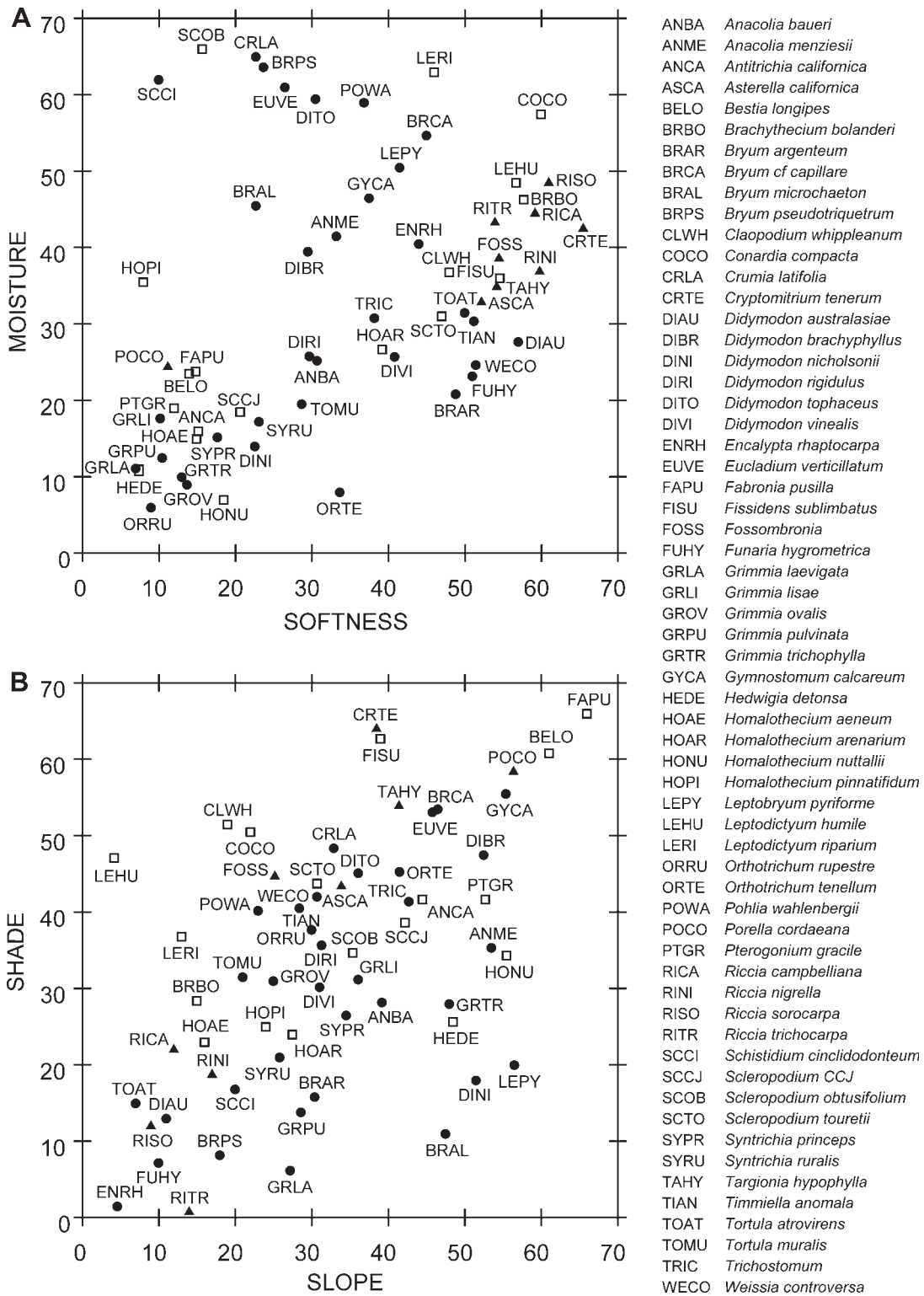
An understanding of the species is gained by comparing their niches. For example, *Orthotrichum rupestre* (ORRU in the lower left corner of **Fig. 2**, Panel **A**) was consistently found on hard dry rock on a medium incline in medium shade, whereas *Conardia compacta* (COCO in the upper right corner of **Fig. 2**, Panel **A**) was found on soft soil saturated with water in flat shaded microsites. *Fabronia pusilla* (FAPU in the upper right corner of **Fig. 2**, Panel **B**) was found in the steepest and shadiest of microsites, whereas *Encalypta rhaptocarpa* (ENRH in the lower left corner of **Fig. 2**, Panel **B**) was found on nearly the flattest and sunniest of microsites. The pleurocarpous *Homalothecium arenarium* (HOAR) and the acrocarpous *Didymodon vinealis* (DIVI) were close to one another in terms of moisture, softness and slope, but *Didymodon vinealis* preferred deeper shade and *Homalothecium arenarium* liked sunnier places. All *Grimmia* species tended toward dry hard substrates (lower left of **Fig. 2**, Panel **A**), but they spread out in Panel **B**, with *G. trichophylla* (GRTR) living on steeper surfaces followed by *G. liseae* (GRLI), then *G. ovalis* (GROV) and *G. pulvinata* (GRPU) living on sunnier spots, followed by *G. laevigata* (GRLA) on even sunnier spots. *Hedwigia detonsa* (HEDE), another species in the dry rock guild with *Grimmia*, appears in **Fig. 2**, Panel **A** practically on top of GRLA, but Panel **B** reveals how HEDE grew on shadier steeper faces of the boulders than GRLA.

