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

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ABSTRACT

• **Premise of the study**: Worldwide, 36% of all plant species are exceedingly rare, and are at the highest risk of extinction. Extinction risk has also been observed to be phylogenetically clustered, threatening the loss of lineages that contribute unique evolutionary diversity to communities. Rare plants' contributions to phylogenetic diversity are largely unknown, however. We investigate whether rare species (as measured by local abundance and range size) contribute disproportionately to phylogenetic diversity in a subalpine plant community.

• **Methods:** We collected abundance data at three sites in Washington Gulch near the Rocky Mountain Biological Laboratory (RMBL, Gothic, Colorado, USA) in 2021 and 2022. We then calculated range size for each species. 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.

• **Key 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 and groups of rare species than when we removed single common species and groups of common species.

• **Conclusions**: Overall, we found that rare species do not disproportionately contribute to phylogenetic diversity. This suggests that rare species likely provide phylogenetic redundancy with common species, and losing rare species may not cause disproportionate drops in phylogenetic diversity in this system.

KEY WORDS: local abundance; phylogenetic diversity; rare species; range size; Rocky Mountain Biological Laboratory

INTRODUCTION

Worldwide, 36% of all plant species are exceedingly rare (observed only five or fewer times globally; (Enquist et al., 2019), and are at the highest risk of extinction (Yessoufou and Davies, 2016; Enquist et al., 2019). At the same time, extinction risk has been observed to be phylogenetically clustered (Willis et al., 2008; Eiserhardt et al., 2015; González-Orozco et al., 2016), threatening the loss of lineages that contribute unique evolutionary diversity to communities. The exact ecological contributions of rare species need more clarification in many systems (Violle et al., 2017; Dee et al., 2019), but they are known to provide key ecosystem functions ranging from providing pollinator resources to fire resilience to diversity across trophic levels (Bracken and Low, 2012; Mouillot et al., 2013; Leitão et al., 2016). However, their contributions to phylogenetic diversity have been explored in very few systems (but see (Anderson et al., 2004; Mi et al., 2012; Herzog and Latvis, 2022).

Understanding factors impacting phylogenetic diversity is key, as it is more positively correlated with biomass than species richness or functional diversity (Cadotte et al., 2008). Phylogenetic diversity also promotes ecosystem stability and productivity (Cadotte et al., 2012; Cadotte, 2013; Davies et al., 2016), diversity in other taxonomic groups (Dinnage et al., 2012; Milcu et al., 2013), and can increase resistance to invasion (Galland et al., 2019; Delavaux et al., 2023). More broadly, phylogenetic diversity can capture variation between species that is missed when only studying one or a few traits (Cadotte et al., 2009; E-Vojtkó et al., 2023) and more accurately reflects niche differences (Huang et al., 2020). It is also an increasingly important axis

of diversity to consider in plant conservation (Tucker et al., 2012; Molina-Venegas et al., 2021). Given the benefits of phylogenetic diversity, the contributions of rare species are important to clarify in light of ongoing species losses (White et al., 2023).

Rarity can be categorized in multiple ways in terms of small population size, small range size, narrow habitat specificity, or combinations thereof (Rabinowitz, 1981). Here we investigate two major axes of rarity: local abundance and range size. Species can be categorized as rare using these metrics individually or in combination, and they do not always correlate (Sexton et al., 2009), so it is unclear whether range size might follow the same phylogenetic diversity patterns as abundance. For example, a species may have very high local abundance but have a very restricted distribution or vice versa. Species' range sizes and limits are shifting, shrinking or expanding with global change (Hardie and Hutchings, 2010; Chen et al., 2011; Sheth and Angert, 2018). Like low-abundance species, species with small ranges are also at higher risk of extinction (Harnik et al., 2012; Manes et al., 2021). To our knowledge, there has never been a test of rare species' contributions to phylogenetic diversity based on range size.

We might expect both low abundance and small-ranged species to be more phylogenetically diverse than random (overdispersed) in relation to each other and their larger community (Mi et al., 2012). The niche differentiation hypothesis suggests that each species within a community occupies its own niche, that rare species use distinct resources, and that rare species will be distinct from each other and more abundant species (Hanski, 1982; Gaston, 1994; Grime, 1998). We now know that phylogenetic diversity is rarely a suitable proxy for functional diversity (Gerhold et al., 2015; Cadotte et al., 2019; E-Vojtkó et al., 2023), though the association of phylogenetic diversity with ecosystem properties suggests that it can capture

aspects of community-level function (Cadotte et al. 2009; E-Vojtkó et al. 2023; Cadotte et al. 2008; Davies et al. 2016).

Previous work supports rare species' distinctiveness in some systems and by some metrics. A study by Jiao et al. (2017) found that rare microbes have higher alpha and beta diversity than their abundant counterparts, but this study did not test phylogenetic diversity. In desert annual plants, rare species do not closely exhibit a well-established functional tradeoff between water use efficiency and relative growth rate seen in the dominant species, suggesting niche differentiation in physiological traits (Ge et al., 2019). Like Jiao et al. (2017), Ge and colleagues (2019) did not test the relatedness of species evading the tradeoff, leaving open an important question about how phylogenetic relatedness may explain differences in rare species' ecological strategies. In tropical tree plots worldwide, rare species were found to be phylogenetically more diverse than abundant species, although this only held true in less disturbed plots (Mi et al., 2012). In yeasts growing in decaying cactus tissue, researchers found that abundance was linked to phylogenetic relatedness, but it varied depending which subfamily of cactus the yeast was growing within (Anderson et al., 2004).

Alternatively, both low abundance and small-ranged species may be randomly distributed across the phylogeny. In this case, we would not expect low abundance and small-ranged species to disproportionately contribute to overall phylogenetic diversity, and instead they would provide phylogenetic redundancy with more abundant species. In tall grass prairies, rare species indeed did not contribute disproportionate phylogenetic diversity, and provided phylogenetic redundancy within the community (Herzog and Latvis, 2022).

Here, we investigate whether low abundance and small-ranged species contribute disproportionately to phylogenetic diversity in a subalpine plant community. Consistent with the

idea that rare species are unique from more common ones, we hypothesize that rare species disproportionately contribute to phylogenetic diversity. We test this idea across an elevational gradient in the Colorado Rocky Mountains near the Rocky Mountain Biological Laboratory (RMBL, Gothic, Colorado, USA). We first predict (1) that range size and local abundance will both show phylogenetic signal, indicating that common and rare species occupy different phylogenetic lineages. Then, we predict (2) that weighting phylogenetic diversity metrics by high abundance or large range size will decrease phylogenetic diversity, consistent with the prediction that rare species contribute more to diversity than common species. Finally, we predict (3) that removing species according to rarity will decrease phylogenetic diversity more when the removed species are rare than when they are common.

MATERIALS & METHODS

Study system & abundance data

We collected abundance data for an angiosperm community at three sites in Washington Gulch near the Rocky Mountain Biological Laboratory (RMBL, Gothic, Colorado, USA) from June to August in 2021 and 2022. RMBL is located in the East River valley of the West Elk mountains, approximately 10 kilometers from Crested Butte, Colorado. Study sites were located at 2815 m (38°53'50"N, 106°58'43"W), 3165 m (38°57'38"N, 107°01'53"W), and 3380 m (38°58'10"N, 107°01'53"W) in elevation. At each of the three sites, we had five 1.2 m x 1.2 m plots that were randomly placed within each site each summer (see more detailed description of sites and plots in (Veldhuisen et al., 2023) and (Sloat et al., 2015)).

Within each 1.2 m x 1.2 m plot at the three sites, we identified all vascular plants to species level and 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 unknown and non-native species were excluded from all analyses. To quantify abundance, we averaged local abundance across all five plots at each site and the two data collection years. We did not include invasive species or species that were only identified to genus in any of our analyses.

