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ABSTRACT. A long and steep elevational gradient presents the opportunity to study the niches of a large number of species within a small geographic area. Along such a gradient in the Sierra Nevada of California, all bryophytes were recorded in 253 plots. Along with species occurrence, the wetness, incline, shadiness and substrate type of the spot where each bryophyte was living were recorded. The average of these ecological traits (i.e., the central tendency of the species niche) was tabulated along with a determination of whether the species was a specialist or generalist for that niche dimension. Moving to guilds, co-occurrence in plots was used to aggregate species into ecological coalitions using the program RCLUS. These coalitions occupy different parts of an ordination of species, but they reveal more subtlety than the ordination itself. An ecotone was evident between the foothill bryophyte vegetation zone and a higher elevation zone. Other ecotones were not obvious; for example, we did not detect a sharp boundary between a conifer zone and a subalpine zone, rather the turnover of species was incremental and individualistic. For naturalists who know the species, being able to characterize them ecologically contributes to thoughts of the assembly of communities and the conservatism of clades.

KEYWORDS. Coalition, R mode, RCLUS, Sequoia National Park, Nevada, turnover.

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When studying a landscape, much may be gained by learning in what sorts of spots each kind of organism lives. This learning can be acquired by a bryophyte collector who takes very careful notes on micro- and meso-habitats. However, the description of the niches and guilds of the various bryophytes can be made more disciplined by gathering one's observations in the form of plots. With plots, one gathers data on the co-occurrence of this and that kind of organism, and one can sample in a way that results in, for instance, a comparable number of plots at each elevation in a landscape. Here we describe the niches of the common bryophytes that occurred in plots located along a 3000-m elevational gradient on the western slope of the Sierra Nevada of California. In addition, we explore ways to group species into guilds, or (to follow the terminology of the software we use) "coalitions of species".

For our purposes, the **niche** of a species is simply the ecological characteristics of the species that potentially differ on average from other species. A **guild** is a set of species with similar niches. The species of a guild are not necessarily related, so a guild is a grouping that is not necessarily a taxonomic grouping, though in some cases a guild corresponds to a taxon (e.g., various kinds of *Fontinalis* characteristically live in perennial streams of clean water). Under Huchinson's (1978) niche concepts, one sometimes distinguishes between the niche (which is something that is characteristic of the organisms) and the biotope (which is of the environment and could also be called "the habitat"). One might speak of elevation as being an environmental gradient in the biotope, and the part of the elevational range that tends to be used by, say, *Brachytheciastrum collinum* as being a dimension of its niche (Colwell & Rangel 2009). *Brachytheciastrum collinum* lives at high elevations, in deep shade, on boulders, often on the underside of overhangs.

We will be focusing on analyses in **R mode**, as opposed to **Q mode** (McCune et al. 2002). With both types of analyses, one starts with a matrix of species-by-plots. A typical Q-mode analysis yields an

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ordination of plots in species space, and one might go on to break the plots up into vegetation types with indicator species. An R-mode analysis involves studying the associations between every species and every other species, and one might go on to search for coalitions of species united by their co-occurence. Furthermore, one does not have to use associations per se; one can use similarities (or conversely dissimilarities). Since Q mode is more "normal", R mode is sometimes referred to as an "inverse" analysis (Williams & Lambert 1961). We emphasize R mode, and for clarity of contrast, in a supplemental file, we briefly present a corresponding analysis in Q mode. At its heart, our report is about species, not about plots or maps, although plots and even maps are a way of learning about species. A coalition of species based on co-occurrence is a kind of guild, although guilds may alternatively be based on more explicitly specified dimensions of niches.

Landscapes with large changes in elevation over short distances allow one to explore the niches of species beyond what is observable about the micro-sites where one finds the bryophytes (Watson 1981). Presumably, in the course of centuries, any species found in the landscape had the capacity to disperse from the lowest to highest elevations and vice versa. We would not say that every species can instantly disperse to every point. No, autocorrelation in the Mojave Desert suggests that at a very fine scale, dispersal shortcomings are at play (Smith & Stark 2014), but such evidence does not contradict the conclusion that each bryophyte moves tens (probably hundreds) of kilometers over the course of time and would be sorted into some microsites at both ends of a gradient if it could thrive at both (Mota de Oliveira et al. 2009). Having dismissed dispersal limitation, studies of the differences in elevational preferences among species hint at the dynamics of community assembly (Vitt 2006). Elevation represents major changes in climate, and species sort themselves out into various elevations. In California's western Sierra Nevada, the foothills present a winter growing season, whereas the growing season in the alpine zone is during the summer (Schoenherr 2017). No one will think that elevation itself is what the bryophytes key in on, but elevation affects important aspects of niche space; it is a surrogate for a confounded set of variables that includes the form of precipitation (rain versus snow), dew point, temperature, and in all these things seasonality (Körner 2007).

For this paper, we give an attempt at (1) organizing our observations into characterizations of the niche of each common species, (2) quantifying how constant species niches are between two widely separated areas, (3) finding how species form coalitions, (4) at where those coalitions fall on R-mode ordinations, (5) discerning additional coalitions on ordinations of wet-loving, medium, and dry-loving sets of species, and (6) asking to what extent do the bryophytes fall into elevational zones separated by ecotones.

MATERIALS AND DATA

Study area and vascular vegetation zones. We worked in the Kaweah River watershed in and just outside Sequoia National Park, in California's southern Sierra Nevada (latitude from 36°18′ to 36°42′N, longitude from 118°14′ to 118°55′W). Kaweah's landscape displays glacier-carved valleys and exposed granitic peaks with lenses of meta-sedimentary parent rock overlain, most notably patches of marble. The area we studied climbs up steeply to the Great Western Divide, which runs north-south parallel to and west of the Sierran Crest, with ridges reaching up to 3658 m.

Continuous change in vascular vegetation follows this steep and long elevational gradient and includes representations of many of California's floristic communities (Shevock 1996). Gradient analysis by Vankat (1982) found that elevation largely structures the vascular plant vegetation. The vascular vegetation has been carefully mapped, and features of the physical environment, including meso-scale climatic conditions, are well described in maps maintained at the headquarters of Sequoia and Kings Canyon National Parks (e.g., https://irma.nps.gov/DataStore/Reference/Profile/2252079).

As one explores the elevational gradient from 380 to 3556 m, it is convenient to speak of four vascular vegetation zones:

1. The **foothill** zone occurs up to approximately 1200 m. Vegetation types include chamise/yucca chaparral, mixed chaparral, and blue oak/California buckeye woodland. The Mediterranean climate of the foothills is characterized by hot, dry summers. Winters are cool, and usually above freezing with precipitation mainly in the form of rain. Almost all rainfall occurs from November to April, often as consecutive rainy days. On subsequent days, fog is

very common, extending the intervals during which bryophytes are hydrated. Rainfall is approximately 63 cm per year, which is lower than the other elevational zones along the gradient.

2. The **lower conifer** zone spans elevations from approximately 1200 to 2440 m. Stands of giant sequoia (*Sequoiadendron giganteum*) occur on relatively flat shelves. Elsewhere dense stands of incense cedar (*Calocedrus decurrens*), jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), and sugar pine (*Pinus lambertiana*) occur, interspersed with wet meadows and rock outcrops. In the lower conifer zone, precipitation (114 cm per year) transitions from being primarily in the form of rain at 1200 m to being primarily in the form of snow at 2440 m. Summers here are still very dry; however, when the foothills have tanned in early summer, the montane forest is green and relatively cool from the previous winter's snow, which has seeped into soils with high organic content.

3. The **upper conifer** zone starts at about 2440 m and reaches more or less to 2750 m, depending on topography. Winter air temperatures are too low and the growing season is too short for the conifers found lower down. Instead, one finds extensive stands of red fir (*Abies magnifica*) and lodgepole pine (*Pinus contorta* subspecies *murrayana*), dissected by streams. In flatter areas, wet meadows occur. Rocky outcrops are often sunny with too little soil for trees. Dead wood increasingly stays hard on the surface facing up rather than rotting and becoming spongy where bryophytes would grow.

4. The **high country** includes the subalpine zone, starting at about 2750 m, and transitions to the alpine at approximately 3050 m. Tall trees are absent. Shorter whitebark pine (*Pinus albicaulis*) or foxtail pine (*Pinus balfouriana*) are scattered but dense only in small patches. Dry areas feature bare rock outcroppings and talus slopes. Fed by snowmelt, wet habitats increase in the high country and include streamlets, seasonal seepages, lakes, meadows, and fens that support graminoids and perennial forbs (Barbour et al. 2007; Storer 1963). The winters are cold and long, the summers short, cool and dry. The Sierra has much less of a monsoon season than the Rocky Mountains. Although sporadic short thunderstorms result in more precipitation than at lower elevations, still most of the moisture is due to snow melt, creating a highly contrasting mosaic of wet and dry areas. Winds can kick up any time of the year. In summer they have a drying effect, and in winter they move snow from unsheltered areas to thick drifts. In the high country, evaporation is rapid.

Sampling plots and herbarium work. As a flexible goal, plots were sampled in sets of three or four in close proximity, with one plot being wetter, such as including a stream, one plot being drier, such as a rock outcrop, and the third to fourth plots chosen to capture mesosite diversity. Other than the wet and dry plots, the subsequent plots were chosen to include variety, such as flat compact soils at low elevations, rotten logs at mid elevations, and the edges of seasonal tarns at high elevations. Sampling in this way ensured that we had equal representation of wet and dry plots at all elevations (Coleman 2014). The median elevational gap between plots adjacent in elevation was 5.4 m, and the 95th percentile of gaps was 50.2 m. Our total plot number was 253.