Major taxonomic groups of bryophytes tended to occupy different "adaptive zones" (Huttunen 2004; Proctor 1984). Except for the leafy liverwort *Porella cordaeana* (POCO), liverworts tended to occupy softer places than the average moss (**Table 1**), and pleurocarpous mosses tended to prefer deeper

shade than acrocarpous mosses, but otherwise these three groups of bryophytes did not clearly gravitate to distinct parts of the four-axis niche space. In general, species seem to be spread across niche space without the different niche axes being redundant. However, the softest substrates in the driest places, the flattest areas in deep shade, and the steep inclines in high light were unoccupied or not present.

Two notes on the above analysis are in order. First, very similar results for local bryophyte species' habitat preferences were obtained when we left out the rare species and re-ran the program with only the 45 species found in eight or more mesosites. The correlations of the axes obtained with species found in three or more mesosites versus eight or more mesosites were always  $r > 0.99$ . Second, averaging the index values across the 103 mesosites gave similar results to the above method in which comparisons were made only within mesosites. The correlations between these two methods were always  $r > 0.9$  for each of the four environmental variables. This also implies that the subjective opinions about categories of softness, moisture, slope and shadiness must not have drifted very much over the two year period of data collection as they were assessed from mesosite to mesosite. Still, the within-site axes are in principle better because they do not rely on the observer being consistent.

**Ordination of mesosites.** An indirect gradient analysis was done to separate the mesosites based on the bryophyte composition. Analyses were done in PC-ORD (McCune & Mefford 1999). A matrix of the observation point scores of species by mesosites was created. The number of species or groups of related species (hornworts, *Fossombronia* spp., small *Scleropodium* spp. and *Trichostomum* spp.) that were found in two or more mesosites was 73. Beals smoothing was applied to the data because many mesosites were about equally different from one another, and most samples contained a fairly small proportion of the species. Smoothing the data helps discern better the favorability of a site to a species that was absent at that site through its association with other species at other sites (McCune 1994). Bray-Curtis distances were calculated, and non-metric multidimensional scaling was used to produce a two-dimensional ordination (**Fig. 3**). The two



**Figure 2.** Niche axes for 61 common bryophytes. **A.** substrate softness versus moisture. **B.** slope versus shade. Circles depict acrocarpous mosses, squares pleurocarpous mosses and triangles liverworts. For each of the four axes, distances were portrayed on the axis in a way that maximized the correlation between these distances and the observed dissimilarities of one species to the next within sites.

