Elevational Distributions of Forest Floor Mosses and a Test of Competition at Two Elevations in Western Oregon

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Abstract

Factors controlling mosses on the forest floor in western North America are poorly understood. We examined elevational distributions for six of the most abundant large forest floor mosses; based on those distributions, a transplant experiment of two species evaluated if interspecific interactions can be mediated by climatic context. Mosses had species-specific elevational profiles, with *Rhytidiopsis robusta* more prominent at higher elevations, while *Hylocomium splendens*, *Kindbergia oregana*, *Rhytidiadelphus loreus*, and *Rhytidiadelphus triquetrus* were more prominent at lower elevations. *Homalothecium megaptilum* was bimodal, peaking at middle and low elevations. We selected *Rhytidiadelphus triquetrus* and *Rhytidiopsis robusta* for a transplant experiment because each is prominent at different elevations and they are similar in stature. Moss mat squares cut from the forest floor at middle elevations were transplanted in a single- or mixed-species pattern at two sites, one high elevation and one low elevation. We recorded changes in percent cover within the squares over one year as well as outgrowth onto bare soil and litter. Hypothesized relative species performances based on elevational distributions were mostly not supported. The low-elevation associated species (*Rhytidiadelphus triquetrus*) outperformed the high-elevation species (*Rhytidiopsis robusta*) at the high-elevation site, both in a mixture and as a monoculture. At the lower site, *Rhytidiadelphus triquetrus* grew well in a mixture, but the monoculture declined. Furthermore, *Rhytidiopsis robusta* grew faster at low elevation than at high, both in a mixture and monoculture, despite being more abundant at high elevations. Poor performance of both species at high elevations raises interesting questions about what factors limit moss mats in general at higher elevations in the Cascade Range.

Key Points

- *Rhytidiopsis robusta* frequents higher elevations; *Hylocomium splendens, Kindbergia oregana*, *Rhytidiadelphus loreus*, and *R. triquetrus* frequent lower elevations.
- Elevational distributions of dominant forest floor moss species do not predict responses to transplantation to sites at different elevations.
- The generally poor performance of transplants to higher elevations and lower abundance of forest floor mosses at higher elevations raise the question of what factors limit these moss mats at higher elevations in the Cascade Range.

Keywords: *Homalothecium megaptilum*, *Hylocomium splendens, Kindbergia oregana, Rhytidiadelphus triquetrus, Rhytidiopsis robusta*

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Introduction

In the Pacific Northwest of North America, bryophytes are prominent and a functionally important part of the vegetation (Smith et al. 2015, 2017), yet we know little of the factors that structure the distribution and abundance of mosses on the forest floor. Observational studies (e.g., Peck et al. 1995; Jonsson 1996; Rambo and Muir 1998a,b; Root and McCune 2010; Evans et al. 2012) have revealed species–environment covariation and disturbance effects on the bryoid layer (bryophytes and lichens on the forest floor; Lesica et al. 1991, Nelson and Halpern 2005, Dovĉiak et al. 2006, Baldwin and Bradfield 2007, Waxwing et al. 2021), but the environmental and interspecific drivers of variation in even the major forest floor species remain poorly understood. We found no studies on broad-scale distribution and abundance of forest floor mosses in western Oregon and Washington. Lacking this, and because we wished to contrast species interactions at different elevations, we generated elevational profiles for six of the most common forest floor mosses of the region. These elevational distributions provide both guidance for selection of species for experimental work as well as a reference for evaluating future distributional shifts with climate change.

Transplant experiments have had a central role in developing our understanding of plant ecology, helping to separate environmental from genetic effects on phenotypes, such as the classic experiments by Clausen, Keck, and Hiesey (Clausen et al. 1948, Núñez-Farfán and Schlichting 2001). This approach has also been applied to bryophytes, using transplant experiments to examine phenotypic plasticity (e.g., Hassel et al. 2005), reproductive biology (Bisang et al. 2004), air pollution effects (Bates 1993), ecotypic variation (Merinero et al. 2020), and the differences between geographic distribution and climatic tolerances (Dahlberg et al. 2014, Merinero et al. 2020, Greiser et al. 2021). Bryophyte transplants have also been used to investigate species interactions, including facilitative effects on higher plants (Groeneveld et al. 2007), competition among mosses (Rydin 1993), and interactions of environment and bryophyte host identity on N-fixing associates (Stuart 2021).