The area of each plot was 25 m^2, and shape followed the natural contours of the plot's central features. For example, a plot along a stream might be long and narrow. Capturing the change in species that occurs with change in habitat was ensured through sampling at a variety of meso-habitats such as meadows, soil banks, streams, lakes, and large boulders. Plots were intentionally chosen for the presence of bryophytes. A site had to have at least two species present to become a plot. Randomly selecting small pieces of land to be plots would have led to many plots with no bryophytes. The fact that our plots were *not* selected randomly means we cannot address such issues as how absolute abundance changes across elevation. However, our study can still address interesting questions of how habitat types affect niche differences and how this changes with elevation.

Information for every plot included variables across the micro-, meso-, and macro-site scales (Sagar & Wilson 2007). Plots were assigned a number. Longitude and latitude were read using a GPS navigator. The GPS unit also gave elevation, but we redetermined plot elevations from latitude and longitude using the website GPS Visualizer. For each plot, we recorded a general description of location and vegetation, parent rock type (granite, grano-diorite, marble, schist, quartzite, slate), topographic position (ridge top, slope, valley, gorge bottom, plateau, ravine bottom) and vascular vegetation type (alpine, sub-alpine, red fir forest, mixed conifer forest, oak woodland, chaparral,

savannah, treeless prairie, etc.). Gross slope and aspect were also estimated.

Every bryophyte species within a plot was identified. If we recognized the species in the field, we did not collect it. Field identifications were aided using hand lenses. For species we were unsure of, we made a herbarium specimen. Location and ecological information were recorded. Macro photographs were taken of many of the specimens as they were collected. Representative specimens are deposited in the herbaria of California State University, Northridge (SFV) and of Sequoia and Kings Canyon National Parks (THRI).

Microhabitats were recorded for each species in a plot following the protocol of Sagar (2007). These microsite dimensions include substrate, shade, incline, and wetness. Shadiness, incline, and wetness were recorded on a 5-level ordinal scale. Substrate was categorical. If a species occupied more than one category or level, they were all recorded.

Substrate types were the microsite surfaces a bryophyte grew on. We recognized ten categories: hard rock, soft rock (rare in the Kaweah), compact mineral soil (we do not characterize any organic soil as compact), loose mineral soil, organic soil, soft rotten wood (not necessarily from a "softwood" conifer), hard dead wood (not necessarily from a "hardwood" angiosperm), bark of dead wood, trunk of live tree, limbs >20 cm in diameter, branches <20 cm in diameter.

The **wetness** of a spot was meant to represent its drainage and how fast it would dry out after a rain: 0–dries easily and quickly in a day; 1–usually dries over the course of days; 2–moist for prolonged periods maybe over a week; 3–usually wet; or 4–submerged at least seasonally. It was important to have a predefined idea of these five ranks based on considerable prior field experience in order to be consistent in our judgment of wetness values (as with the other microsite scores).

Shadiness categories were as follows: 0–full sun; 1–¼ shade; 2–½ shade; 3–¾ shade; or 4–full shade. This variable represented our estimation of how much sun a microsite would experience in a 24-hour period based on its aspect relative to the path of the sun and on surrounding features that cast shadows.

The **Incline** of a microsite was measured with a clinometer at first and after experience estimated by eye: 0–0° to 30°; 1–31° to 45°; 2–46° to 70°; 3–71° to 90°; or 4–>90°.

Microsite categories were recorded not as 1-versus-blank for a particular moss species, but using a crude rank of abundance. Each species abundance value in each category was estimated recording tally marks up to five: 1–one clump; 2–two clumps; 3–one large patch up to about 1 m^2 in area; 4–several large patches or >1 m^2; and 5–patches covering a large proportion of the 25 m^2 plot. When we ended up with multiple records of the same species in a plot, we used the maximum number of tally marks for any microsite category. It was also frequently the case that a species was found as a contaminant in another packet. For such contaminants, the original microsite categories were used but with only one mark per category.

Collected specimens were taken back to the herbarium for identification. Specimens were sorted into genera to organize the identification process. Specimens were examined macroscopically with a dissecting scope, then usually further examined microscopically using a compound microscope. Through the compound scope, micrographs were taken for future reference. Species were determined using *Flora of North America* (2007, 2014), Norris & Shevock (2004), Malcolm et al. (2009), Paton (1999) and Doyle & Stotler (2006).

For over a decade, we spent our spare time doing our best to identify all the specimens. Quite a number of species that we found have been described as new to science since we started. A number of putative species remain undescribed. Our identifications of *Syntrichia* are the most problematic. Determinations for representative specimens were done by D. Toren (CAS), J. Spence (then of the National Park Service), B. Carter (SJSU), B. Mishler (UC), J. Shaw (DUKE), N. Mendez (SFV), and Daniel Palmer (SFV). Even though we know how to identify the mosses of California much better than when we started, imperfect taxonomic resolution persists. Sadly, we had to lump some of our entities into operational taxonomic units of two or more (putative) species, as noted in **Supplementary File S1**, which also provides the raw data. Throughout the paper, we will refer to the species or lumps of species as "species". We recorded 2049 occurrences of 255 species.

STATISTICAL METHODS

Niche dimensions. The elevational central tendency was calculated as the average elevation of all the plots in which a species was found. For

wetness, incline, and shadiness, each tendency was calculated as the tally-mark-weighted average for each species. Substrate tendency, being more or less an unordered categorical variable, was a bit harder to report as an average: for species in which 75% or more of the tally marks were for one substrate category, we simply declared it had a tendency for that category; when <75% of the tally marks were in one substrate category we pooled the categories enough to make the number >75%, so for example, *Meiotrichum lyallii* had 60% of its marks on organic soil and 31% of its marks on loose mineral soil, so we described its substrate as "soil (often organic)"; finally, some species were found growing on such a variety of substrates that they were declared "substrate generalists". We also figured in a generalist designation for elevation, wetness, incline, and shadiness. First, we calculated the 12.5th and the 87.5th percentiles; 75% of the occurrences fall between these two percentiles. We then calculated the 87.5th minus the 12.5th percentile and asked if this span of the niche dimension was more than half the theoretically possible gradient. If so, the species was labeled a "generalist" for that niche dimension.

Species that occurred in both the Kaweah and the Santa Monica Mountains. For a subset of 37 species, we have data on niche tendency not only from the Kaweah but also from the Santa Monica Mountains as reported in Sagar & Wilson (2009). Hence, we calculated three correlations—for average wetness, average incline, and average shadiness. Species were included when found in three or more plots in both studies. The macrosites are 270 km apart in a straight line, which is very close to north-south, and they differ in climate due to Kaweah being more continental and at a higher latitude. The Santa Monica Mountains are not of high elevation or even mid elevation by the standards of the Sierra Nevada, which is why so few species are shared in common.

Coalitions based on co-occurrence at the plot level. For the Kaweah data set, RCLUS was used to search for coalitions of species (Ott et al. 2015; Sanderson et al. 2006). It is written as a macro in Excel[1]. It randomly starts with a species and searches for other species that are close in terms of co-occurrence, here expressed as Sørensen similarity.

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[1] RCLUS (18 February 2014 version) was kindly provided by one of its authors, Jeffrey E. Ott (jeott@fs.fed.us).

When a species is above a threshold similarity, it is provisionally agglomerated to the coalition. A subsequent species is agglomerated when its average similarity to the species already in the provisional coalition is above the threshold. New coalitions are initiated by considering species not already in a coalition. Then the program improves the lists of coalitions by iteratively considering dropping or adding species to each coalition. A species can belong to two or more coalitions, and many species do not end up belonging to any coalition. The whole process is repeated for numerous runs (100 by default) that vary in their initial species, and the frequency of runs that yielded an exact coalition list is reported for each such search.

R-mode ordination. To visualize the RCLUS coalitions, we ordinated the species, i.e. we carried out an R-mode scaling. This was done with PC-ORD (McCune & Mefford 2017). An **A** matrix was prepared of 253 plots by 186 species found in two or more plots (species that were in only one plot were not included). This matrix was imported into PC-ORD. We immediately applied Beals smoothing, which changed the matrix from zeros and ones to probabilities of finding a species in a plot even if it was not actually found, based on its occurrences with species that were found in the plot (regarding Beals smoothing, see Discussion). We then transposed the smoothed **A** matrix. We used PC-ORD's thorough autopilot to derive an optimal non-metric multidimensional scaling based on Sørensen distances between every species and every other species. Generally speaking, Sørensen coefficient (whether expressed as similarity or dissimilarity) tends to give less importance to instances in which two species are jointly absent, and more generally Sørensen is less affected than other coefficients by the problem of a large number of zeros in one's data matrix (Clark et al. 2006 elaborate on the topic and provide a modified coefficient). The ordination was rotated so that Axis 1 was maximally correlated with the number of plots a species occurred in, i.e. with **prevalence**. With the linear effect of prevalence accounted for, we then studied the spread of species along Axes 2 and 3.

Chunking by wetness. The large data matrix was sliced into three chunks—one with species whose average wetness was >2.5, one in the middle, and one whose average wetness was <1.5. Species found

in >2 more plots were kept, and then plots with >2 species were kept. The sub-matrix of wet-loving species consisted of 94 plots by 34 species. The middle sub-matrix consisted of 191 plots by 62 species. The sub-matrix of dry-loving species consisted of 191 plots by 62 species. For each chunk, RCLUS was used to search for coalitions. Separately, each sub-matrix was Beals smoothed, transposed, and ordinated. Coalitions were color-coded on the ordinations.

