Alpine Botany
https://doi.org/10.1007/s00035-021-00261-y

ORIGINAL ARTICLE

Contrasting patterns of phylogenetic diversity and alpine specialization across the alpine flora of the American mountain range system

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Received: 28 January 2021 / Accepted: 31 May 2021

Abstract

Although mountainous habitats contribute substantially to global biodiversity, comparatively little is known about biogeographic patterns of distributions of alpine species across multiple mountain ranges. Here, we present a detailed analysis of the distributions and phylogenetic affinities of alpine seed plant lineages across North, Central, and South American mountain systems. Using a large dataset that characterizes the elevational niches of American seed plants in a continuously valued way, we related the proportion of alpine habitat occupied by plant lineages to their biogeographic distributions at a regional scale and place these results in a phylogenetic context. We found alpine species diversity to be greatest in the central Andes and western North America, and that assemblages with lower phylogenetic diversity contained species with a greater degree of alpine specialization. In particular, near-Arctic/boreal alpine communities were characterized by low phylogenetic diversity and higher degrees of alpine specialization, whereas the opposite was observed for southern Patagonian communities. These results suggest that abiotic filtering alone in these climatically similar regions is unlikely to explain alpine community assembly. Nevertheless, the overall relative rarity of alpine specialists, and the tendency for such specialists to be most closely related to montane lineages, suggested that filtering was still an important factor in shaping alpine community structure. This work corroborates the importance of a nuanced and scale-dependent perspective on the 'history-filtering' debate axis, as both factors have likely contributed to modern biodiversity patterns observed in alpine plant communities across the Americas.

Keywords Alpine flora · American flora · Elevation niche · Montane flora · Phylogenetic diversity

Introduction

Despite representing less than 25% of terrestrial surface (Körner et al. 2011), mountains harbor exceptional biodiversity (Myers et al. 2000; Körner 2003, 2004; Kreft and Jetz 2007; Kier et al. 2009; Körner et al. 2011; IPBES 2019; Rahbek et al. 2019a, b; Brummitt et al. 2021). High-elevation habitats offer potential cooler-climate corridors for plant dispersal (Antonelli et al. 2009), and their topographic complexity provides myriad microclimatic niche space for

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plants to become established and survive (Körner 2003). Nevertheless, many questions remain unanswered regarding the biogeography (Rahbek et al. 2019a, b) and phylogenetic composition (González-Caro et al. 2020) of higher-elevation assemblages. Additionally, historical and biogeographic processes, such as climatic cycles and glaciations, have fragmented and reconnected alpine "sky islands" (Marx et al. 2017). This intermittent connectivity across time has further promoted high levels of diversification and endemism in some of the hottest spots of diversity, such as the Andean mountain chain (Hughes and Eastwood 2006; Flantua et al. 2019) and the Tibet–Himalaya–Hengduan region (Hughes and Atchison 2015; Ding et al. 2020).

The complexity of mountain biodiversity is further evidenced by changes in species richness (Guo et al. 2013) and turnover (McFadden et al. 2019; Smithers et al. 2020) across elevational gradients. Such patterns have prompted researchers to delimit different elevational zones across the globe in a systematic way. In particular, Körner et al. (2011) defined seven life thermal belts based on bioclimatic and topographic characteristics: the nival (perpetual snowline), upper alpine, lower alpine (tree line estimate), upper montane, lower montane, remaining mountain area with frost, and remaining mountain area without frost. These thermal zones account for latitudinal differences in the absolute elevation of alpine and montane habitats (Körner et al. 2011) and provide a biologically meaningful and geographically robust assessment of different elevational belts. Further, these elevational categories allow for comparisons of biodiversity patterns across different mountain ranges at large biogeographic scales (Körner et al. 2011). Such a systematic approach is invaluable for studies seeking to draw general, macro-ecological and biogeographic inferences about processes structuring higher-elevation assemblages across different mountain systems. This is especially important since, although it is clear that the combined history of orogeny, uplift, erosion, and climatic cycles has altered the landscape of mountains and mountain ranges in complex ways, the proximate sequence and timing of events that built the biodiversity we observe is still an open question.

Despite the importance of mountains for biodiversity, few studies have formally synthesized plant diversity patterns within and across mountain regions (Körner 1995,2004). In particular, comparatively little is known about the biodiversity of the alpine life zone (including the nival, upper and lower alpine thermal belts). Alpine zones are characterized by extreme environments at the physiological limits of plant life (Körner 2003) and represent one end of the available niche spectrum in mountain regions. Alpine zones are also at the elevational limits of available terrestrial terrain (Elsen and Tingley 2015), and lineages specializing in this niche space are at risk for being extirpated as lowland species move up slope as a result of climate change and potentially outcompete alpine endemics or leave them with no further habitat upslope (Millar and Fagre 2007; Kelly and Goulden 2008; Morueta-Holme et al. 2015; Steinbauer et al. 2018; Moret et al. 2019).

Crucially, several knowledge gaps about general patterns of alpine plant diversity remain: (1) how alpine community richness varies across latitude and among different mountain regions; (2) whether alpine communities are phylogenetically clustered or over-dispersed relative to the regional (e.g., montane) species pool (but see the recent study by Qian et al. 2021); (3) which lineages dominate in alpine communities and which lineages exhibit the highest turnover (beta-diversity) between mountain regions; and (4) how such lineage-specific patterns relate to processes of abiotic filtering, dispersal limitation, and historical (biogeographic) contingency.

Such macro-scale patterns in the composition and diversity of alpine communities likely arise from differing richness and phylogenetic diversity patterns among individual lineages comprising these assemblages. Therefore, an appreciation for the contributions that specific lineages make to total alpine diversity is also needed, as such contributions may reflect the confluence of historical processes, filtering, and ecological dynamics. For example, the *Astragalus/Oxytropis* complex is a primary component of Fabaceae diversity across the Americas (Amiri et al. 2020), including alpine habitats; however, the origins of the clade are likely Eurasian (Bagheri et al. 2017; Amini et al. 2019). It is therefore plausible that adaptations to cold or higher elevations arose in this lineage prior to the assembly of any one particular modern American alpine community. In contrast, Solanales diversity in the Americas is concentrated within South America, where the clade is believed to have originated (Olmstead 2013). The contribution Solanales make to American alpine assemblages might therefore be expected to reflect this distinct biogeographic history. Synthesizing how different biogeographic legacies of particular alpine lineages combine with lineage-specific physiological constraints and ecological filters to produce modern alpine assemblages would greatly enhance our current understanding of alpine biodiversity overall.

In addition to these questions regarding alpine community assembly and dynamics, the ability to discern macroecological patterns is also limited by data availability. Alpine floras, especially those in the Andes, are often composed of numerous range-limited endemics (Hughes and Eastwood 2006), sometimes known only from single mountain peaks. Data for such species can be equally scattered and diffuse (e.g., Sklenář and Balslev 2005; Al-Shehbaz 2018), creating significant challenges for addressing general questions regarding alpine plant ecology across different mountain ranges or through time. Defining the distributions of such narrowly distributed species and assessing the contributions of these lineages to the overall patterns of alpine biodiversity at larger spatial scales is an ongoing challenge.

In this study, we use georeferenced species occurrence records from digitized herbarium databases and climate data to build species distribution models (SDMs) and present a detailed investigation of alpine seed plant biodiversity across North, Central, and South American mountain ranges. We use this dataset to achieve two broad goals. First, we characterize general, macro-ecological and biogeographic diversity patterns among alpine communities, such as latitudinal diversity gradients, phylogenetic diversity of alpine assemblages, and turnover in alpine community composition. Distribution models allowed us to continuously define the niche space of each species in the American mountains, distinguishing alpine specialists from generalists and mapping their diversity to quantify the degree of alpine specialization across different mountains. Second, we use our conservative data cleaning protocol to critically assess the quality of currently available occurrence data for such macro-ecological questions of alpine communities and address potential regional biases in data availability whose eventual resolution might greatly enhance the current state of knowledge on alpine community assembly.

Methods

Species distributions and niche characterization

For this study, we utilized a previously assembled dataset characterizing the elevation and climate niches of 72,372 seed plant species across the Americas using occurrence records and species distribution models (SDMs; Figueroa et al. *in review*). Briefly, this dataset was assembled by aggregating georeferenced occurrence records from the Global Biodiversity Information Facility (GBIF) and Integrated Digitized Biocollections (iDigBio). Occurrence records were initially cleaned separately using aggregator-specific flags detailed in Figueroa et al. (*in review*). The full dataset of occurrence records is accessible and fully described in the Dryad data repository at (https://doi.org/10.5061/dryad.9cnp5hqgx) and (https://doi.org/10.15468/dl.gtgtt5).