Although these studies have shown the potential value of bryophyte transplant experiments, they remain underutilized for answering questions about how bryophyte communities may respond to a changing climate. Specifically, transplant experiments may be useful for understanding the question of how species interactions may mediate species responses to a changing climate (Alexander et al. 2016).

Here, we transplanted mosses as part of a broader, multi-taxon study designed to test the degree to which species interactions vary as a function of environmental context, specifically microclimate and forest structure (e.g., stand density, tree size distribution, overstory species composition). We transplanted mixtures of two dominant forest floor mosses in contrasting environments. The transplanted species, *Rhytidiadelphus triquetrus* (Hedw.) Warnst. and *Rhytidiopsis robusta* (Hook.) Broth., are similar in stature and general growth form (Figure 1) but are prominent at low and high elevations, respectively, on the west slope of the Cascade Range. *Rhytidiadelphus triquetrus* is a shaggy, coarse forest floor species with broad ecological tolerances, often achieving high dominance in the moss layer, and has a wide distribution throughout temperate to arctic regions of the Northern Hemisphere (McCune and Hutten 2018). *Rhytidiopsis robusta* is another large forest floor moss, abundant in many montane to subalpine forests, but it appears to have narrower environmental tolerances and is endemic to oceanic and suboceanic climates of the Pacific Northwest of North America. It occurs from coastal Alaska south to northern California, and inland to western Montana and Alberta. We have no prior evidence on the relative growth rates of these species, apart from the limited inference afforded by their similarity of size in a range of habitats.

We hypothesized that in an environment where the two species have similar biomass growth rates, *Rhytidiadelphus triquetrus* would be the superior competitor, since its open, loose growth form might rapidly build tall mats, while *Rhytidiopsis robusta* is somewhat more compact and might be overtopped by *Rhytidiadelphus triquetrus*. In contrast, at high elevations, *Rhytidiopsis robusta*

should be the better competitor, simply because it appears to tolerate colder, wetter habitats than *Rhytidiadelphus*. These hypotheses led to three specific predictions:

1. In monoculture, a species should increase in cover more at the site closer to its distributional maximum; i.e., the low-elevation species *(Rhytidiadelphus triquetrus)* should perform better at the low-elevation site and the high-elevation species *(Rhytidiopsis robusta)* should perform better at the high-elevation site.
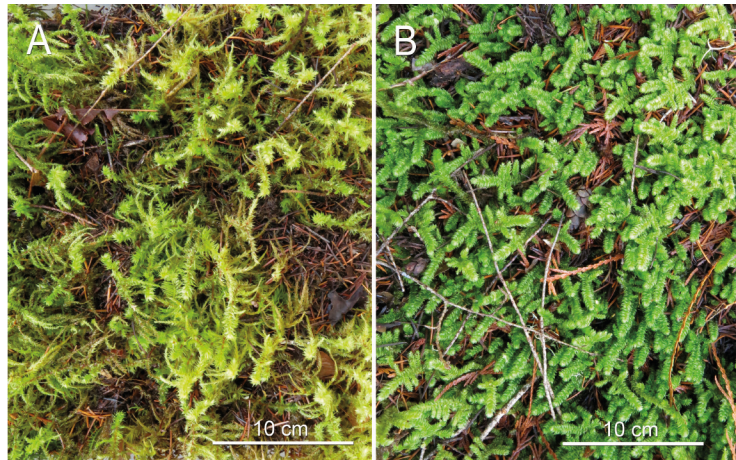

Figure 1. Two dominant forest floor mosses in the western Cascades used in our transplant experiment. A. *Rhytidiadelphus triquetrus*. B. *Rhytidiopsis robusta*.

2. In a mixture with *Rhytidiadelphus triquetrus* at the low elevation site, *Rhytidiopsis robusta* will perform worse than in a monoculture, due to the greater hypothesized competitive ability of *Rhytidiadelphus triquetrus*.