**Table 1.** Comparing the niches of acrocarps, pleurocarps and liverworts. Numbers are means  $\pm$  standard errors. The *P*-values are from ANOVAs. Means followed by similar letters are not significantly different by Tukey multiple comparisons tests.

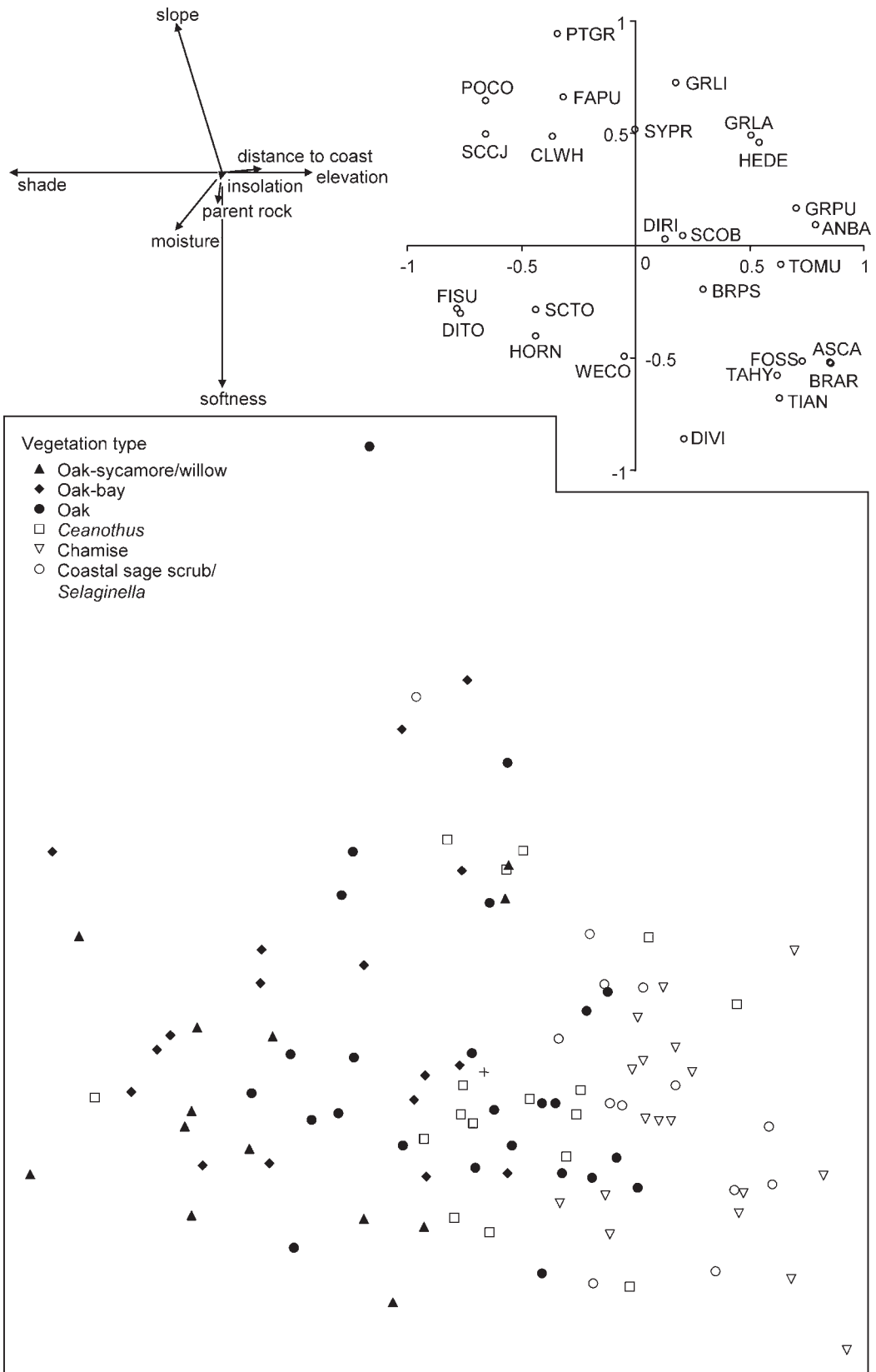
	acrocarps	pleurocarps	liverworts	<i>P</i>
Softness	30.56a $\pm$ 2.47	30.48a $\pm$ 4.66	52.35b $\pm$ 5.34	0.002
Moisture	32.16 $\pm$ 3.19	32.21 $\pm$ 4.21	38.45 $\pm$ 2.42	0.606
Slope	32.99 $\pm$ 2.42	34.18 $\pm$ 4.25	27.44 $\pm$ 5.36	0.556
Shadiness	29.23a $\pm$ 2.61	40.86b $\pm$ 3.19	35.27ab $\pm$ 7.50	0.049
<i>n</i>	34	18	9	