Aggregated GBIF and iDigBio records were further processed by excluding points with any of the following issues: (1) falling outside the study area (the Americas); (2) less than four decimal point precision (~ 11 m near the equator); (3) duplicate localities for a species (rarefaction); (4) falling outside polygons describing accepted species' distributions (as defined by Plants of the World Online, POWO; www.github.com/tdwg/wgsrpd; Brummitt 2001); and (5) species with fewer than twelve records (to build reliable models). Cleaned records were then passed to MaxEnt (version 3.1.4; www.github.com/mrmaxent/Maxent; Phillips et al. 2004, 2006) along with 2.5' resolution climate data from WorldClim (Fick and Hijmans 2017) to build SDMs for the range of each species across the Americas (full set of models available at https://doi.org/10.5061/dryad.9cnp5hqgx).

Having obtained SDMs for all 72,372 species in our dataset, we characterized elevational niches by parsing each SDM into different elevational categories. We first used the 2.5' shapefiles from the Global Mountain Biodiversity Assessment (GMBA 2010; Körner et al. 2011, 2017) to spatially define mountainous habitats (376 individual mountains, and 8 large-scale mountain ranges: Andes, Appalachia, Columbia, Cascades, Interior, Rockies, Sierra Madre, West Coast) in the Americas and then used the seven isothermal belt zones of (Körner and Paulsen 2004; Körner et al. 2011) to delimit elevational categories as montane, alpine, and lowland habitat areas within each mountain range. These zones integrate temperature, growing season length, and topographic information to provide a robust and biogeographically relevant assessment of the extent and type of montane and alpine habitat across the globe. They further permit an assignment of species distributions along elevational gradients despite latitudinal differences in what constitutes montane and alpine areas (see Table 2 in Körner et al. 2011 for precise climatic zone definitions). Because these elevational categories were built at 2.5' resolution, all of our analyses were matched to this for consistency.

To accommodate lineages that experience varied climate across their ranges, we characterized niches as continuously valued distributions and not as discrete scalar values. This allowed us to quantify the fraction of each species' range falling within either alpine, montane, or lowland habitat, rather than having to bin species arbitrarily in each category. This distinction is important for how biologists classify alpine species (Körner 2003) and allowed us to distinguish between species whose ranges were centered in alpine habitat (termed 'specialists'; defined below) from those whose ranges extended into the alpine zone but were centered elsewhere (termed 'generalists'; defined below and in Fig. 1). Except when drawing comparisons with non-alpine species, the analyses presented here were performed only on species with elevational niches falling within the alpine (specialist or generalist) elevation category (Fig. 1).

Assigning alpine specialist and generalist categories

Using the SDMs and niche characterization described above, each of the 72,372 species in the dataset was assigned one of five, mutually exclusive, categories, as detailed in Fig. 1: (1) alpine specialist; (2) alpine generalist-primarily montane; (3) alpine generalist-primarily lowland; (4) non-alpine primarily montane; or (5) non-alpine primarily lowland. Alpine specialists were defined as having at least 50% of their modeled

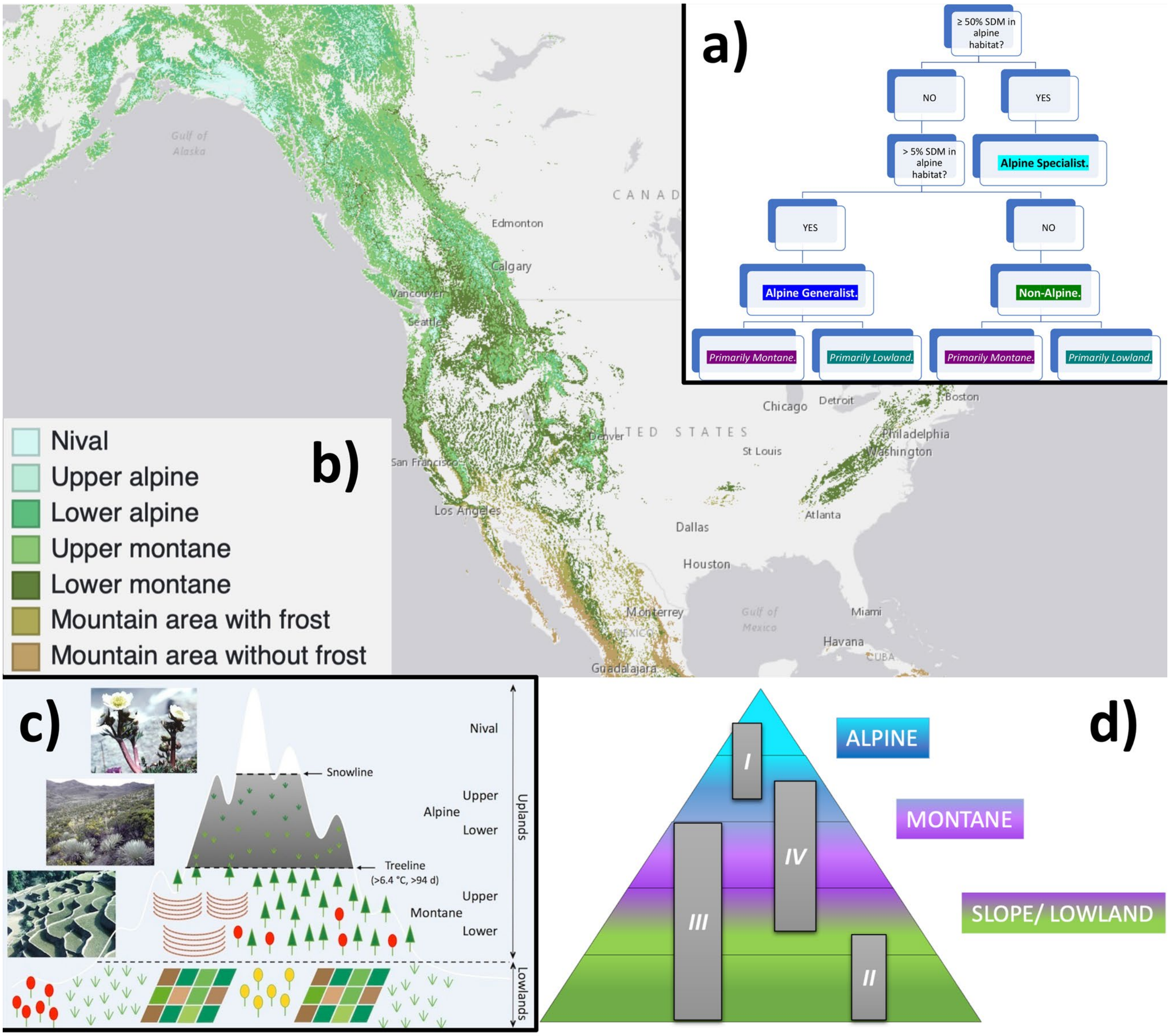

Fig. 1 Conceptual illustration of elevational categories and species pool differences. **a** Decision tree used to categorize American seed plants as alpine specialists or generalists based on their species distribution model (SDM). The sub-categories of primarily montane or lowland were assigned based on where the majority of the non-alpine range occurred. **b** The seven thermal life belts of Korner et al. (2017) shown in geographic context of North America as an example. **c** Schematic depiction of the seven thermal life belts of Korner et al. (2017) along a single mountain. The illustrations in (**b**) and (**c**) were adapted directly from (https://www.gmba.unibe.ch), which defined these categories. (**d**) Schematic illustrating how species (indicated by roman numerals) might be distributed along elevational gradients, with gray bars indicating the elevational niche breadth of each species. *Species I* has a range centered in the alpine belt and therefore would be classified as an alpine specialist. *Species II* has a range centered in lowlands that does not extend into the alpine region and would thus be a non-alpine and primarily lowland species. Both *Species III* and *IV* have ranges that extend into the alpine belt but are centered elsewhere and would therefore be classified as alpine generalists. The range of *Species IV* is centered in montane habitat, giving this species a sub-category of primarily montane

range in alpine habitat. Alpine generalists had less than 50% but at least 5% of the modeled range in alpine areas. Non-alpine species had less than 5% of the modeled range within alpine regions. The sub-categories of primarily montane or lowland were assigned based on whether a majority of the remaining (i.e., non-alpine) range occurred in montane or lowland habitat, respectively. By categorizing the elevational strategy of every species in the dataset, we were also able to examine the distribution of elevational strategies for the closest relatives of each alpine species (phylogenetic relationships among species defined as described below), and to assess whether alpine specialists were more closely related to other specialists or species occurring primarily at lower elevations.

