

RESEARCH ARTICLE

Rare species do not disproportionately contribute to phylogenetic diversity in a subalpine plant community

Leah N. Veldhuisen^{1,2}  | Verónica Zepeda³  | Brian J. Enquist^{1,2}  |
Katrina M. Dlugosch¹ 

¹Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

²Rocky Mountain Biological Laboratory, 8000 County Rd. 317, Box 519, Crested Butte, CO 81224, USA

³Laboratorio Nacional de Ciencias de la Sostenibilidad, Instituto de Ecología, Universidad Nacional Autónoma de México, México City 04510, México

Correspondence

Leah N. Veldhuisen, PO Box 210088, Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ 85721 USA.
Email: leah.veldhuisen@gmail.com

Abstract

Premise: Within plant communities, few species are abundant, and most are locally rare. Worldwide, 36% of plant species are exceedingly rare and often face high extinction risk. However, the community phylogenetic impact of the loss of rare plants is largely unknown in many systems. We address this gap by investigating how rare species contribute to phylogenetic diversity, considering multiple metrics of rarity and multiple elevations in a subalpine plant community.

Methods: We collected abundance data at three sites near the Rocky Mountain Biological Laboratory (Colorado, USA). We calculated each species' range size from public occurrence data. We calculated phylogenetic signal for abundance and range size, compared community phylogenetic metrics weighted by range size and abundance to unweighted metrics, and quantified the change in phylogenetic diversity when removing single species and groups of species ranked by rarity.

Results: We found phylogenetic signal for abundance, but not range size. There was no difference between rarity-weighted and -unweighted phylogenetic diversity metrics. Finally, phylogenetic diversity did not decline more when we removed single rare species or groups of rare species than when we removed single common species and groups of common species.

Conclusions: We found that rare species, whether at low abundance or with a small range, do not disproportionately contribute to phylogenetic diversity in our subalpine plant community. These results were consistent across elevations. Instead, rare species might provide phylogenetic redundancy with common species. Deeper understanding of functional differentiation is needed to understand contributions of rare species to this system.

KEYWORDS

local abundance, phylogenetic diversity, range size, rare species, Rocky Mountain Biological Laboratory

Worldwide, 36% of all plant species are exceedingly rare (observed five or fewer times globally; Enquist et al., 2019) and are often at high risk of extinction (Yessoufou and Davies, 2016; Enquist et al., 2019). Even if not globally rare, the majority of plant species in a community are locally rare and most likely to go locally extinct if conditions change (Matthies et al., 2004; Zavaleta and Hulvey, 2004; Zettlemoyer et al., 2019). While rare species have been observed to perform critical ecosystem functions, such as

supporting pollinators, enhancing fire resilience, and contributing to food web diversity (Bracken and Low, 2012; Mouillot et al., 2013; Leitão et al., 2016), their contributions to evolutionary diversity and associated ecosystem functions are unknown in most systems (Violle et al., 2017; Dee et al., 2019). In particular, their role in maintaining phylogenetic diversity remains poorly understood, with few studies addressing this question (Anderson et al., 2004; Mi et al., 2012; Herzog and Latvis, 2022). Here we contribute to

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2025 The Author(s). *American Journal of Botany* published by Wiley Periodicals LLC on behalf of Botanical Society of America.

this gap by examining how major axes of rarity contribute to phylogenetic diversity in a subalpine plant community, for which little is known about phylogenetic diversity (Bryant et al., 2008; Veldhuisen et al., 2023).

Understanding community phylogenetic diversity is essential because it is strongly linked to ecosystem processes. It correlates more positively with biomass than does species richness or functional diversity (Cadotte et al., 2008) and promotes ecosystem stability, productivity, and resistance to invasion (Cadotte et al., 2012; Cadotte, 2013; Davies et al., 2016; Galland et al., 2019; Delavaux et al., 2023). In plant communities specifically, species richness increases arthropod diversity more when diversity is also high (Dinnage et al., 2012), and phylogenetic diversity predicts soil microbial diversity better than plant species richness (Milcu et al., 2013). Despite the increasing recognition of the importance of phylogenetic diversity, it is unclear how rare species contribute to phylogenetic diversity in most systems, which is especially critical to understand in the face of ongoing species losses (White et al., 2023).

The niche differentiation hypothesis suggests that rare species use distinct resources and that they are distinct from each other and from more abundant species (Hanski, 1982; Gaston, 1994; Grime, 1998). Previous studies do support the functional distinction of rare species (Mouillot et al., 2013; Leitão et al., 2016; Jiao et al., 2017; Ge et al., 2019; Coulon et al., 2023). For example, Ge et al. (2019) found that rare desert annual plants do not exhibit the same well-established functional trade-off between water-use efficiency and relative growth rate as dominant species, suggesting niche differentiation in physiological traits. However, linking rarity to traits and niche space has proven to be complex (Crisfield et al., 2024). Phylogenetic divergence can potentially capture multivariate niche differences more holistically than single-trait approaches (Cadotte et al., 2009; Huang et al., 2020; E-Vojtkó et al., 2023). If rare species have unique combinations of genetic variants that allow them to persist (Mouillot et al., 2013), they will be more evolutionarily divergent than other species, leading to higher phylogenetic diversity in the community (Mi et al., 2012).

Alternatively, rare species might not contribute uniquely to community phylogenetic diversity, for several reasons. First, if ecologically important traits in a particular habitat are not phylogenetically conserved, niche differentiation will be decoupled from phylogenetic relationships (Cavender-Bares et al., 2009; Swenson and Enquist, 2009), and rare species with unique niches could have any relationship to the rest of the community. Second, ecologically important traits could be conserved phylogenetically but also constrained ecologically, such that species with traits adapted to a particular habitat are closely related (known as “environmental filtering”; Cavender-Bares et al., 2009; Mayfield and Levine, 2010; Kraft et al., 2015). Filtering could lead to phylogenetic “redundancy” among species (Webb et al., 2002; Cavender-Bares et al., 2009). Rare species might also be closely related to others in their community because they speciated locally, which may be a particular issue in

areas with a history of rapid diversification (Klak et al., 2004; Hughes and Eastwood, 2006; Hughes and Atchison, 2015; Xing and Ree, 2017). Despite these possibilities, the observation of unique contributions of phylogenetic diversity to ecosystem functions suggests that pervasive phylogenetic redundancy and relatedness may not be the norm (Cavender-Bares et al., 2009; Cadotte et al., 2008, 2012; Cadotte, 2013; Davies et al., 2016).

Given these alternative possibilities, it is critical to assess the contributions of rare species to phylogenetic diversity independently of measures of functional diversity (Gerhold et al., 2015; Cadotte et al., 2019; Hahn et al., 2024). To date, we know of only two studies investigating the contributions of rare plants to phylogenetic diversity. Mi et al. (2012) found that rare tree species in temperate, subtropical, and tropical forests were phylogenetically more diverse than abundant species when in less-disturbed plots. In contrast, a recent study of North American tall-grass prairies (Herzog and Latvis, 2022) found that rare species were randomly distributed across the phylogeny, providing phylogenetic redundancy with more abundant species. Herzog and Latvis (2022) noted that their tall-grass prairies are dominated by species from only a small subset of families and are significantly less diverse than expected by chance. It is unsurprising that tall-grass prairies would be less diverse than the tropical forests studied by Mi et al. (2012) (Tietje et al., 2023). Our subalpine communities are somewhat more phylogenetically diverse than tall-grass prairies (Bryant et al., 2008; Herzog and Latvis, 2022; Veldhuisen et al., 2023), and so we may expect higher contributions by rare species.

Rarity can be categorized in multiple ways, including small population size, limited range, narrow habitat specificity, or combinations thereof (Rabinowitz, 1981). These metrics can independently or jointly categorize species as rare, but they are not always correlated (Sexton et al., 2009; Jain et al., 2014; Crisfield et al., 2024). For example, a species may have a high local abundance but a restricted distribution or vice versa. Because range size and local abundance can differ for a single species, it is possible that rare species quantified by range size would impact phylogenetic diversity in different ways than rare species quantified by abundance, and therefore it is key to investigate different metrics separately. Indeed, a previous study found that the functional diversity contributions of a rare species depend on how rarity is measured (Jain et al., 2014). Within local communities, low local abundance is a typical metric of rarity, but range size is also an important axis of rarity to address, given that species with low local abundance may or may not be buffered by persisting across a wide geographical distribution and niche space (Rabinowitz, 1981; Johnson, 1998). Indeed, both low-abundance and range-restricted species are observed to be at higher risk of extinction (Staudte et al., 2020a, b; Manes et al., 2021).