dimensions of the ordination cumulatively reflected the distance matrix at  $r^2 = 0.921$ .

Meso-environmental variables were then overlain on the ordination (upper left inset in **Fig. 3**). Correlations were 0.525 for elevation (possibly reflecting whether a mesosite was exposed in a high place or moist and shady in a low coastal place), 0.363 for distance to the ocean, 0.303 for parent rock type and 0.126 for insolation; these numbers are proportional to the length of the vectors on the upper left inset in **Fig. 3**. Vectors are also shown for the four micro-habitat characteristics: softness, moisture, slope and shadiness. For each mesosite, the common species' niche position was multiplied by the number of observations; these numbers were summed across species; and divided by the sum of observations of all species. The resulting mesosite values were overlain on the ordination along with other mesosite characteristics. Mesosites to the left had an abundance of shade-loving mosses. Mesosites on the lower half of the ordination had an abundance of mosses that do well on soft substrate. The separation of mesosites could be accounted for by the variation in abundance of species that do well on soft-substrates at  $r = 0.796$ , by abundance of moisture-loving mosses at  $r = 0.469$ , by the abundance of mosses that live on steep micro-slopes at  $r = 0.677$  or by the abundance of shade-loving mosses at  $r = 0.791$ . Strangely, topographic positions as we scored them did not occupy noticeably different parts of the ordination. Vascular vegetation was a bit better at accounting for differences among mesosites (main graph in **Fig. 3**). There was some tendency for the mesosites with woodland vegetation types to be more similar to each other in terms of bryophytes than to the mesosites with shrubland vegetation. Nevertheless, the different vascular

vegetation types grade broadly into each other in terms of bryophyte composition.

To appreciate the ordination better, it is helpful to know which sectors of it are likely to have which bryophytes. For the more common species, the upper right inset in **Fig. 3** shows the correlations between the species abundance and the two ordination axes. Mesosites with a high abundance of FISU (*Fissidens sublimbatus*) and DITO (*Didymodon tophaceus*) were on the left side of the ordination (higher in elevation), whereas mesosites tending to have a high abundance of GRPU (*Grimmia pulvinata*) and ANBA (*Anacolia baueri*) tended to be on the right side (lower in elevation). PTGR (*Pterogonium gracile*) was most abundant at mesosites toward the top of the ordination (sandstones) and DIVI (*Didymodon vinealis*) was most abundant at mesosites toward the bottom of the ordination (volcanics). All three common liverworts (FOSS, ASCA and TAHY) (*Fossombronia* spp., *Asterella californica* and *Targionia hypophylla*) were most common in mesosites in the lower right quadrant, where there are more than twice as many mesosites with shrubland vegetation types than mesosites in woodlands. Five of the nine pleurocarpous mosses found at more than 15 mesosites were common at mesosites on the left half of the ordination where the most mesosites are dominated by oak-sycamore/willow, oak-bay or oak type vegetation. Only a few mesosites on the left side of the ordination have *Ceanothus* vegetation type, one mesosite is dominated by coastal sage scrub/*Selaginella* and no mesosites are of the chamise vegetation type. DITO (*Didymodon tophaceus*) and WECO (*Weissia controversa*) occurred in mesosites in the lower left of the ordination where there are many low elevation mesosites with vegetation types that are associated with live oak.