3. In a mixture with *Rhytidiopsis robusta* at the high elevation site, *Rhytidiadelphus triquetrus* will perform equally poorly as in a monoculture, due to a lower tolerance to high elevation conditions and only a small competitive effect by *Rhytidiopsis robusta*.

Methods

Elevational Distributions

As context for selecting two species for a transplant experiment, we generated the elevational distributions of six dominant forest floor moss species in western Oregon (west of -121.5°W) based on 573 georeferenced herbarium records in the Consortium of Bryophyte Herbaria (2023), excluding duplicates. The six species were: *Homalothecium megaptilum* (Sull.) H. Rob., $n = 112$; *Hylocomium splendens* (Hedw.) Schimp., $n = 41$; *Kindbergia oregana* (Sull.) Ochyra, $n = 258$; *Rhytidiadelphus loreus* (Hedw.) Warnst., $n = 58$; *R. triquetrus*, $n = 63$; and *Rhytidiopsis robusta*, $n = 41$. Probability density functions estimate relative likelihood of occurrence at a given elevation; each function

has an area under the curve equal to 1.0. Curves were fitted by two methods (both in McCune and Mefford 2018). Kernel 1 uses a cross-validated smoothing parameter (Bowman and Azzalini 1997, p. 37), simplified to the case of a constant smoothing parameter. Kernel 1 minimizes the integrated mean squared error between the density estimates and the true underlying density function. Kernel 2 is optimized under the assumption that the underlying distribution is normal. Bowman and Azzalini (1997) considered kernel 2 to be a useful, simple method for choosing a smoothing parameter with unimodal distributions.

Transplants

We performed a transplant experiment in the H. J. Andrews Experimental Forest in the McKenzie River watershed east of Eugene, Oregon. Average annual temperature varies topographically but is approximately 10 °C, with January and July means of 2 °C and 22 °C, respectively. Average annual precipitation is about 2,400 mm, with 70% of that from November through March. Elevations range from 410 to 1,630 m.

We selected the target species *Rhytidiadelphus triquetrus* and *Rhytidiopsis robusta* because each one is a dominant forest floor moss, similar in stature, but prominent at different elevations,

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based on the elevational distributions as determined above. The sources for transplant material were single-species patches on gently sloping benches well above Lookout Creek at middle elevations between the two transplant destinations. *Rhytidiopsis robusta* was gathered at 986 m (44.23112°N, 122.12640°W) in a multi-aged *Thuja plicata–Tsuga heterophylla* forest with some large old *Pseudotsuga menziesii* (nomenclature of vascular plants follows Hitchcock and Cronquist [2018]). Where forest floor mosses were abundant, the undergrowth was rather open with *Berberis nervosa, Chimaphila umbellata, Goodyera oblongifolia, Linnaea borealis, Trientalis latifolia,* and *Xerophyllum tenax. Rhytidiopsis robusta* was common at this site, growing intermixed with *Kindbergia oregana, Homalothecium megaptilum*, and other species, but also in pure patches, which we sampled. *Rhytidiadelphus triquetrus* was gathered at 662 m (44.23109°N, 122.17822°W) in a young *Pseudotsuga–Tsuga* forest with an undergrowth of *Polystichum munitum* and young *Acer macrophyllum*; we detected no *Rhytidiopsis robusta* at this site. The moss layer was dominated by *Rhytidiadelphus triquetrus* and *Kindbergia oregana.*

Transplant destinations were two old forests with complex canopy structures, one higher elevation at 1,273 m (44.2738°N, 122.1395°W) and one lower elevation at 514 m (44.2213°N, 122.2405°W). Both forests had multilayered canopies with a wide range of tree sizes, small canopy gaps, and low to moderate shrub and herb densities. Each site received four arrays (replicates) of each of the four treatments (see below). Note that we only had one site at each elevation, which precludes inference to elevational effects in general. Based on data from nearby H. J. Andrews Reference Stands (04 and 17) for the period of shared record (1972–1995), the higher elevation forest averaged 5.9 °C (1.3 °C SD) and the lower elevation forest averaged 8.9 °C (1.0 °C SD; data from Daly and McKee 2019). Snow cover lasts for 5–8 months at the higher site and 0–3 months at the lower site. The higher elevation forest was dominated by *Abies procera*, *A. amabilis*, *Pseudotsuga menziesii,* and *Tsuga heterophylla*, while the lower elevation forest
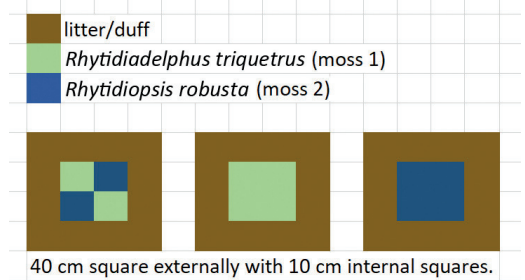

