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Calcicolous and calcifugous bryophytes along the desert edge of the California Floristic Province

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Abstract. We studied the habitat preferences of various bryophytes on a landscape in which calcareous and granitic rocks interdigitate. On both substrates, plots were placed in sunny dry locations, shady dry locations, and along streams in wet locations. In other words, six habitat types were studied in a factorial design involving edaphics × moisture. Wet granitic habitat had the highest species richness, whereas wet calcareous habitat had the lowest species richness. In dry sites, shady plots had higher richness than sunny plots, regardless of edaphics. Particular species varied widely in their preferences with at least one species being an indicator for each of the six habitats, e.g.: "fan-form tubers Bryaceae" was specialized on granitic wet habitat; *Grimmia lisae* was specialized on granitic shady habitat; *Grimmia montana* was specialized on granitic sunny habitat; *Didymodon tophaceous* was specialized on calcareous wet habitat; *Orthotrichum cupulatum* + *hallii* was specialized on calcareous shady habitat; *Grimmia anodon* was specialized on calcareous sunny habitat. The composition of the bryophyte assemblages was very strongly affected by the interaction of calcareous-versus-granitic × dry-versus-wet; the wet calcareous assemblage was the most distinctive. To the extent possible, we classified the various species into guilds (e.g., the calcicolous rheophyte guild) taking into account generalization versus specialization. In summary, we found remarkable interactions between edaphics and wetness.

Keywords. Edaphic specialist, guilds, niches, Mojave Desert, Tehachapi Mountains.

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Plants that thrive on calcium-rich substrates like marble are termed **calcicoles**, while those that prefer something like granite are called **calcifuges** (Lee 1999). When a species is found predominantly on a specific rock or soil derived from that rock, it is called an **edaphic specialist**. Plot-based studies such as those by Glime & Vitt (1987), Sekulová et al. (2011) and Abay et al. (2014) establish that some bryophytes, calcicoles, do best at higher pH, whereas other species, calcifuges, prefer neutral or even low pH. In other words, both kinds of edaphic specialists exist. Still other species are found on a wide range of parent rock types, and these may be called **edaphic generalists**. In the interest of avoiding clumsy compound words, we will refer to substrates and/or streams differing in parent rock type as "edaphics."

A number of past studies done in dry habitats have found that species richness is positively correlated with pH (e.g., Löbel et al. 2006; Tyler & Olsson 2016). In other words, more species tend to be calcicoles than calcifuges, at least in high-latitude species pools in the mesic climates where the previous studies have been done. In wet habitats, such as in streams, the pattern might be different (though Glime & Vitt 1987 reported a positive correlation). Plants in streams, **rheophytes**, are bathed in solution continuously, so the concentration of H^+ or other ions might be toxic or might dampen photosynthesis (Tremp et al. 2012). Even if high pH does not preclude many species, the assemblage as a whole might show an edaphics × wetness interaction. The direction of such an interaction is not easy to predict from the previous literature: should we expect dry spots to have more disparity or less in their bryophytes between basic and neutral rocks than wet spots?

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Outside of wetlands, where mosses dry out, edaphics and moisture have been shown, at least in part, to have an effect on substrate fidelity. Cleavitt (2001) did regeneration experiments showing substrate chemistry to be an important factor in bryophyte establishment. Tng et al. (2009) compared two regions in Tasmania, and found that, in the wetter climate, liverworts occurred on both trees and soil more frequently than in the relatively drier climate. In other words, species showed less niche fidelity and more off-substrate occurrence in the wetter climate. Even on the same dry substrate, some sunny spots are occupied by **thermophytes**, whereas other shady spots dry out much less frequently and are preferred by **umbrophytes**.

Granitic and calcareous rocks interdigitate on the southern slope of Tejon Ranch, in the Tehachapi Mountains, on the desert edge of the California Floristic Province. The geology is a mosaic in which the underlying parent rocks consists of plutonic granitics with lenses of calcareous metamorphics spottily overlain (Critelli & Nilsen 2000; Nilsen 1987). The area has an arid climate with low general suitability for bryophytes (Geffert et al. 2013), and their cover on trees and dead wood is almost non-existent, even on species of oaks that 100 miles north are covered with mosses (Coleman 2014).

Here we report on a study in which plots were placed on granite or on marble and in sunny, shady or wet locations. Thus, we compared six habitat types. The data were queried as follows. (1) We wanted to know how species richness is affected by edaphics and wetness, to look for statistical interactions, and to see how the pattern scales up as plots are aggregated. (2) We wanted to see to what extent species could be characterized as calcicoles or calcifuges, one species at a time. (3) In terms of the composition of the bryophyte community as a whole, we tested for interactions between edaphics and wetness to see, for instance, if one assemblage (it turned out streams flowing over marble) was especially distinctive. (4) On the possibility that all the habitats have specialists, we attempted to group species niches together into guilds, recognizing a potential spectrum of specialization-to-generalization in the context of our six habitat types.

METHODS

Along the rain-shadow side of Tejon Ranch, facing the desert, we did a stratified plot study comparing the bryophytes on calcareous marble versus pH-neutral granitic rocks. Plots were positioned to maximize interspersion of calcareous and granitic substrates. We worked in a narrow elevational band between 1,100 and 1,900 m.a.s.l.