**Table 2.** Bryophyte species that were significant indicators of a single vascular vegetation type. Numbers in the body of the table are Indicator Values (Dufrêne & Legendre 1997), with the **bold** value showing the vascular vegetation type of maximal indication. *P* is the result of a Monte Carlo test, and it is based on the proportion of randomized trials with indicator value equal to or exceeding the observed indicator value. CSS = coastal sage scrub.

	oak-sycamore/ willow	oak/bay	oak	<i>Ceanothus</i>	chamise	CSS/ <i>Selaginella</i>	<i>P</i>
<i>Conardia compacta</i> (COCO)	17	0	0	1	0	0	0.017
<i>Fissidens sublimbatus</i> (FISU)	28	22	12	9	0	2	0.011
<i>Didymodon tophaceus</i> (DITO)	33	17	1	1	0	0	0.003
<i>Bestia longipes</i> (BELO)	1	26	0	0	0	0	0.006
<i>Eucladium verticillatum</i> (EUVE)	5	21	0	0	0	0	0.006
<i>Porella cordaeana</i> (POCO)	4	29	7	1	0	1	0.006
<i>Pohlia wahlenbergii</i> (POWA)	0	20	0	0	0	0	0.007
<i>Scleropodium CCJ</i> (SCCJ)	3	26	20	2	0	0	0.012
<i>Pterogonium gracile</i> (PTGR)	2	19	3	4	0	0	0.035
<i>Asterella californica</i> (ASCA)	1	3	8	6	30	23	0.003
<i>Bryum pseudotriquetrum</i> (BRPS)	4	4	0	5	21	7	0.038
<i>Fossombronia</i> spp. (FOSS)	0	0	1	5	31	3	0.003
<i>Targionia hypophylla</i> (TAHY)	0	5	4	3	10	26	0.028
<i>Bryum argenteum</i> (BRAR)	0	0	2	2	22	27	0.014
<i>Tortula atrovirens</i> (TOAT)	0	5	0	0	1	20	0.010
#plots	13	17	25	17	18	13	

Since vascular vegetation type explained some variation in the bryophyte community, it is interesting to know which bryophyte species distinguished the various vascular vegetation types. The vascular vegetation types were recognized as *a priori* groups, and indicator species analysis was run in PC-ORD for the bryophytes. In this context, indicator species are those bryophytes characteristic of one vascular vegetation type as opposed to all others (Dufrêne & Legendre 1997). The program calculated the proportional abundance of each species in a particular group relative to its abundance in all groups, and expressed it as a percentage

(Table 2). If both proportions were high, the species was considered a good indicator. The highest indicator value for a given species across the groups was presented as a summary of the overall indicator value of that species. The statistical significance of the indicator values was evaluated by a Monte Carlo test. Fifteen indicator species were identified as faithful to one particular vegetation type. Oak/bay vegetation type had six significant indicator species. Oak-sycamore/willow, chamise and coastal sage scrub/*Selaginella* had three each. There were no species that were significant indicators for oak or *Ceanothus* types, even though the former had the largest

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**Figure 3.** Lower panel shows an ordination of sites based on bryophytes with vascular vegetation type overlain. Woodland (closed symbols) and shrubland (open symbols) types show some separation, although the six vegetation types broadly grade from one to the next. The ordination was rotated to make the horizontal axis maximally correlated with elevation. The upper left inset shows how environmental variables change with direction from the origin of the ordination. The upper right inset shows the correlation of bryophyte species abundances against the ordination's axes. Position of a species relative to the origin of this graph indicates at which sites it was generally abundant in the same position on the ordination; for example, POCO (*Porella cordaeana*) was found at sites in the upper left quadrant of the ordination. The species shown are those that were found at more than 15 sites, and full names are given in Table 3. Correlations were based on Beals smoothed data.

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number of plots (25) and the latter had as many plots as the oak/bay type (17 plots). There were no species with a perfect indicator value of 100. In other words, no species was present at all mesosites of a particular vegetation type and only those mesosites. In fact, it seems that bryophytes are not very strong indicators of vascular plant communities. The most important indicator species were *Didymodon tophaceus* with indicator value of 33 for oak-sycamore/willow type, *Asterella californica* with indicator value of 30 for chamise type and *Porella cordaeana* for oak/bay with indicator value of 29.