Figure 2. Pattern of moss mat transplants: interspecific (checkerboard pattern), and intraspecific for each species (solid pattern).

was dominated by *P. menziesii* and *T. heterophylla*. In both locations, the larger overstory trees were well over 300 years old.

Moss mats were transplanted as 20 × 20 cm squares of single species (*Rhytidiopsis robusta* or *Rhytidiadelphus triquetrus*) or in 10 × 10 cm squares placed in a checkerboard pattern to force competition (Figure 2). For both treatments, mats were cut from the forest floor on 3 December 2021 at the source locations described above. We cut mats with a serrated bread knife and pruning clippers, lifted mats by hand (methods in Smith et al. 2015, 2017), and then divided mats into squares. Mineral soil was not included in the mats.

Moss mats were stored under shelter at ambient temperatures for 36 hours and then were transplanted to destination sites on 5 December 2021. Transplanted mats were placed into 20 × 20 cm holes cut into the litter and duff of recipient sites such that each square had a 10 cm buffer strip of litter and duff on all sides and transplant mats were nestled into the forest floor. We used four arrays (replicates) of the three treatments in each destination site. Each array was arbitrarily placed at least 5-10 m from its nearest neighbor, avoiding areas of dense shrubs and complete voids in the herb layer. Each transplant mat and the surrounding buffer was photographed with a Canon G10 camera mounted on a tripod, with timed shutter release and aperture priority mode set to maximize depth of field. Photography was timed to avoid sun flecks. We used red/white chaining pins and a measuring tape to temporarily mark corners of the 20 cm squares, while leaving two

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pins in the outer-lower corners for relocating the transplant corners the following year. Large nails were added later to facilitate exact relocation of corners.

Transplants were rephotographed on 13–14 October 2022 using the original equipment and method (Figure 3). For both original and follow-up photos, we visually estimated percent cover of green, living mosses in Photoshop. Dead shoots were not included in our cover estimates. For each photo, we superimposed a 10×10 cm grid, aligned the grid cells with the edges of the transplanted mat, then visually scored percent cover by species both inside the grid and any extension or growth (cm^2) into the surrounding

Figure 3. Example of a transplanted mat after one year: a *Rhytidiopsis robusta* mat transplanted to the low elevation site. Two corners are marked with chaining pins. A 10×10 cm grid was superimposed in Photoshop. The superimposed green squares are reference patches of known area ($1 \ cm^2$ and $4 \ cm^2$) used to help estimate areas.

10 cm buffer. Percent cover within the squares was converted to cm^2 then summed with cover in the buffer. We also recorded *Kindbergia oregana* cover, which was initially present as a very minor component of the transplanted mats but thrived and expanded in some of the mats. Cover of litter was estimated by subtraction of moss cover from the total area. Total growth (or loss) was expressed in cm^2 as the difference in absolute cover between the two dates.

We analyzed the data with two-way factorial ANOVAs using JMP Pro 16 (JMP Statistical Discovery LLC, Cary, NC), performing one ANOVA for each of the two target species and one for the interloper *Kindbergia oregana*. The dependent variable was growth as defined above. One independent factor was "site", with one high-elevation site and one low-elevation site. The second factor was "treatment", contrasting whether a species was grown as a monoculture (intraspecific) versus in a checkerboard mixture with the other species (interspecific). We considered including treatment

arrays as blocks, but the sample size was so small ($n = 4$ arrays within each cell of the design) that this was impossible. Note that the interspecific competition term is a main effect, not an interaction term: "treatment" contrasts an interspecific competitor versus single species transplants. We visually checked distributions for normality and homogeneity of variance and set alpha for Type 1 error = 0.05 for reporting a difference.