Range size

We calculated range size as Extent of Occurrence (EOO) and Area of Occupancy (AOO) (Gaston and Fuller, 2009; Staude et al., 2020). To obtain these values, we downloaded occurrence data for each species using the 'RGBIF' package (Appendix S1; Chamberlain and Boettiger, 2017) and calculated AOO and EOO with the 'red' package (Cardoso, 2017). We restricted GBIF downloads to occurrences in North America with <1000m coordinate uncertainty and observations that have been made since 1990 to ensure coordinate accuracy. 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 extreme and outlier observations (Gaston and Fuller, 2009; Staude et al., 2020).

Phylogenetic metrics

To calculate phylogenetic signal and community phylogenetic diversity, we used the 'ALLMB.tre' angiosperm phylogeny from (Smith and Brown, 2018). This phylogeny includes

all genera in our dataset and 54 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 replaced *Senecio integerrimus* Nutt. with sister species *S. triangularis* Hook (Pelser et al., 2007). 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* and *Erigeon glacialis* from all analyses.

We calculated phylogenetic signal for both abundance and range size with Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999). We calculated Blomberg's K with the "phylosignal()" function in the 'picante' R package (Kembel et al., 2010) with 5000 randomizations, and Pagel's λ with the function "phylosig()" in the 'phytools' R package (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, while K less than 1 or Pagel's λ near zero suggest 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 dataset. 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, and so it also increases as evolutionary relationships are more distant across the tree, but will be less sensitive to rare cases of very 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 so it reflects the typical distance to any species' closest relative in the dataset 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 each metric's "sample.pool" null model to draw species from the RMBL community with 5000 iterations randomly. 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, and indicate statistical significance of the 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, and indicate statistical significance of the 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 by abundance, we used the "ses.mpd" function in 'picante' (Kembel et al., 2010), but switched the "abundance.weighted=" parameter from *false* to *true*. To weight by range size, we weighted by the log of the AOO value. PD cannot be weighted by abundance, since it is directly correlated with species richness. We defined a significant change

in diversity in response to weighting as a sign change in the SES or if SES absolute values became greater than 1.96.

Removing species

To test prediction 3, we removed individual species and groups of 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. This resulted in two separate rankings of rarity, one for local abundance and one for range size. Then, we removed one species at a time in order of increasing rarity (removing 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 across species of adjacent ranks 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.

To test the impact of removing groups of species at a time, we removed groups of ten species, also in order of abundance and range size. Using a sliding window approach, we created groups of ten 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 & 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. 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 (*Noccaea fendleri, Primula pauciflora* and *Rumex densiflorus* at the low elevation site, *Eucephalus breweri* at the middle and *Arctostaphylos uva-ursi, Erigeron speciosus, Hydrophyllum capitatum, Senecio integerrimus* and *Erigeron eatonii* at the high elevation site). At the low elevation site, the most abundant species was *Collomia linearis* with an average abundance of 573.5. At the middle elevation site, *Heliomeris multiflora* was the most abundant with an average of 253.5 individuals in the site, and at the high elevation site *Polygonum douglasii* was the most abundant with an average of 130 individuals in the site. Range size measured as AOO spanned from 108 km^2 for *Rumex densiflorus* to 469,436 km^2 for *Achillea millefolium,* with a median range size 2316 km^2. Both abundance and range size followed standard rank abundance curves (Fig. 1A-B).

We found phylogenetic signal for abundance with only Blomberg's K (Blomberg's K = 0.304, P-value = 0.04; Pagel's λ = 0.926, P-value =0.17; Fig. 2A), but not for range size with either metric (Blomberg's K = 0.09, P-value = 0.7; Pagel's $\lambda = 7.3 \times 10^{-5}$, P-value =1; Fig. 2B).

Weighting community phylogenetic metrics

Weighting MPD and MNTD by abundance (Fig. 3A) and range size (Fig. 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 but both SES

values were still very near zero and nonsignificant (Fig. 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 (Fig. 3A-B), but never caused the SES values to be statistically significant.

Removing species

Because range size did not show phylogenetic signal, we only show results for abundance (for single species range size removal results see Appendix S3). For abundance, removing species in order of decreasing abundance impacted SES values inconsistently across metrics and sites (Fig. 4). Removing the rarest species did not consistently decrease phylogenetic diversity by any metric. At the high elevation site, removing the most abundant species did not change the SES for PD, slightly lowered SES for MPD, and increased the SES for MNTD (Fig. 4). Removing the least abundant species increased the SES for PD, MPD and MNTD, and the middle abundance species both increased and decreased SES values for all metrics depending on the species (Fig. 4).

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

Finally, at the low elevation site removal of the most and least abundant species lowered SES values by all metrics (Fig. 4). For both PD and MTD, SES values decreased with the removal of each of the top five most abundant species (Fig. 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 (Fig. 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 (Fig. 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 S4).

Removing groups of ten species in order of abundance also did not produce consistent patterns (Fig. 5). Removing the groups with the most rare species did not decrease SES for PD, and instead increased SES at all sites (Fig. 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 (Fig. 5). We only show results for PD here, as results for MPD and MNTD were similarly inconsistent (Appendix S5). Like the removal of individual species, we only removed groups of species based on abundance, because we found no phylogenetic signal in range size (Fig. 2B).

DISCUSSION

We hypothesized that rare species (quantified by local abundance and range size) would contribute disproportionately to phylogenetic diversity, but our results do not support our associated predictions. 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 this was not consistently the case. Our results are strikingly consistent in suggesting that rare species do not have disproportionately high contributions to phylogenetic diversity in this system.

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 percent cover. They then calculated breakpoints where phylogenetic diversity changed significantly from one species' addition to the next, but found that the location of statistically significant breakpoints was not consistently associated with more rare species (Herzog and Latvis, 2022). While we did not calculate breakpoints in our data, Herzog and Latvis's results are similar in that species' phylogenetic contributions are not consistently predictable based on rarity.

Based on our results, we find no evidence that rare species are phylogenetically distant from the rest of the community. However, we did not investigate their functional uniqueness, which would likely produce a different pattern. Phylogenetic diversity often correlates poorly with variation in individual traits (CaraDonna and Inouye, 2015; Gerhold et al., 2015; Maitner et al., 2022; E-Vojtkó et al., 2023), indicating that phylogenetic and functional diversity patterns are not interchangeable. Similarly, prioritizing phylogenetic diversity for conservation efforts does not always maximize functional diversity, even when traits show phylogenetic signal (Mazel et al., 2017). 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). Whether our rare RMBL plant

community members are functionally unique or redundant is unknown, but our results suggest at least that low abundance and small range size do provide redundancy in terms of phylogenetic diversity.

In contrast, Mi at al. (2012) tested for niche differentiation by comparing the phylogenetic diversity of rare and common species in temperate and tropical tree plots, and suggested that the niche differentiation hypothesis is supported in some of their plots because of rare species' phylogenetic distinctiveness. While we now know we cannot assume relatedness predicts niche space in a straightforward way (Mason and Pavoine, 2013; Davies et al., 2016; Blonder, 2018), Mi and colleague's results 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 are still present. If this were the case, it may still be true that rare species historically contributed the most phylogenetic diversity, but we would not know. We also measured the impact of the removal of one species at a time and in groups of ten, but patterns of actual loss in this system 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). We did not evaluate disturbance or historical species loss at our sites, and this would be an important avenue for future research in this system.

The addition of new species via invasions or range shifts may also drive declines in phylogenetic diversity (Selvi et al., 2016; Fitt and Lancaster, 2017; Daru et al., 2021), regardless of whether native species are declining. We know that range shifting and invasive species are impacting this system at the same time others are declining (Renwick et al., 2016; Zorio et al.,

2016; Shepard et al., 2022). We did not include non-native species in our analyses since quantifying their range size is more complex, and only four non-native species occur at low abundance in our plots to begin with. 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 newcomers may be important for future work.