Turnover. We attempted a graphical visualization of turnover along the 3000-m elevational gradient. Arranging the plots by elevation, we calculated what the **penalty** would be for drawing a line (candidate ecotone) between adjacent plots. Penalty was an average across all species that occurred in two or more plots. The contribution to penalty of each species was the smaller of two tails of its elevational distribution, which was the smaller number of occurrences below or above the line, proportionalized by the total number of occurrences. Species whose occurrences were entirely above or below the line did not penalize the line. Species whose occurrences were mostly above or mostly below penalized the line only a small amount. If a species was half above and half below the line, then it would penalize the line the maximum amount. If a strong ecotone presented itself, it would appear as a sharp dip between two peaks in a graph of penalty on elevation.

Results

Given our taxonomic resolution, 68 species were found in only one plot, 30 in two plots, 20 in three plots, 16 in four, 15 in five, 8 in six, 4 in seven, 8 in eight, 7 in nine, and 69 were found in ten or more plots. These last **common species** that were found in ten or more plots will be dwelt on at greater length, since the average for a (niche) trait is more meaningful when based on an adequate sample size.

Niche dimensions. Niche central tendencies for the 69 common species are given in **Table 1**. Also in the table, some of the species are noted as "generalists" for one or more niche dimensions. For example, row 1 *Tortula hoppeana* was characteristically of high elevations, in medium wetness, in medium shadiness, but it was a generalist on substrates and the incline of the substrates it grew on. **Supplementary File S2** gives the tendencies for

the rarer species, as well as the numerical values of degree of niche generalization (rather than the generalist/specialist dichotomy).

Among the common species, *Tortula hoppeana* (row 1) was specialized to the highest elevations, whereas *Orthotrichum bolanderi* (row 69) was the common species specialized to the lowest elevations. *Grimmia brevirostris* (32) had the lowest wetness tendency, and *Chiloscyphus pallescens* (24) had the highest wetness tendency. *Imbribryum alpinum* (10) was the most specialized on horizontal surfaces, whereas *Fabronia pusilla* (58) was the most specialized at growing on the undersurface of overhangs (though it is a substrate generalist on rock and bark). *Imbribryum alpinum* (10), again, was the most specialized for growing with very little shade, whereas *Pohlia cruda* (12) was the most specialized for growing in shade. As for substrate specialists, 100% of *Orthotrichum pylaisii* (23) tally marks were from occurrences on rock, 91% of *Aulacomnium palustre* (4) tally marks were from organic soil, 75% of *Dicranoweisia cirrata* (41) tally marks were from soft rotten wood with another 20% from hard dead wood or dead bark, and 100% of *Orthotrichum lyellii* (65) tally marks came from occurences on trees.

Twelve species that occurred in 10 or more plots were specialists for all five niche dimensions ("penta-specialists" in **Table 1**): *Brachytheciastrum collinum* (row 11), *Orthotrichum pylaisii* (12), *Homalothecium nevadense* (30), *Porella cordaeana* (39), *Orthotrichum papillosum* (43), *Weissia controversa* (45), *Didymodon vinealis* (48), *Homalothecium pinnatifidum* (53), *Orthotrichum lyellii* (65), *Didymodon eckeliae* (66), *Grimmia laevigata* (67) and *Hedwigia detonsa* (68). None of these were species of wet spots. None of them were specialists on soft rotten wood or organic soils. Perhaps more of them were of low elevations than high elevations, but several were of middle elevations. Some are thought of as common by California bryologists. Most notably *Didymodon vinealis,* when all its segregate taxa are segregated, was surprisingly specialized for such a familiar moss.

Ceratodon not splitup (row 38) was the only generalist for all five niche dimensions, and we are inclined to think that the genus as found in the Kaweah might contain multiple species or ecotypes (Jules & Shaw 1994). A number of other "species" seemed suspiciously broad in their elevational niche and might similarly contain considerable

Table 1. For each of the common species (rows), tendencies on five gradients (columns) are provided. Rows are sorted from species that tend to occur at the highest elevations to species that tend to occur at the lowest elevations (in meters). Consider cells without the word "generalist" as more of a specialist for that niche dimension. Wetness, Incline and Shadiness range from 0 to 4. **Bold** is used to emphasize extreme or unusual niches. *n* reports the number of plots a species was found in, but some tendencies were based on a slightly smaller sample size in cases where we failed to record more than presence.

		n	Substrate	Elevation	Wetness	Incline	Shadiness
1	*Tortula hoppeana*	11	generalist rock/soils (various)	3121	2.14	generalist 1.57	2.52
2	*Pohlia bolanderi*	26	generalist rock/soils (various)	3061	generalist 1.72	generalist 1.60	**3.01**
3	*Grimmia alpestris*	26	rock	**3029**	**0.88**	generalist 1.47	generalist 2.83
4	*Aulacomnium palustre*	17	**organic soil**	2998	**2.59 meadows**	0.61	generalist 1.38
5	*Pohlia nutans*	12	generalist soils/rock/wood	2936	generalist 2.00	generalist 0.79	generalist 2.29
6	*Polytrichum piliferum*	31	generalist soil (often organic)/rock	generalist 2904	generalist 1.43	**0.44**	generalist 1.85
7	*Scapania undulata*	16	generalist rock/organic soil	2786	**3.46 streams**	generalist 1.29	generalist 2.78
8	*Meiotrichum lyallii*	30	**soil (often organic)**	2781	1.90	generalist 0.99	2.53
9	*Hygrohypnum ochraceum*	12	rock	2766	3.04	generalist 1.02	**3.40**
10	*Imbribryum alpinum*	11	generalist soils (various)/rock	2752	generalist 2.04	**0.11**	1.30
11	*Brachytheciastrum collinum* penta-specialist	20	**rock**	2705	1.55	2.18	2.88
12	*Pohlia cruda*	19	generalist rock/soils (various)	2697	2.66	generalist 1.29	**3.43**
13	*Imbribryum muehlenbeckii*	20	generalist rock/soils (various)	2650	2.43	generalist 0.76	generalist 2.02
14	*Grimmia hamulosa*	11	rock	2512	generalist 1.50	generalist 1.08	1.57
15	*Polytrichum juniperinum*	44	soil (often organic)	generalist 2473	generalist 1.67	**0.56**	1.71
16	*Ptychostomum pallescens*	12	generalist soils (various)/rock	2462	2.45	**0.60**	2.45
17	*Philonotis fontana*	57	generalist rock/soil	generalist 2380	2.65	generalist 1.26	generalist 2.60
18	*Eurhynchiastrum pulchellum*	16	generalist rock/soils (various)	2369	2.56	generalist 1.56	generalist 3.16
19	*Syntrichia* "*bartramii*"	10	rock	2204	1.50	generalist 1.90	3.10
20	*Ptychostomum pseudotriquetrum*	40	generalist soil (often organic)/rock	generalist 2197	2.86	generalist 1.01	generalist 2.52
21	*Marchantia polymorpha*	16	organic soil, adjacent rock	2174	3.00	0.66	generalist 3.08
22	*Plagiomnium medium*	22	organic soil	2107	2.93 streams	generalist 0.80	generalist 2.75
23	*Orthotrichum pylaisii* penta-specialist	12	rock face	2101	1.18	2.83	2.38
24	*Chiloscyphus pallescens*	12	generalist rock/organic soil/rotten wood	2079	3.54 streams	generalist 1.13	generalist 3.08

Table 1. Continued.

		n	Substrate	Elevation	Wetness	Incline	Shadiness
25	*Dichodontium pellucidum*	15	rock	2064	3.09 streams	generalist 1.23	3.06
26	*Grimmia montana*	28	rock	2040	0.86	generalist 1.58	generalist 2.20
27	*Riccia sorocarpa*	11	soils (various)	generalist 1989	2.09	generalist 1.00	generalist 1.59
28	*Brachythecium frigidum*	29	generalist rock/organic soil	1954	2.89	generalist 1.41	2.52
29	*Brachythecium albicans*	13	generalist rock/soils (various)	1954	2.16	generalist 1.67	2.61
30	*Homalothecium nevadense* penta-specialist	22	rock face	1933	1.55	2.53	2.86
31	*Aulacomnium androgynum*	27	**wood (often rotten)**	1895	1.88	generalist 1.60	2.69
32	*Grimmia brevirostris*	17	rock	1861	0.34	generalist 1.55	generalist 1.40
33	Bryaceae *torenii*+B	24	rock/mineral soil	1852	generalist 2.13	generalist 1.68	2.25
34	*Syntrichia ruralis*	29	rock	1844	1.42	generalist 1.65	generalist 2.51
35	*Brachytheciastrum velutinum*	33	generalist rock/wood/soil	1833	1.74	generalist 2.13	generalist 3.16
36	*Orthodicranum tauricum*	12	**wood (often rotten)**	1759	1.78	generalist 1.90	2.67
37	*Kindbergia praelonga*	19	generalist rock/organic soil	1750	2.97 seeps	generalist 1.19	2.79
38	*Ceratodon*	36	generalist rock/soil	generalist 1642	generalist 1.51	generalist 0.92	generalist 2.27
39	*Porella cordaeana* penta-specialist	13	rock face	1614	1.90	2.59	3.40
40	*Grimmia trichophylla*	26	rock	1612	1.11	generalist 2.06	2.50
41	*Dicranoweisia cirrata*	10	**wood (often rotten)**	1612	1.58	generalist 1.77	generalist 2.41
42	*Scleropodium obtusifolium*	32	**rock**	1569	**3.15** streams	generalist 2.03	2.65
43	*Orthotrichum papillosum* penta-specialist	10	trees and adjacent rocks	1383	1.74	2.38	2.73
44	*Orthotrichum rupestre*	35	rock	1293	1.44	generalist 2.10	2.62
45	*Weissia controversa* penta-specialist	10	**compact soil**	1264	1.85	2.33	2.88
46	*Syntrichia princeps*	53	rock	1151	1.51	generalist 1.69	2.35
47	*Scleropodium touretii*	23	generalist rock/soils (various)	1135	2.28	generalist 1.71	2.89
48	*Didymodon vinealis* penta-specialist	24	rock/mineral soil	1124	1.80	2.19	2.76
49	*Didymodon brachyphyllus*	17	rock/mineral soil	1103	1.55	generalist 2.12	2.26
50	*Grimmia lisae*	32	rock	generalist 1076	1.02	generalist 1.37	2.09