Here we tested whether rare plant species, defined by low local abundance and a small range, disproportionately contribute to phylogenetic diversity in subalpine plant

communities. We hypothesized that rare species contribute more to phylogenetic diversity due to their evolutionary distinctiveness and that losing rare species will cause greater declines in diversity metrics compared to common species. We tested this idea across an elevational gradient in the Colorado Rocky Mountains near the Rocky Mountain Biological Laboratory (RMBL; Gothic, Colorado, USA). In this system, plant communities are known to be more phylogenetically overdispersed at higher elevations (Bryant et al., 2008; Veldhuisen et al., 2023), indicating greater potential for rare species to play unique roles at higher elevation. We first predicted (1) that range size and local abundance will show phylogenetic signals, indicating that common and rare species occupy different phylogenetic lineages. Then, we predicted (2) that weighting phylogenetic diversity metrics by high abundance or large range will decrease phylogenetic diversity, consistent with the prediction that rare species contribute more to diversity than common species. As a consequence, we predicted (3) that removing species from the data set according to rarity will decrease phylogenetic diversity more when the removed species are rare than when they are common. Finally, we predicted (4) that removing rare species will have the strongest impact on phylogenetic diversity at high elevation sites. Our study is particularly novel in considering multiple metrics of rarity, multiple elevations, and subalpine plant communities in the investigation of the contributions of rarity to community phylogenetic diversity.

MATERIALS AND METHODS

Study system and abundance data

We collected abundance data for a forb community at three sites in Washington Gulch near RMBL from June to August in 2021 and 2022. The RMBL is located in the East River Valley of the West Elk Mountains, approximately 10 km from Crested Butte, Colorado. Study sites were located at 2815 m a.s.l. (38°53'50"N, 106°58'43"W), 3165 m a.s.l. (38°57'38"N, 107°01'53"W), and 3380 m a.s.l. (38°58'10"N, 107°01'53"W). At each of the three sites, we had five 1.2 × 1.2 m plots that were randomly placed within each site each summer. (Sites and plots were described by Veldhuisen et al., 2023 and Sloat et al., 2015.)

We identified all vascular plants to species level within each 1.2 × 1.2 m plot at the three sites. We confirmed our identifications against RMBL Herbarium specimens (herbarium code RMBL) and iNaturalist observations. Each plot was sampled once per year near the peak of the growing season (approximately mid July, depending on the year and elevation). Plant sampling dates were staggered to ensure all communities had the same relative phenological time point. In each plot, we counted all individuals of every species. We only counted plants rooted within the plot, and unidentifiable individuals and non-native species were excluded from all analyses. To ensure consistency, we established clear

guidelines for decision-making and had everyone collect data from the same plot and compare results to standardize protocol. To quantify abundance and generate a single number by which to rank a species, we averaged local abundance across all five plots at each site and the two data collection years. Overall, we collected data for 39 species at the low-elevation site, 27 at the middle-elevation site, 36 at the high-elevation site, and 59 species total.

Range size

We calculated range size as extent of occurrence (EOO) and area of occupancy (AOO) (Gaston and Fuller, 2009; Staude et al., 2020b). To obtain these values, we downloaded occurrence data for each species using the R package *rgbif* (Chamberlain and Boettiger, 2017) and calculated AOO and EOO with the R package *red* (Cardoso, 2017). We restricted GBIF downloads to occurrences in North America with <1000 m coordinate uncertainty and observations made since 1990 to ensure coordinate accuracy (Appendix S1). We focused on North American observations because the continent spans a wide range of environmental conditions that are also accessible to the same lineages present at our site. In addition, all but eight species were endemic to North America, and thus their global distributions were fully captured by this area. The package *red* calculates AOO as the total cells occupied by the provided points at a 2 × 2 km resolution, which aligns with IUCN resolution requirements (Cardoso, 2017). We used only the AOO values to calculate phylogenetic signal (Prediction 1) and rank species for testing the impact of their removal (Prediction 2) because AOO is less sensitive to extremes and outlier observations (Gaston and Fuller, 2009; Staude et al., 2020b).

Phylogenetic metrics

To calculate phylogenetic signal and community phylogenetic diversity, we used the ALLMB.tre angiosperm phylogeny of Smith and Brown (2018). This phylogeny includes all genera in our data set and 55 of 68 species. If a species was missing from the phylogeny but was the only member of its genus in the plots, we replaced it with a closely related congener in the Smith and Brown phylogeny (Appendix S2). Only the genus *Senecio* had multiple species in the plots missing from the phylogeny. We removed *S. crassulus* A. Gray and *S. bigelovii* A. Gray from all phylogenetic analyses because they have no available genetic or phylogenetic information. We could not find an up-to-date genus-level phylogeny for *Erigeron* to inform replacements, so we removed *Erigeron elatior* (A. Gray) Greene and *Erigeron glacialis* (Nutt.) A. Nelson from all analyses. All pruned phylogenies were fully resolved.

To test Prediction 1, we calculated phylogenetic signal for both abundance and range size using Blomberg's *K* (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999). We calculated

Blomberg's K with the function `phylosignal()` in the R package `picante` (Kembel et al., 2010) with 5000 randomizations, and Pagel's λ with the function `phylosig()` in the R package `phytools` (Revell, 2011) with 5000 iterations and model set to `lambda`. Blomberg's K or Pagel's λ values near 1 indicate trait evolution consistent with Brownian motion. In contrast, K less than 1 or Pagel's λ near zero suggests less phylogenetic signal than expected by Brownian motion.

We calculated Faith's phylogenetic diversity (PD; Faith, 1992), mean phylogenetic distance (MPD), and mean nearest taxon distance (MNTD) and their associated standard effect sizes (SES) in `picante` (Kembel et al., 2010). Faith's phylogenetic diversity (Faith, 1992) is the total evolutionary distance (branch length) across a phylogenetic tree describing the relationships among the taxa in a data set. This metric will increase if relationships are more distant across the tree (species are more evolutionarily divergent). Mean phylogenetic distance is the mean distance between pairs of species. As such, it also increases as evolutionary relationships are more distant across the tree. However, it will be less sensitive to rare cases of distantly related species that would otherwise elevate Faith's phylogenetic diversity. Mean nearest taxon distance is the mean of the distance to the closest relative of each taxon and reflects the typical distance to any species' closest relative in the data set and increases as closest relatives are more distant. Therefore, MNTD is more reflective of the tendency of species to have closer relatives than it is of the overall evolutionary diversity across the entire tree (community of species) that is captured by the former metrics. (For further discussion, see review by Tucker et al., 2017.)

To calculate SES, we used the `sample.pool` null model for each metric to randomly draw species from the RMBL community with 5000 iterations. Positive SES values indicate that the species group in question is more phylogenetically diverse than a random draw of the same number of species from the regional species pool (overdispersion). SES values above 1.96 will have P -values above 0.975, indicating statistical significance of SES. Negative SES values indicate that the species group in question is less phylogenetically diverse than a random draw of the same number of species from the regional species pool (underdispersion). SES values below -1.96 will generate P -values below 0.025, indicating statistical significance of SES.

Weighting by abundance and range size

To test Prediction 2, we calculated MPD and MNTD weighted by abundance and range size. We then compared the weighted versus unweighted standard effect sizes for each community. To weight these metrics, we used the function `ses.mpd` in `picante` (Kembel et al., 2010), but switched the parameter `abundance.weighted=` from `false` to `true`, and weighted by local abundance and log of the AOO value. Since PD is directly correlated with species richness, it cannot be weighted by abundance. We considered

changes in diversity in response to weighting significant if the SES absolute values became greater than 1.96.

Removing species

To test Prediction 3, we removed species and recalculated phylogenetic diversity after the removal. For each site, we ranked species in order of decreasing rarity in terms of both local abundance and range size, such that the most abundant and largest range-size species were ranked first and the lowest abundance and smallest range-size species were ranked last. Then, we removed one species at a time in order of increasing rarity (removing the most abundant and largest range sizes first) and calculated the SES for PD, MPD, and MNTD of the resulting community. We also tested for autocorrelation of residuals from a regression between standard effect size and the abundance rank of removed species within each site using the Durbin–Wallis test with 1, 2, and 3 steps to see if removal of similarly ranked species had similar effects. Finally, we also tested for the effects of leaving out single species at the plot level at each site, which offers increased replication but smaller community sizes (and therefore smaller observed community phylogenies, which are likely to increase variance in the resulting phylogenetic diversity estimates).