Plots were 25 m^2. For each plot, a species list was made, and a specimen of any bryophyte that could not be identified on sight was collected. For each species, abundance was scored as crude categories (**Supplementary File S1**), but most of the analyses presented below were based on presence/absence.

On calcareous parent material, 23 plots were sunny, 19 plots were shady but dry, and 11 plots were along wet streams. On granitic parent material, 22 plots were sunny, 28 plots were shady but dry, and 15 plots were along wet streams. It was impossible to find more streams without going beyond the confines of the study region and the zone of the rain shadow. The average pH for calcareous streams was 8.23 ± 0.074 SE, and for the granitic streams was 7.42 ± 0.137.

Specimens were identified consulting with experts, including David Toren (California Academy of Sciences), Brent Mishler (University of California, Berkeley), John Brenda (Missouri Botanical Garden), and John Spence (National Park Service). Vouchers will be deposited at the herbarium of California State University, Northridge (SFV).

Statistics. Species richness within a plot was analyzed by two-way pure model I ANOVA (R core team 2013). One ANOVA was done (excluding the wet plots) comparing sunny-versus-shady by calcareous-versus-granitic, and a second ANOVA was done comparing wet-versus-dry plots (the latter being shady and sunny plots pooled) by calcareous-versus-granitic. Following a significant interaction term, *t*-tests were run to compare species richness between wet and dry plots within an edaphic type. After the ANOVAs, we asked, how does the species richness pattern scale up considering an aggregate of plots in one habitat type? PC-ORD (McCune & Mefford 2017) calculates "species-area curves" sampling plots with replacement. This allowed the six habitat types to be compared in terms of the number of species, after aggregating eleven plots at a time (eleven being the smallest sample size, from calcareous wet plots).

Preferences of particular species were analyzed using Fisher's exact 2 × 2 tests of independence of edaphics × presence/absence (using R). This was only done for species found in at least six plots of the same shadiness or wetness counting both calcareous and granitic plots. Species with sample sizes lower than this cannot yield significant differences. For this set of analyses, we pooled *Orthotrichum cupulatum* + *O. hallii* and two closely related forms of *Syntrichia princeps* s.l. Splitting would have yielded similar graphs. In addition to the 2 × 2 tests, PC-ORD's indicator species analysis was run to quantify the species' importance in *one* of the six habitat types and its unimportance in the other five types (Dufrêne & Legendre 1997). Indicator species analysis is not sensitive to the situation in which a species is specialized on, say, calcareous rock but indifferent to shade-versus-sun. Such a species would have lower indicator values than a species that is specialized on calcareous sunny habitat and is absent from other habitats including calcareous shady habitat. Indicator values range from 0 to 100.

Assemblages by habitat were studied in PC-ORD by running two non-metric multidimensional scaling ordinations with accompanying factorial perMANOVAs. The first was a contrast of sunny-versus-shady by edaphics, and the second a contrast of shady-versus-wet by edaphics. The perMANOVAs had to be done on four groups with equal sample sizes. This meant trimming the data back to 19 plots per treatment for the sunny-versus-shady perMANOVA (though the ordination shows all the plots). For the wet-versus-shady plots, the data had to be trimmed to just 11 plots per treatment (and only those plots are show in the ordination). Species that were only found once were excluded from the ordinations and analyses since they do not inform similarity between plots. The data were Beal's smoothed, which uses only presence/absence information, and Sorensen's distances were used. The perMANOVA was based on 33 taxa for sunny-versus-shady. For wet-versus-shady, the perMANOVA was based on 35 taxa. As a supplementary file, we also present a third ordination based on all the plots, though without any perMANOVA.

To prepare the data for a classification into guilds, species were retained only if they occurred in at least six plots. This left 23 common species. *Orthotrichum cupulatum* + *O. hallii* were again treated as one taxonomic unit (if they are distinct, they have very similar niches). Abundance scores were averaged over all plots for each of the six habitat types. Sorensen's distances were used to make a two-way classification, agglomerating plots on the one hand and species niches on the other (PC-ORD). Guilds were reified based on the habitats in which they were found and considering how generalized they were across habitat types.