Results and Discussion

Elevational Distributions

Elevational distributions showed that *Rhytidiopsis robusta* was more prominent at higher elevations, in contrast to *Hylocomium splendens*, *Kindbergia oregana*, *Rhytidiadelphus loreus*, and *Rhytidiadelphus triquetrus* as lower elevation species (Figure 4). *Homalothecium megaptilum* was bimodal, with a smaller peak of abundance at < 100 m and a stronger peak at about 800 m. On the west slope of the Cascade Range, *Rhytidiadelphus triquetrus*
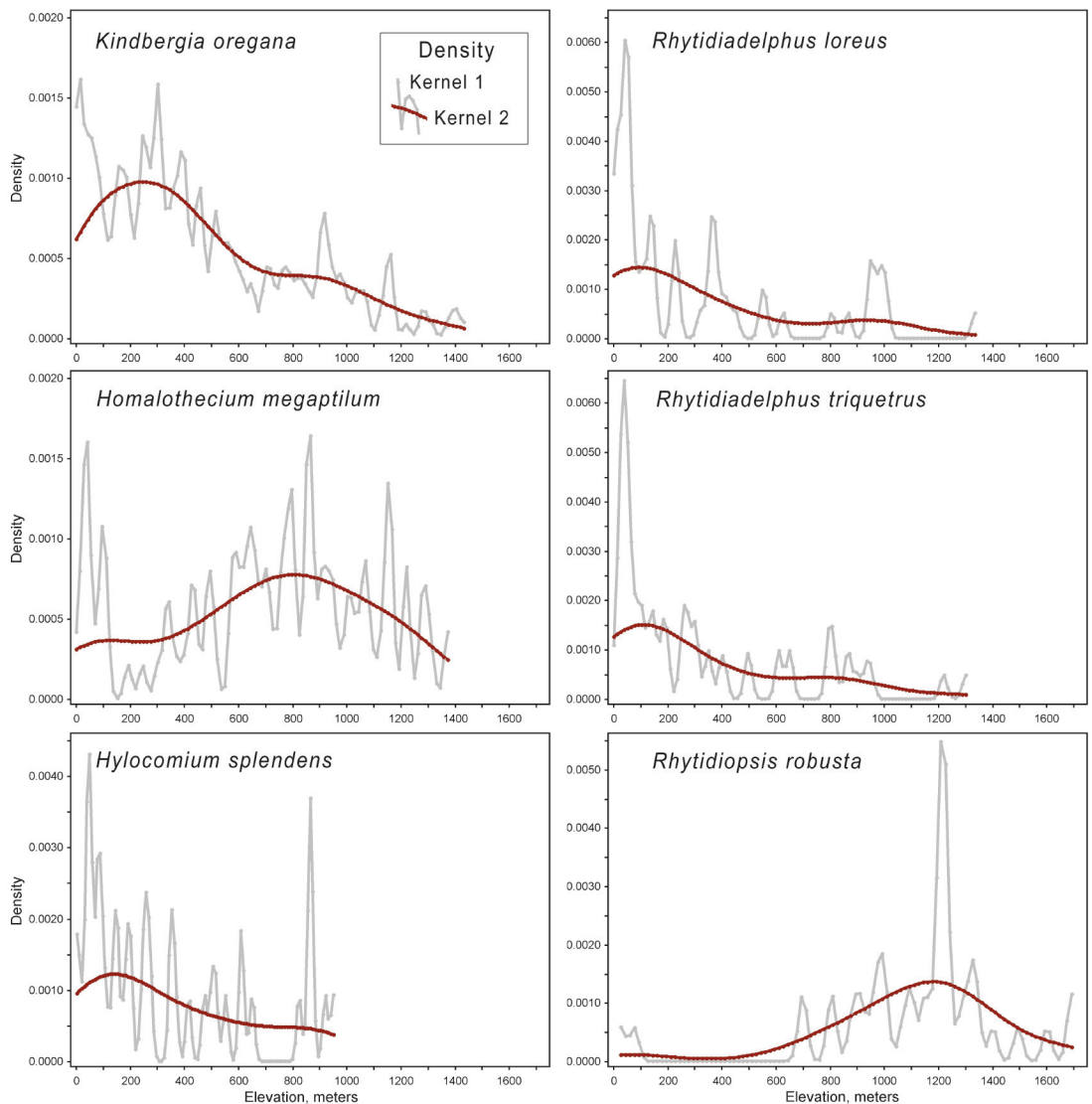
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Figure 4. Elevational distributions of six dominant forest floor moss species in western Oregon (west of -121.5°W) based on 573 georeferenced herbarium records in the Consortium of Bryophyte Herbaria, April 2023, excluding duplicates. Probability density functions estimate relative likelihood of occurrence at a given elevation. Kernels 1 and 2 represent two smoothing parameters with different optimization principles (see Methods).