Removing individual species is likely to result in a noisy signal, especially given that estimates of abundance and range size will themselves include error, resulting in imperfect ranking of species according to rarity. Moreover, rare species could be lost in groups rather than individually during periods of change, and the loss of multiple species will have strong phylogenetic effects if extinctions are phylogenetically clustered, which has been observed (Willis et al., 2008; Eiserhardt et al., 2015; González-Orozco et al., 2016). To test the impact of losing groups of species at a time, we removed groups of 10 species in order of abundance and range size. Using a sliding window approach, we created groups of 10 species, starting with the top 10 most-abundant species, then shifting to species ranked 2–11, 3–12, and so on until the 10 least-abundant species. We then calculated the SES of phylogenetic diversity for the community with each group of 10 removed. We analyzed all data in R version 4.3.1 (R Core Team, 2023).

RESULTS

Community composition and phylogenetic signal

The low-elevation site contained 39 species across 17 families, the middle site had 27 species across 14 families, and the high site had 36 species across 20 families. We found that local abundance ranged from 0.5 to 573.5 individuals per site when pooled across plots and averaged across years, with a median average abundance of 10.5 individuals per

site (Figure 1). At all three sites, the least-abundant species had only one individual in one year with an average of 0.5 individuals per site across years. These species were *Noccaea fendleri* (A. Gray) Holub, *Primula pauciflora* (Greene) A.R. Mast & Reveal, and *Rumex densiflorus* Osterh. at the low-elevation site (Figure 1A); *Eucephalus breweri* (A. Gray) G.L. Nesom at the middle (Figure 1B); and *Arctostaphylos uva-ursi* L., *Erigeron speciosus* DC., *Hydrophyllum capitatum* Douglas ex Benth., *Senecio integerrimus* Nutt., and *Erigeron eatonii* A. Gray at the high-elevation site (Figure 1C). The most-abundant species at the low-elevation site was *Collomia linearis* Nutt. with an average abundance of 573.5 individuals (Figure 1A). At the middle-elevation site, *Heliomeris multiflora* Nutt. was the most abundant with an average of 253.5 individuals (Figure 1B), and at the high-elevation site *Polygonum douglasii* Greene was the most abundant with an average of 130 individuals (Figure 1C). Range size measured as AOO spanned from 108 km² for *Rumex densiflorus* to 469,436 km² for *Achillea millefolium* L., with a median range size 2316 km² (Figure 1).

We found phylogenetic signal for abundance with only Blomberg's *K* (Blomberg's *K* = 0.304, *P* = 0.04; Pagel's λ = 0.926, *P* = 0.17; Figure 2A), but not for range size with

either metric (Blomberg's *K* = 0.09, *P* = 0.7; Pagel's λ = 7.3×10^{-5} , *P* = 1; Figure 2B).

Weighting community phylogenetic metrics

Weighting MPD and MNTD by abundance (Figure 3A) and range size (Figure 3B) did not significantly change phylogenetic diversity at any of our sites. At the low-elevation site, MPD SES was positive when unweighted and negative when weighted by range size. However, both SES values were still very near zero and nonsignificant (Figure 3B). Also at the low-elevation site, weighting by abundance increased SES values for MPD and MNTD, but SES values stayed nonsignificant. At other sites, impacts of weighting were variable and depended on the metric in question (Figure 3A, B), but never caused the SES values to be statistically significant.

Removing species

In general, removing species according to rarity did not reveal consistent effects on phylogenetic diversity. Because

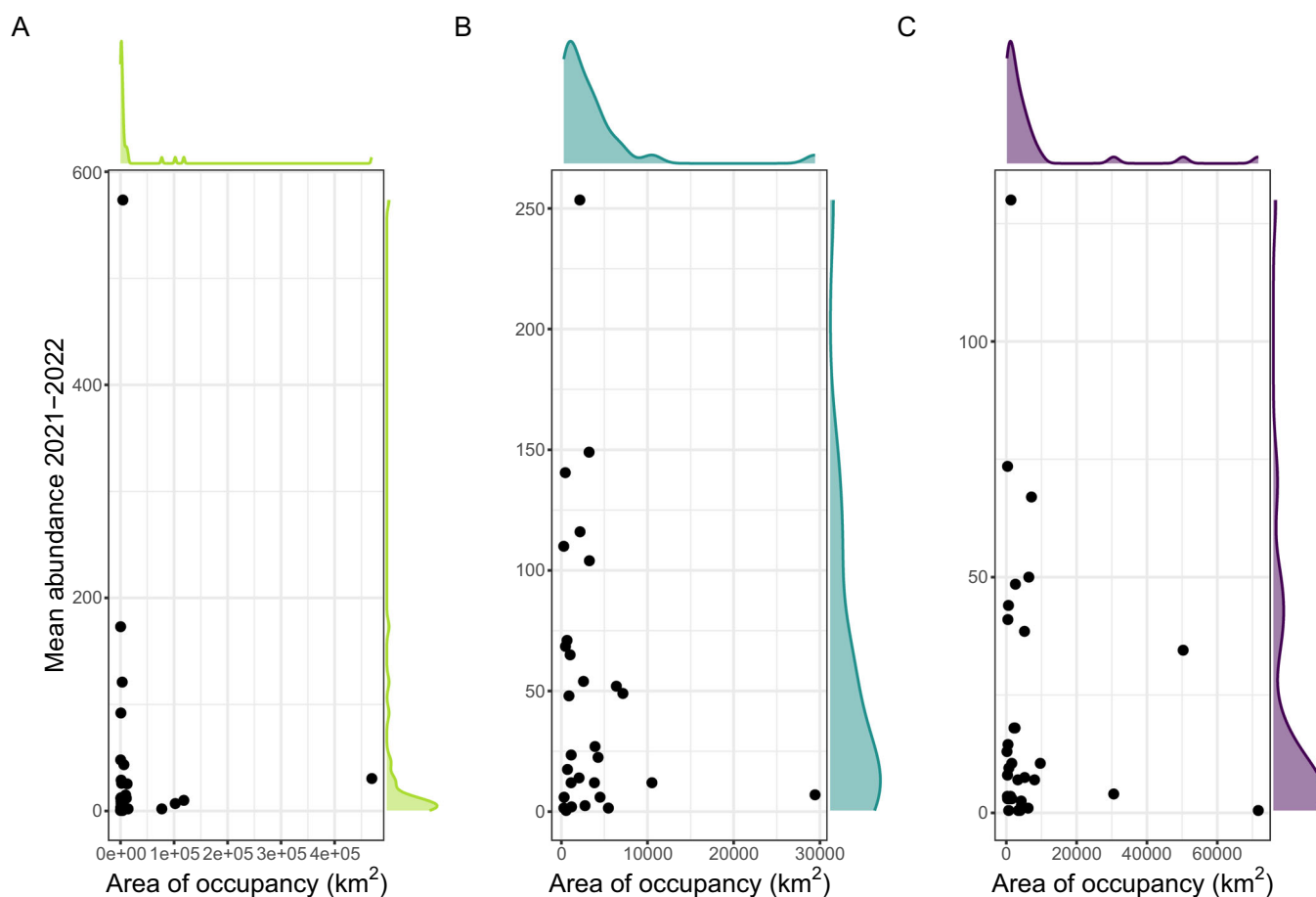


FIGURE 1 Range sizes of species plotted against their mean local abundance with rank abundance and range size curves plotted on the edge. (A) Low-elevation site at 2815 m a.s.l., (B) middle-elevation site at 3165 m a.s.l., and (C) is the high-elevation site at 3380 m a.s.l.