Alpine species richness and biogeographic variation in specialization

To investigate spatial diversity patterns of alpine species across the American mountain systems, we gridded North, Central, and South America (the 'study area') into 0.5° cells (termed 'sites'). We then used a combination of approaches to determine species presence within a given site. First, we converted the SDMs describing species ranges into binary matrices indicating potential presence or absence (potential presence was defined as the SDM scoring at least 2% for that species in that site). We then masked these binary matrices by GMBA mountain shapefiles defining the geographic boundaries of all mountains and mountain ranges within the study area (Körner et al. 2017). These steps produced a potential species list for all sites within higher-elevation habitat. We then filtered potential lists by including only those species categorized as alpine specialists or generalists (Fig. 1). Summarized alpine species lists (i.e., only including those species categorized as alpine specialist or generalist) based on these methods are deposited with Dryad (https://doi.org/10.5061/dryad.4qrfj6q8v), along with a taxonomy for these alpine species (Online Resource 2).

Species richness was obtained by counting the number of alpine species predicted to be present within each site. Each phylogenetic diversity metric was similarly calculated based on the alpine species predicted to be present at each site. We also provide a metric summarizing each site's average degree of alpine habitat specialization. To assess this, we asked which species were present at each site as well as what fraction of each species' total modeled range (i.e., across all American mountains) fell within alpine habitat. We then averaged this fraction of alpine habitat among all species present within each site.

Phylogeny, taxonomy, and phylogenetic diversity

Phylogenetic relationships among American seed plants were defined by Smith and Brown (2018; ALLMB phylogeny), and polytomies were left unresolved. The backbone taxonomy from the World Checklist of Selected Plant Families (WCSP 2020) was used to match species to taxonomic families and orders as defined by the Angiosperm Phylogeny Group (APG IV 2016). Such taxonomic categories (e.g., in comparisons of relative occurrence) were used to highlight the distributions and prevalence of biologically relevant groups that are of interest to alpine botanists and not meant to imply that such rankings demarcate equivalent biological units. There were relatively few gymnosperms among the alpine species in our dataset, and none among alpine specialists. Among these, only *Lepidothamnus fonkii* and species of *Ephedra* were likely true alpine (i.e., non-tree) species. The remaining gymnosperms (*Pinus, Picea, Larix, Tsuga, Abies*, and *Thuja*) were tree species whose ranges extend to such high elevations that they sometimes fell within the GMBA lower alpine belt and were therefore classified as alpine generalists. As a result, we did not organize gymnosperm taxonomic families or orders as we did with angiosperms. However, because our broader dataset includes all American gymnosperms, these species are represented in the figures and phylogenetic diversity analyses where relevant.

Phylogenetic diversity was measured with the Phylogenetic Diversity Index (PDI), Mean Nearest Taxon Distance (MNTD), and Mean Pairwise Distance (MPD) using the 'PHYLOMEASURES' package (Tsirogiannis and Sandel 2017) in the R statistical computing environment (R Core Team 2020). This package provides functionality to standardize phylogenetic diversity metrics by species richness to overcome some of the non-independence between richness and phylogenetic diversity measures (Tsirogiannis and Sandel 2016; but see Sandel 2018). Sites with negative phylogenetic diversity values were interpreted as 'clustered', and sites with positive values as 'over-dispersed' (or phylogenetically 'even'). Although we acknowledge that quantitative comparisons of such diversity metrics across sites with very different richness and filtering/ selective processes should be taken with caution (Sandel 2018), here we have drawn general comparisons along the mountain systems of the Americas that do not depend on strict quantitative comparisons between individual sites. We assessed phylogenetic diversity among American alpine species (as defined in Fig. 1), American high-elevation seed plant species (defined as having at least 5% of their SDM in montane or alpine habitat), and among all American seed plants in the larger dataset of Figueroa et al. (*in review*). Note that clustering of alpine sites here therefore indicates assemblages more closely related than expected in the context of American alpine lineages, whereas the assessment of phylodiversity in Qian et al. (2021) compares alpine phylodiversity to the surrounding communities at lower elevations.

Dataset considerations

Our data cleaning and filtering methods created a robust, biologically informed, and conservative estimate of the distributions of seed plants across the Americas well-suited for addressing general macro-scale questions of biodiversity patterns. However, because our methods involved excluding species with fewer than twelve occurrence records to have sufficient climate variability when building reliable models, there was the possibility of missing small-scale endemic species that might be of particular relevance to alpine biodiversity (discussed in Figueroa et al. *in review*). One type of bias that could occur with this method would be preferential loss of species from alpine communities. Examining the geographic distribution of seed plant records before and after the filtering step that excluded species with fewer than twelve points did not reveal any elevational biases based on the number of records available (Supplemental Fig. S1). Geographic bias in species excluded by our method was another possibility, particularly for Andean alpine communities which are rich in endemic species (Hughes and Eastwood 2006). Online Resource 3 provides a list of some Andean alpine taxa excluded by our conservative data cleaning and filtering protocol that demonstrate such a geographic bias in data availability (see "Discussion").

Results

Dataset coverage and species richness

Data cleaning and filtering methods resulted in a dataset of 2937 American alpine seed plants (~ 7% of all higher-elevation species, alpine or montane, $N = 35{,}952$). Of these, 96 (representing 54 genera) were classified as alpine specialists, whose modeled range was centered (i.e., at least 50%) within alpine habitat. The remainder ($N_{\text{species}} = 2841$; representing 709 genera) were classified as alpine generalists (i.e., between 5 and 50% of modeled range within alpine regions). Alpine species richness did not follow a unimodal latitudinal gradient (Fig. 2; see Supplemental Fig. S2 for combined alpine and montane American seed plant species richness). Instead, richness was highest in both the northern Rockies/western ranges of North America, and the central Andes of South America (i.e., species richness was latitudinally bimodal). Summarized species lists of alpine communities within each mountain and major mountain ranges were deposited with Dryad (https://doi.org/10.5061/dryad.4qrfj6q8v).

Phylogenetic distribution of alpine taxa

Alpine species were distributed broadly across the American seed plant phylogeny, with specialists occurring in most major angiosperm clades (Fig. 3 and Supplemental Fig. S3). Overall, 717 genera contained at least one alpine species (specialist or generalist), spread across 131 taxonomic families (41% of all families represented in our dataset). Nevertheless, alpine species were not distributed evenly across clades. Ten families (Fig. 4) contained ~ 50% of all alpine species, and Asteraceae and Poaceae jointly accounted for just under 23%. Additionally, many families (~ 59%, $N = 187$) represented in the American angiosperm phylogeny did not include a single alpine species (Supplemental Table S1a, b), and, in fact, entire orders were without alpine species in the Americas (~ 31%, or $N = 20$, orders present in the dataset but absent from alpine communities). Online Resource 2 provides a taxonomy of alpine species included in this study along with their familial and ordinal placements as defined by APG IV.

Spatial distribution of alpine taxa

At the family level, alpine diversity varied among different American mountain ranges. Although ten families comprised almost half of all alpine species in our dataset, the relative frequencies of these ten families differed markedly between mountain ranges (Fig. 4). For instance, Solanaceae in our dataset occurred exclusively in the Andes, and Poaceae dominated in the Sierra Madre. Although Cyperaceae ranked as only 4th overall among all alpine species, this family was either the first or second most species-rich family in all major mountain ranges except the Andes and Sierra Madre. Additionally, familial prevalence varied according to the mountain range (Supplemental Fig. S4). For instance, Poaceae were more frequent in Central and South American mountains whereas Asteraceae occurred more commonly in North America.

Distributional biodiversity patterns at the level of plant orders mostly mirrored those of the overall bimodal diversity across all alpine species (Supplemental Fig. S5). However, some orders, such as Fabales and Lamiales, were much more diverse in the Andes, whereas other orders, such as Ericales, Brassicales, and Saxifragales, had higher diversity in the northern Rockies and West Coast mountains. Regardless of spatial scale (individual mountains or mountain ranges), Poales were always the most dominant order. Figure 5 highlights latitudinal turnover in alpine community composition for the Rockies and the Andes (see Supplemental Fig. S6 for other mountain range systems).