was the most prominent large forest floor moss at low elevations but diminished in frequency above about 1,000 m. Within its range, *Rhytidiopsis robusta* was most frequent above 800 m but was occasionally found at lower elevations. Based on their similarities in growth form and differential abundances by elevation (Figure 4), we selected

Rhytidiopsis robusta and *Rhytidiadelphus triquetrus* for our transplant experiment.

Transplants

Most of the transplant blocks were healthy and quite well integrated with the surrounding forest floor after ten months, suggesting successful
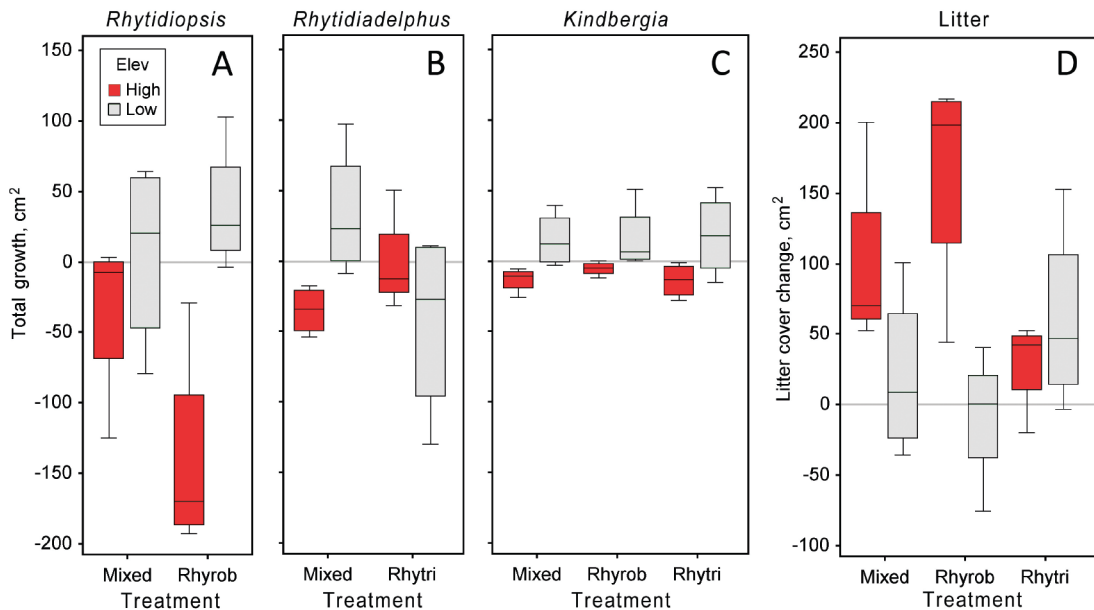
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Figure 5. Absolute growth in cm² (early December 2021 to mid-October 2022), summing increases or decreases within transplanted squares and outgrowth from the transplants into the surrounding 10 cm buffer (bare litter). Boxplots contrast growth (or loss) of the mosses. A. *Rhytidiopsis robusta,* B. *Rhytidiadelphus triquetrus*, C. *Kindbergia oregana*, and D. litter, each in relation to elevation of the transplant destination and treatment. "Mixed" treatments were adjacent squares in a 2 × 2 checkerboard pattern of *Rhytidiopsis robusta* and *Rhytidiadelphus triquetrus*, and "Rhyrob" and "Rhytri" treatments were a single 20 × 20 cm square monoculture of those same two species, respectively. *Kindbergia oregana* was present as a minor admixture in the surrounding forest and in the transplants. Litter results show the change in cover of bare litter. Boxplots show medians (central black line), 25th and 75th percentiles (boxes), and 5th and 95th percentiles (whiskers). Corresponding statistical results are in Table 1.