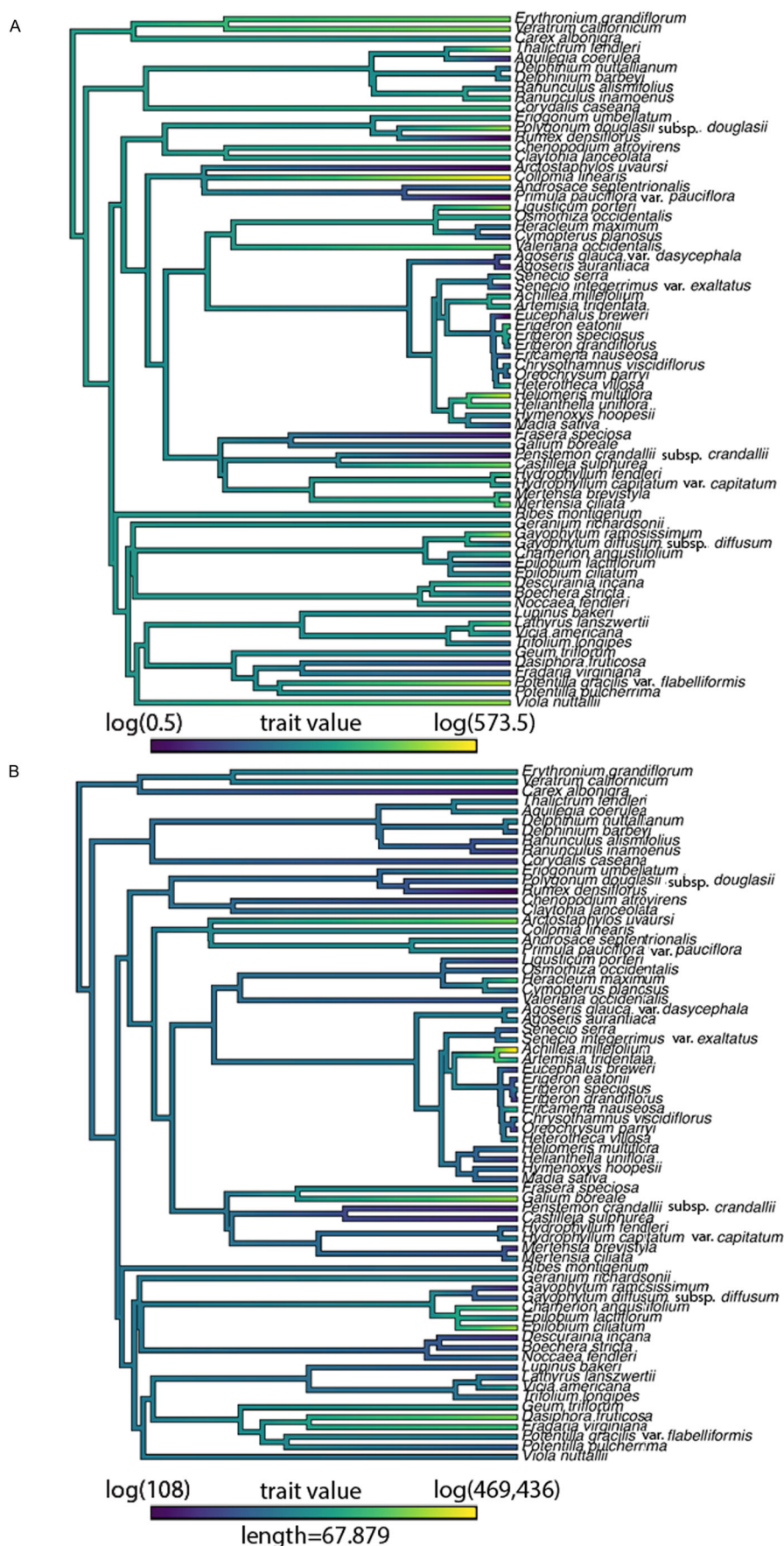


FIGURE 2 (See caption on next page).

range size did not show phylogenetic signal (i.e., particular lineages did not tend to be represented by small range sizes), this was expected, and here we focus on results for abundance, which did show phylogenetic signal (results for single species removal according to range size are available in Appendix S3). For abundance, removing species in order of decreasing abundance impacted SES values inconsistently across metrics and sites, and removing the rarest species did not consistently decrease phylogenetic diversity by any metric (Figure 4). These site level results were also reflected at the plot level, though variability was even greater, as expected for the smaller community sizes (Appendix S4).

At the high-elevation site specifically, removing the most-abundant species did not change the SES for PD, slightly lowered SES for MPD, and increased the SES for MNTD (Figure 4). Removing the least-abundant species

increased the SES for PD, MPD, and MNTD. The middle-abundance species both increased and decreased SES values for all metrics depending on the species (Figure 4).

At the middle-elevation site, removal of the most- and least-abundant species increased SES across all metrics (Figure 4). Removing other low-abundance species (ranked 20–26 of 29) both increased and decreased SES values depending on metric and individual species (Figure 4). As for the high-elevation site, removing the middle-ranked abundance species had mixed impacts on community phylogenetic diversity by all metrics (Figure 4).

Finally, at the low-elevation site removal of the most and least-abundant species lowered SES values by all metrics (Figure 4). For both PD and MTD, SES values decreased with the removal of each of the top five most-abundant

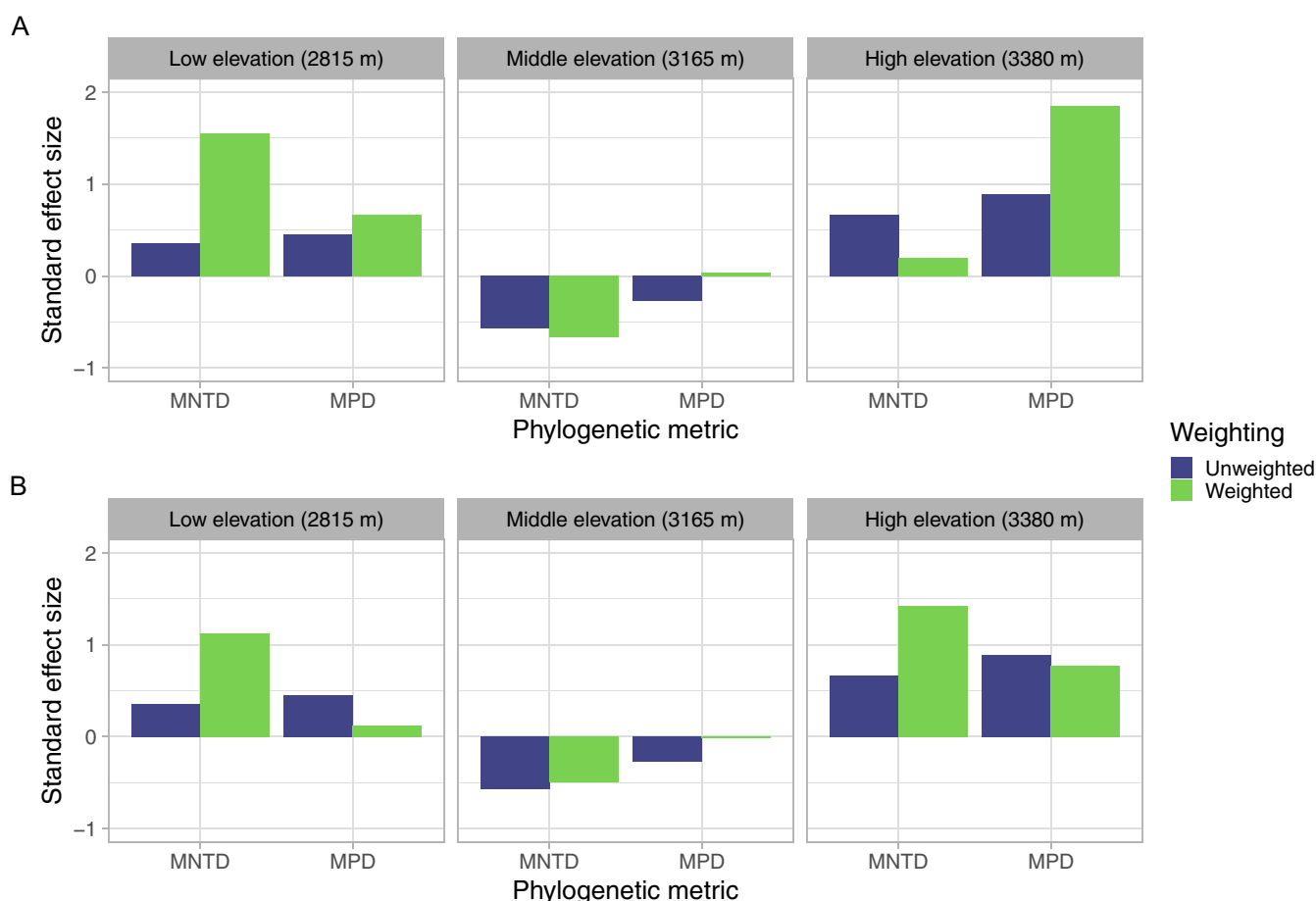


FIGURE 3 Standard effect sizes to compare weighted and unweighted mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD). Unweighted values are in blue; weighted values are in green. (A, B) Weighting by (A) abundance and (B) range size at the three elevational sites. Weighting by abundance and range size does not significantly change MPD or MNTD for the sites. At the middle-elevation site, range size-weighted MPD has a standard effect size and is nearly invisible in panel B.

FIGURE 2 Phylogenies with log values of abundance (A) and range size (B) indicated by branch colors. (A) Abundance shows significant phylogenetic signal for Blomberg's K only ($K = 0.304$, $P = 0.04$, Pagel's $\lambda = 0.93$, $P = 0.168$); (B) range size does not show any significant signal ($K = 0.09$, $P = 0.7$, Pagel's $\lambda = 7.3 \times 10^{-5}$, $P = 1$).