Phylogenetic diversity and alpine specialization

This montane and alpine dataset is nested within a larger dataset describing the climatic niches of 72,372 American seed plants (described elsewhere, Figueroa et al. *in review*). To examine the phylogenetic affinities of alpine specialists, we summarized the elevational strategies of each specialist species' phylogenetic nearest neighbor within the American seed plant phylogeny. Among alpine specialists in our dataset, ~ 62% ($N = 59$) did not have another specialist among their closest relatives, and for 89% ($N = 85$) the most common strategy among nearest phylogenetic neighbors was a primarily montane distribution.

We measured phylogenetic diversity among American alpine species within each range using species-richness standardized versions of the Phylogenetic Diversity Index

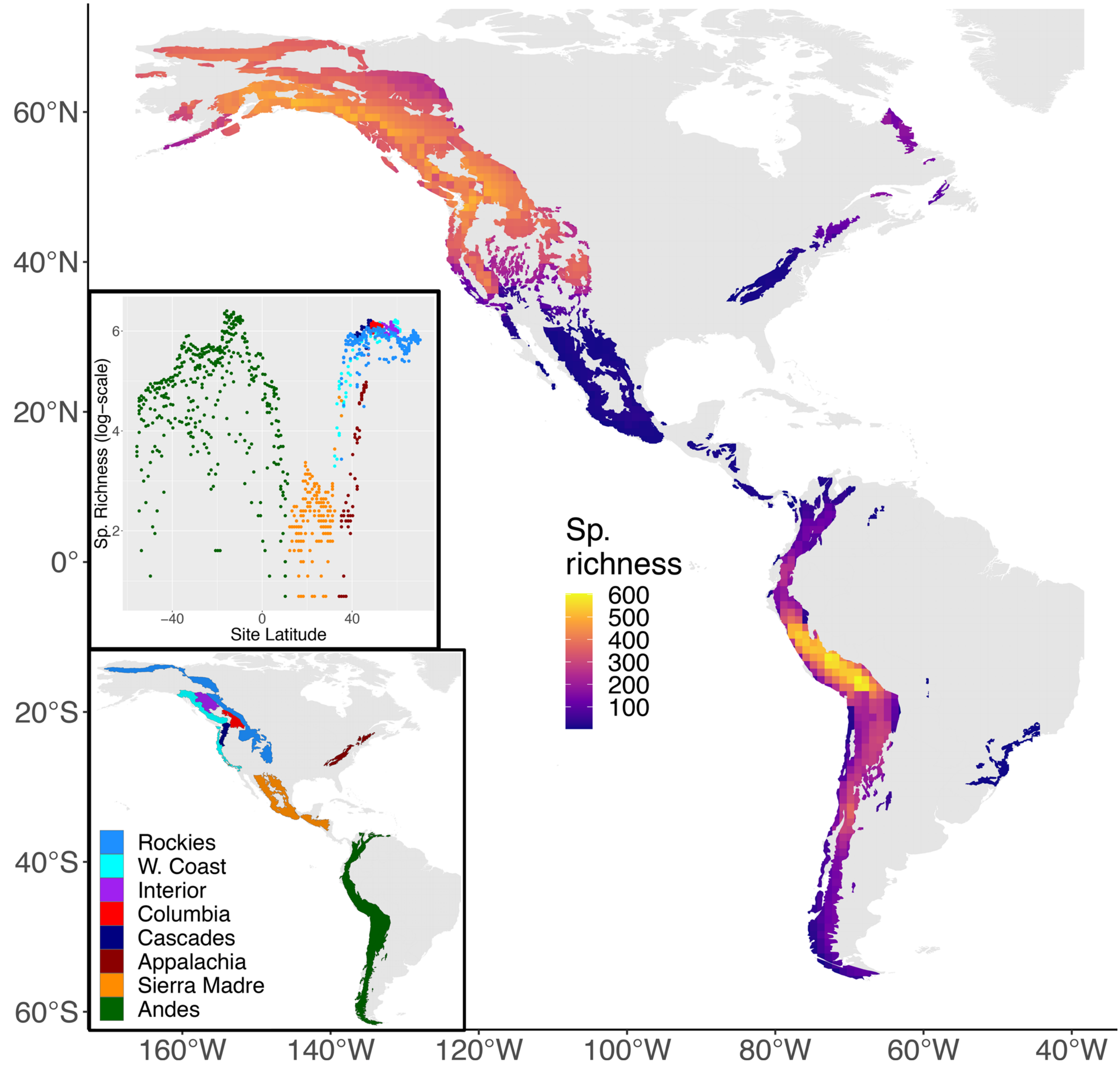

Fig. 2 Heat map showing how alpine species richness across the Americas did not follow a simple latitudinal gradient. Richness was highest (warm tones) in both the central Andes and the northern Rockies/western North American ranges (in contrast, combined montane and alpine species richness peaked near the equator; see Supplemental Fig. S2). Central American mountain ranges had noticeably lower numbers of alpine species (cool tones), which might indicate under-sampling in these regions (see "Discussion"). *Inset scatter plot*: Alpine species richness (logged) vs. latitude across (equal area) sites within 8 major mountain ranges emphasizing the bimodal aspect of alpine diversity. *Inset map*: Major mountain ranges described throughout this study (Appalachia, Andes, Cascades, Columbia, Interior, West Coast, and Rockies). *Color correspondences for these mountain ranges are consistent throughout*

(PDI), Mean Nearest Taxon Distance (MNTD), and Mean Pairwise Distance (MPD; Fig. 6). The majority of the Rockies and Alaskan ranges were significantly more phylogenetically clustered than expected by chance (i.e., negative PDI values), whereas the Sierra Madre were phylogenetically over-dispersed (i.e., positive PDI values). For the Andes, we observed mixed results, though sites tended to be more clustered; in particular, the central Andes showed significant phylogenetic clustering. MNTD was closely correlated with PDI ($R^2 = 0.94$, $p < 0.001$) and showed similar spatial patterns. In contrast, however, MPD was significantly greater in the mid-Rockies/western North American mountains. Overall, the Rockies were characterized by low phylogenetic diversity and MNTD but higher MPD. In the Andes, the