Finally, it is notable that we did find phylogenetic signal in abundance but not in range size. Herzog & 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 for phylogenetic signal in range size with mixed results (Morin and Lechowicz, 2013; Zacaï et al., 2017; Pigot et al., 2018). Pigot and colleagues (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 is unique to introduced species. Morin and Lechowicz (2013) found weak but significant signal in range size in tree species in forest plots worldwide. Zacaï (Morin and Lechowicz, 2013; Zacaï et al., 2017; Pigot et al., 2018) and colleagues (2017) found that phylogenetic signal in range size varies regionally, and is likely influenced by spatio-temporal environmental stability over geological time. Each of these studies address range size across very broad spatial and temporal scales (Morin and Lechowicz, 2013; Zacaï et al., 2017; Pigot et al., 2018), while our study only includes present-day species native to the North American Rocky Mountains. This indicates that the scale tested likely influences whether or not range size shows phylogenetic signal, which is consistent with other scale-dependent community phylogenetic patterns (Cavender-Bares et al., 2009; Willis et al., 2009; Park et al., 2020).

CONCLUSIONS

We found that rare species do not contribute disproportionately to phylogenetic diversity, and both raise and lower phylogenetic diversity relative to richness depending on the identity of the species, elevation and phylogenetic metric. This finding is consistent with previous work (Mi et al., 2012; Herzog and Latvis, 2022), and suggests that rare species may add phylogenetic redundancy rather than diversity in this community. To further clarify the impact of rare species on biodiversity, future work should assess which species are disappearing, which species may have already gone locally extinct, the functional redundancy of rare species, and the impact of incoming species to the system.

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AUTHOR CONTRIBUTIONS

L.N.V. and K.M.D. conceived of the study. V.Z. collected field data. L.N.V. generated range size data and analyzed 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.

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.

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

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

Appendix S2: Species in our research sites listed with replacement species used from Smith & Brown's ALLMB.tre phylogeny (see also Methods).

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

Appendix S4: 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 S5: Results of additional phylogenetic diversity metrics (MPD & MNTD) from removing groups of species based on abundance.

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FIGURES & CAPTIONS

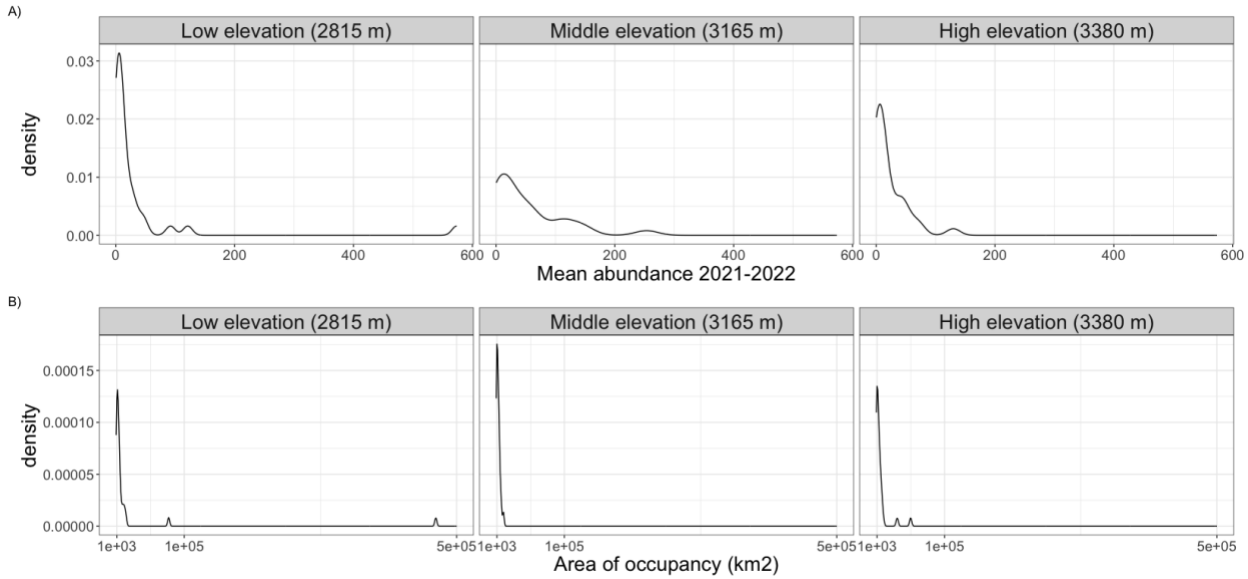
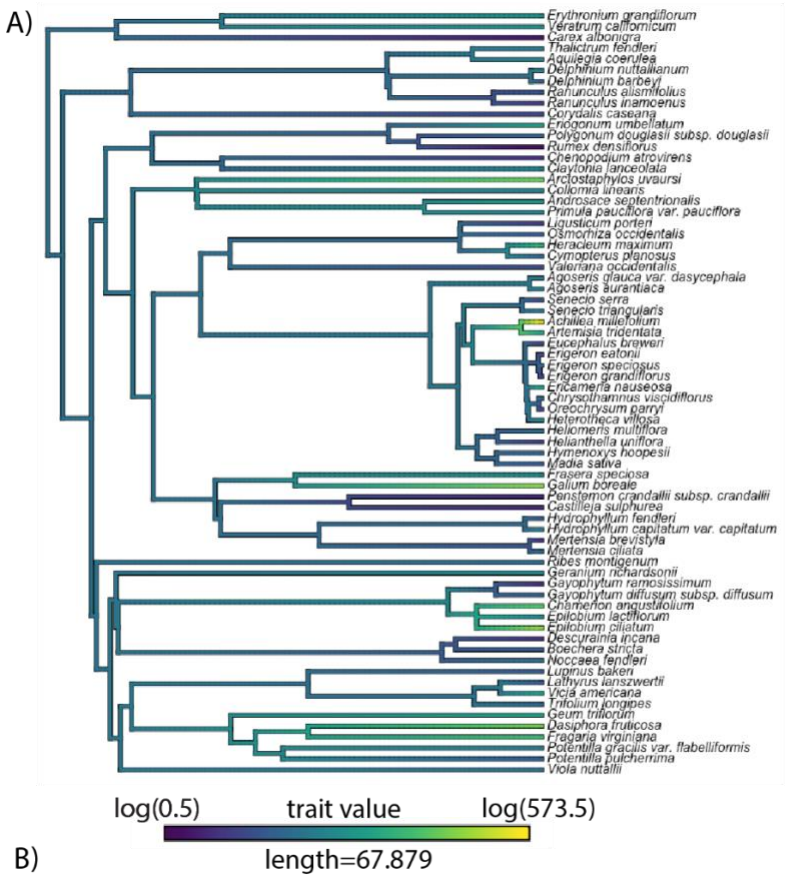
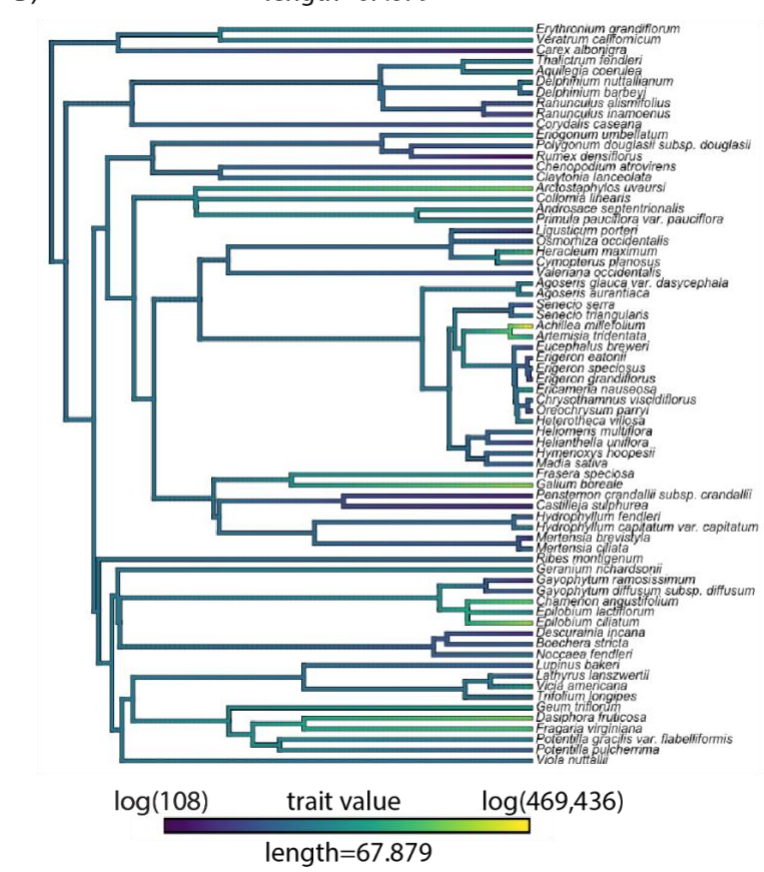


Figure. 1: Rank abundance (A) and range size (B) curves for RMBL species at each site.