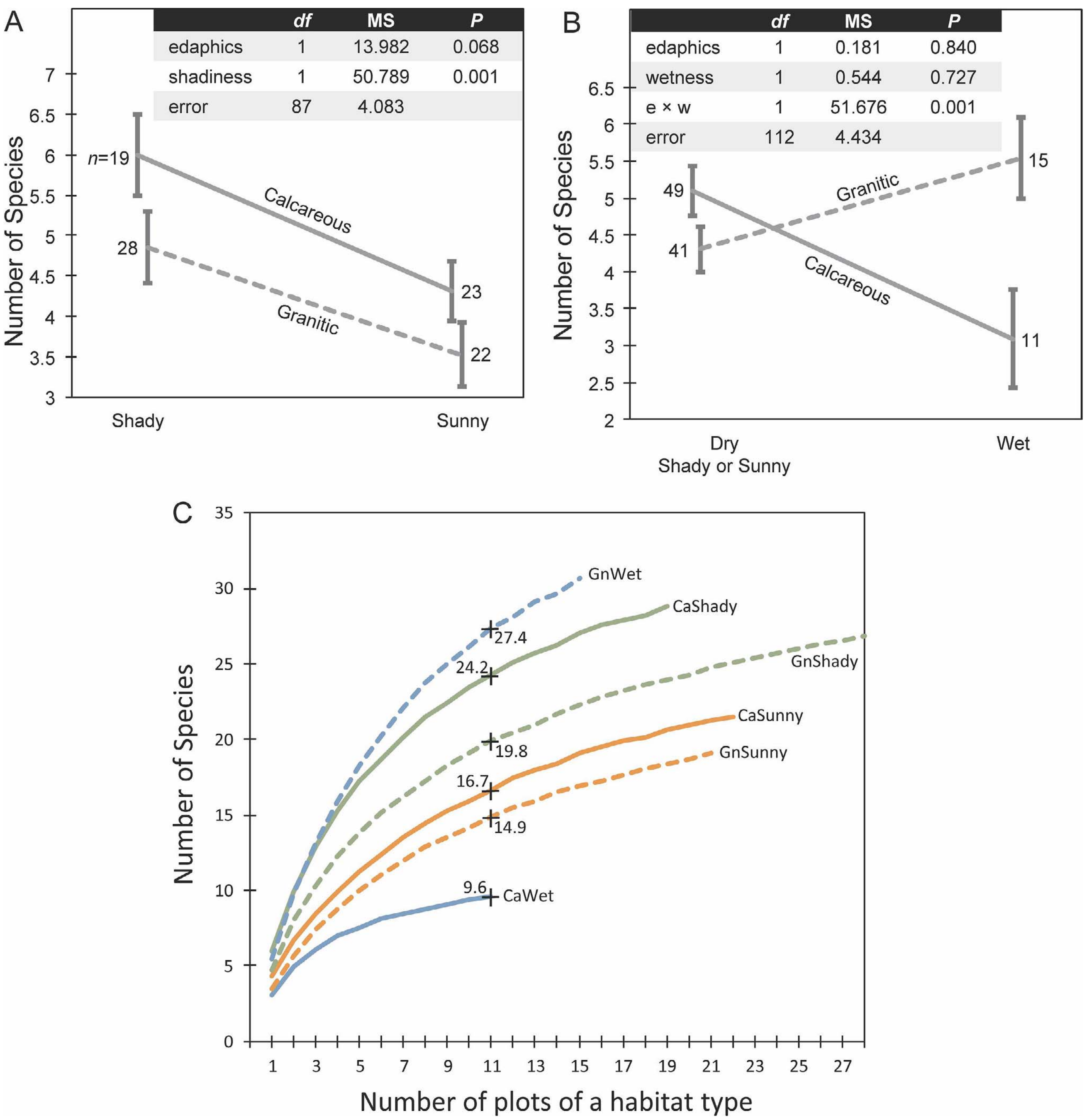
RESULTS

Species richness. In the 116 plots taken together, 91 species were found in at least one plot, and 55 were found in two or more plots.

Fig. 1A considers only dry plots, either shady or sunny and either calcareous or granitic. Sunny granitic plots had on average 3.7 bryophytes. Shady granitic plots had about one species more, at 4.8 species. Calcareous plots had about one species more than the granitic plots, 4.3 for sunny ones and 6.0 for shady ones. Edaphics × shadiness was not significant ($P=0.543$), rather edaphics was marginally non-significant ($P=0.068$) and shadiness was highly significant ($P_{\text{shadiness}}=0.001$), with the effects being additive.

Fig. 1B considers the wet stream plots versus the dry plots (the latter being shady and sunny plots pooled). Edaphics × wetness was highly significant ($P<0.001$). Unexpectedly, calcareous wet plots had fewer species at 3.2 than dry plots at 5.1 (equal variances difference between two means $t_{50}=2.9078$, $P=0.005$). On the other hand, granitic wet plots had more species than dry plots, though with marginal significance, 5.5 versus 4.3 (Welch $t_{23.597}=1.941$, $P=0.064$).

Species-area curves indicated that, for a hypothetical aggregate of eleven granitic sunny plots, 14.9 species would be found on average, for eleven shady plots 19.8 species, and for eleven granitic stream plots 27.4 species (**Fig. 1C**). The moister the habitat, the more species coexist. However, the pattern was not so straightforward for calcareous plots. For eleven calcareous sunny plots aggregated 16.7 species would be found on average, for shady plots 24.2 species, but for eleven calcareous wet stream plots only 9.6 species would be found. As with species richness in single plots, there was evidence of



	df	MS	*P*
edaphics	1	13.982	0.068
shadiness	1	50.789	0.001
error	87	4.083	

	df	MS	*P*
edaphics	1	0.181	0.840
wetness	1	0.544	0.727
e × w	1	51.676	0.001
error	112	4.434	

Figure 1. A. Effects of edaphics and shadiness, excluding consideration of wet plots, and with the interaction term dropped because it had a $P>0.25$. Mean numbers of species (± SE) in 5 × 5 m plots of different habitat types. Sample sizes near means are numbers of plots of a habitat type. **B.** Effects of edaphics and wetness, pooling shady and sunny plots under the category of dry. **C.** Species-area curves showing the hypothetical number of species found in 1 to many plots in the aggregate of one habitat type. Numbers show the estimated species richness found in eleven plots.

an interaction whereby calcareous streams have surprisingly few species. Also of note, these curves do not level off, suggesting that if more plots had been sampled, many more than 91 species would have been found.