Table 1. Growth responses of moss transplants due to site (contrasting two elevations) and treatment (species). These analyses of variance (ANOVAs) test whether the total growth of the target species (*Rhytidiadelphus triquetrus* and *Rhytidiopsis robusta*) and *Kindbergia oregana* is affected by the transplant elevation destination (site) and treatment (interspecific competition vs. single species). Thus, the treatment term measures the effect of the interspecific interaction. We report degrees of freedom (d.f.), sum of squares (SS), F ratio (F), and P(type I) error rates (P). To avoid the implication of growth of a species where we did not put it, for a given species' test, only transplant squares that included a target species are compared, except for *Kindbergia oregana*, which was included as a small admixture in many mats of both target species. In other words, each species' test compares two treatments instead of three. Asterisks indicate $P < 0.05$.

ANOVA	d.f.	SS	F	P
Rhytidiopsis robusta				
Treatment	1	5588	1.4	0.260
Site	1	47852	12.0	0.005*
Site × Treatment	1	18975	4.7	0.050*
Rhytidiadelphus triquetrus				
Treatment	1	1870	0.9	0.358
Site	1	743	0.4	0.558
Site × Treatment	1	12155	5.9	0.031*
Kindbergia oregana				
Treatment	2	80	0.1	0.890
Site	1	4455	13.0	0.002*
Site × Treatment	2	113	0.2	0.849

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transplantation of each species. Individual squares had minor soil disturbance, potentially caused by rodents, but each square provided useful data on the performance of each species. Some squares were relatively unchanged, whereas others showed considerable lateral expansion, and some (mainly at the higher elevation site) showed declines in cover. The initial checkerboard pattern had been altered in most cases by partial gains and losses, sometimes with one species encroaching on another. Even though the sample sizes were small, statistically significant differences emerged (Figure 5, Table 1), yielding some interesting and unexpected results. We address each hypothesis below.

Although we predicted that at the low elevation site *Rhytidiopsis robusta* would have worse performance in a mixture with *Rhytidiadelphus triquetrus* than as a monoculture transplant, *Rhytidiopsis robusta* showed similar, modest but positive growth in both monocultures and mixtures. At the low elevation site, we predicted that *Rhytidiadelphus triquetrus* should grow well, both in a mixture with *Rhytidiopsis robusta* and as a monoculture, but while *Rhytidiadelphus triquetrus* grew well in a mixture at the low elevation site, it declined in cover when growing in monocultures (Figure 5).

We predicted that at the high elevation site, *Rhytidiadelphus triquetrus* should decline both in a mixture and in a monoculture, based on its low abundance at higher elevations in the western Cascades (Figure 4). In actuality, *Rhytidiadelphus triquetrus* declined in a mixture at the high elevation site but changed little as a monoculture at this site. This finding suggests the importance of interspecific competition in determining nonvascular plant performance. However, the pattern of greater interspecific competitive effects in more stressful environments runs counter to the long-held hypothesis that competition should be greatest in warmer, wetter, and more aseasonal environments and relatively weak in seasonal, climatically stressful environments (Schemske et al. 2009, Freeman et al. 2022, LaManna et al. 2022).

Because of its frequency at high elevations (Figure 4), we predicted that *Rhytidiopsis robusta* should grow more in monoculture at the high elevation site than *Rhytidiadelphus triquetrus*. While we found *Rhytidiadelphus triquetrus* monocultures to be static at high elevations, *Rhytidiopsis robusta* monocultures declined sharply in cover, suggesting that despite being a high elevation site, the microhabitat was not favorable for *Rhytidiopsis robusta.* Further, in contrast to our prediction that in a monoculture, the low-elevation species *Rhytidiadelphus triquetrus* should grow faster at the low elevation site than at the high elevation site, it actually grew slightly better at the high elevation site (Figure 5). Conversely, we predicted that the high-elevation species *Rhytidiopsis robusta* should grow equally well or faster in a monoculture at the high elevation site than at the low elevation site. However, the opposite was true, with all monoculture squares showing positive growth at the low elevation site and loss of cover at the high elevation site. Thus, both species, when growing in a monoculture, performed worse at their "home" elevation and worse than when they grew in competition with the other species. Although this study does not have the ability to identify the mechanisms, this result suggests the possibility of strong negative intraspecific density-dependence that could result from competition or host-specific pathogens. Negative intraspecific density-dependence tends to promote species coexistence within communities (Janzen 1970, Connell 1971), and future studies might further test how prevalent this phenomenon is in bryophyte communities.