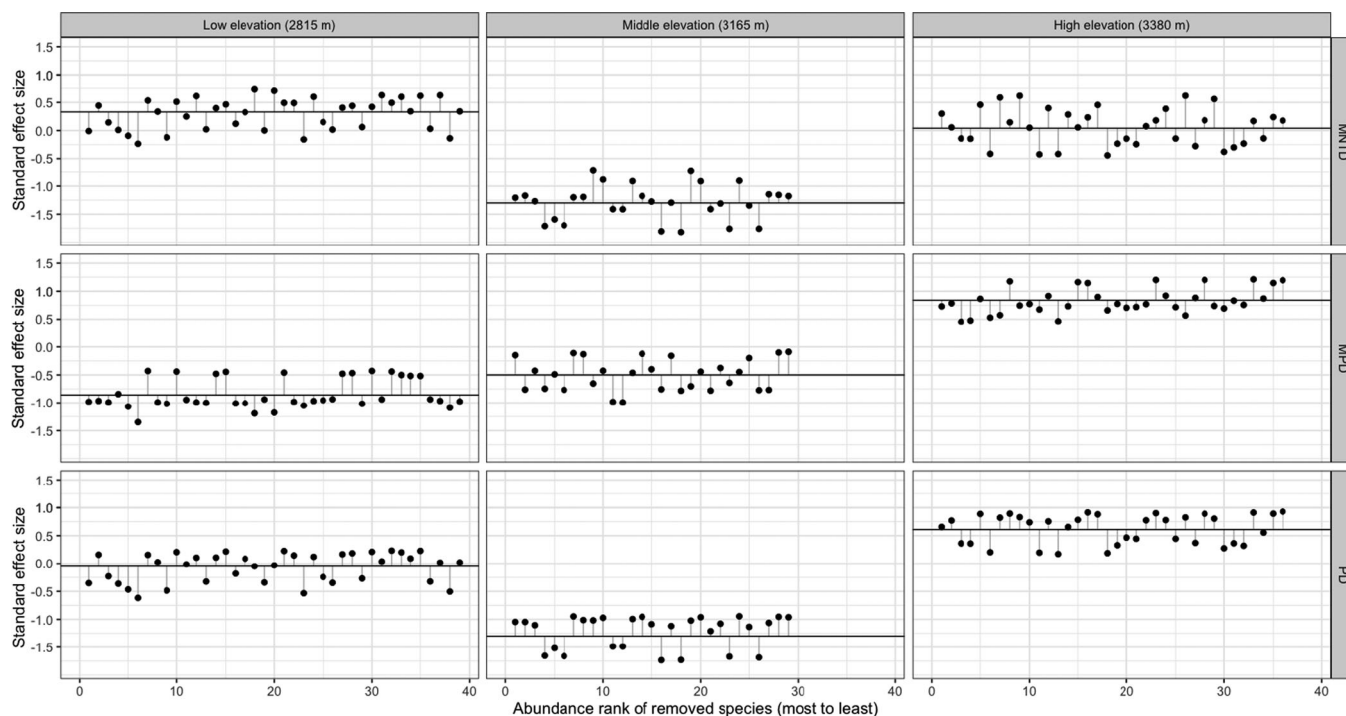


FIGURE 4 Change in standard effect size (SES) when individual species are removed in order of decreasing abundance at the three elevational sites. The horizontal black line in each graph shows the SES of the metric for the overall community at each site; the dots show how the SES changes when the species at the rank indicated on the x-axis is removed. Mean nearest taxon distances (MNTD) are shown in the top row, mean phylogenetic distances (MPD) are in the middle row, and phylogenetic diversities (PD) are on the bottom. No clear pattern suggests that removing rarer species (right side of each panel) decreases MNTD, MPD, or PD more than removing more-abundant species (left side of each panel).

species (Figure 4). This decrease in SES was also mostly true for MPD, except that the removal of the third most-abundant species did not change the SES value. While the removal of the least-abundant species decreased SES values for all metrics, removal of the next three least-abundant species either did not change or increased SES values depending on metric and species (Figure 4). Like the middle- and high-elevation sites, removing the middle-ranked species at the low-elevation site had variable impacts on SES values for all metrics (Figure 4). We tested for autocorrelation between points within each site at one, two, and three steps and found no significant autocorrelation ($P > 0.05$ for all; Appendix S5).

Removing groups of 10 species in order of abundance also did not produce consistent patterns (Figure 5). Removing the groups with the rarest species did not decrease SES for PD and instead increased SES at all sites (Figure 5). At the low-elevation site, removing groups of common species had the most-negative impact on SES values, while removing the most common species did not impact SES at the high-elevation site and increased the SES at the middle-elevation site (Figure 5). We only show results for PD here because results for MPD and MNTD were similarly inconsistent (Appendix S6). Like the removal of individual species, we only removed groups of species based on abundance because we found no phylogenetic signal in range size (Figure 2B).

DISCUSSION

We hypothesized that rare species (quantified by local abundance and range size) would contribute disproportionately to phylogenetic diversity, especially at higher elevations, but our results were not consistent with this idea. We found that abundance did show phylogenetic signal, but range size did not. We predicted that weighting MPD and MNTD by higher abundance and larger range size would decrease phylogenetic diversity (consistent with disproportionately high contributions by rare species), but it did not. Finally, we predicted that removing rare species (individually or in groups) would decrease phylogenetic diversity more than removing common species, but diversity dropped more with the removal of rare species only occasionally and not more so at high elevations. Our results are strikingly consistent in suggesting that rare species do not contribute disproportionately to phylogenetic diversity in this system.

Our results may be influenced by limitations on our ability to detect the effects of rarity on community phylogenetic diversity, stemming from both the calculation of rarity and the calculation of diversity. An important contribution of our study is its examination of multiple axes of rarity (abundance and range size), but separating these axes also has the potential to obscure the effects of an integrated metric of rarity. How best to quantify rarity remains an

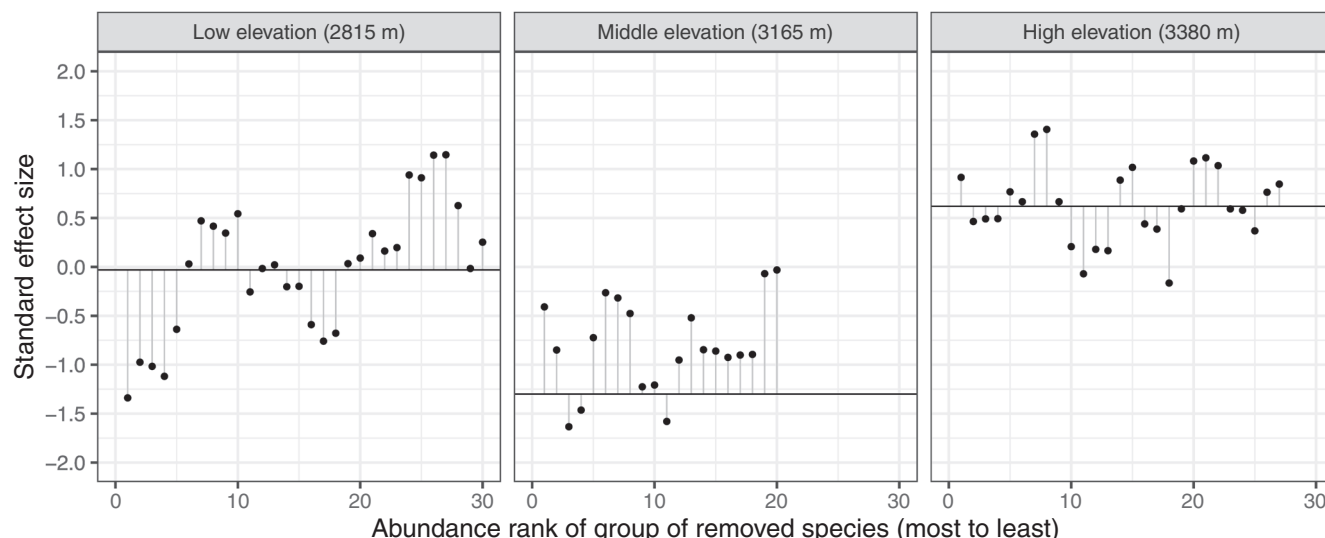


FIGURE 5 Change in standard effect size (SES) for phylogenetic diversity (PD) when groups of 10 species are removed in order of decreasing abundance at the three elevational sites. The horizontal black line in each graph shows the SES of the metric for the overall community at each site; dots show how the SES changes when the group is removed. Numbers on the x -axis rank the most-abundant species in the group that was removed. For example, for the point at $x=5$, the species that were removed were ranked 5–14. No clear pattern suggests that removing rarer species (right side of each panel) decreases PD more than removing more-abundant species (left side of each panel).

active area of discussion in the field (Crisfield et al., 2024; Falaschi et al., 2025). Our focus was also on local rarity contributions to local community composition (though range size estimates were global for most species), and different patterns might arise across larger scales (Hartley and Kunin, 2003). Finally, our power to detect deviations of community phylogenetic diversity from expected phylogenetic diversity is limited by the regional species pool, which here was only modestly larger (same order of magnitude) than community composition.