Preferences of particular species. Comparing sunny-versus-shady × edaphics, many species stood out as being strong calcicoles or strong calcifuges. The species showed a range of preferences from the likes of *Grimmia anodon* strongly preferring marble

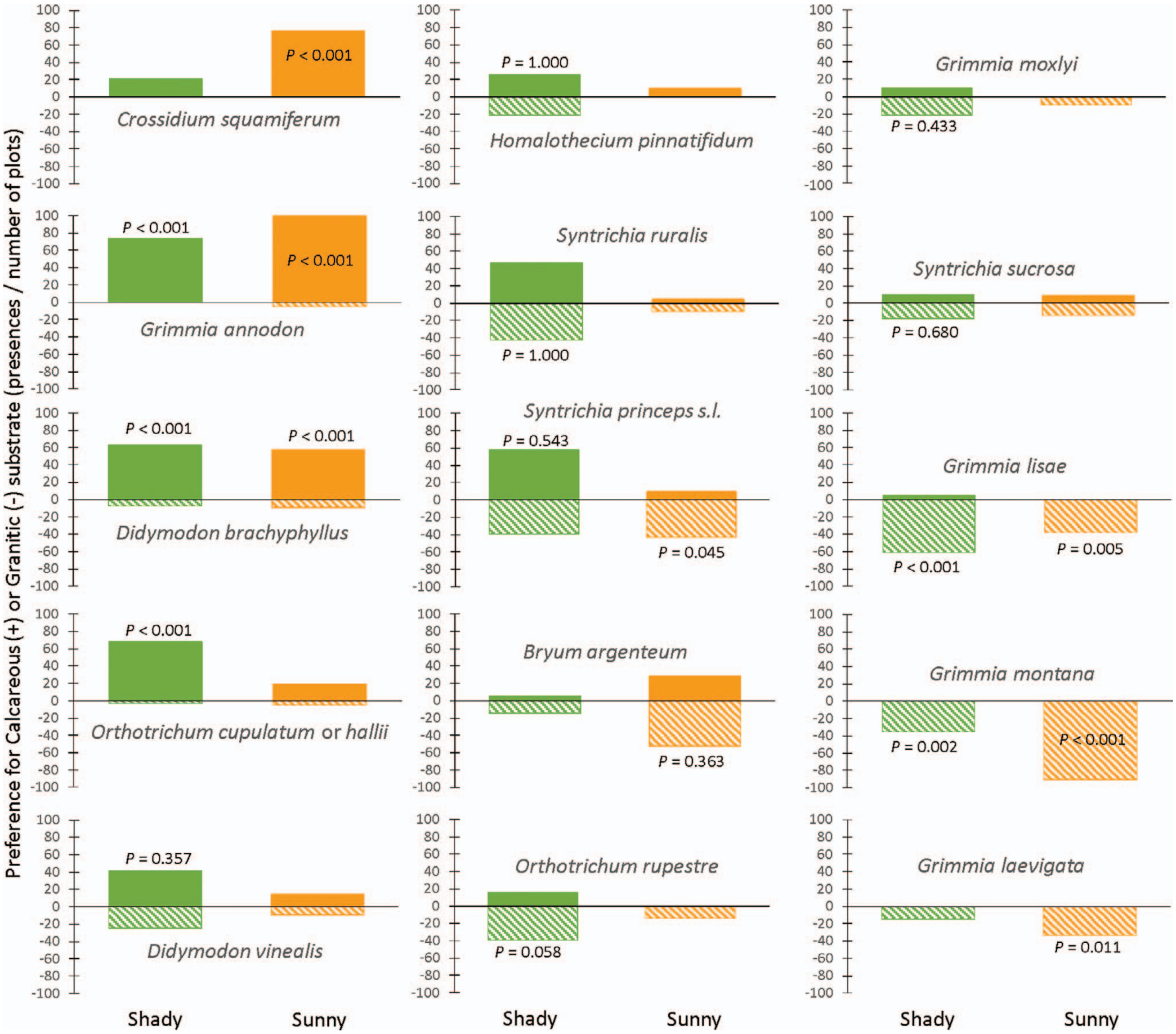


Figure 2. Percent present in plots of a habitat type. Species arranged from calcicoles in upper left to calcifuges in lower right. Upward pointing bars are calcareous; downward pointing bars are granitic. P-values are from Fisher's exact tests comparing calcareous to granitic plots in terms of percent present versus absent. Numbers of plots of each of the six habitat types are given in Fig. 1. When P-values are not given, $n<6$ and no test was done.