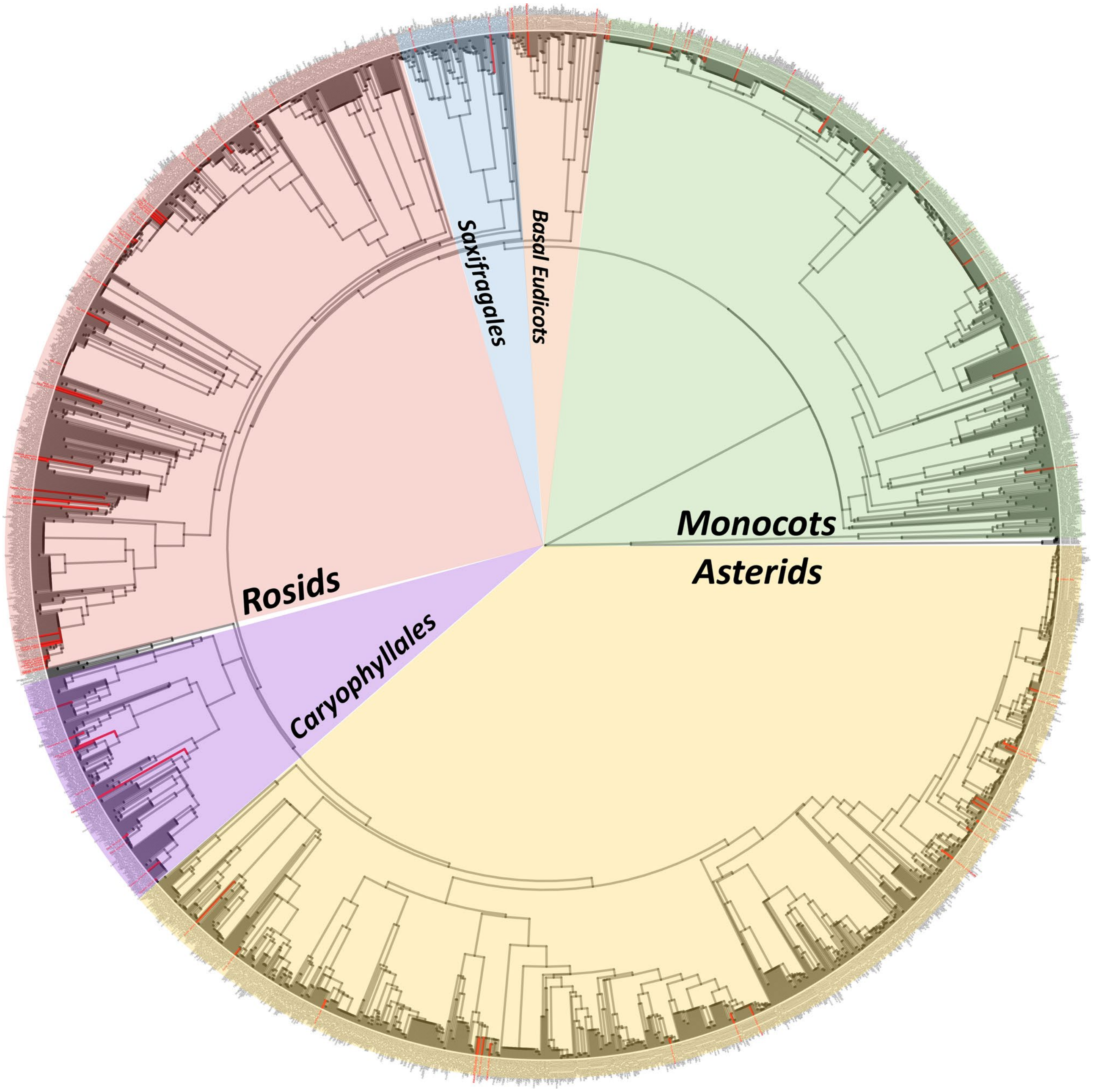

Fig. 3 Phylogenetic distribution of all 2937 alpine species from North, Central, and South America in our dataset. Alpine specialist species (defined here as having at least 50% of the species' modeled range within alpine habitat) are marked in red. Most major plant groups (clades highlighted with colored panels) contain alpine specialists. *Supplemental Fig. S3 provides a phylogeny of just the alpine specialists in our dataset. Supplemental Table S1 lists American angiosperm orders and families without alpine species*

central cordillera was characterized by low PDI, MNTD, and MPD, whereas the southern cordillera had moderately high values of all three metrics, indicating a general phylogenetic diversity gradient along the Andean mountains, increasing from north to south. These patterns were particular to alpine communities in our study area and were in contrast with the overall patterns of phylogenetic diversity among all angiosperms in the Americas as well as patterns observed when montane species were included (Supplemental Figs. S7 and S8; see "Discussion").

Additionally, we examined spatial variation in the degree of alpine specialization (Fig. 6d) by calculating the average amount of American alpine habitat occupied by all species found within sites (see "Methods"). The northern Rockies and Alaskan Ranges had greater proportions of alpine specialization, whereas the Sierra Madre region was more

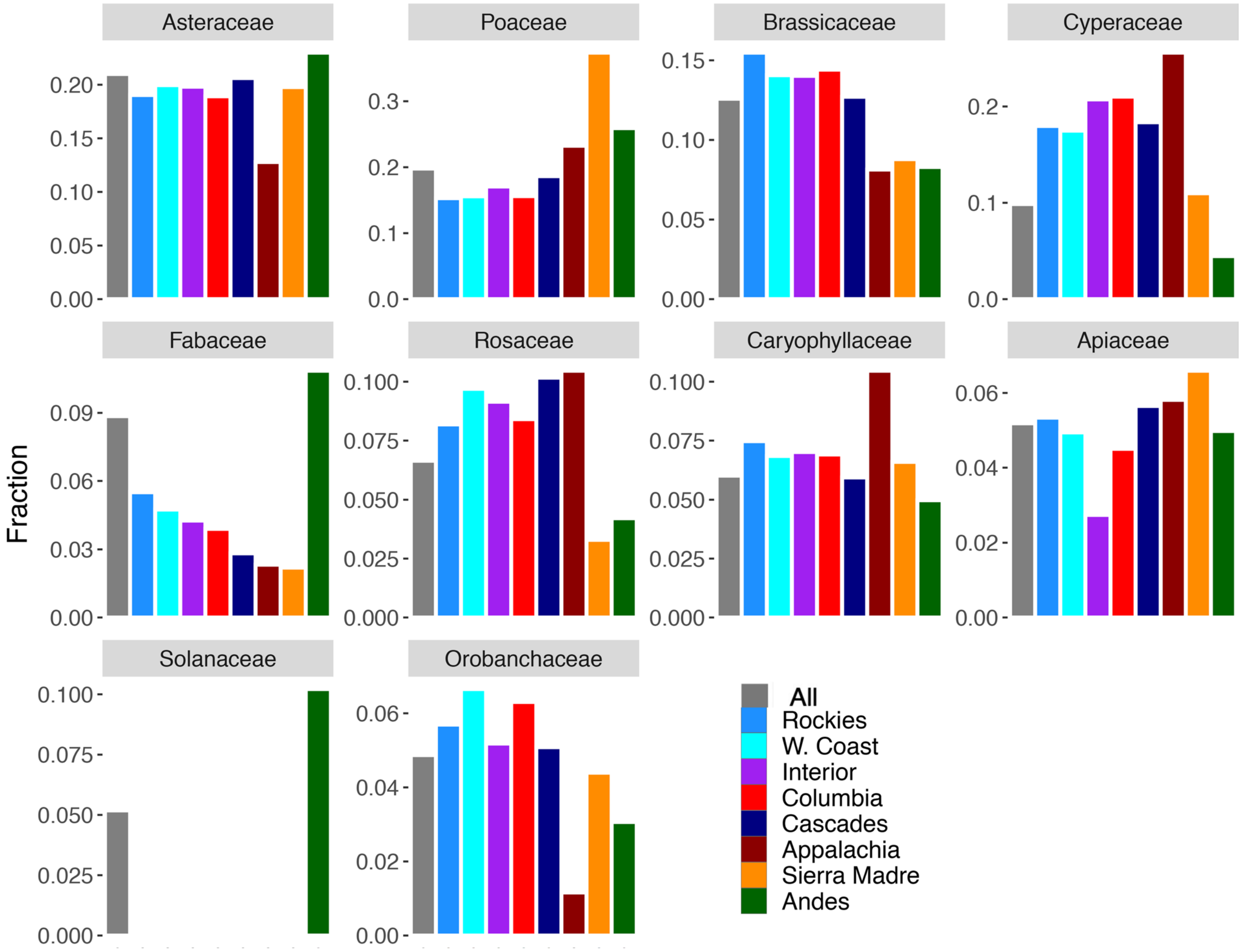

Fig. 4 Distribution of the top ten most dominant taxonomic families with alpine species across eight major American mountain range systems (colors indicate Appalachia, Andes, Cascades, Columbia, Interior, West Coast, and Rockies). At this spatial scale, the relative frequencies of these families varied substantially between mountain ranges. For instance, Cyperaceae were dominant in all mountain ranges except the Andes and Sierra Madre, despite being only the fourth most frequent family when looking across all mountain ranges. Poaceae dominated in the Central American mountains to a greater extent than they did in other regions, and Solanaceae were absent from all major mountain range systems except the Andes. *Families are ordered by their frequency across the entire alpine species dataset (e.g., Asteraceae possess more alpine species than any other family), as indicated by gray bars (note each panel has an independent vertical axis)*

composed of generalists. In other words, the northern Rockies/Alaskan ranges were composed of a greater fraction of phylogenetically clustered alpine specialists and the Sierra Madre represented more phylogenetically over-dispersed generalists. In contrast to the patterns of increased specialization near the Arctic (above approx. 50° N), sites in the extreme Southern Andes (below approx. 40° S) contained a greater fraction of generalists. Thus, the alpine flora of boreal/near-Arctic regions differed in phylogenetic diversity patterns and degree of alpine specialization from the Patagonian region of the Andes. In general, phylogenetic diversity was significantly and negatively correlated with the degree of alpine specialization ($R^2 = 0.59$ across all mountains; $p < 0.001$). The strength of this relationship was markedly greater when considering only the major mountain ranges (Fig. 6d; $R^2 = 0.76$; $p < 0.001$).