Our results are consistent with a similar recent study that found that rare and common species contribute similarly to phylogenetic diversity in tallgrass prairies (Herzog and Latvis, 2022). The authors sampled 21 tallgrass prairie communities and calculated PD each time they added increasingly rare species, which were quantified by percentage cover. They then calculated breakpoints where phylogenetic diversity changed significantly from the addition of one species to the next. Still, they found that the location of statistically significant breakpoints was not consistently associated with rare species (Herzog and Latvis, 2022). Although we did not calculate breakpoints in our data, the results of Herzog and Latvis are similar in that the phylogenetic contributions of a species are not consistently predictable based on rarity.

In contrast to our results, Mi et al. (2012) compared the phylogenetic diversity of rare and common species in temperate and tropical tree plots and found that rare species were phylogenetically distinct, which they framed as support for the niche differentiation hypothesis. While we now know we cannot assume that relatedness predicts niche space in a straightforward way (Mason and Pavoine, 2013; Davies et al., 2016; Blonder, 2018), the results of Mi and

colleagues are informative. In particular, they found that rare species contribute more phylogenetic diversity only in plots with lower levels of disturbance (Mi et al., 2012). If disturbance has caused local extinctions of rare species before the time frame of our study, the rarest species will no longer be present, and we would instead be observing the less-rare species that still occur. If previous disturbance has already caused the local extinction of rare species, it may still be true that rare species historically contributed the most phylogenetic diversity, but we would not be able to observe it. Similarly, disturbance could also lower phylogenetic diversity if only a subset of related species survived (Helmus et al., 2010). It is worth noting that none of our species are listed in the Colorado Rare Plant Guide (Colorado Natural Heritage Program, 2023), so our species with the smallest ranges and lowest abundance may not, in fact, be considered rare in a global context, and rarer species may already have been lost. We measured the impact of the removal of one species at a time and in groups of 10, but patterns of actual loss in this system (e.g., sets of related species) are unknown and are likely to be highly system-specific (Zavaleta and Hulvey, 2004; Hooper et al., 2012; Sanders et al., 2018; Chase et al., 2020; Carmona et al., 2021). Evaluating disturbance or historical species loss at our sites would be an important avenue for future research in this system.

Regardless of whether native species are changing, the addition of new species via invasions or range shifts may also alter phylogenetic diversity, and some work suggests such newcomers can cause declines diversity (Selvi et al., 2016; Fitt and Lancaster, 2017; Daru et al., 2021). We know that range shifts and invasive species are impacting this system, while other species are declining (Renwick et al., 2016; Zorio et al., 2016;

Shepard et al., 2022). We did not include non-native species in our analyses because our plots included only four non-native species, all of which currently occur at low abundance. Three of the four non-native species are in Asteraceae, and as such would likely not change our results. Evidence does suggest plants are shifting their elevational ranges in this system (Zorio et al., 2016), however, so investigating the phylogenetic impact of range-shifting newcomers may be important for future work.

We found phylogenetic signal in abundance but not in range size. Herzog and Latvis (2022) tested for phylogenetic signal in abundance in their tall grass prairie communities and found signal at the regional scale and in 5 of their 21 communities. Previous work has tested phylogenetic signal in range size with mixed results (Morin and Lechowicz, 2013; Zacaï et al., 2017; Pigot et al., 2018). Pigot et al. (2018) found that introduced bird species have strong phylogenetic signal in their native range size, but random samples of birds do not show phylogenetic signal in range size, so this finding was unique to introduced species. Morin and Lechowicz (2013) found weak but significant signal in range size in tree species in forest plots worldwide. Zacaï et al. (2017) found that phylogenetic signal in range size varies regionally and is likely influenced by spatiotemporal environmental stability over geological time. Each of these studies addressed range size across broad spatial and temporal scales (Morin and Lechowicz, 2013; Zacaï et al., 2017; Pigot et al., 2018), while we only included present-day species native to the North American Rocky Mountains. Previous work indicates that including non-native species or broadening our spatial scope to include more species may change our phylogenetic signal results, which is consistent with other context-dependent community phylogenetic patterns (Cavender-Bares et al., 2009; Willis et al., 2009; Park et al., 2020).

Work in other systems has suggested that rare species provide the most unique functional trait combinations (Mouillot et al., 2013) and contribute significantly to functional diversity (Leitão et al., 2016; Coulon et al., 2023), although results depend on how rarity is quantified (Jain et al., 2014). Our results show no evidence that rare species are phylogenetically distant from the rest of the community; however, we did not investigate their functional uniqueness, which may produce a different pattern. Phylogenetic diversity is expected to reflect the broad multivariate trait combinations of species, but often correlates poorly with variation in individual traits, which in some cases may be critical for structuring communities (CaraDonna and Inouye, 2015; Gerhold et al., 2015; Maitner et al., 2022; E-Vojtkó et al., 2023). Similarly, one study using a theoretical modelling approach found that prioritizing phylogenetic diversity for conservation efforts did not always maximize functional diversity, even when traits showed phylogenetic signal (Mazel et al., 2017). Whether our rare RMBL plant community members are functionally unique or redundant is unknown, but our results suggest that species with low abundance and a small range may provide redundancy in terms of phylogenetic diversity.

Taken together, our results raise important questions about the potential contributions of rare species to other dimensions of biodiversity, such as functional diversity and functional rarity. The contributions of rare species to all facets of diversity are particularly important to understand because extinction risk threatens the loss of lineages that contribute unique evolutionary diversity to communities (Willis et al., 2008; Eiserhardt et al., 2015; González-Orozco et al., 2016). Violle et al. (2017) emphasized the critical role of functional rarity in maintaining ecosystem processes and resilience. Future research should explore whether the rare species in this system possess unique functional traits that contribute disproportionately to ecosystem functioning, even if they do not increase phylogenetic diversity. Understanding the interplay between phylogenetic and functional rarity will help clarify the broader ecological significance of rare species and inform conservation strategies to preserve biodiversity and ecosystem stability in the face of global change. Integrating functional trait data with evolutionary frameworks will allow us to better assess whether rare species provide irreplaceable ecosystem functions or reinforce redundancy within ecological communities.

CONCLUSIONS

Our study aimed to test whether rare species contribute disproportionately to phylogenetic diversity in our sub-alpine plant community, a question central to understanding their ecological and evolutionary significance. Contrary to our hypothesis, we found that rare species in our system do not uniquely increase phylogenetic diversity, and their contributions to phylogenetic diversity vary inconsistently with the identity of the species, elevation, and phylogenetic metric. These findings challenge assumptions that rare species increase evolutionary diversity and raise questions about their broader ecological roles.

AUTHOR CONTRIBUTIONS

L.N.V. and K.M.D. conceived the study. V.Z. collected field data. L.N.V. generated and analyzed range size data. L.N.V. wrote the original draft with input from K.M.D. and V.Z. All authors provided feedback. L.N.V., B.J.E., and K.M.D. acquired funding. All authors approved the final version of the manuscript.

ACKNOWLEDGMENTS

This study was conducted on the traditional and unceded land of the Ute People. The authors thank RMBL and private landowners for land access, RMBL for securing permits, Dlugosch lab members for manuscript feedback, and Dan Park for discussing analyses and results. Suggestions from Melanie Tietje and one anonymous reviewer greatly improved this work. This work was funded by Rocky Mountain Biological Laboratory, Botanical Society of America, and University of Arizona Graduate & Professional Student Council awards to L.N.V. and U.S. National

Science Foundation grant 1750280 to K.M.D. B.J.E. acknowledges that this material is based upon work supported by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research, Earth and Environmental Systems Sciences Division and Data Management Program, under Award Number DEAC02-05CH11231, as part of the Watershed Function Scientific Focus Area and the ExaShed project. B.J.E. was also supported by NSF awards 2225078 and 2225076.

DATA AVAILABILITY STATEMENT

Range size and abundance data can be accessed at <https://doi.org/10.6073/pasta/320111b8e067c3b443fa25a719aac7ae>. Code is available at <https://github.com/lveldhuisen/phylogenetics-and-ranges>.