A)
Erythronium grandiflorum
Veratrum californicum
Carex albonigra
Thalictrum fendleri
Aquilegia coerulea
Delphinium nuttallianum
Delphinium barbeyi
Ranunculus alismifolius
Ranunculus inamoenus
Corydalis caseana
Eriogonum umbellatum
Polygonum douglasii subsp. douglasii
Rumex densiflorus
Chenopodium atrovirens
Claytonia lanceolata
Arctostaphylos uvaursi
Collomia linearis
Androsace septentrionalis
Primula pauciflora var. pauciflora
Ligusticum porteri
Osmorhiza occidentalis
Heracleum maximum
Cymopterus planosus
Valeriana occidentalis
Agoseris glauca var. dasycephala
Agoseris aurantiaca
Senecio serra
Senecio triangularis
Achillea millefolium
Artemisia tridentata
Eucephalus breweri
Erigeron eatonii
Erigeron speciosus
Erigeron grandiflorus
Ericameria nauseosa
Chrysothamnus viscidiflorus
Oreochrysum parryi
Heterotheca villosa
Helomeris multiflora
Helianthella uniflora
Hymenoxys hoopesii
Madia sativa
Frasera speciosa
Galium boreale
Penstemon crandallii subsp. crandallii
Castilleja sulphurea
Hydrophyllum fendleri
Hydrophyllum capitatum var. capitatum
Mertensia brevistyla
Mertensia ciliata
Ribes montigenum
Geranium richardsonii
Gayophytum ramosissimum
Gayophytum diffusum subsp. diffusum
Chamerion angustifolium
Epilobium lactiflorum
Epilobium ciliatum
Descurainia incana
Boechera stricta
Noccaea fendleri
Lupinus bakeri
Lathyrus lanszwertii
Vicia americana
Trifolium longipes
Geum triflorum
Dasiphora fruticosa
Fragaria virginiana
Potentilla gracilis var. flabelliformis
Potentilla pulcherrima
Viola nuttallii
log(0.5)
trait value
log(573.5)
length=67.879


B)
Erythronium grandiflorum
Veratrum californicum
Carex albonigra
Thalictrum fendleri
Aquilegia coerulea
Delphinium nuttallianum
Delphinium barbeyi
Ranunculus alismifolius
Ranunculus inamoenus
Corydalis caseana
Eriogonum umbellatum
Polygonum douglasii subsp. douglasii
Rumex densiflorus
Chenopodium atrovirens
Claytonia lanceolata
Arctostaphylos uvaursi
Collomia linearis
Androsace septentrionalis
Primula pauciflora var. pauciflora
Ligusticum porteri
Osmorhiza occidentalis
Heracleum maximum
Cymopterus planosus
Valeriana occidentalis
Agoseris glauca var. dasycephala
Agoseris aurantiaca
Senecio serra
Senecio triangularis
Achillea millefolium
Artemisia tridentata
Eucephalus breweri
Erigeron eatonii
Erigeron speciosus
Erigeron grandiflorus
Ericameria nauseosa
Chrysothamnus viscidiflorus
Oreochrysum parryi
Heterotheca villosa
Helomeris multiflora
Helianthella uniflora
Hymenoxys hoopesii
Madia sativa
Frasera speciosa
Galium boreale
Penstemon crandallii subsp. crandallii
Castilleja sulphurea
Hydrophyllum fendleri
Hydrophyllum capitatum var. capitatum
Mertensia brevistyla
Mertensia ciliata
Ribes montigenum
Geranium richardsonii
Gayophytum ramosissimum
Gayophytum diffusum subsp. diffusum
Chamerion angustifolium
Epilobium lactiflorum
Epilobium ciliatum
Descurainia incana
Boechera stricta
Noccaea fendleri
Lupinus bakeri
Lathyrus lanszwertii
Vicia americana
Trifolium longipes
Geum triflorum
Dasiphora fruticosa
Fragaria virginiana
Potentilla gracilis var. flabelliformis
Potentilla pulcherrima
Viola nuttallii
log(108)
trait value
log(469,436)
length=67.879

628

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 (Blomberg's K = 0.304, P-value = 0.04, Pagel's λ = 0.926, P-value =0.168), while B) range size does not show any significant signal (Blomberg's K = 0.09, P-value = 0.7, Pagel's λ = 7.3×10^{-5}, P-value =1).

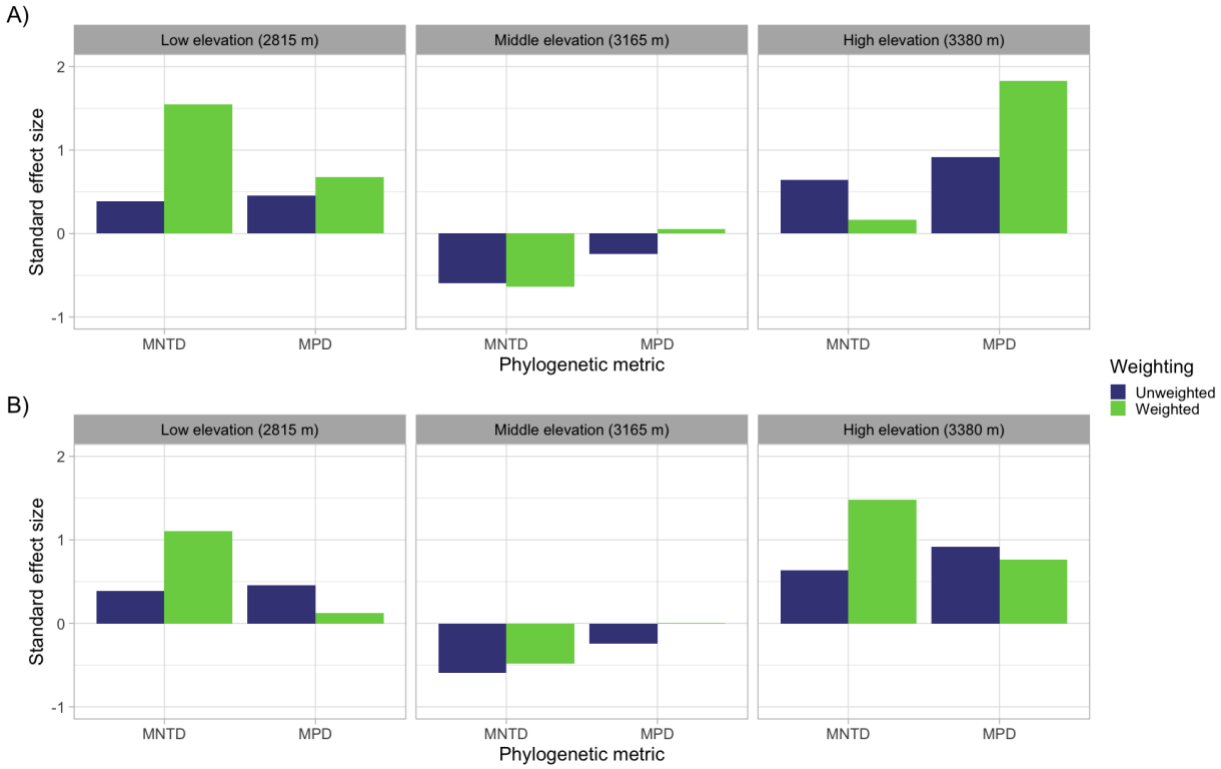


Figure 3: Standard effect sizes to compare weighted and unweighted MPD and MNTD. Unweighted values are in blue and weighted are in green. A) shows weighting by abundance. B) shows weighting by range size. Each of the three panels in A) and B) show the different sites. Weighting by abundance and range size does not significantly change MPD or MNTD in any of the sites.