to the likes of *Grimmia montana* strongly preferring granitic substrate (**Fig. 2**). In no case did a species significantly prefer one edaphic type in shady plots and significantly prefer the other edaphic type in sunny plots. Some mosses seemed to prefer shadier plots (*Orthotrichum cupulatum* + *hallii*), whereas others preferred sunnier plots (*Crossidium squamiferum*). Most of the taxa that preferred sunny plots are extreme in their edaphic preference with the exception of *Bryum argenteum*. The rule may be exemplified by *Crossidium squamiferum* which had an indicator value for sunny calcareous plots of 59.1 (P=0.001). For sunny granite, *Gimmia montana* had an indicator value of 54.4 (P=0.001). *Orthotrichum cupulatum* + *hallii* had an indicator value of 48.6 (P=0.001) for shady calcareous rock. For shady granite, *Grimmia lisae* had an indicator value of 47.8 (P=0.001). The three *Syntrichia* taxa shown in **Fig. 2** seem to show little edaphic preference (although sample size precludes *Syntrichia caninervis*, which might be calcicolous).

Species that preferred stream plots were all but absent in drier plots (**Fig. 3**). In the wet streams, *Hygroamblystegium varium* was an indicator for

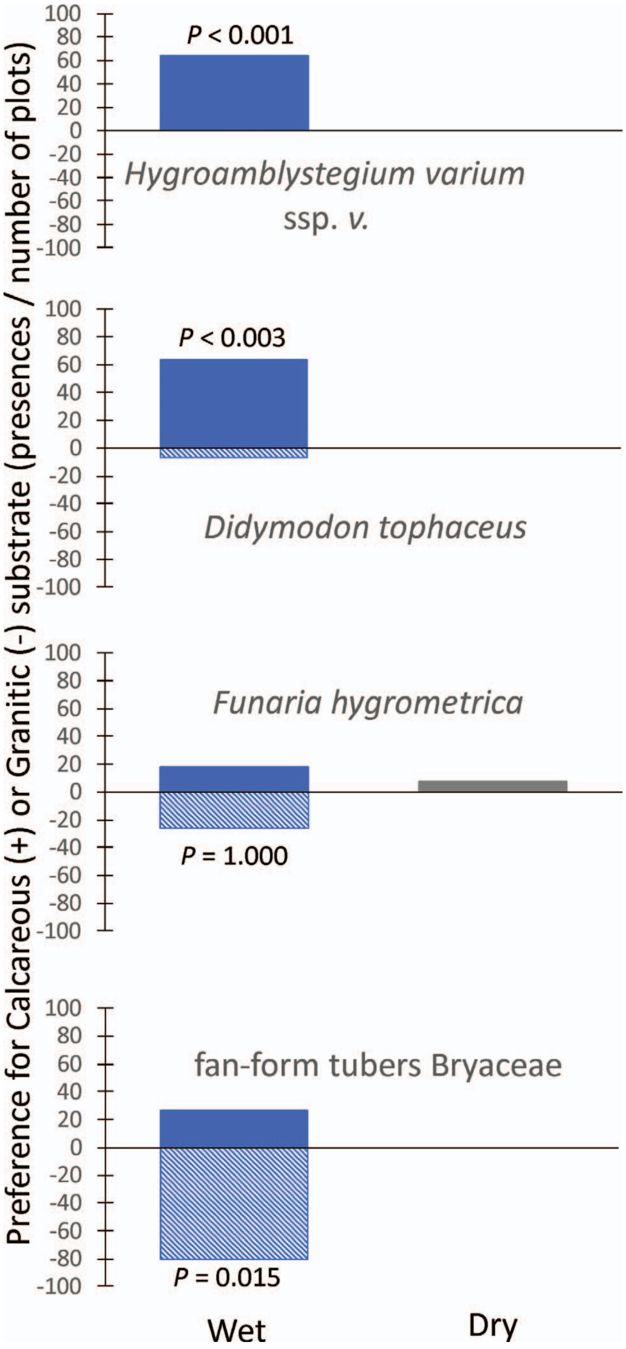


Figure 3. Percent present in plots of a habitat type. "Dry" represents shady and sunny plots pooled. Conventions as in Fig. 2.

calcareous habitat at 63.6 (this was the highest indicator value in the data set; $P=0.001$). *Didymodon tophaceus* also preferred wet calcareous habitat, with an indicator value of 58.8 ($P=0.001$). For granitic streams, the species call "fan-form tubers Bryaceae" had an indicator value of 39.8 ($P=0.001$). Species preferring dry plots were only found in wet plots in dry microhabitats. The species shown in **Fig. 2** all had very low occurrences in wet plots, generally being absent from the stream itself.