ORCID

Leah N. Veldhuisen  <https://orcid.org/0000-0002-7094-0108>

Verónica Zepeda  <https://orcid.org/0000-0001-8559-2882>

Brian J. Enquist  <https://orcid.org/0000-0002-6124-7096>

Katrina M. Dlugosch  <https://orcid.org/0000-0002-7302-6637>

REFERENCES

- Anderson, T. M., M. Lachance, and W. T. Starmer. 2004. The relationship of phylogeny to community structure: the cactus yeast community. *American Naturalist* 164: 709–721.
- Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57: 717–745.
- Blonder, B. 2018. Hypervolume concepts in niche- and trait-based ecology. *Ecography* 41: 1441–1455.
- Bracken, M. E. S., and N. H. N. Low. 2012. Realistic losses of rare species disproportionately impact higher trophic levels: loss of rare ‘cornerstone’ species. *Ecology Letters* 15: 461–467.
- Bryant, J. A., C. Lamanna, H. Morlon, A. J. Kerkhoff, B. J. Enquist, and J. L. Green. 2008. Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences, USA* 105: 11505–11511.
- Cadotte, M. W. 2013. Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences, USA* 110: 8996–9000.
- Cadotte, M. W., M. Carboni, X. Si, and S. Tatsumi. 2019. Do traits and phylogeny support congruent community diversity patterns and assembly inferences? *Journal of Ecology* 107: 2065–2077.
- Cadotte, M. W., B. J. Cardinale, and T. H. Oakley. 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences, USA* 105: 17012–17017.
- Cadotte, M. W., J. Cavender-Bares, D. Tilman, and T. H. Oakley. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One* 4: e5695.
- Cadotte, M. W., R. Dinnage, and D. Tilman. 2012. Phylogenetic diversity promotes ecosystem stability. *Ecology* 93: S223–S233.
- CaraDonna, P. J., and D. W. Inouye. 2015. Phenological responses to climate change do not exhibit phylogenetic signal in a subalpine plant community. *Ecology* 96: 355–361.
- Cardoso, P. 2017. red - an R package to facilitate species red list assessments according to the IUCN criteria. *Biodiversity Data Journal* 5: e20530.
- Carmona, C. P., R. Tamme, M. Pärtel, F. de Bello, S. Brosse, P. Capdevila, R. González-M, et al. 2021. Erosion of global functional diversity across the tree of life. *Science Advances* 7: eabf2675.
- Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.
- Chamberlain S, and C. Boettiger. 2017. R Python, and Ruby clients for GBIF species occurrence data. *PeerJ* <https://doi.org/10.7287/peerj.preprints.3304v1> [preprint].
- Chase, J. M., S. A. Blowes, T. M. Knight, K. Gerstner, and F. May. 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature* 584: 238–243.
- Colorado Natural Heritage Program. 2023. Colorado rare plant guide. Website <https://cnhp.colostate.edu/rareplant> [accessed 20 March 2025].
- Coulon, N., M. Lindegren, E. Goberville, A. Toussaint, A. Receveur, and A. Auber. 2023. Threatened fish species in the Northeast Atlantic are functionally rare. *Global Ecology and Biogeography* 32: 1827–1845.
- Crisfield, V. E., F. Guillaume Blanchet, C. Raudsepp-Hearne, and D. Gravel. 2024. How and why species are rare: towards an understanding of the ecological causes of rarity. *Ecography* 2024: e07037.
- Daru, B. H., T. J. Davies, C. G. Willis, E. K. Meineke, A. Ronk, M. Zobel, M. Pärtel, et al. 2021. Widespread homogenization of plant communities in the Anthropocene. *Nature Communications* 12: 6983.
- Davies, T. J., M. C. Urban, B. Rayfield, M. W. Cadotte, and P. R. Peres-Neto. 2016. Deconstructing the relationships between phylogenetic diversity and ecology: a case study on ecosystem functioning. *Ecology* 97: 2212–2222.
- Dee, L. E., J. Cowles, F. Isbell, S. Pau, S. D. Gaines, and P. B. Reich. 2019. When do ecosystem services depend on rare species? *Trends in Ecology & Evolution* 34: 746–758.
- Delavaux, C. S., T. W. Crowther, C. M. Zohner, N. M. Robmann, T. Lauber, J. van den Hoogen, S. Kuebbing, et al. 2023. Native diversity buffers against severity of non-native tree invasions. *Nature* 621: 773–781.
- Dinnage, R., M. W. Cadotte, N. M. Haddad, G. M. Crutsinger, and D. Tilman. 2012. Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecology Letters* 15: 1308–1317.
- Eiserhardt, W. L., F. Borchsenius, C. M. Plum, A. Ordóñez, and J.-C. Svenning. 2015. Climate-driven extinctions shape the phylogenetic structure of temperate tree floras. *Ecology Letters* 18: 263–272.
- Enquist, B. J., X. Feng, B. Boyle, B. Maitner, E. A. Newman, P. M. Jørgensen, P. R. Roehrdanz, et al. 2019. The commonness of rarity: global and future distribution of rarity across land plants. *Science Advances* 5: eaaz0414.
- E-Vojtkó, A., F. de Bello, Z. Lososová, and L. Götzenberger. 2023. Phylogenetic diversity is a weak proxy for functional diversity but they are complementary in explaining community assembly patterns in temperate vegetation. *Journal of Ecology* 11: 2218–2230.
- Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61: 1–10.
- Falaszchi, M., E. Lo Parrino, R. Manenti, and G. F. Ficetola. 2025. Differences in estimates of extinction risk between occupancy and abundance data. *Conservation Biology*: e70020. <https://doi.org/10.1111/cobi.70020>
- Fitt, R. N. L., and L. T. Lancaster. 2017. Range shifting species reduce phylogenetic diversity in high latitude communities via competition. *Journal of Animal Ecology* 86: 543–555.
- Galland, T., G. Adeux, H. Dvořáková, A. E-Vojtkó, I. Orbán, M. Lussu, J. Puy, et al. 2019. Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Journal of Ecology* 107: 2090–2104.
- Gaston, K. J. 1994. Biodiversity - measurement. *Progress in Physical Geography: Earth and Environment* 18: 565–574.
- Gaston, K. J., and R. A. Fuller. 2009. The sizes of species' geographic ranges. *Journal of Applied Ecology* 46: 1–9.
- Gerhold, P., J. F. Cahill, M. Winter, I. V. Bartish, and A. Prinzing. 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* 29: 600–614.
- Ge, X.-Y. M., J. P. Scholl, U. Basinger, T. E. Huxman, and D. L. Venable. 2019. Functional trait trade-off and species abundance: insights from a multi-decadal study. *Ecology Letters* 22: 583–592.
- González-Orozco, C. E., L. J. Pollock, A. H. Thornhill, B. D. Mishler, N. Knerr, S. W. Laffan, J. T. Miller, et al. 2016. Phylogenetic