Table 1. Continued.

		n	Substrate	Elevation	Wetness	Incline	Shadiness
51	*Anacolia baueri*	14	rock	1075	1.54	generalist 2.45	2.50
52	*Claopodium whippleanum*	23	generalist: compact soil/rock/ organic soil	1054	generalist 2.21	generalist 1.84	**3.26**
53	*Homalothecium pinnatifidum* penta-specialist	48	rock	1029	1.52	2.33	2.49
54	*Antitrichia californica*	27	rock and adjacent tree trunks	1028	1.66	generalist 2.07	2.52
55	*Timmiella anomala*	26	compact soil	1014	2.01	generalist 1.45	2.54
56	*Asterella californica*	16	mineral soil/rock	978	generalist 2.31	generalist 2.18	generalist 3.05
57	*Syntrichia laevipila*	11	trees	963	2.18	generalist 1.39	2.66
58	*Fabronia pusilla*	15	generalist rock/bark	945	1.71	**3.22**	3.23
59	*Fissidens sublimbatus*	29	**compact soil**	936	2.26	generalist 1.73	3.35
60	*Grimmia pulvinata*	24	rock top	905	0.81	generalist 1.00	generalist 1.63
61	*Targionia hypophylla*	14	soils (often compact)	841	generalist 1.95	generalist 1.95	generalist 2.67
62	*Bryum argenteum*	27	generalist on soil (often mineral)/ rock	839	generalist 1.23	generalist 1.47	generalist 1.67
63	*Fossombronia longiseta*	13	soils (often compact)	838	2.08	generalist 1.17	generalist 2.62
64	*Syntrichia* "*obtusissima*"	24	rock	837	0.95	generalist 1.52	1.67
65	*Orthotrichum lyellii* penta-specialist	10	**trees**	803	1.90	2.39	2.29
66	*Didymodon eckeliae* penta-specialist	15	mineral rock/soil	793	1.89 riparian	2.35	2.84
67	*Grimmia laevigata* penta-specialist	21	rock top	761	0.71	**0.29**	1.32
68	*Hedwigia detonsa* penta-specialist	14	rock face	740	0.77	**2.53**	2.16
69	*Orthotrichum bolanderi*	18	generalist rock/bark	735	1.18	2.37	2.36

eco-genetic diversity. *Polytrichum piliferum* (6) was an elevation generalist, and our observation was that the low elevation occurrences were of a moss with a larger body size than the high elevation occurrences, which are similar to *P. piliferum* as known north of California. *Polytrichum juniperinum* (15) was also an elevational generalist. We are suspicious of our sample of *Riccia sorocarpa* (27); it had a broad elevational niche and might contain some low elevation occurrences of a different species that we were unable to discern. Two "species" that experienced bryologists would not

be surprised to find to be taxonomically heterogeneous and that we found to be elevational generalists were *Philonotis fontana* (17) and *Ptychostomum pseudotriquetrum* (20).

At this point, we now stop our narration of niche generalists; elevation was worth dwelling on because it was scored with more accuracy. Especially curious readers will want to closely study the other four microhabitat dimensions, comparing species of particular interest. We now turn to comparing ecological differences between closely related species in **Table 1**.

- *Grimmia brevirostris* and *Grimmia hamulosa* (rows 32 versus 14) are often lumped, and like many *Grimmia* species they both live on rock; yet they differ in elevational tendency (1861 m versus 2512 m), and perhaps the former lives in drier spots on average. Jim Shevock (personal communication) thinks of *G. brevirostris* as not extending as far south as the Kaweah, so conceivably future research might recognize both species but with all our specimens belonging to *G. hamulosa*.

- *Orthotrichum lyellii* with its asexual propagules seems to differ elevationally from *Orthotrichum papillosum* which lacks such gemmae (row 65 at 803 m versus row 43 at 1383 m). How to handle this complex has been debated for decades, and the forms differ in their niches (Montalvo 1982). Since we identified our specimens, Lara et al. (2020) have reworked the group, recognizing four distinct species in the segregate genus *Pulvigera*. What we called *O. papillosum* seems likely to be their *Pulvigera howei*, although *Pulvigera papillosa* in the strict sense cannot be ruled out.

- The taxonomic gap between *Grimmia montana* and *Grimmia alpestris* is not debated, but the two are closely related. Our data confirmed that *G. montana* is a mid-elevation species whereas *G. alpestris* is of high elevations (26 at 2040 m versus 3 at 3029 m). Both live on hard, quickly drying rock.

- *Homalothecium pinnatifidum* is a low elevation species, whereas *Homalothecium nevadense* is of mid elevations (row 53 at 1029 m versus 30 at 1933 m). They are similarly specialized on rock in fairly shady spots.

A few not-quite-terminal taxa remain regretfully confusing in terms of us being able to always identify them on the basis of morphology.

- *Imbribryum torenii* was described as new to science after we started our study, and we mixed up its occurrences with those of what appears to be another undescribed and common species, "Bryaceae species B". We were forced to lump (as row 33). However, the niche breaths give some weak suggestion that the two entities might differ in substrate, wetness, and/or incline. They occurred similarly in the Kaweah's lower conifer zone in partial shade.

- Another taxonomically difficult pair of species was *Grimmia lisae* and *Grimmia trichophylla* (rows 50 and 40). They were remarkably similar or generalized in the five niche dimensions and often found in the same plot. Our sample of the former might contain some aberrant specimens of some third species that we could not find another name for, yet Daniel Palmer who identified each of these specimens worked very carefully at distinguishing the two entities on the basis of number of leaf cross-section cells, a spiral twist or lack thereof in terms of leaf posture, and basal cell length.

- Finally, we segregated several 'species' of *Syntrichia*, shown fully in our larger **Supplementary File S2**, and the averages for the various named species and unsettled segregates suggested niche differences. Clearly more ecological work is needed on this genus after the species come to be easily identified in the field.

Species that occurred in both the Kaweah and the Santa Monica Mountains. In cases where the same species occurred in our study of the Kaweah and in Sagar and Wilson's 2009 study of the Santa Monica Mountains, did the species retain their relative relationships? Yes, the correlation between the two studies for average wetness was $r = 0.713$; for average incline was $r = 0.582$; and for average shadiness was $r = 0.817$.

Coalitions based on co-occurrence at the plot level. Up to this point, we have summarized niche dimensions that were directly observed. Now, we go on to indirectly cluster species based on their co-occurrences. Crudely put, we searched the data set for species that are similar in their plot occurrences taking into account joint presences.

Our most thorough search was done using only the species found in 10 or more plots. Using the common species only, we varied the affinity threshold level and scrutinized the resulting list of coalitions. Threshold levels that were stringent (high Sørensen such as 0.28) yielded many small clusters. While many small clusters might be useful for purposes more detailed than ours, a handful of groups is easier to narrate, so we ended up using a somewhat lower threshold. RCLUS runs its algorithm a large number of times, and typical output from RCLUS includes some clusters that were found

in few runs, i.e. had low frequency. We shortened the list of clusters by dismissing clusters that were found at low frequency. Also, RCLUS sometimes yields two clusters that have high overlap, i.e. that are almost redundant, in which cases, one or the other was chosen. (Those who want this process automated can use the condensed set of coalitions that RCLUS gives as extra output.) If one scrutinizes the results of different searches using different cutoff values, some of the clusters have very similar membership; in our experience, the search with the more stringent cutoff value simply has extra clusters, and either search may have some extra infrequent or nearly redundant clusters. We settled on a Sørensen threshold of 0.21 and did that search with 1000 runs. Five clusters were worth noting.