Discussion

Dataset considerations

In this study, we offer a detailed investigation of alpine seed plant diversity across the Americas using occurrence records to build SDMs characterizing the extent of alpine habitat encountered by American seed plants. Our methods

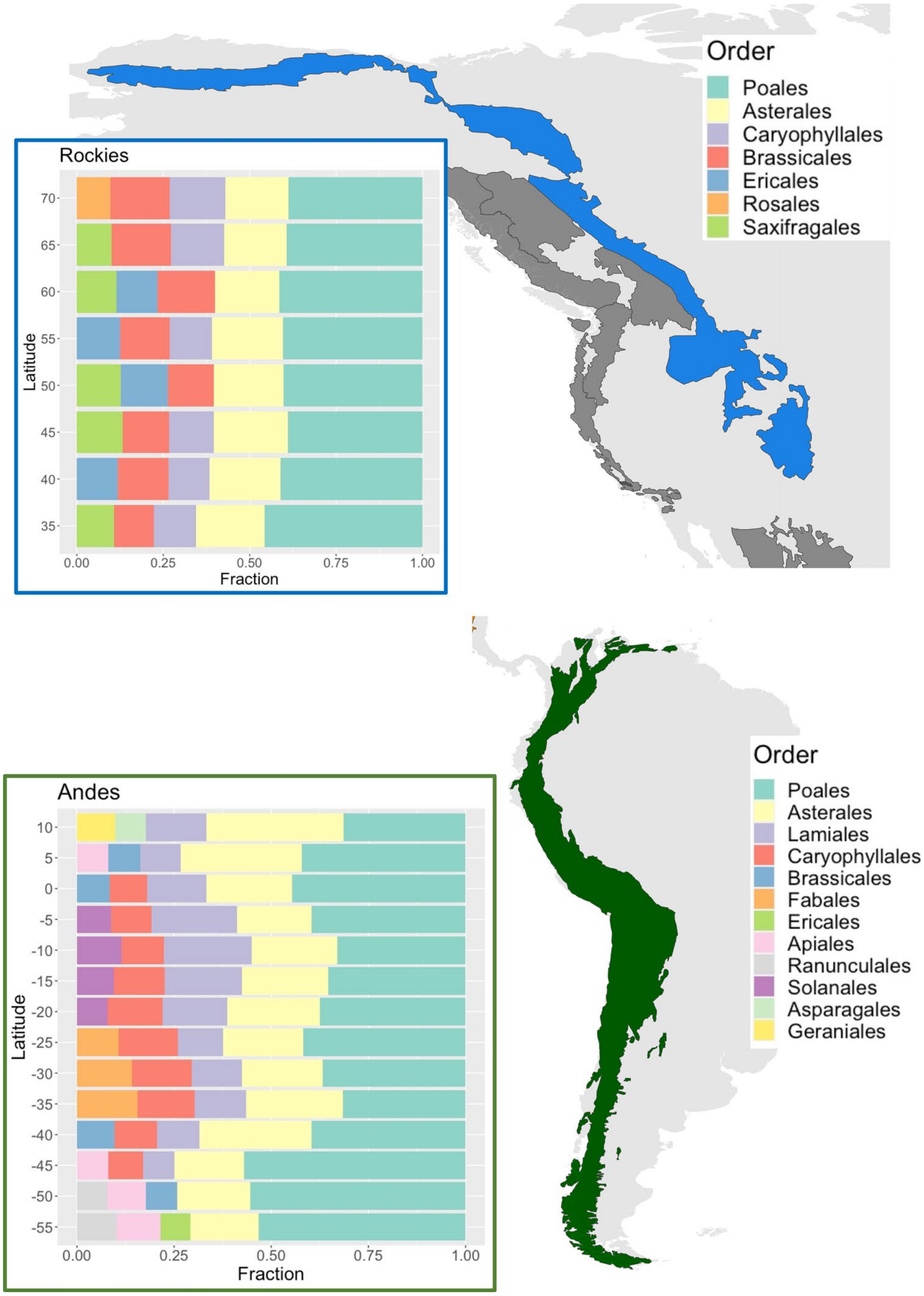

Fig. 5 Patterns of ordinal-level alpine community turnover over the latitudinal extent of the Rockies (*top panel, blue*), and the Andes (*bottom panel, green*). Bar plots show the relative dominance of the top five most abundant orders among communities found within 5° latitudinal sections of each mountain range. Community composition varied between the Rockies and Andes; for example, Solanales were absent in alpine communities from the Rockies, and Saxifragales were never among the most dominant Andean orders. Dominance patterns also varied along the latitudinal extent of each mountain range. For example, the relative dominance of Poales increased moving southward along the Andes while that of Asterales decreased. Some orders, such as Caryophyllales and Saxifragales in the Rockies, varied in their relative frequency along latitudinal ranges and are not represented as top taxa in all zones

to build SDMs allowed us to overcome some of the limitations of incomplete sampling inherent in the direct use of georeferenced point occurrence records by providing broader geographic distributions of species (Barthlott et al. 2007; Meyer et al. 2015; Brummitt et al. 2021) and to describe the elevational niches of plants in our dataset in a graded and more biologically meaningful way. To build reliable climatic niche models, we employed a threshold minimum requirement of twelve records per species. Although this did not appear to introduce any elevational biases through the preferential exclusion of alpine taxa (Supplemental Fig. S1), it certainly excluded numerous range-limited species, such as endemics. Further, this conservative occurrence record threshold is likely to disproportionately impact representation of Andean alpine lineages, where the degree of alpine endemism is substantial (Hughes and Eastwood 2006), and we offer a partial list of such potential exclusions in Online Resource 3. Thus, our dataset also represents an assessment of where focused collecting efforts and increased sampling of alpine plants could enhance our understanding of alpine biodiversity.