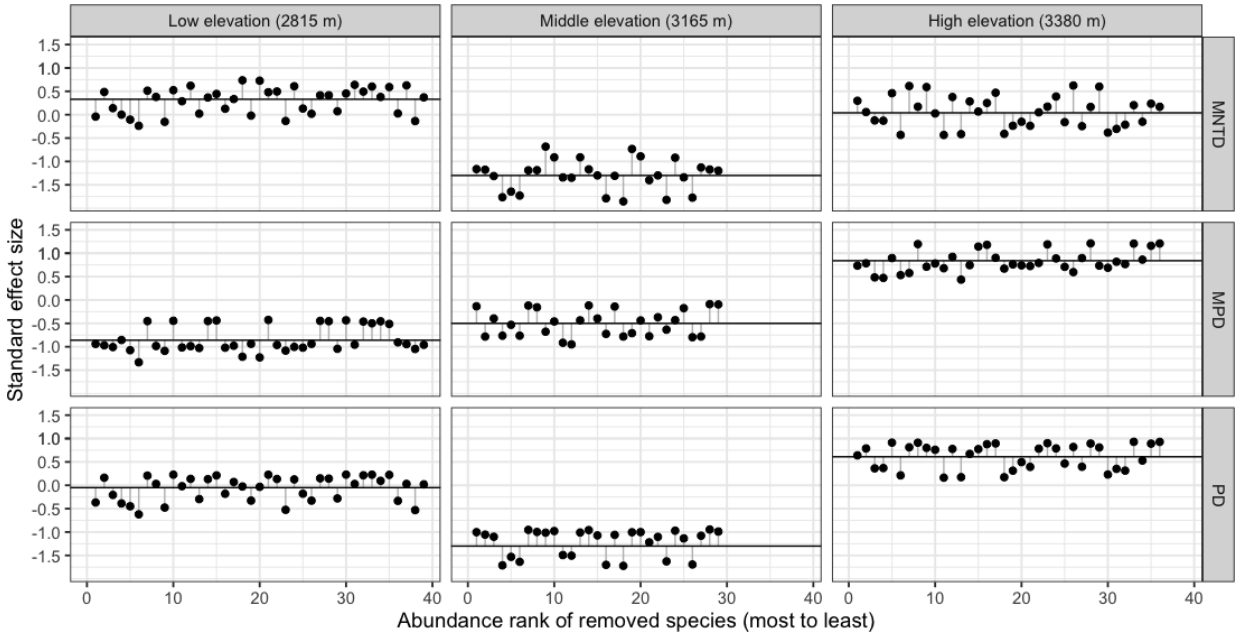


Figure 4: Change in SES values when individual species are removed in order of decreasing abundance. The horizontal black line in each figure shows the standard effect size of the metric for the overall community at each site, and dots show how the SES changes when the species at the rank indicated on the x-axis is removed. MNTD values are shown in the top row, MPD values are in the middle row, and PD are on the bottom. The left column shows the low elevation site, middle column is the middle elevation site, and right is the high elevation site. There is no clear pattern suggesting 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).

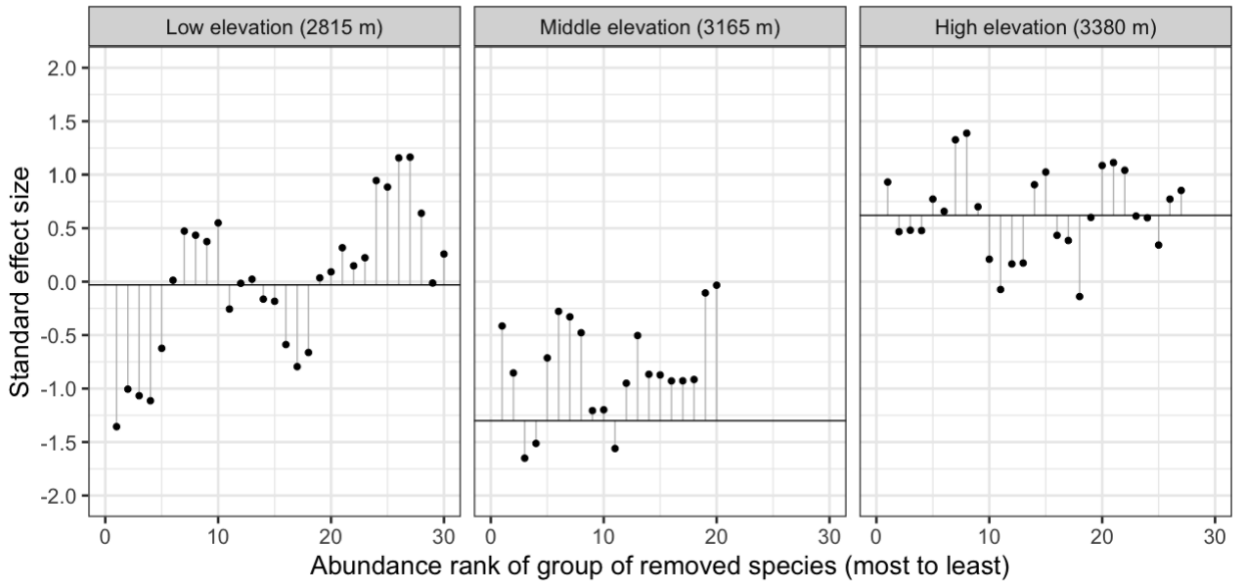
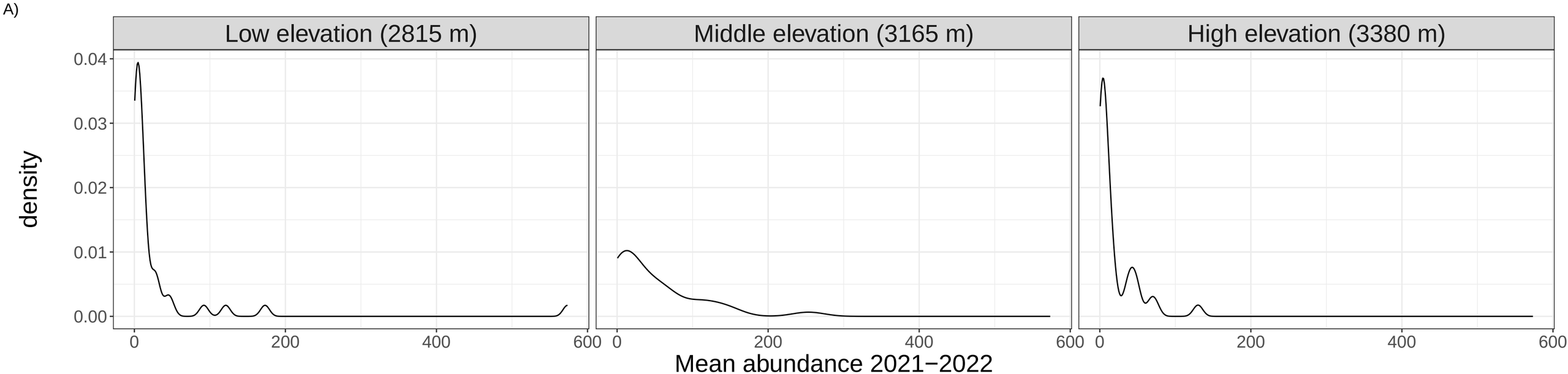
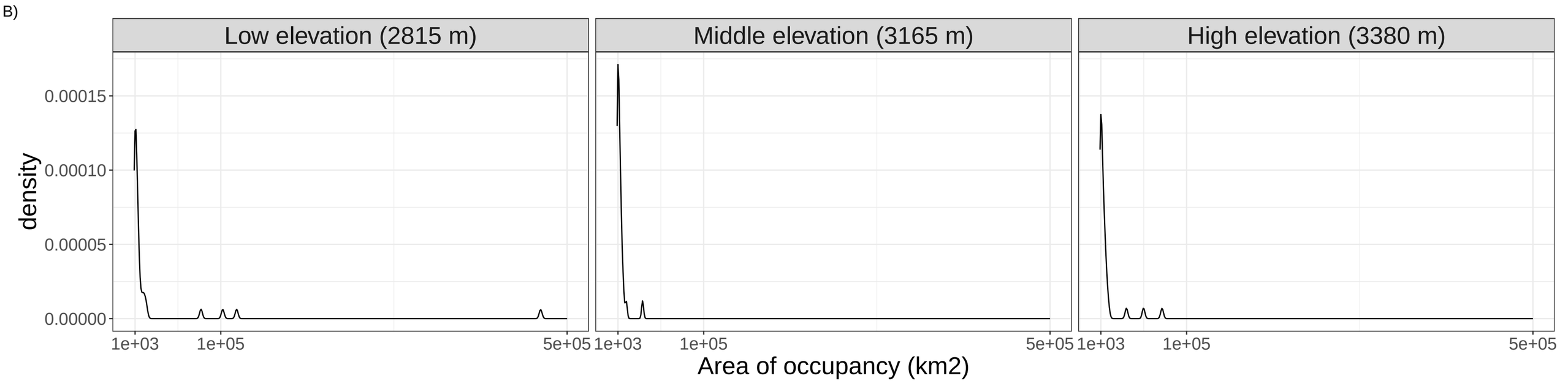
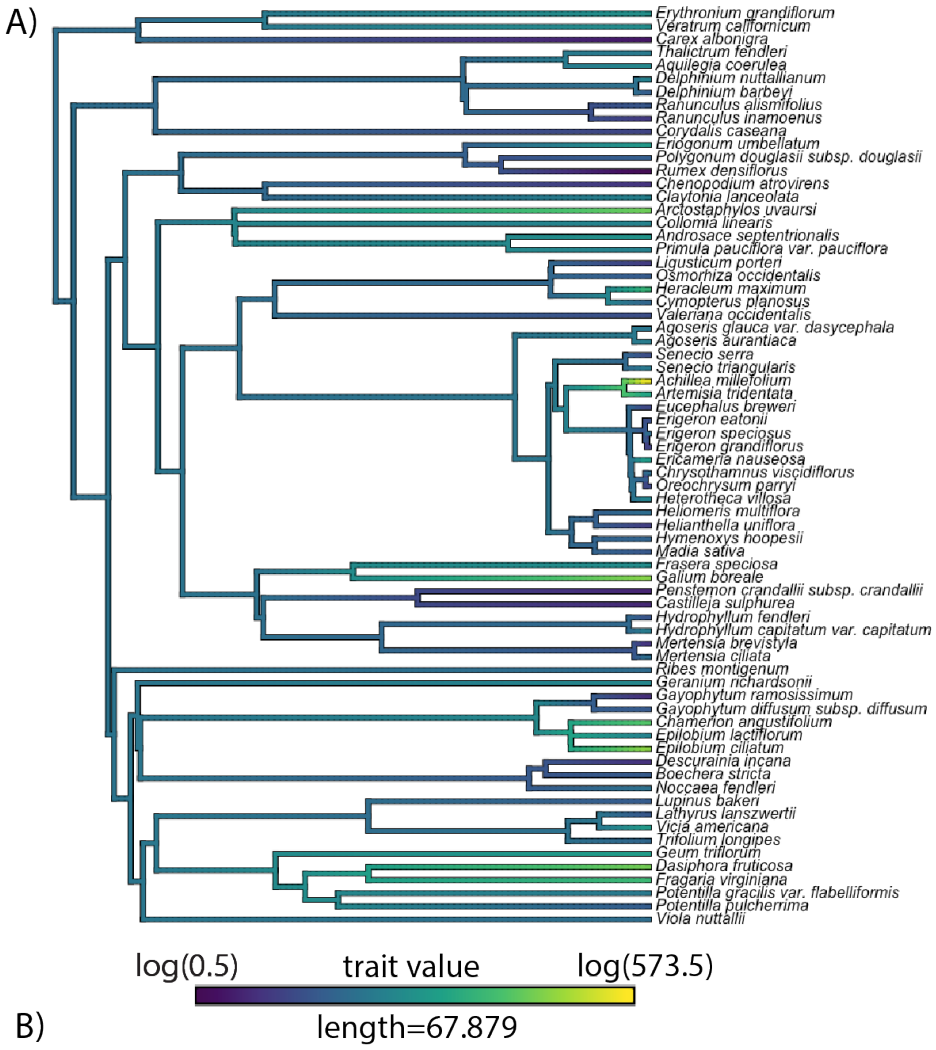