## DISCUSSION

Our primary contribution is descriptive: someone interested in how the habitat of two bryophyte species differs can compare the species on **Figs. 2 and 3**. Previous studies like ours (reviewed by Slack 1990) have been done in much less arid regions and often have tackled just one guild within a community. Glime and Vitt (1987) showed how species distributions correlated with environmental gradients among Canadian montane streams. Kenkel and Bradfield (1986) examined epiphytic species composition on big-leaf maple in British Columbia, and found that particular epiphytic species tended to occupy similar niches at different sites, and that the shifts in species' microhabitat use appeared to be greatest between sites that had the most different meso-environmental conditions. Other studies have focused on a single genus, contrasting various species' habitat parameters. Vitt et al. (1975) and others (McQueen 1990; Vitt & Slack 1984) looked at the correlation of *Sphagnum* species to ion and moisture gradients. Watson (1981) compared the microhabitat use of six species of Polytrichaceae along an altitudinal gradient. In the mesic northwestern corner of California, Williams and Sillett (2007) contrasted the habitats of various epiphyte species growing on large redwood trees.

In the semi-arid SMM, we found that the within-mesosite differences in microsite extrapolated up well, explaining much of the variation among mesosites. Other characteristics recorded for mesosites seemed poorly correlated with position on the ordination. One would imagine that mesosite variables like how much sun the site receives would

affect wetting-and-drying cycles and thence the bryophyte species composition. Surprisingly, though, insolation showed almost no correlation with the major axes of bryophyte community structure. Perhaps the insolation values we used were too coarse to resolve mesosite differences, or perhaps there was so much microsite variation in shadiness within mesosites as to make the mesosite's overall insolation irrelevant. Elevation had some explanatory power. Probably in the SMM elevation represents something about topography, e.g., the tops of ridges receive more precipitation than lower flatter areas. Curiously, however, the variable we called "topography" seemed of little explanatory power. Our mesosites were weakly separated by vascular vegetation type. In other climates, vascular vegetation type has often but not always been found to be indicative of bryophyte species composition (Mills & Macdonald 2004; Motzkin et al. 1999; Rambo & Muir 1998; Vitt et al. 2003). Possibly the reason vascular vegetation in the SMM had only weak explanatory power is because only a few SMM bryophytes are epiphytic, and even the litter from woody vegetation is sparse with relatively little deciduous overstory. Overstory vegetation contributes to shade, but even without trees, steep canyon walls and rock outcrops can provide shade.

Our study considered only a few aspects of the niche. Species presumably differ in other ways as well. They probably differ in their preference for substrate pH (Downing & Selkirk 1993), the recruitment environment (Poorter 2007) and their response to seasonal or environmental variations in light (Proctor 2000). Also, species have different competitive abilities, and cooccurrence of species will alter the relationship between the fundamental and realized niche (Pulliam 2000). We did not study successional changes that may be important in explaining the structure of the bryophyte community. Species vary in the ways they disperse and how easily they cover new ground (During 1992), but from our data one cannot tell how the different species got into their meso- and microsites.

Other studies parallel to ours in areas with slightly different climates would be interesting. We wonder how the niche structure of such places differs from the niche structure of the SMM as it is

illustrated in **Figs. 2** and **3**. As one moves to slightly moister climates, do the species change their relative order (Palmer 1986; Schmitt & Slack 1990)? Our list of 122 species joins a number of other bryoflorulas from various areas in California (listed in Norris & Shevock 2004). Two that the SMM may be compared to are Harpel's (1980) for Mount San Jacinto, which is higher in elevation than the SMM, and Kellman's (2003) for Santa Cruz County, which is higher in latitude. In general, the SMM are floristically in between the other two, and have relatively few species not found in one or the other (Sagar & Wilson 2007). The other bryoflorulas within California, though, have not provided rankings of the ecological preferences of the species.

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