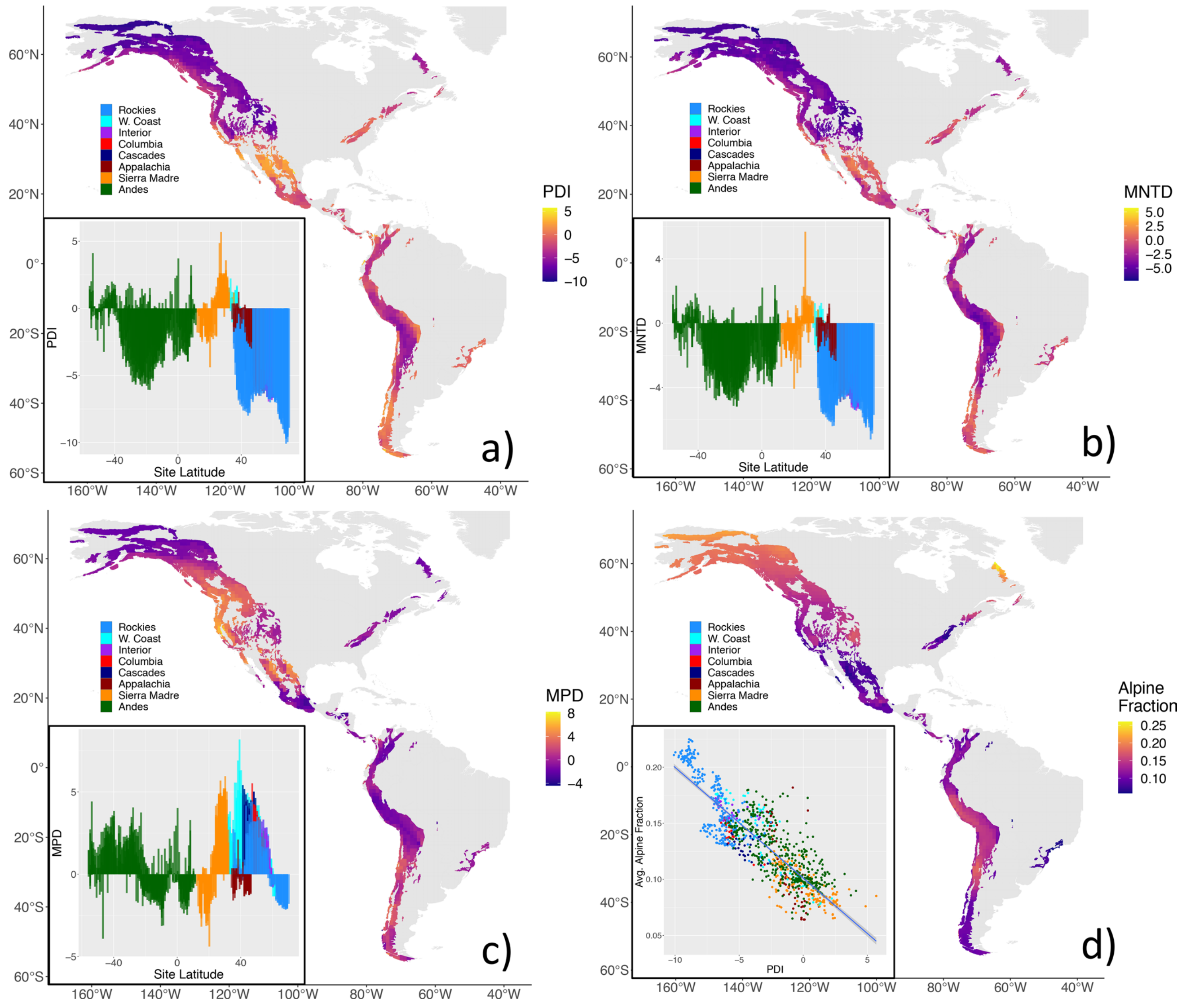

Fig. 6 Phylogenetic diversity of American alpine species and the degree of alpine specialization across American mountain ranges. Each value was calculated among all species present within sites across the study area. (**a**) Phylogenetic Diversity Index (PDI) values indicate either phylogenetic clustering (PDI < 0; observed in the Rockies) or overdispersion (PDI > 0; observed in the Sierra Madre and Patagonian Andes). The inset plot shows PDI values at each site vs. latitude, with bars colored according to major mountain ranges. (**b**) Mean Nearest Taxon Distance (MNTD) generally mirrored the spatial patterns observed for PDI. (**c**) Mean Pairwise Distance (MPD), in contrast, was relatively high in the Rockies and western North America. Negative (positive) values of both MNTD and MPD were interpreted as indicating sites less (more) closely related than expected by chance. Inset plots as in (*a*). (**d**) Community-averaged degree of alpine specialization. Inset plot shows that regions with low PDI (e.g., the northern Rockies) also had a greater degree of alpine-specialized species, and vice versa ($R^2 = 0.76$ for major mountain ranges, or $R^2 = 0.59$ across all mountains; $p < 0.001$ in both cases). In this way, alpine species found in near-Arctic/boreal regions (above approx. 50° N; typified by low PDI and higher degree of specialization) differed from southern Patagonian alpine species (below approx. 40° S; typified by higher PDI and a greater proportion of generalists). *Plots represent metrics only among alpine species (both generalists and specialists); see Supplemental Figs. S7 and S8 for the same metrics across all American angiosperms (e.g., including lowland taxa and montane endemics) and combined montane and alpine species in our dataset*

With these limitations in mind, we have attempted to draw broad, macro-ecological conclusions that are unlikely to be significantly impacted by lack of distribution models for range-limited endemics. Nevertheless, species excluded as a result of the conservative nature of our data cleaning protocol draw critical attention to the need for increased sampling of range-limited endemics to enhance the broader understanding of how such species impact macro-ecological patterns and conclusions. Further, although we have used our dataset to draw comparisons among alpine assemblages occurring across the entire American mountain range system, important differences between Northern and Southern Hemisphere alpine habitats, such as the degree of seasonality, growing season length, and extent and duration of snow cover, should be taken into account when forming conclusions from this macro-ecological dataset. Future studies should investigate how more local-scale processes (e.g., orogeny, climate, erosion) acting within individual mountain regions might be influencing the observed macro-ecological patterns we find here.

Biodiversity patterns

Using the continuous extent of the SDMs, we were able to distinguish between species whose ranges were centered in alpine habitat (termed "specialists" here) from those whose ranges extended above the treeline but were centered elsewhere ("generalists"). These distinctions have been important for how biologists classify alpine species (Körner 2003), which we have previously corroborated by showing statistically significant differences between the temperature niches of alpine seed plant specialists and generalists across the Americas (Figueroa et al. *in review*). Nevertheless, our SDM approach relied solely on American occurrence records. Incorporating global records might change the categorization of specialist and generalist species presented here, as some taxa might be generalists in the Americas but quite restricted to alpine habitat elsewhere or vice versa.

Generally, alpine seed plant diversity was latitudinally bimodal, with the greatest species richness occurring in sites within the central Andes and northern Rockies/western mountains of North America (Fig. 2). These diversity patterns contrasted with those observed among seed plants generally or when combining alpine and montane species (Supplemental Fig. S2), which in both cases were centered on the equator. It is possible that these differences were influenced by under-sampling in Central American alpine communities and the southwest region of North America, and we suggest that increased sampling in these areas might be of high value to alpine biologists. At the same time, these results have important implications for viewing western North American mountain ranges as important centers of alpine biodiversity in conservation efforts (Myers et al. 2000; IPBES 2019), particularly as North American alpine diversity stayed relatively high across a much greater latitudinal extent than observed in the Andes. This contrast between North and South alpine diversity patterns could reflect differing biogeographic histories or filtering effects operating in these two geographically disparate regions, and potentially suggests that dispersal between North and South American mountain ranges may be more limited for alpine plants than montane ones—a hypothesis which should be tested explicitly in future studies.

Lineage-specific patterns

Although we found that most major American seed plant lineages contained at least one alpine species (generalist or specialist; Fig. 3, Supplemental Fig. S3), there was strong unevenness in the phylogenetic distribution of alpine species. Additionally, there were substantial differences in the taxonomic composition of different mountain ranges (Fig. 4) and latitudinal turnover in richness patterns of alpine communities within individual mountain ranges (Fig. 5, Supplemental Fig. S6). Although grouping species by higher taxonomic ranks does not result in comparisons of equivalent biological units, by presenting results on specific clades, we highlight groups that may be of particular biological relevance to alpine botanists. For example, in the Andes, Fabaceae and Solanaceae were relatively more dominant than in any other mountain range (Fig. 4). In fact, Solanaceae was absent from alpine communities outside the Andes, and yet was dominant enough within the Andes that this family still ranked among the top ten families contributing most to American alpine biodiversity overall, congruent with previous biogeographic studies in this family (Olmstead et al. 2008; Dupin et al. 2017).

Phylogenetic and biogeographic analyses of Solanaceae (reviewed in Olmstead 2013) suggest a South American origin for this family. The modern distributions of Solanaceae clades appear to be limited ecologically, rather than by dispersal, with modern ranges shaped by relatively strong niche conservatism of both cold and xeric intolerance (Olmstead 2013). Thus, the absence of Solanaceae from non-Andean mountain ranges might be due to ecological/physiological limits rather than dispersal limitation. This might also explain why, despite their relatively higher frequency in the Andes, none of the Solanales in our dataset ($N=84$) are alpine specialists. The modern Solanaceae distributions thus reflect the influence of both abiotic filtering (limiting their latitudinal and elevational extents) as well as historical processes (substantially greater diversity in South America).

Excluding its higher diversity in the Andes, Fabaceae diversity otherwise declined moving southward along the American mountain ranges. In Northern Hemisphere sites, Fabaceae diversity was driven primarily by the *Astragalus/Oxytropis* complex, whose origins are likely broadly Eurasian (e.g., Bagheri et al. 2017; Amini et al. 2019). This could suggest the high diversity of *Astragalus/Oxytropis* species in the Americas is ultimately due to dispersal from Siberia and surrounding regions. Moving southward, Fabaceae diversity declined due to gradual loss of *Oxytropis* and *Hedysarum*. In contrast, the relative frequencies of *Astragalus* and *Lupinus* remained fairly high and consistent across the mountain ranges. In the Andes, the relatively higher Fabaceae prevalence was driven jointly by *Astragalus* and *Lupinus*, as well as several ($N=10$) Andean-specific genera, primarily

Adesmia (the most species-rich Andean alpine Fabaceae genus in our dataset) but also less prevalent groups, such as *Anarthophyllum* and *Desmodium*. These patterns highlight the scale-dependent interplay of how abiotic filtering and historical contingency shape species turnover among alpine communities.

Despite differences in taxonomic composition between mountain ranges, some broad similarities existed as well. Regardless of spatial scale (i.e., mountain ranges, individual mountains, or latitudinal sections within mountain ranges), Poales were always the most dominant order in American alpine communities, driven jointly by the presence of Poaceae and Cyperaceae in these sites. This result is perhaps not surprising given that Poales tend to dominate in open and dry habitats, and recent work has suggested this clade may have occupied such habitats since the Cretaceous (Bouchenak-Khelladi et al. 2014), which might have preadapted some lineages to success in alpine habitat. The only exception to this pattern was in the northernmost Andes (Fig. 5), where Asterales prevailed. Here, Poales dominance increased moving north to south along the Andes, driven primarily by a general increase in the relative frequency of genera in the Poaceae moving southward, and not the total number of genera representing each order (for example, there were more Asteraceae than Poaceae genera in the Andes at all latitudes above 40° S) or abrupt changes in the genera present along the latitudinal extent of the Andes.