Figure 5: Change in SES values for PD when groups of ten species are removed in order of decreasing abundance. The horizontal black line in each figure shows the standard effect size of the metric for the overall community at each site, and dots show how the SES changes when the group is removed. Numbers on the x-axis are the ranking of 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. The left panel shows the low elevation site, middle panel is the middle elevation site, and right is the high elevation site. There is no clear pattern suggesting that removing rarer species (right side of each panel) decreases PD more than removing more abundant species (left side of each panel).


A)
Low elevation (2815 m)
Middle elevation (3165 m)
High elevation (3380 m)
density
0.04
0.03
0.02
0.01
0.00
0
200
400
600
Mean abundance 2021−2022


B)
Low elevation (2815 m)
Middle elevation (3165 m)
High elevation (3380 m)
density
0.00015
0.00010
0.00005
0.00000
1e+03
1e+05
5e+05
Area of occupancy (km2)


A)
Erythronium grandiflorum
Veratrum californicum
Carex albonigra
Thalictrum fendleri
Aquilegia coerulea
Delphinium nuttallianum
Delphinium barbeyi
Ranunculus alismifolius
Ranunculus inamoenus
Corydalis caseana
Eriogonum umbellatum
Polygonum douglasii subsp. douglasii
Rumex densiflorus
Chenopodium atrovirens
Claytonia lanceolata
Arctostaphylos uvaursi
Collomia linearis
Androsace septentrionalis
Primula pauciflora var. pauciflora
Ligusticum porteri
Osmorhiza occidentalis
Heracleum maximum
Cymopterus planosus
Valeriana occidentalis
Agoseris glauca var. dasycephala
Agoseris aurantiaca
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Helianthella uniflora
Hymenoxys hoopesii
Madia sativa
Frasera speciosa
Galium boreale
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Mertensia ciliata
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Geranium richardsonii
Gayophytum ramosissimum
Gayophytum diffusum subsp. diffusum
Chamerion angustifolium
Epilobium lactiflorum
Epilobium ciliatum
Descurainia incana
Boechera stricta
Noccaea fendleri
Lupinus bakeri
Lathyrus lanszwertii
Vicia americana
Trifolium longipes
Geum triflorum
Dasiphora fruticosa
Fragaria virginiana
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Viola nuttallii
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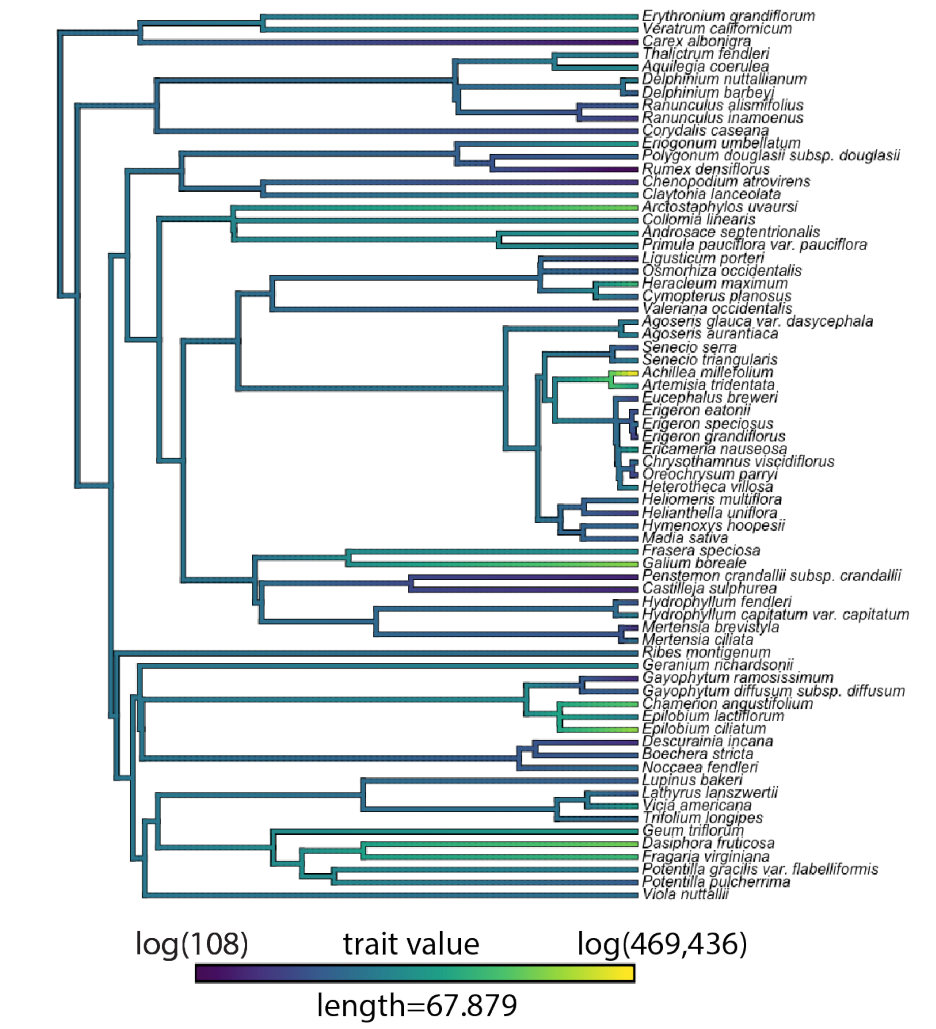
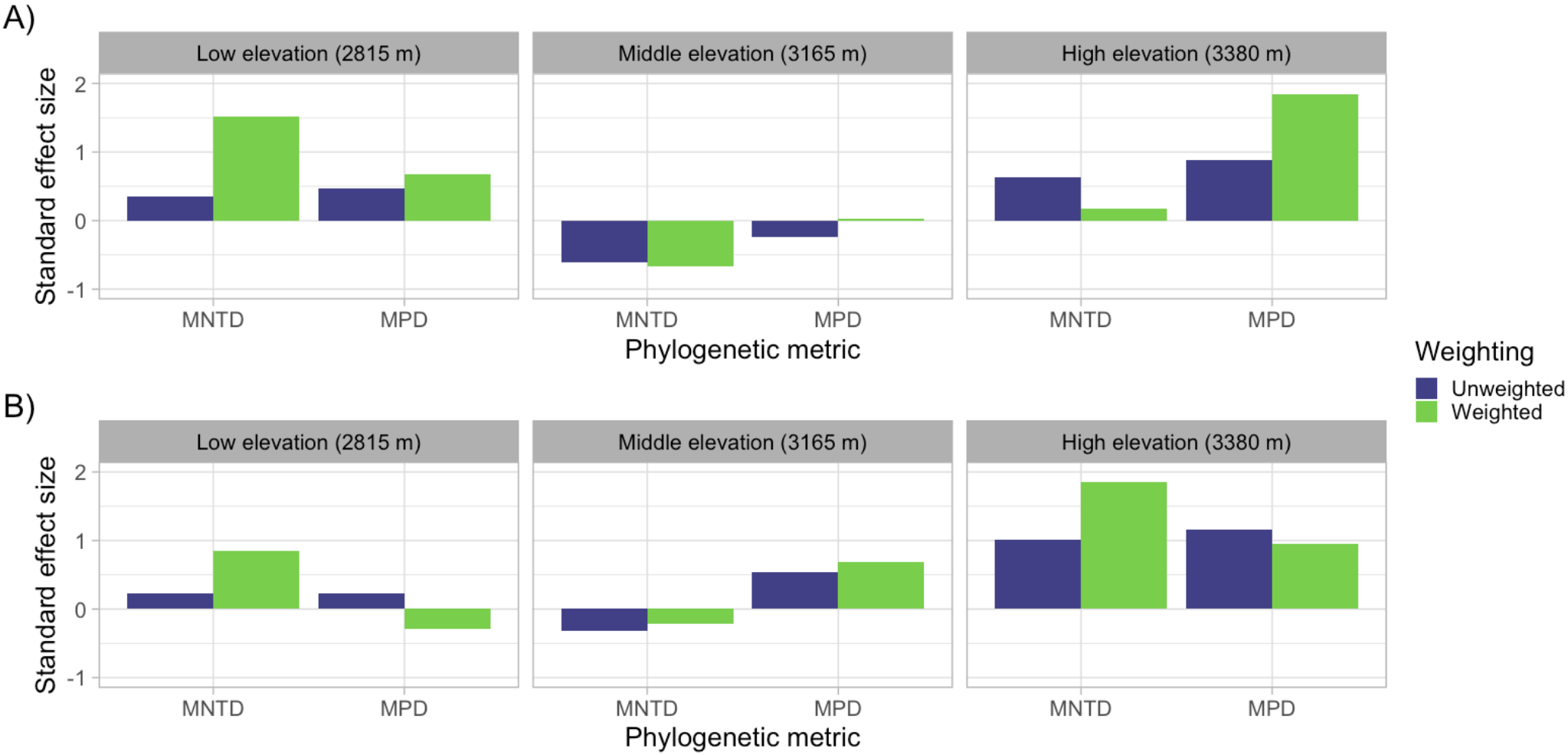
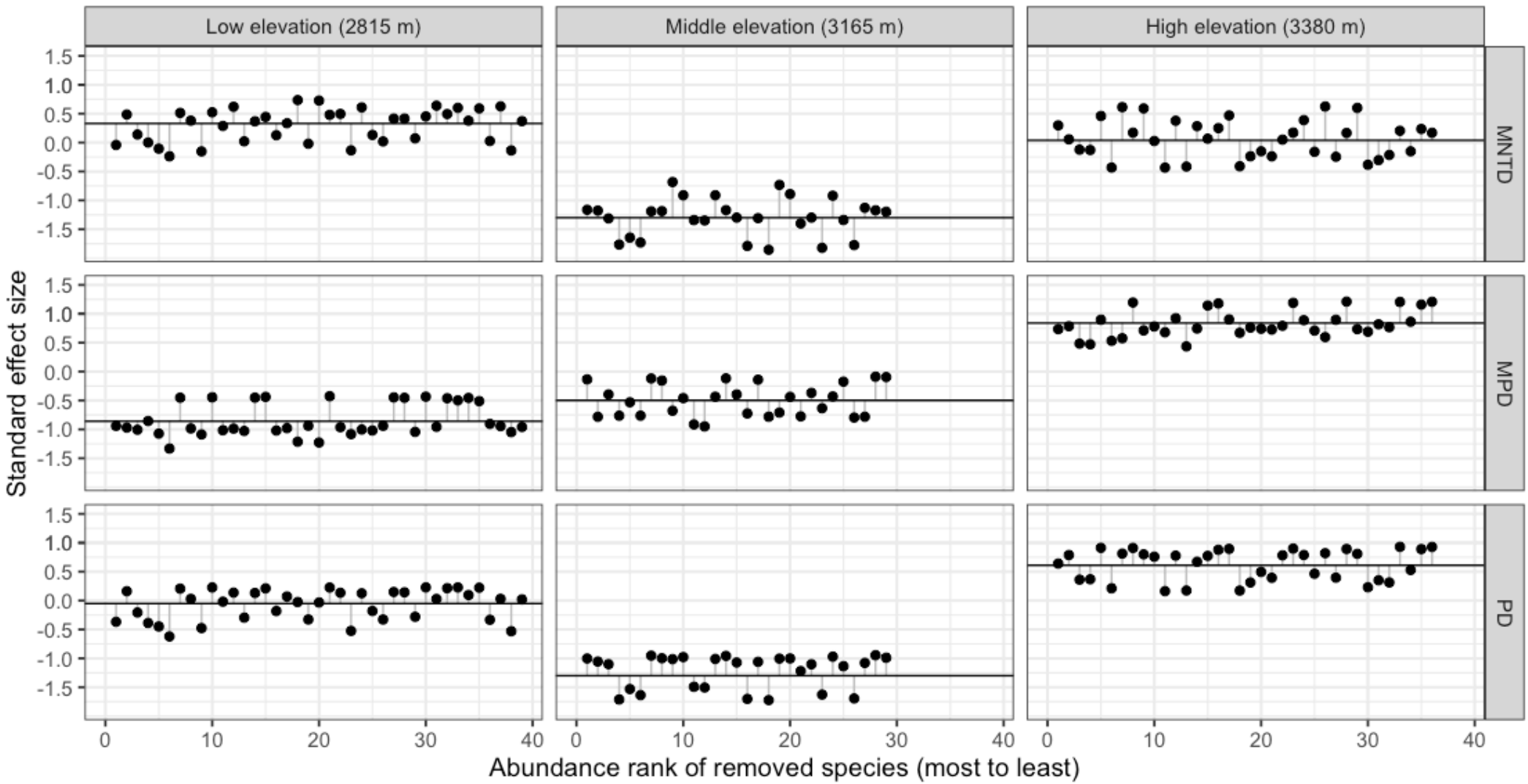
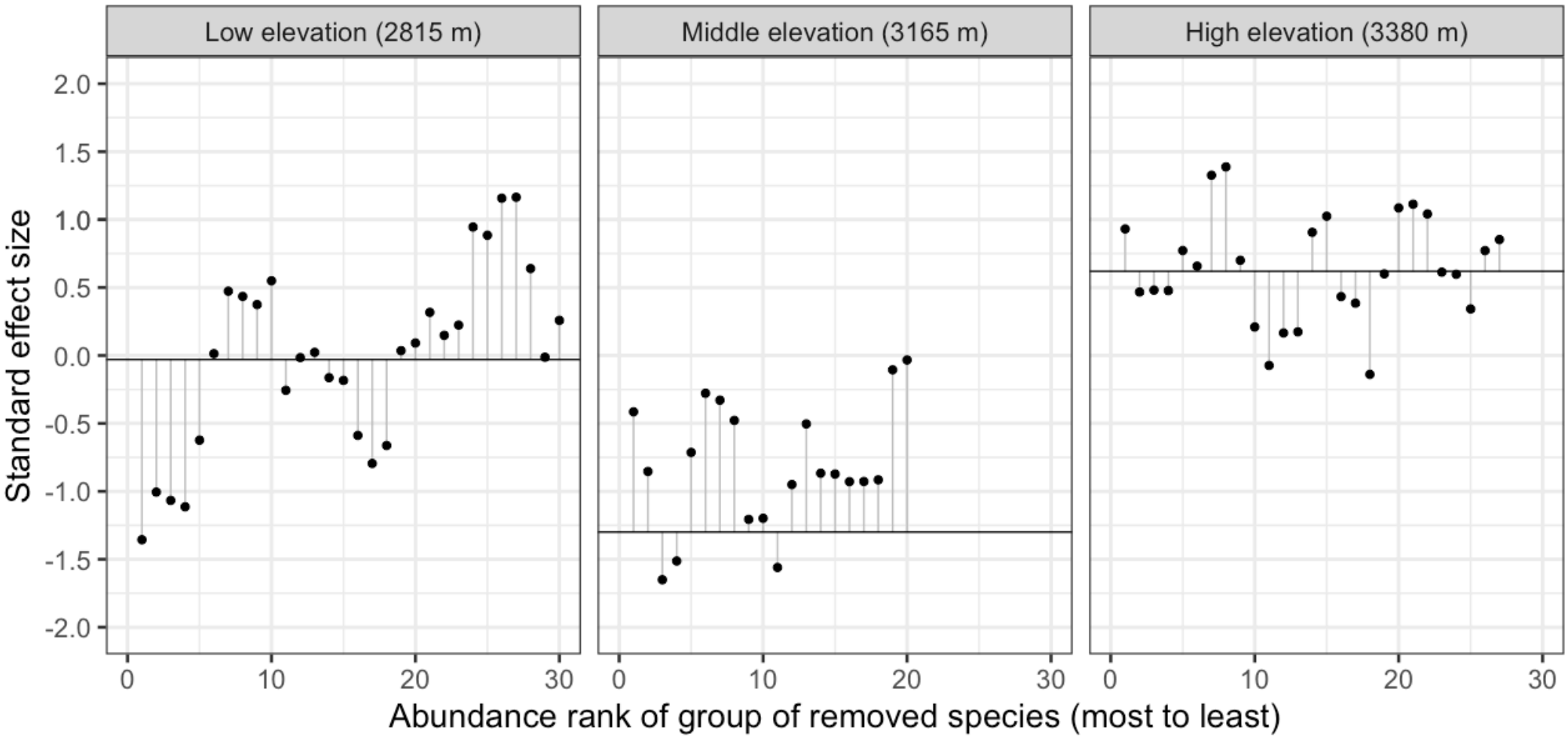