- The **Green** coalition, found in all 1000 runs, consists of eighteen species occurring at low elevation. It is helpful to break the eighteen into two lists, rock specialists and non-rock specialists (species are usually labeled using the first two letters of genus and the first two letters of epithet; **Supplementary File S1** lists all abbreviations). Rock specialists—*Homalothecium pinnatifidum, Syntrichia princeps, Grimmia lisae, Hedwigia detonsa, Orthotrichum rupestre, Grimmia laevigata, Grimmia pulvinata,* and *Syntrichia* "*obtusissima*"; species not so specialized on rock—*Antitrichia californica, Orthotrichum bolanderi, Didymodon eckeliae, Fabronia pusilla, Claopodium whippleanum, Orthotrichum lyellii, Syntrichia laevipila, Fissidens sublimbatus, Didymodon vinealis,* and *Scleropodium touretii.* An idealized 25 m² plot with most of them would have some boulders, some compact soil banks perhaps of a seasonally dry stream bank, and an oak tree. In other words, it would look like a postcard landscape from the California foothills.
- The **Orange** coalition, found in 921 of 1000 runs, consisted of twelve species: *Syntrichia princeps, Orthotrichum rupestre, Dicranoweisia cirrata, Grimmia trichophylla, Homalothecium pinnatifidum, Orthotrichum papillosum, Orthodicranum tauricum, Homalothecium nevadense, Aulacomnium androgynum, Syntrichia ruralis, Brachytheciastrum velutinum,* and *Antitrichia californica.* Four of the species were also in the Green coalition. Species in the Orange coalition oc-

curred a bit higher in elevation in somewhat shadier plots, often with conifers and a log rotting from the outside inwards with soft rotten wood.

- The **Blue** coalition, found in all runs, was made up of ten species, none of them in either the Green or Orange coalitions: *Brachythecium frigidum, Plagiomnium medium, Chiloscyphus pallescens, Kindbergia praelonga, Dichodontium pellucidum, Scleropodium obtusifolium, Scapania undulata, Ptychostomum pseudotriquetrum, Marchantia polymorpha,* and *Philonotis fontana.* Blue species are found in plots with perennial streams or at least in seeps, often in deep shade at mid-elevations.
- The **Purple** coalition was found in 475/1000 runs; however, a largely redundant group was found in 525/1000 runs. We presume that one or the other was found in all runs. The purple coalition's six common species sometimes occurred at the side of a wet meadow or lake or at least in a low spot where water would puddle up seasonally. All of the species occur at fairly high elevations, although some also occur at lower elevations: *Polytrichum juniperinum, Philonotis fontana, Imbribryum muehlenbeckii, Ptychostomum pseudotriquetrum, Eurhynchiastrum pulchellum* and *Imbribryum alpinum.* Two of the Purple coalition's species were in the Blue coalition as well.
- The **Red** coalition was found in 999/1000 runs and consisted of five common species none shared with any other coalition: *Pohlia bolanderi, Grimmia alpestris, Brachytheciastrum collinum, Meiotrichum lyallii,* and *Polytrichum piliferum.* A couple of the species might be characterized as high-elevation specialists, but *Polytrichum piliferum* was a generalist in elevation (and body size).

At first we were disappointed that RCLUS did not find a wet-meadow coalition. *Marchantia polymorpha* (of the Blue coalition) would be in it, as would *Aulacomnium palustre* (which also occurred in many plots but was not part of the five coalitions). As we will discuss below, many other species found in fewer than 10 plots would be good candidates for a wet-meadow coalition. Perhaps RCLUS failed to find one because we did not have enough plots in wet meadows or perhaps the search was thrown off by inconsistency in which particular

wet-meadow species occurred among wet-meadow plots?

We did some other searches to see if we would find the same five coalitions. First, we searched with the same Sørensen cutoff of 0.21 but using species found in 3 or more plots rather than 10 or more. More coalitions were found, and a few more species were found in the named coalitions; still, in general, the five named coalitions were obvious, and no wet-meadow coalition was stable. Second, we varied the Phi coefficient instead of Sørensen. Settling on a Phi of 0.14 resulted in clusters that were similar to the named ones after the usual shortening of the set based on low frequency and near redundancy. These exercises reassured us that our choices of focusing on only the common species and using Sørensen's coefficient as the criterion for clustering were not terribly consequential.
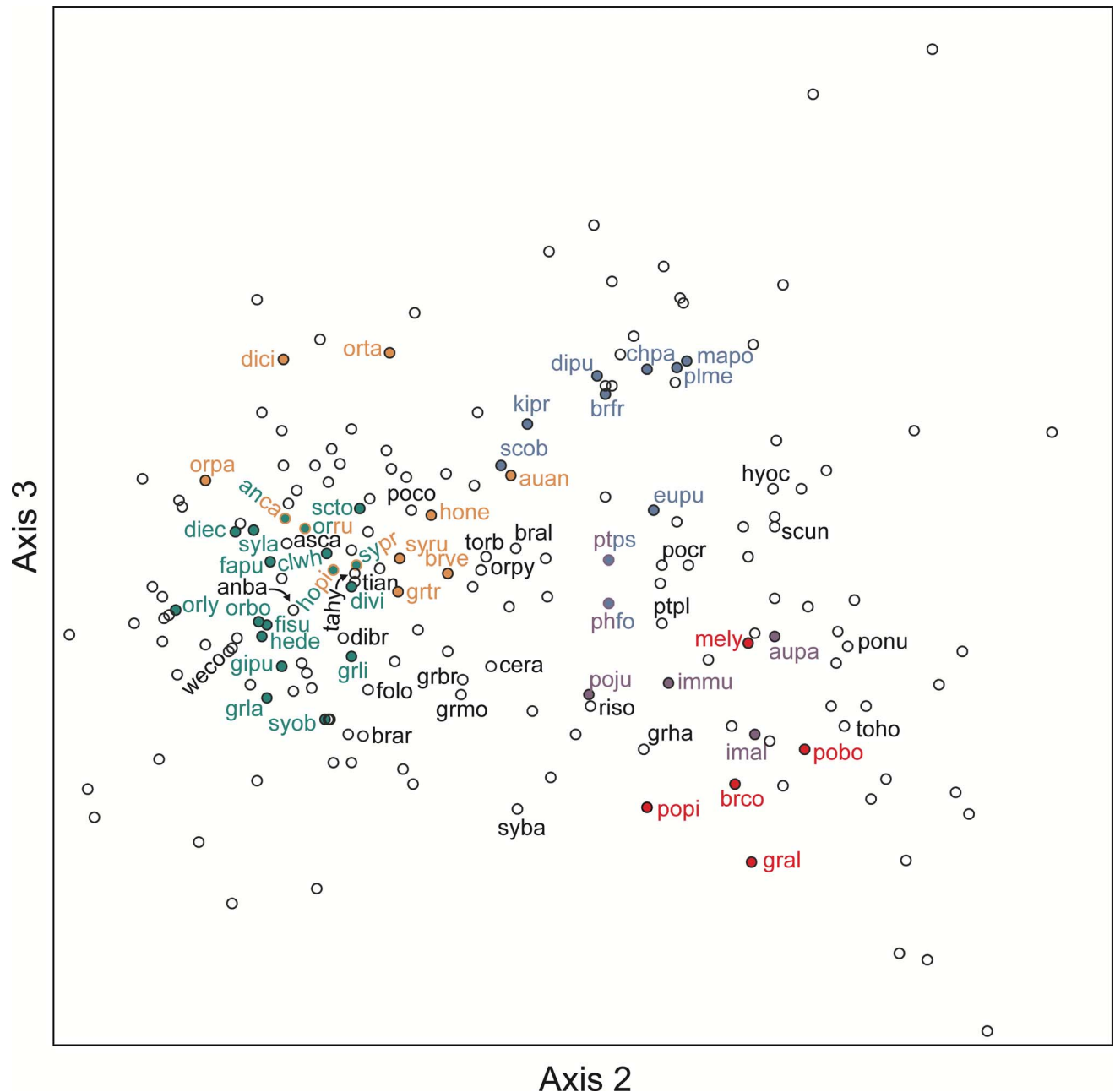
R-mode ordination. We ordinated species in R mode. (A more "normal" ordination of plots in Q mode is shown in **Supplementary File S3**.) The autopilot recommended a 3-dimensional solution (3-dimensions were also its recommendation on runs in Q mode and in R mode with only common species). The final stress was 8.10 ($R^2_n = 0.993$). After rotation, prevalence was strongly correlated with Axis 1 ($r = 0.872$), and none of the directly observed niche dimensions were strongly correlated with Axis 1 (all $|r| < 0.2$). Axis 1 was not of interest in itself, but Axes 2 and 3 were perpendicular to it, and so in a limited sense they had the linear effect of prevalence removed. After rotation, Axis 2 was correlated with elevation ($r = 0.922$), with average wetness ($r = 0.556$), and negatively correlated with average incline ($r = -0.346$). Axes 3 was weakly correlated with average wetness ($r = 0.413$). All other $|r| < 0.2$.

The rotated R-mode ordination is presented in **Fig. 1** with the five coalitions color-coded after the ordination was made. Clearly, RCLUS did more than just cut up the ordination. (1) Some species on the ordination seem to be in the middle of a coalition but were not part of that coalition. (2) Other sectors on the ordination contain several seemingly close species that did not form a coalition. (3) And of course, some species are in more than one coalition, perhaps because their many occurrences were varied in terms of their co-occurrences. In sum, RCLUS found associations that would have been foggy if only seen as a graph of Axes 2 and 3.

The same ordination but labeled quite differently is given in **Fig. 2** Instead of color-coding the coalitions, substrate specialists were color-coded. The few specialists on trees had low values on Axis 2 (were at lower elevations). The specialists on mineral soil also had low values on Axis 2 (were at lower elevations where soils often become quite compact), whereas the specialists on organic soil had high values on Axis 2 (occurred at higher elevations). On the other hand, the many species specializing on rock were scattered throughout the ordination, as were substrate generalists.