- approaches reveal biodiversity threats under climate change. *Nature Climate Change* 6: 1110–1114.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.
- Hähn, G. J. A., G. Damasceno, E. Alvarez-Davila, I. Aubin, M. Bauters, E. Bergmeier, I. Biurrun, et al. 2024. Global decoupling of functional and phylogenetic diversity in plant communities. *Nature Ecology & Evolution* 9: 237–248.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38: 210–221.
- Hartley, S., and W. E. Kunin. 2003. Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology* 17: 1559–1570.
- Helmus, M. R., W. Keller, M. J. Paterson, N. D. Yan, C. H. Cannon, and J. A. Rusak. 2010. Communities contain closely related species during ecosystem disturbance. *Ecology Letters* 13: 162–174.
- Herzog, S. A., and M. Latvis. 2022. Community-level phylogenetic diversity does not differ between rare and common lineages across tallgrass prairies in the northern Great Plains. *Ecology and Evolution* 12: e9453.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486: 105–108.
- Huang, M., X. Liu, M. W. Cadotte, and S. Zhou. 2020. Functional and phylogenetic diversity explain different components of diversity effects on biomass production. *Oikos* 129: 1185–1195.
- Hughes, C., and R. Eastwood. 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences, USA* 103: 10334–10339.
- Hughes, C. E., and G. W. Atchison. 2015. The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. *New Phytologist* 202: 275–282.
- Jain, M., D. F. Flynn, C. M. Prager, G. M. Hart, C. M. Devan, F. S. Ahrestani, M. I. Palmer, et al. 2014. The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecology and Evolution* 4: 104–112.
- Jiao, S., W. Chen, and G. Wei. 2017. Biogeography and ecological diversity patterns of rare and abundant bacteria in oil-contaminated soils. *Molecular Ecology* 26: 5305–5317.
- Johnson, C. N. 1998. Species extinction and the relationship between distribution and abundance. *Nature* 394: 272–274.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.
- Klak, C., G. Reeves, and T. Hedderson. 2004. Unmatched tempo of evolution in Southern African semi-desert ice plants. *Nature* 427: 63–65.
- Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29: 592–599.
- Leitão, R. P., J. Zuanon, S. Villéger, S. E. Williams, C. Baraloto, C. Fortunel, F. P. Mendonça, and D. Moullot. 2016. Rare species contribute disproportionately to the functional structure of species assemblages. *Proceedings of the Royal Society, B, Biological Sciences* 283: 0160084.
- Maitner, B. S., D. S. Park, B. J. Enquist, and K. M. Dlugosch. 2022. Where we've been and where we're going: the importance of source communities in predicting establishment success from phylogenetic relationships. *Ecography* 2022: e05406.
- Manes, S., M. J. Costello, H. Beckett, A. Debnath, E. Devenish-Nelson, K.-A. Grey, R. Jenkins, et al. 2021. Endemism increases species' climate change risk in areas of global biodiversity importance. *Biological Conservation* 257: 109070.
- Mason, N. W. H., and S. Pavoine. 2013. Does trait conservatism guarantee that indicators of phylogenetic community structure will reveal niche-based assembly processes along stress gradients? *Journal of Vegetation Science* 24: 820–833.
- Matthies, D., I. Bräuer, W. Maibom, and T. Tschardt. 2004. Population size and the risk of local extinction: empirical evidence from rare plants. *Oikos* 105: 481–488.
- Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.
- Mazel, F., A. O. Mooers, G. V. D. Riva, and M. W. Pennell. 2017. Conserving phylogenetic diversity can be a poor strategy for conserving functional diversity. *Systematic Biology* 66: 1019–1027.
- Mi, X., N. G. Swenson, R. Valencia, W. J. Kress, D. L. Erickson, Á. J. Pérez, H. Ren, et al. 2012. The contribution of rare species to community phylogenetic diversity across a global network of forest plots. *American Naturalist* 180: E17–E30.
- Milcu, A., E. Allan, C. Roscher, T. Jenkins, S. T. Meyer, D. Flynn, H. Bessler, et al. 2013. Functionally and phylogenetically diverse plant communities key to soil biota. *Ecology* 94: 1878–1885.
- Morin, X., and M. J. Lechowicz. 2013. Niche breadth and range area in North American trees. *Ecography* 36: 300–312.
- Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, et al. 2013. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology* 11: e1001569.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.
- Park, D. S., X. Feng, B. S. Maitner, K. C. Ernst, and B. J. Enquist. 2020. Darwin's naturalization conundrum can be explained by spatial scale. *Proceedings of the National Academy of Sciences, USA* 117: 10904–10910.
- Pigot, A. L., E. E. Dyer, D. W. Redding, P. Cassey, G. H. Thomas, and T. M. Blackburn. 2018. Species invasions and the phylogenetic signal in geographical range size. *Global Ecology and Biogeography* 27: 1080–1092.
- Rabinowitz, D. 1981. Seven forms of rarity. In H. Synge [ed.], *The biological aspects of rare plant conservation*, 205–217. Wiley, NY, USA.
- R Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website: <https://www.R-project.org/>
- Renwick, K. M., M. E. Rocca, and T. J. Stohlgren. 2016. Biotic disturbance facilitates range shift at the trailing but not the leading edge of lodgepole pine's altitudinal distribution. *Journal of Vegetation Science* 27: 780–788.
- Revell, L. J. 2011. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology & Evolution* 3: 217–223.
- Sanders, D., E. Thébault, R. Kehoe, and F. J. Frank van Veen. 2018. Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences, USA* 115: 2419–2424.
- Selvi, F., E. Carrari, and A. Coppi. 2016. Impact of pine invasion on the taxonomic and phylogenetic diversity of a relict Mediterranean forest ecosystem. *Forest Ecology and Management* 367: 1–11.
- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40: 415–436.
- Shepard, I. D., S. A. Wissinger, Z. T. Wood, and H. S. Greig. 2022. Predators balance consequences of climate-change-induced habitat shifts for range-shifting and resident species. *Journal of Animal Ecology* 91: 334–344.
- Sloat, L. L., A. N. Henderson, C. Lamanna, and B. J. Enquist. 2015. The effect of the foreshadower drought on carbon exchange in subalpine meadows. *Ecosystems* 18: 533–545.
- Smith, S. A., and J. W. Brown. 2018. Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany* 105: 302–314.
- Staude, I. R., L. M. Navarro, and H. M. Pereira. 2020a. Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography* 29: 16–25.
- Staude, I. R., D. M. Waller, M. Bernhardt-Römermann, A. D. Bjorkman, J. Brunet, P. De Frenne, R. Hédal, et al. 2020b. Replacements of small-by large-ranged species scale up to diversity loss in Europe's temperate forest biome. *Nature Ecology & Evolution* 4: 802–808.
- Swenson, N. G., and B. J. Enquist. 2009. Opposing assembly mechanisms in a neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology* 90: 2161–2170.

- Tietje, M., A. Antonelli, F. Forest, R. Govaerts, S. A. Smith, M. Sun, W. J. Baker, and W. L. Eiserhardt. 2023. Global hotspots of plant phylogenetic diversity. *New Phytologist* 240: 1636–1646.
- Tucker, C. M., M. W. Cadotte, S. B. Carvalho, T. J. Davies, S. Ferrier, S. A. Fritz, R. Grenyer, et al. 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews of the Cambridge Philosophical Society* 92: 698–715.
- Veldhuisen, L. N., B. J. Enquist, and K. M. Dlugosch. 2023. Phylogenetic diversity of flowering plants declines throughout the growing season across a subalpine elevational gradient. *bioRxiv* <https://www.biorxiv.org/content/10.1101/2023.11.06.565878v1> [preprint].
- Violle, C., W. Thuiller, N. Mouquet, F. Munoz, N. J. B. Kraft, M. W. Cadotte, S. W. Livingstone, and D. Mouillot. 2017. Functional rarity: the ecology of outliers. *Trends in Ecology & Evolution* 32: 356–367.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475–505.
- White, H. J., C. M. McKeon, R. J. Pakeman, and Y. M. Buckley. 2023. The contribution of geographically common and rare species to the spatial distribution of biodiversity. *Global Ecology and Biogeography* 32: 1730–1747.
- Willis, C. G., M. Halina, C. Lehman, P. B. Reich, A. Keen, S. McCarthy, and J. Cavender-Bares. 2009. Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography* 33: 565–577.
- Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. Davis. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences, USA* 105: 17029–17033.
- Xing, Y., and R. H. Ree. 2017. Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot. *Proceedings of the National Academy of Sciences, USA* 114: E3444–E3451.
- Yessoufou, K., and T. J. Davies. 2016. Reconsidering the loss of evolutionary history: How does non-random extinction prune the tree-of-life? In R. Pellens and P. Grandcolas [eds.], *Biodiversity conservation and phylogenetic systematics: preserving our evolutionary heritage in an extinction crisis*, 57–80. Topics in biodiversity and conservation, 14. Springer, Cham, Switzerland.
- Zacari, A., E. Fara, A. Brayard, R. Laffont, J.-L. Dommergues, and C. Meister. 2017. Phylogenetic conservatism of species range size is the combined outcome of phylogeny and environmental stability. *Journal of Biogeography* 44: 2451–2462.
- Zavaleta, E. S., and K. B. Hulvey. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306: 1175–1177.
- Zettemoyer, M. A., D. D. McKenna, and J. A. Lau. 2019. Species characteristics affect local extinctions. *American Journal of Botany* 106: 547–559.
- Zorio, S. D., C. F. Williams, and K. A. Aho. 2016. Sixty-five years of change in montane plant communities in western Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research* 48: 703–722.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Citations for GBIF downloads used to calculate range size.

Appendix S2. Species in our research sites listed with replacement species from the ALLMB.tre phylogeny of Smith and Brown (2018; see also Materials and Methods).

Appendix S3. Results of phylogenetic diversity (PD, MPD, and MNTD) from removing single species based on range size.

Appendix S4. Results of phylogenetic diversity (just PD) from removing single species based on abundance at the plot level.

Appendix S5. *P*-values for autocorrelation tests at each site for both abundance and range size, all three phylogenetic metrics and 1, 2, and 3 steps.

Appendix S6. Results of additional phylogenetic diversity metrics (MPD and MNTD) from removing groups of species based on abundance.

How to cite this article: Veldhuisen, L. N., V. Zepeda, B. J. Enquist, and K. M. Dlugosch. 2025. Rare species do not disproportionately contribute to phylogenetic diversity in a subalpine plant community. *American Journal of Botany* 112(6): e70061. <https://doi.org/10.1002/ajb2.70061>