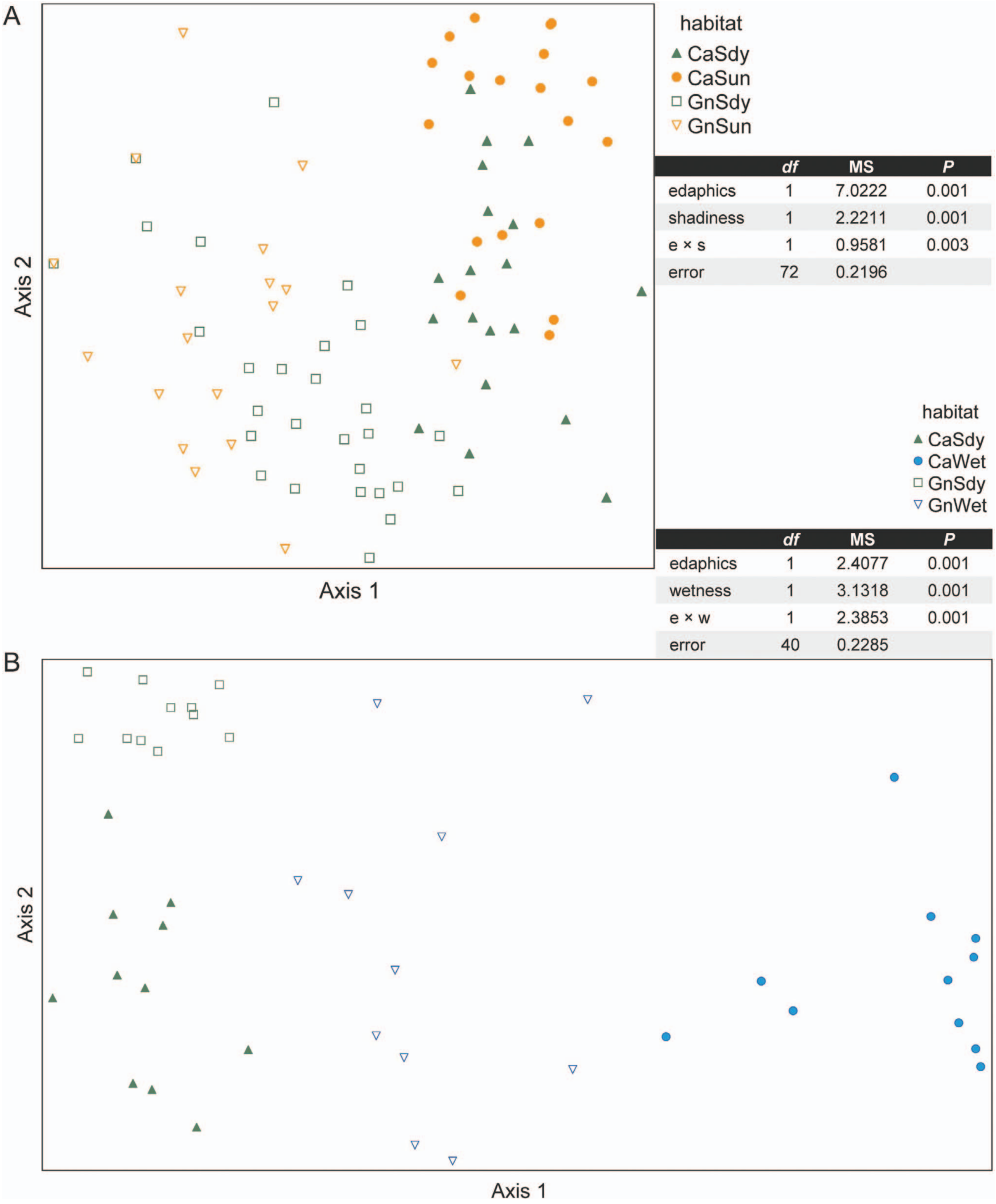
Assemblages by habitat. Moving from a consideration of species one at a time to the composition of assemblages in the six habitats, we ask, does including *all* the species yield responses for the bryophytes *as a whole*?

The ordination that excluded wet plots had a stress=9.01 and a nonmetric $R^2=0.99$ (**Fig. 4A**). According to perMANOVA, edaphics × sunny-versus-shady significantly interacted, with calcareous sunny less similar to calcareous shady and granitic sunny closer to granitic shady ($P=0.003$); however, this interaction seems relatively weak. In this ordination, edaphics overlapped very little left to right, and sunny-versus-shady overlapped more in the vertical direction on the graph.

In the ordination that excluded the sunny plots, stress=7.46 and nonmetric $R^2=0.99$ (**Fig. 4B**). Edaphics interacted much more strongly with wet-versus-dry than it had with shady-versus-sunny. Shady plots were placed to the left of the ordination, wet granitic plots lay in the middle, and wet calcareous plots were to the right, very far from shady calcareous plots. Vertically, shady calcareous plots were lower on the ordination and shady granitic plots were higher. The edaphics × wetness interaction was very strong, on an order with the strength of the main effects.

An ordination of all the plots from all six habitats revealed an axis of greatest variation that separated the calcareous wet plots as distinct from the granitic wet plots as almost distinct from all the dry plots whether sunny or shady and whether calcareous or granitic (**Supplementary File S2**). Dry plots—sunny and shady, calcareous and granitic—were more likely to have species in common, whereas the two kinds of wet plots shared few species in common with each other and few in common with dry plots.