Another feature of **Fig. 2** is that some of the rarer species labels are shown, unlike in **Fig. 1**. This allows us to entertain the possibility of a wet-meadow guild, and wet-meadow candidates are to be seen toward the right (at higher elevations) with slanted labels. At the highest values of Axis 3 are placed *Ptychostomum pacificum* and *Cratoneuron filicinum*. A bit lower down are *Philonotis fontana* var. *americana* and *Marchantia polymorpha* (the latter a common species). Near the middle of Axis 3 are *Drepanocladus aduncus* and *Straminergon stramineum*, and a bit lower on Axis 3 are *Sarmentypnum exannulatum* and *Aulacomnium palustre* (another common species). Although not all eight of these species would be characterized as very high-elevation specialists, they all are quite high on Axis 2. The ordination failed to pull out a meadow dimension independent of elevation. In addition, the meadow candidates show wide scatter on Axis 3 and are often closer on the ordination to one or another species that would be better thought of as being of streams or seeps or even of drier microhabitats. Maybe a wet-meadow coalition is just not to be found in our data at the among-plot scale.

Some kind of ordination is worth presenting to visualize the separation of coalitions. **Fig. 1**'s R-mode ordination of species makes straightforward sense as both are based on the relationship of one species to the next. Nevertheless, in purely practical terms, the Q-mode ordination of plots and species (**Supplementary File S3**) would have been equally serviceable, even though the connection between coalitions and Q mode is more circuitous. On the other hand, R-mode analyses bring with them some annoying challenges (McCune et al. 2002). Generally speaking, and in our case, the number of plots species occur in (prevalence) varies more than the

Figure 1. R-mode ordination of species with five coalitions from RCLUS color-coded. Species in two coalitions are labeled in both colors, different letters of their species code. Black points were not in the coalitions. Unlabeled points occurred in fewer than 10 plots. **anba** *Anacolia baueri*, **anca** *Antitrichia californica*, **asca** *Asterella californica*, **auan** *Aulacomnium androgynum,* **aupa** *Aulacomnium palustre*, **bral** *Brachythecium albicans*, **brar** *Bryum argenteum*, **brco** *Brachytheciastrum collinum,* **brfr** *Brachythecium frigidum*, **brve** *Brachytheciastrum velutinum*, **cera** *Ceratodon*, **chpa** *Chiloscyphus pallescens*, **clwh** *Claopodium whippleanum*, **dibr** *Didymodon brachyphyllus*, **dici** *Dicranoweisia cirrata*, **diec** *Didymodon eckeliae*, **dipu** *Dichodontium pellucidum*, **divi** *Didymodon vinealis*, **eupu** *Eurhynchiastrum pulchellum*, fapu *Fabronia pusilla*, **fisu** *Fissidens sublimbatus*, **folo** *Fossombronia longiseta*, **gipu** *Grimmia pulvinata*, **gral** *Grimmia alpestris*, **grbr** *Grimmia brevirostris*, **grha** *Grimmia hamulosa*, **grla** *Grimmia laevigata*, **grli** *Grimmia lisae*, **grmo** *Grimmia montana*, **grtr** *Grimmia trichophylla*, **hede** *Hedwigia detonsa*, **hone** *Homalothecium nevadense*, **hopi** *Homalothecium pinnatifidum*, **hyoc** *Hygrohypnum ochraceum*, **imal** *Imbribryum alpinum*, **immu** *Imbribryum muehlenbeckii*, **kipr** *Kindbergia praelonga*, **mapo** *Marchantia polymorpha*, **mely** *Meiotrichum lyallii*, **orbo** *Orthotrichum bolanderi*, **orly** *Orthotrichum lyellii*, **orpa** *Orthotrichum papillosum*, **orpy** *Orthotrichum pylaisii*, **orru** *Orthotrichum rupestre*, **orta** *Orthodicranum tauricum*, **phfo** *Philonotis fontana*, **plme** *Plagiomnium medium*, **pobo** *Pohlia bolanderi*, **poco** *Porella cordaeana*, **pocr** *Pohlia cruda*, **poju** *Polytrichum juniperinum*, **ponu** *Pohlia nutans,* **popi** *Polytrichum piliferum*, **ptpl** *Ptychostomum pallescens*, **ptps** *Ptychostomum pseudotriquetrum*, **riso** *Riccia sorocarpa*, **scob** *Scleropodium obtusifolium*, **scto** *Scleropodium touretii*, **scun** *Scapania undulata*, **syba** *Syntrichia* "*bartramii"*, **syla** *Syntrichia laevipila*, **syob** *Syntrichia* "*obtusissima*"*,* **sypr** *Syntrichia princeps*, **syru** *Syntrichia ruralis*, **tahy** *Targionia hypophylla*, **tian** *Timmiella anomala*, **toho** *Tortula hoppeana*, **torb** Bryaceae *torenii*+B, **weco** *Weissia controversa*. In color in the online pdf.
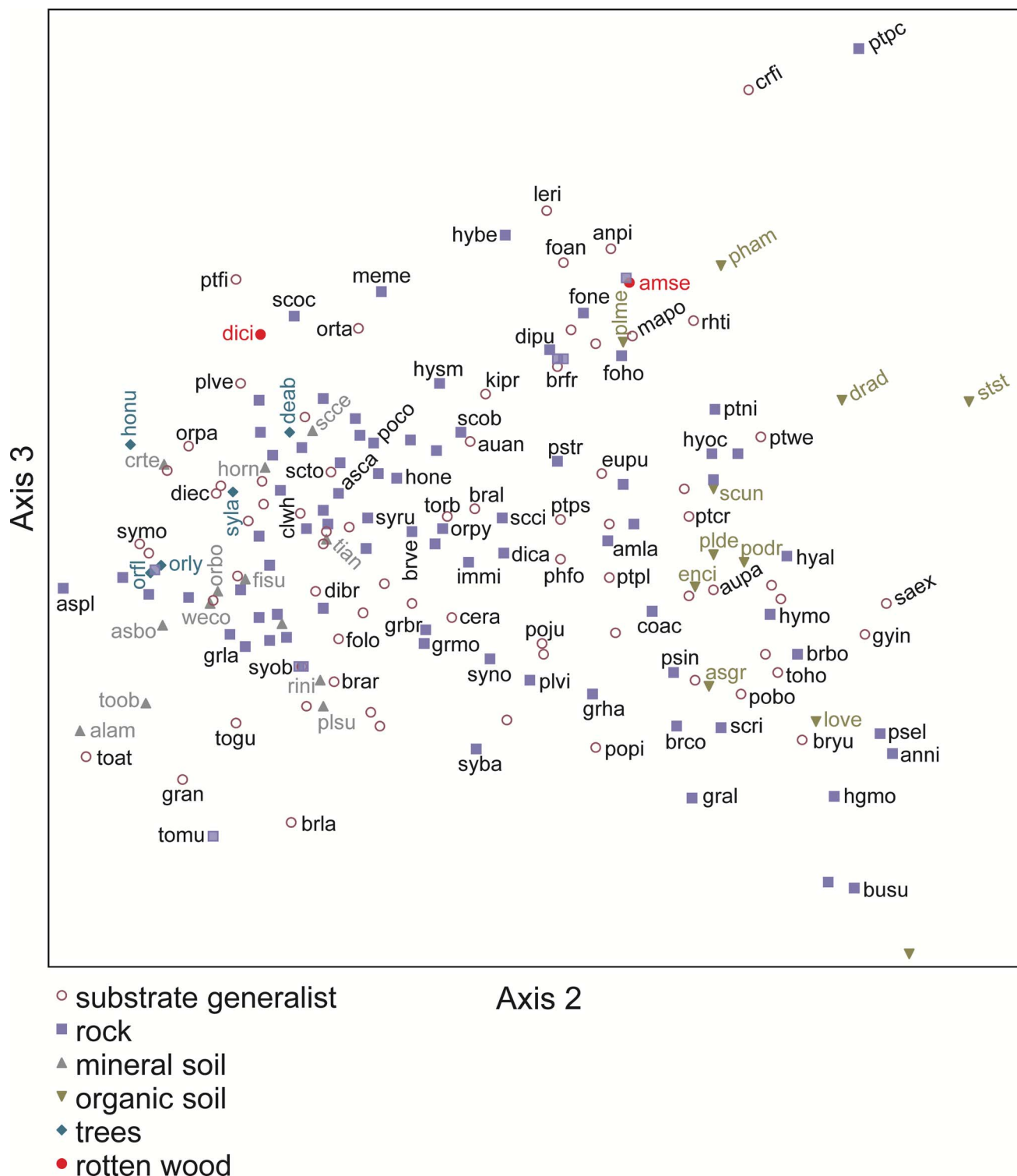
Figure 2. R-mode ordination of species in plot space. Axes 2 and 3 shown (Axis 1 largely represented the number of plots a species was found in). The labels for many species are not shown because they got in the way of other information. Codes additional to those given in the caption of Figure 1: **alam** *Aloina ambigua*, **amla** *Amphidium lapponicum*, **amse** *Amblystegium serpens*, **anni** *Andreaea nivalis*, **anpi** *Aneura pinguis*, **asbo** *Asterella bolanderi*, **asgr** *Asterella gracilis*, **aspl** *Asterella palmeri*, **brbo** *Bruchia bolanderi*, **brla** *Bryum lanatum,* **bryu** *Bryum* sp. 1, **busu** *Bucklandiella sudetica*, **coac** *Codriophorus acicularis*, **crfi** *Cratoneuron filicinum*, **crte** *Cryptomitrium tenerum*, **deab** *Dendroalsia abietina*, **dica** *Distichium capillaceum*, drad *Drepanocladus aduncus*, **enci** *Encalypta ciliata*, **foan** *Fontinalis antipyretica*, **foho** *Fontinalis howellii*, **fone** *Fontinalis neomexicana*, **gran** *Grimmia anodon*, **gyin** *Gymnocolea inflata*, **hgmo** *Hydrogrimmia mollis*, **honu** *Homalothecium nuttallii*, **horn** hornwort, **hyal** *Hygrohypnum alpinum*, **hybe** *Hygrohypnum bestii*, **hymo** *Hygrohypnum molle*,

number of species that occur in plots (richness). By ignoring Axis 1, we removed only the linear effect of prevalence (the effect of the number of plots a species occurred in), but prevalence also likely affected Axes 2 and 3 in a non-linear way, perhaps placing the common species towards the center of the ordination. Maybe there is a better way to remove the effect of prevalence before one calculates distances by somehow standardizing one species to the next. Alternatively, Jackson et al. (1989) suggest that use of a different coefficient than Sørensen would be less affected by prevalence (e.g., Phi).