B)
Erythronium grandiflorum
Veratrum californicum
Carex albonigra
Thalictrum fendleri
Aquilegia coerulea
Delphinium nuttallianum
Delphinium barbeyi
Ranunculus alismifolius
Ranunculus inamoenus
Corydalis caseana
Eriogonum umbellatum
Polygonum douglasii subsp. douglasii
Rumex densiflorus
Chenopodium atrovirens
Claytonia lanceolata
Arctostaphylos uvaursi
Collomia linearis
Androsace septentrionalis
Primula pauciflora var. pauciflora
Ligusticum porteri
Osmorhiza occidentalis
Heracleum maximum
Cymopterus planosus
Valeriana occidentalis
Agoseris glauca var. dasycephala
Agoseris aurantiaca
Senecio serra
Senecio triangularis
Achillea millefolium
Artemisia tridentata
Eucephalus breweri
Erigeron eatonii
Erigeron speciosus
Erigeron grandiflorus
Ericameria nauseosa
Chrysothamnus viscidiflorus
Oreochrysum parryi
Heterotheca villosa
Heliomeris multiflora
Helianthella uniflora
Hymenoxys hoopesii
Madia sativa
Frasera speciosa
Galium boreale
Penstemon crandallii subsp. crandallii
Castilleja sulphurea
Hydrophyllum fendleri
Hydrophyllum capitatum var. capitatum
Mertensia brevistyla
Mertensia ciliata
Ribes montigenum
Geranium richardsonii
Gayophytum ramosissimum
Gayophytum diffusum subsp. diffusum
Chamerion angustifolium
Epilobium lactiflorum
Epilobium ciliatum
Descurainia incana
Boechera stricta
Noccaea fendleri
Lupinus bakeri
Lathyrus lanszwertii
Vicia americana
Trifolium longipes
Geum triflorum
Dasiphora fruticosa
Fragaria virginiana
Potentilla gracilis var. flabelliformis
Potentilla pulcherrima
Viola nuttallii
log(108)
trait value
log(469,436)
length=67.879


A)
Low elevation (2815 m)
Middle elevation (3165 m)
High elevation (3380 m)
Standard effect size
2
1
0
-1
MNTD
MPD
Phylogenetic metric
Weighting
Unweighted
Weighted
B)
Low elevation (2815 m)
Middle elevation (3165 m)
High elevation (3380 m)
Standard effect size
2
1
0
-1
MNTD
MPD
Phylogenetic metric


Low elevation (2815 m)
Middle elevation (3165 m)
High elevation (3380 m)
MNTD
MPD
PD
Standard effect size
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
0
10
20
30
40
Abundance rank of removed species (most to least)


Low elevation (2815 m)
Middle elevation (3165 m)
High elevation (3380 m)
Standard effect size
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
0
10
20
30
Abundance rank of group of removed species (most to least)