Agglomerating species into guilds? Taking the six habitats as units, the niches of the most common species were agglomerated into guilds (**Fig. 5**).The five species listed toward the top of the figure—*Grimmia anodon*, *Encalypta vulgaris*, *Crossidium squamiferum*, *Syntrichia caninervis*, and to a lesser degree *Didymodon brachyphyllus*—were calcicolous specialists; because of these species, shady and sunny



	df	MS	*P*
edaphics	1	7.0222	0.001
shadiness	1	2.2211	0.001
e × s	1	0.9581	0.003
error	72	0.2196	

	df	MS	*P*
edaphics	1	2.4077	0.001
wetness	1	3.1318	0.001
e × w	1	2.3853	0.001
error	40	0.2285	

Figure 4. A. Ordination of sunny-versus-shady by calcareous-versus-granitic plots (excluding wet plots) based on all species presence/absence. The ordination was rotated so that edaphics would line up as contrasting left to right. **B.** Ordination of wet-versus-dry by calcareous-versus-granitic plots (excluding sunny plots). Data were abbreviated to 11 plots of each of four habitats. All species were included with the ordination based on presence/ absence.

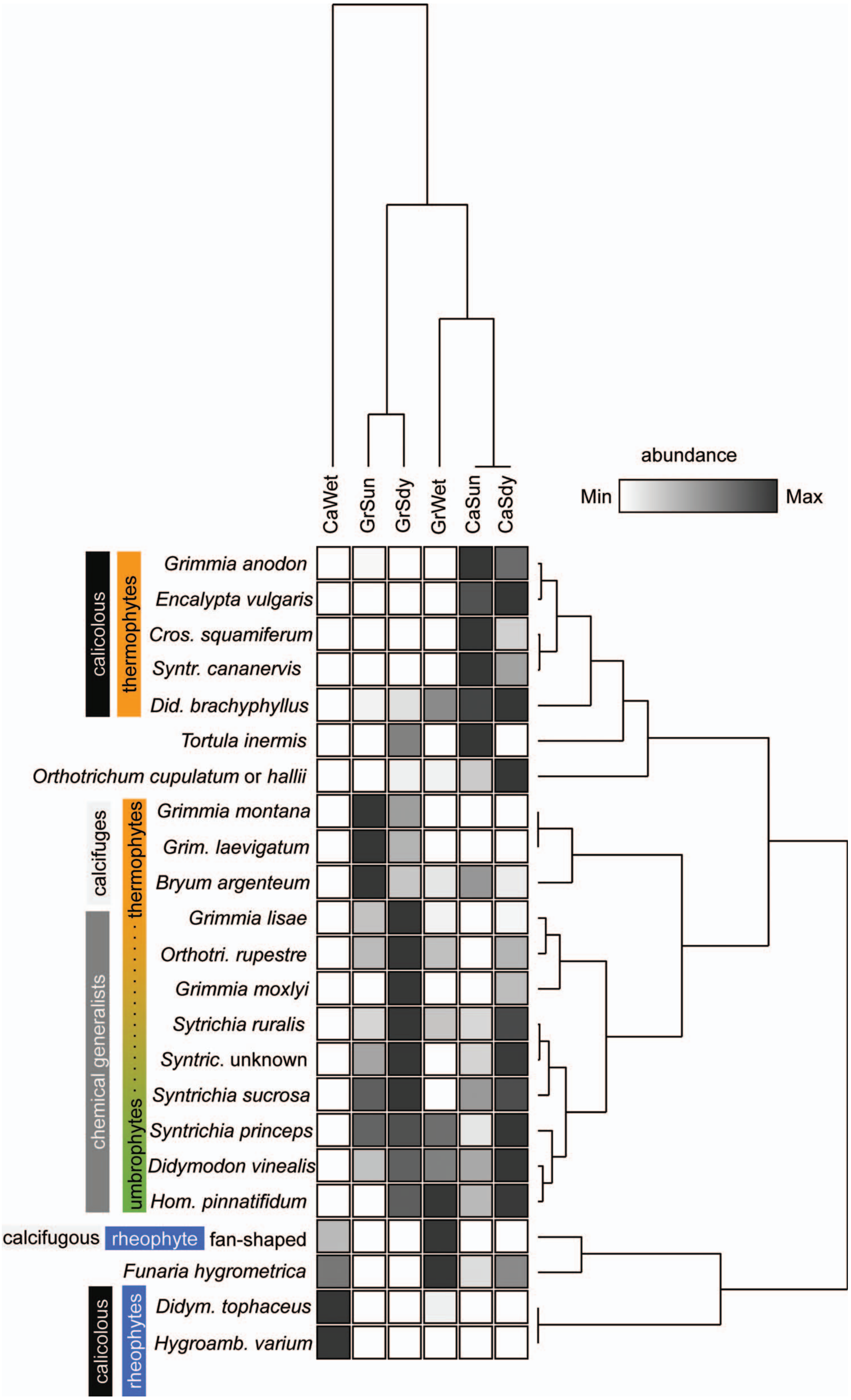


Figure 5. Two-way grouping of habitat types (shown horizontally) and of species niches (shown vertically). Only the most common species were included in this analysis. Highlighted guild labels were added as interpretation after the analysis.

habitats clustered tightly. As for granitic habitats, shady and sunny were clustered based on many species, some specialists like *Grimmia montana* and *Grimmia laevigata*, and others generalists. These calcifuges and generalists range from loving sun (thermophytes) to preferring shade (umbrophytes). Somewhat independent of the spectrum from thermophyte to umbrophyte, the spectrum from specialist to generalist was incremental. *Bryum argenteum* was an edaphic generalist more on the thermophyte end of the spectrum, and *Didymodon vinealis* was an edaphic generalist that was more of an umbrophyte. Calcareous wet habitat did not cluster with granitic wet habitat, the latter being more similar to granitic dry habitat. *Didymodon tophaceous* and *Hygroamblystegium varium* were specialized calcicolous rheophytes. Calcifugous rheophytes seemed to show more crossover into calcareous streams. In contrast to the specialized calcicoles, the calcifuge specialists tended to be fewer with more calcifuges being less specialized.