Kindbergia oregana, present in very small amounts in many of the transplanted mats, consistently increased in cover at the low elevation site but consistently decreased at the high elevation site. This species naturally occupies both sites but is more common at lower elevations. We hypothesize that the horizontal growth form of *Kindbergia* allowed it to quickly invade unoccupied space, taking advantage of the minor disturbance to the mats and surrounding forest floor. The poor performance of *Kindbergia* at the high elevation site was consistent with the general attrition of the mats at the high site, in contrast

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with generally positive growth of all species at the low elevation site.

The area covered by bare litter also increased for all treatments at the high elevation site but changed little at the low elevation site, except for *Rhytidiadelphus triquetrus* in monoculture, where it increased by about 50% (Figure 5). Bare litter in the plots can increase due to mortality of the moss transplants as well as fresh deposition of litter on top of slow-growing mosses. The balance of litter net accumulation rates and moss growth rates appears critical to survival of forest floor mosses (Jean et al. 2020). One might hypothesize that the expansion of litter at the high elevation site resulted from higher deposition rates or lower decomposition rates, relative to moss growth rates. Further studies could test this hypothesis by measuring litter inputs, decomposition, and moss growth rates.

Poor Performance of Moss Mats at Higher Elevations

Moss mat transplants of *Rhytidiopsis robusta* lost cover at the high elevation site while *Rhytidiadelphus triquetrus* showed no net change at that site (Figure 5). Although an unexpected result, given the higher relative abundance of *Rhytidiopsis robusta* versus *Rhytidiadelphus triquetrus* at higher elevations (Figure 4), the lackluster performance of both species was not surprising, considering the generally lower moss cover at higher elevations in the H. J. Andrews Experimental Forest (J. Worthley, A. Neat, and J. LaManna, unpublished data). These results raise the question: what factors limit moss mats in general at higher elevations in the Cascade Range? Although we can speculate several possible reasons for this trend, none are compelling enough to present here. We know of no literature demonstrating a consistent pattern of dependence of moss cover on elevation in temperate climates, nor would we expect one because of the complexity of the problem; however, in our case there appears to be a strong regional pattern for which the limiting factors are unknown. Moss mat transplants and microenvironmental manipulations can be used to directly answer

questions of limiting factors over regional gradients. For example, based on moss transplants and environmental measurements at many sites in Sweden, Greiser et al. (2021) found that competition, shading by leaf litter, and water scarcity might be more important than the direct effects of temperature for performance at the species' warm range margin.

Future Work

Because our findings are based on a small sample size, no site (elevation) replication, and only one year of data, we urge caution in interpreting and applying our results. For instance, some of the counterintuitive results that we report (e.g., *Rhytidiopsis robusta* declines in its native elevational range) could be due to a particularly wet and cold La Niña winter in 2022 (Wills et al. 2022) or due to a site-specific effect that we were unable to test without replication at numerous high elevation sites. Nonetheless, this study offers a promising proof-of-concept that a mixture of observational distribution models and experimental transplants is a viable option for learning more about bryophyte species' distributions. A multi-year experiment with multiple recipient sites at each elevation would more convincingly address long-term outcomes of competitive interactions. Moss mats on the forest floor are often complex mixtures, and to better understand the environmental controls of competitive outcomes, we recommend including multiple species. For our area in the western Cascade Range, prime candidates are *Homalothecium megaptilum, Hylocomium splendens, Kindbergia oregana,* and *Rhytidiadelphus loreus*.

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

Contributions of individual authors: conceptualization (all), funding (MB, JL, BM), fieldwork (BM, JD, MB), lab work (BM), methodology, data curation and analysis (BM), visualization (BM), writing and editing (all).

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