Chunking by wetness. At the risk of becoming tedious, realize that our large **A** matrix can be sliced into chunks each analyzed on its own. Here we report on three chunks, sliced by average wetness.

In the analysis of only wet-loving species, four coalitions were evident: (1) one similar to the Blue coalition above that includes many species that live in or next to flowing streams; (2) a low-elevation coalition that lives in stream beds that dry out during the summer (*Cryptomitrium tenerum*, *Scleropodium julaceum*, *Fissidens bryoides*); (3) a mid to high-elevation coalition headed by the wet-meadow species *Aulacomnium palustre*, along with *Gymnocolea inflata* and the stream species *Scapania undulata*; finally (4) a mostly high-elevation coalition of alpine swales consisting of *Lophozia ventricosa*, *Hydrogrimmia mollis*, *Pohlia drummondii*, *Andreaea nivalis*, and again the more elevationally wide-ranging stream species *Scapania undulata*. An R-mode ordination separate from the ones above and below was done and is shown in **Fig. S4.1** (in **Supplementary File S4**), with the coalitions color-coded.

For the sub-matrix with only species of medium wetness, RCLUS found coalitions vaguely reminiscent of the Green, Orange, Purple and Red coalitions of the common-species search, as well as a coalition of mostly low-elevation soil species: *Pleuridium subulatum*, *Riccia nigrella*, *Fossombronia longiseta*, *Timmiella anomala*, *Rosulabryum torques-*

cens, *Riccia sorocarpa* (this one also of higher elevations), and *Fissidens sublimbatus*. Other than finding the soil coalition, the analysis of medium-wetness species did little more than reassure the previous analysis of data that had not been sliced into three wetness chunks. No ordination is presented.

Finishing up, the sub-matrix of only dry-loving species yielded coalitions shown on yet another ordination as **Fig. S4.2** (in **Supplementary File S4**). Separation is evident between two dry-rock guilds: one of sunny plots at low elevations—*Grimmia laevigata*, *Syntrichia* "*obtusissima*", *Grimmia lisae*, *Grimmia pulvinata*, *Bryum argenteum*, *Orthotrichum bolanderi*, *Hedwigia detonsa*, *Gemmabryum vinosum*, *Gemmabryum brassicoides*; and a second of slightly shadier plots extending to mid elevations—*Syntrichia ruralis*, *Grimmia montana*, *Grimmia trichophylla*, *Orthotrichum rupestre*, *Orthotrichum pylaisii*.

Of course, it would be possible to chunk the big matrix in other ways, perhaps based on shadiness, and one would surely find that the two or three chunks of any niche dimension would vary in terms of which other niche dimension was evidently important in separating the species of a chunk. In our case, for the wet chunk whether the water was moving fast or slow was important, whereas for the dry chunk the density of the surrounding trees was important and the incline of the microsites of the various species. Such dissections of the data can be quite diverting.

Turnover. It would be analytically consistent to report on turnover only as part of **Supplementary File S3** because it is a Q-mode analysis, but turnover pulls together our interest in elevation, so our analysis of turnover is given as **Fig. 3**. If the bryophyte elevational ranges were to fall into four zones with three sharp ecotones between the zones, the resulting graph would have had four humps (to the right) and three dips (to the left). Instead, a hump for the foothills is separated by a dip (ecotone) as one transitions into the lower conifer

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hysm *Hygrohypnum smithii*, **immi** *Imbribryum miniatum*, **leri** *Leptodictyum riparium*, **love** *Lophozia ventricosa*, **meme** *Metaneckera menziesii*, **orfl** *Orthotrichum flowersii*, **pham** *Philonotis fontana* var. *americana*, **plde** *Plagiothecium denticulatum*, **plsu** *Pleuridium subulatum*, **plve** *Plagiomnium venustum*, **plvi** *Plagiobryoides vinosula*, **podr** *Pohlia drummondii*, **psel** *Pseudotaxiphyllum elegans*, **psin** *Pseudoleskea incurvata* var. *incurvata*, **pstr** *Pseudoleskea tribulosa*, **ptcr** *Ptychostomum creberrimum*, **ptfi** *Pterigynandrum filiforme*, **ptni** *Ptychostomum nitidulum*, **ptpc** *Ptychostomum pacificum*, **ptwe** *Ptychostomum weigelii*, **rhti** *Rhizomnium pseudopunctatum*, **rini** *Riccia nigrella*, **saex** *Sarmentypnum exannulatum*, **scce** *Scleropodium cespitans*, **scci** *Schistidium cinclidodonteum*, **scoc** *Scleropodium occidentale*, **scri** *Schistidium rivulare*, **stst** *Straminergon stramineum*, **symo** *Syntrichia montana*, **syno** *Syntrichia norvegica*, **toat** *Tortula atrovirens*, **togu** *Tortula guepinii*, **tomu** *Tortula muralis*, **toob** *Tortula obtusifolia*. In color in the online pdf.
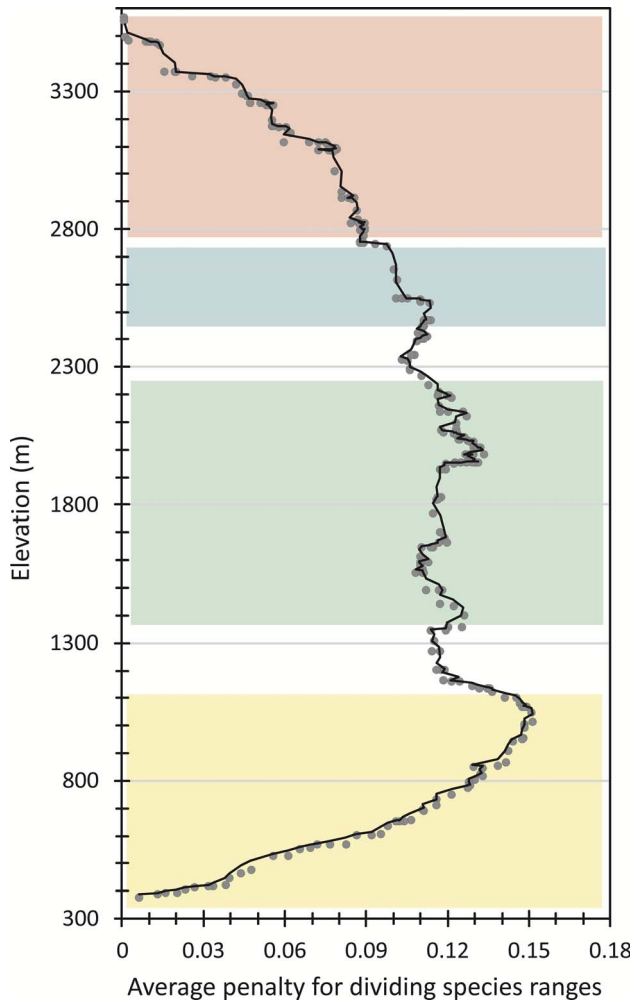
Figure 3. Graphical test of bryophyte elevational zones. If the bryophyte vegetation were in four zones with sharp ecotones, then this graph would display four humps with three dips at the ecotones. In color in the online pdf.

zone. However, the other anticipated zones and ecotones were indistinct. Said another way, numerous species had nearly their entire elevational range within the foothills with few or no occurrences above 1100 m elevation, whereas this was not true regarding the other vascular vegetation zones. Not very many species had elevational ranges restricted to the high country, rather the high-country species extended to varying degrees down the mountain into other zones. We doubt this lack of bryophyte zonation is due to uneven sampling as the number of plots at various elevations was quite even (Coleman 2014). In addition to the lack of a high-country hump, one could say that the ecotones, such as they exist, were not very narrow. Even the ecotone transitioning from the foothills into the lower

conifer zone was at least a couple of hundred meters in relief; it was not like a whole assemblage of conifer-zone bryophytes were reliably found as soon as one climbed up to plots that were amid conifers, although once one did, many foothill species no longer occurred. At any rate, from the lower conifer zone up, the bryophyte species, on the whole, behaved individualistically with regard to elevation (in the sense of Gleason 1926).

DISCUSSION

Our foremost contribution is that we have documented the habitat specialities and generalities, or "niches", of the bryophytes in a landscape. One could do that merely by looking at herbarium labels, but collectors tend to collect a specimen when they see a species in an unusual spot, so the summary averages would not be as accurate as from plot data. It also helps that all the micro-habitat scores were done by the same two people debating each one. Averages were computed, and this brings up an important caution: we are *not* saying that a species is never found outside its average niche; we are *not* saying no one ever finds a patch of *Fabronia pusilla* on top of a flat surface with its ciliate leaves toward the open sky, simply that it was found much more on the underside of an overhang.