Discussion

Statistics on particular species showed that some were under-represented on granitic rock and over-represented on calcareous rock (calcicoles), whereas others had the opposite specialization (calcifuges). At least one species of each type preferred the sunny plots, the shady plots, or the stream plots. In short, edaphic specialization in mosses was confirmed, as has been found in other climates in both dry and wet spots (Downing 1992; Thiebaut et al. 1998; Tyler & Olsson 2016). Not surprisingly, shadiness and wetness play a large role in species preferences. It was generally the case that more species were found in shady places than in the sun. For granitic plots, more taxa were found in wet plots than in shady plots; however, for calcareous sites, fewer species were found in wet plots than in dry plots whether shady or sunny. When considering dry plots only, many more species were found in the shade than in the sun regardless of edaphics. Mosses occurring in shady habitats probably dehydrate more slowly than those in sunny habitats (Potzger 1939). Shade probably enables more species to live within a positive carbon budget (Alpert & Oechel 1985). As can be seen in **Fig. 1**, dry calcareous substrates supported more species than dry granitic substrates, in keeping with a familiar pH trend (Hydbom et al. 2012). Chemical properties of the substrates, particularly pH and its relationship to other chemicals, is likely an important determinant of substrate fidelity (Bates 1992; Tessler et al. 2014; Virtanen et al. 2000). Interestingly, Bates et al. (2004) found edaphic effects on epiphytes even though epiphytes are not in direct contact with rocks or soil.

A clear result was that edaphics interacted with whether the habitat was dry or wet. This interaction was strong for both species richness and community composition. However, it was not evident in the results for any one species. We were interested to find that the calcareous streams were species-poor even though they were wet, and they were very distinctive in their species composition. In other words, the calcareous plots had a reverse relationship with wet/dry when compared to the pH neutral granitic plots. The environmental variable that the bryophytes are actually responding to may not be pH. It might be CO_2 availability versus carbonate concentration or some toxic ionic concentration (Tremp et al. 2012). The effect of edaphics in our streams was different from what Glime & Vitt (1987) found in streams that varied from pH 7.3–7.8 in the Canadian Rockies. They found almost an order of magnitude more species, and the species diversity increased with pH (Vitt et al. 1986). Our regional species pool was presumably poorer. The reason for the low species richness in high-pH streams was unclear. None of our streams are of such a low pH as to be generally unsuitable for bryophytes. In high-pH waters, CO_2 becomes unavailable as it is converted into bicarbonate ions. Bain and Proctor (1980) suggest that mosses, in general, cannot live off of bicarbonate ions and need to use CO_2 as their carbon source. Yet, the calcareous streams we sampled were not of such a high pH and most had turbulent water. So, it seems unlikely that the low diversity was because the plants were less able to make a living.

In plots, we found 91 species. The plots were placed to include rocky outcrops and streams, and they were only in a very narrow elevational band on the rain-shadow side of the mountain range. Surely many more species could be found if one collected the region without these limitations. For example, ephemerals on fine soils and epiphytes would have increased our species count. Even with the limitations imposed by our sampling design, if the landscape had additional streams, we would have probably found additional species as extrapolated from **Fig. 1C**. The landscape-level species pool likely includes many more than 91 species (Palmer M.S. thesis in prep). For example, we did not find *Crumia latifolia* in a plot, but it is present in the regional pool and is probably more or less a calcicole (Harthill et al. 1979). Still, 91 species is quite a lot for such a dry climate, and that number is surely so high because both the marble and the granite plots contribute different specialists.

This study was conducted at the edge of the desert. Trees that elsewhere act as substrate are barely occupied by mosses. This means that rock and soil become the substrates that remain of use, at least outside of wet spots. Due to the limitations in substrate availability and moisture levels, the calcicole/calcifuge contrast is probably sharpened compared to what might be found in a moister climate. However, the contrast does not go to zero even in very moist climates such as the San Juan Islands (Harpel 1997) and the British Isles (Porley & Hodgetts 2009). In addition to discovering the statistical interactions between wetness and edaphic types, our study quantifies the preferences of the various species in this relatively arid ecosystem.

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Supplementary documents online:

Supplementary File S1. Matrix of plots by species. Numbers in the body are abundance classes: 1 for 0.1% or less of the plot; 2 for species found more than 0.1% up to 1%; 3 for species that were found from 1% to 10%; 4 for species found above 10%.

Supplementary File S2. Ordination of all six habitats together. Non-metric multidimensional scaling of Sorensen's distances of Beal's smoothed presence/absence data based on species that occurred in two or more plots.