Our interest in bryophyte niches was originally inspired by studies of the microsite (Vitt et al. 1975). Using crude scores, this is what our **Table 1** summarizes. This type of study can be improved on by use of equipment capable of fine measurements and allowing for quantification of niche breadth and overlap (Slack & Glime 1985; Vitt & Slack 1984). Nevertheless, the law of large numbers implies the averages of our crude scores should approximate fine distinctions as sample size increases. Our idea was to expand on the type of studies that inspired us by scoring microsites (Kenkel & Bradfield 1986) at many mesosites (Stehn et al. 2010) along as long an elevational gradient as we could feasibly visit in a continuous landscape (Mejia et al. 2020). If one studies a long enough ecological gradient, be it elevation or latitude or continentality, that gradient is going to be important. The 3000-m elevational gradient we studied certainly greatly structured the bryophyte community. As one walks from the foothills to the Great Western Divide, almost all of the community composition changes, and the few taxa such as

Polytrichum piliferum that span the whole 3000 m raise questions about cryptic species (Carter 2012) or ecotypes (Pisa et al. 2013).

In our data set, phylogenetic niche conservatism (Wiens et al. 2010) is amply suggested. All three species of *Fontinalis* were found only submerged in streams at mid elevations. The *Riccia* species were on mineral soil, usually nearly horizontal. Many species of Pottiaceae were of low elevations and very few of high elevation. Most Mniaceae were rare or absent from low elevation. Jungermanniales were much more common in the high country than lower down and then only in perennial streams; Marchantiales were the other way around. It should be added that conservatism is suggested relative to specified niche dimensions, while other niche dimensions may be labile. Wetness was a notable axis of diversification among the Pottiaceae. *Orthotrichum* (in the broad sense) displayed striking variety in terms of growing on trees versus on rocks. The two species of *Aulacomnium* have remarkably different niches, with *A. androgynum* often on soft rotten wood in deep shade, and *A. palustre* in wetlands in open sun. It is hoped that our niche characterizations will be combined with a phylogeny to yield results on conservatism and lability. Examples of such **community phylogenetics** include studies of niche dimensions (e.g., Willis et al. 2010) and even elevation (Ndiribe et al. 2013).

The correlations of niche tendencies for species found in both the Kaweah and the Santa Monica Mountains (Sagar & Wilson 2009) indicate considerable stasis in species niches. The correlations were high even though the scoring was done subjectively by different people in the two studies and the averages were calculated differently. It would be quite interesting to carry out studies parallel to ours in places even farther from California's southern Sierra Nevada. Perhaps similar long transects could be run in the Mediterranean climates of Chile and/or Spain where similarly oriented mountain ranges exist presenting similar elevations.

The word "guild" is a general one used by different researchers differently, even with contrasting meanings (Wilson 1999). Sometimes it means species that do similar things in different places; other times it means species that co-occur. This contrast mirrors the equivocation between Eltonian niches and Huchinsonian niches. Elton (1927) wrote: "There is the niche which is filled by birds of prey which eat small mammals such as shrews and mice. In an oak wood this niche is filled by tawny owls, while in the open grassland it is occupied by kestrels." We could say that in the foothills along riparian corridors vertical rock faces are the home of *Porella cordeana*, while in the conifer zone and away from any stream a corresponding niche is occupied by *Orthotrichum pylaisii*. They rarely if ever co-occur. The coalitions that we searched for using RCLUS are another type of guild in the sense that a coalition is recognized based on co-occurrence even if two species are associated because they are facilitating one another in different roles rather than both responding similarly to abiotic conditions. Naturally for bryophytes, using our type of data, we have very little way of even developing hypotheses about specific facilitative (or competitive) roles versus direct relationships with the abiotic habitat. We see co-occurrence as indicative of niche dimensions that are hard for people to see but that bryophytes differ along (Fridley et al. 2007). The closest thing we measured that would capture such a dimension is elevation, and elevation reflects Hutchinsonian differences.

A couple of comments are in order about our experience with RCLUS. First, species found in few plots tended not to be included in coalitions; the lower the prevalence, the harder it apparently was for species co-occurrences to be *disproportionately* high, although in principle it is still possible, for instance when two species are always and only jointly present. Second, RCLUS sometimes reports a coalition of one (or a few) species, but we did nothing with such coalitions. Ecologically, it is reasonable to recognize one species that has a pattern of occurrence unlike all others, a species that is a guild of one. In landscapes with large parts that have burned just recently (not ours when we sampled), *Funaria hygrometrica* might be a noteworthy coalition of one. RCLUS, though, is not programmed to be based on negative affinity, i.e., on not occurring with other species, so we don't know what to think of it reporting a coalition of one. These two mysteries aside, we hope that RCLUS will be used (and perhaps improved upon) by others, and more generally, that R-mode analyses will become more popular among field naturalists.

Before ordinating, we Beals smoothed our **A** matrix. Roughly speaking, Beals smoothing replaces an actual presence/absence datum with the proba-

bility a species should have occurred in a plot based on its co-occurrences with other species (McCune 1994). One would not have to smooth if one had *much* more thorough sampling involving larger plots or maybe elevational bands with subsampling inside bands, resulting in better quantification of abundances; however, such thorough sampling was for us infeasible. The cells of our **A** matrix are mostly filled with zeros (absences), and no small amount of additional effort was going to change what is a very common deficit of **A** matrices. In principle, one might consider smoothing based on the gradient(s) under study (e.g., smoothing a unimodal distribution along the elevation gradient) rather than smoothing based on the other species in the matrix, but this would not have been a complement to RCLUS. De Cáceres & Legendre (2008) warn against the use of Beals smoothing in particular when the data contain many rare species, when species distributions are unrelated to shared environmental gradients, and/or when one is using the smoothed data for inferential statistics. As partial justification, first, in the ordination that we featured the most, we focus on the common species that were also in the RCLUS analysis (**Fig. 1**). Second, we strongly suspect that the common species distributions are related to measured or unmeasured environmental gradients such as elevation and hydrology. Finally, we did not use the resulting ordination to carry out statistical tests. Thus, although Beals smoothing runs the risk of inventing a pattern out of nothing, it is, on the one hand, necessary for us in the sense that we had to do something to stabilize the ordination, and on the other hand, our use was in the type of situation when it is relatively unlikely to mislead. Nevertheless, a larger number of plots and thereby a large number of "common" species would have improved the appropriateness of Beals smoothing (De Cáceres & Legendre (2008) given that our very long gradient is associated with high turnover, and the higher the turnover, the larger the sample size should be to secure reliable Beals favorability estimates.

Even though elevation was principal in our results, we found only one prominent elevational ecotone, between the foothills and everything above them. Thus, recognizing bryophyte elevation zones would be uncomfortably forced. The coalitions of RCLUS were better than vegetation types because RCLUS allows species to be individualistic (Ott et al.

2015). The boundaries of the various species do not have to be coincident cartographically. Further, not all species are part of a coalition; and species are allowed to be part of more than one coalition. Reifying the coalitions that RCLUS found, elevation was always an aspect of the coalition's interpretation. This seemed a bit less true of coalitions of very wet-loving species, but even then some of the species in the coalition had similar elevational preferences. One curious negative finding was that we did not (easily) find a calcicole coalition (cf. Palmer & Wilson 2021). In the Kaweah, marble is a prominent albeit minority parent rock type, and we did indeed have plots on marble at various elevations. However, meta-sedimentary plots were not found to be different from plutonic plots in the Q-mode analysis and few if any common species were associated with the meta-sedimentary plots. Perhaps we did not sample enough of them, or perhaps the rock types in the Kaweah are too varied and complex for our simple dichotomy to be revealing.

For Sierran naturalists, coming to know the bryophytes is part and parcel in coming to contemplate their niches and guilds. One comes to recognize the species and genera based on their morphology while at the same time learning where they are most likely found and with what other bryophytes. Given that the landscape is so small and dispersal is so easy, one comes to believe that each species is excluded more or less along this or that habitat gradient. Conversely, the species have their niches, and while a species might be generalized for some niche dimensions, almost all are probably specialized for some niche dimension or other, apparent or not. Presumably specialization is because tradeoffs have affected the courses of evolution among the many lineages represented in the bryophyte community. Then, over the course of decades or centuries or millennia, but at any rate more recently than the deep history of adaptations and specializations, the species are sorted ecologically. Species that are specialized to live out much of the year sopping wet, are not only excluded from drier spots, but they also are assembled into the various wet places following such features as the speed with which the water flows, its algal load, and its seasonality. Species specialized to live in spots that dry out quickly, not only are excluded from wetter habitat, but they are sorted among themselves following the texture of the substrate, shadiness,

incline, etc. Some of the niche relations are apparent to the naturalist and no doubt other niche dimensions are invisible. In the landscape of the mountains, the available niches vary by elevation because elevation causes differences in the seasonality of every aspect of climate. This is perhaps slightly more so for drier niches than for wet ones, and yet still a stream in the foothills is not the same to the community of bryophytes as a stream in the alpine zone.

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Supplementary documents online:

Supplementary File S1. In Excel with sheets for: Raw data; Full **A** matrix presence/absence; Taxonomic notes; Species abbreviations.

Supplementary File S2. Detailed expansion of Table 1 with numbers instead of the category "generalist". In Excel with a metadata sheet.

Supplementary File S3. Q-mode analysis.

Supplementary File S4. Separate analyses corresponding to species with wet and with dry niches.