Phylogenetic diversity patterns

Our phylogenetic diversity (PDI, MNTD, MPD) and alpine specialization metrics provided a nuanced picture of differences among alpine communities occurring in different American regions (Fig. 6). Near-Arctic/ boreal alpine communities (above approx. 50° N) were typically phylogenetically clustered with a greater degree of alpine specialization, whereas southern Patagonian communities (below approx. 40° S) were more phylogenetically even with a lesser degree of specialization. These patterns differentiate the alpine communities occurring at opposite ends of the American mountain range system, despite broad climatic similarities in the two regions, and suggest an important role for historical factors in the assembly of their floras. Additionally, phylogenetic diversity in the Andes was generally lowest in the central region, and increased moving southward, where alpine specialization was the lowest (Fig. 6). The alpine communities of the Andean mountain range were therefore characterized by their own latitudinal phylogenetic diversity gradient. Across all major mountain ranges, we also found a significant and strongly negative correlation ($R^2 = 0.76$; $p < 0.001$) between a community's phylogenetic diversity and degree of alpine specialization (Fig. 6d). Thus, sites with more phylogenetic clustering were also composed of species exhibiting a greater degree of alpine specialization.

A general trend of increasingly older divergence time estimates moving southward along the Andes, consistent with Andean uplift occurring from south to north, has been previously reported (Luebert and Weigend 2014). Our findings of greater phylogenetic diversity in southern Andean alpine communities are consistent with this reported general trend as well as some clade-specific specific phylogeographic studies on diversification along the Andes (Picard et al. 2008). When alpine and montane species were combined, the southern Andes still showed higher levels of phylogenetic diversity compared to other Andean sites (Supplemental Fig. S7); however, the trend was not as strong.

Historical constraint or abiotic filtering?

A key question concerning alpine community assembly is whether abiotic filtering or historical contingency (e.g., phylogenetic and biogeographic history) plays a greater role (e.g., Hughes and Eastwood 2006; Flantua et al. 2019). Invariably, the answers to such dichotomous questions are that both factors contribute. Nevertheless, the relatively low number of alpine specialists (~ 3% of all alpine species in our dataset) might suggest that abiotic filtering dominates over shorter evolutionary timescales, preventing larger numbers of species from having their range centered in the alpine belt. This might also explain why sites with greater alpine specialization were also more phylogenetically clustered (Fig. 6d)—if there are strong abiotic filters to alpine specialization, then it may be that only certain lineages are able to pass through the filter (Marx et al. 2017). Notably, however, diversity metrics are influenced by both the spatial and taxonomic scale of the observations (e.g., Swenson et al. 2006; Marx et al. 2019). By comparing phylogenetic diversity among solely alpine communities (Fig. 5) to both combined alpine-montane communities and across all seed plants (Supplemental Fig. S7), we were able to gain a better understanding for how alpine biodiversity differs in phylogenetic structure along elevational gradients and among spatially proximate communities.

Consistent with the idea of strong filtering shaping alpine communities, we found that most alpine specialists (~ 62%, $N = 59$) did not have another specialist among their closest relatives. The most common strategy among the closest relatives of alpine specialists, instead, was a primarily montane distribution (89%, $N = 85$). This was in contrast to alpine generalists, for which ~ 20% were most closely related to primarily lowland taxa (data not shown). This suggests that lowland lineages might contribute proportionally more to alpine generalist lineages, whereas alpine specialists have a greater phylogenetic affinity with lineages that are already occupying montane habitats. Additionally, the discussion on whether and in what ways mountain uplift has helped shaped higher-elevation biodiversity patterns is often hampered by our ignorance of the time lag between orogenic effects and species' ability to colonize and survive in novel environments (e.g., Luebert and Weigend 2014). The extent of phylogenetic niche conservatism observed here could be helpful to this discussion insofar as it suggests that, despite older lineages being present in many habitats, the actual number of alpine species is quite low (~ 7% of higher-elevation species) and therefore the lag times could be considerable.

Given the strong asymmetries in how lineages are distributed geographically, the species composition found in a given mountain range will also surely be strongly influenced by phylogenetic history in that region. For instance, Poales dominated all mountain ranges at the regional level (Fig. 5, Supplemental Fig. S6). On the one hand, this could suggest a general ability of Poales to be successful in alpine habitats, consistent with the notion of abiotic filtering driving the composition of alpine communities. However, the individual genera giving rise to the dominance of Poales differed among ranges (Supplemental Fig. S4), with *Carex* (Cyperaceae) being most dominant in the Rockies, *Poa* (Poaceae) in the Andes, and jointly *Carex/Agrostis* (Cyperaceae/Poaceae, respectively) in the Sierra Madre. On the other hand, these results do not negate the notion of a general ability of Poales taxa to disperse to alpine communities. For instance, the dominance of certain species-rich Poalean families, such as Poaceae and Cyperaceae, in open and dry habitats has been attributed to general physiological mechanisms of CO_2 concentration that enhance survival in these ecosystems (Bouchenak-Khelladi et al. 2014). However, these findings do suggest a more nuanced and scale-dependent perspective of the interplay between phylogeny, historical contingency, and abiotic filtering in the assembly of alpine communities (rather than a strictly dichotomous viewpoint).

Conclusion

We have provided a detailed appraisal of American alpine seed plant diversity and major biogeographic patterns given the context of our current sampling of these notoriously remote regions. Employing a conservative and robust data cleaning protocol (Soltis and Soltis 2016; Figueroa et al. *in review*), we highlighted how species distribution models can enhance our understanding of alpine biodiversity. Our results also call attention to key issues in current data availability, such as the need for increased sampling of both range-limited Andean endemics and alpine communities in and around Central America, as well as the conservation importance of the western North American cordillera for alpine biodiversity. In general, we found alpine diversity to be greatest in the central Andes and western North America, and that sites with lower phylogenetic diversity were composed of species with a greater degree of alpine specialization. Additionally, contrasting patterns of phylogenetic diversity may indicate different community assembly processes acting in otherwise climatically similar Arctic/boreal alpine communities and Patagonian ones, such that that abiotic filtering alone cannot explain these biodiversity patterns. At the same time, the relative rarity of alpine specialists and the tendency for alpine species to be most closely related to montane lineages suggest that filtering is still an important determinant of alpine community structure. This work corroborates the importance of a nuanced and scale-dependent perspective on this 'history-filtering' debate axis, as both factors have likely contributed to modern biodiversity patterns observed in alpine seed plant communities across the Americas.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00035-021-00261-y.

Acknowledgements H.F., H.E.M., and S.A.S. were funded by NSF DBI 1930030. Additional funding for H.E.M. was provided by NSF FESD 1338694. P.S. and D.S. were funded by NSF 1930007. C.J.G., J.B., and A.S. were funded by NSF DBI 1930005. The authors would like to acknowledge that portions of this research took place on the traditional Territories of the Three Fire Peoples—the Ojibwe, Odawa and Bodéwadmi—as well as others.

Authors' contributions All authors helped conceive of the study. CJG, and AS wrote the code to assemble the dataset, CJG implemented data aggregation and niche modeling methods, and JB coordinated computational activities. HF, HEM, and SAS developed methods to analyze the dataset and characterize elevational niches. HF and HEM wrote the first draft of the manuscript. All authors contributed to developing methods to aggregate data records and analyze niche models as well as final edits and revisions to the manuscript.

Funding H.F., H.E.M., and S.A.S. were funded by NSF DBI 1930030. Additional funding for H.E.M. was provided by NSF FESD 1338694. P.S. and D.S. were funded by NSF 1930007. C.J.G., J.B., and A.S. were funded by NSF DBI 1930005.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

Data and code availability Links to aggregated occurrence records from GBIF and iDigBio, scripts used to analyze species distribution models and calculate climatic niches, CSV files of climatic niches, and species distribution models generated by MaxEnt are deposited with Dryad at (https://doi.org/10.5061/dryad.9cnp5hqgx). This Dryad deposit contains information on ~ 72,000 American seed plants, not just those described here in the main text and supporting information. Species lists for solely the alpine taxa examined here, organized by individual mountains and mountain ranges, are deposited with Dryad at (https://doi.org/10.5061/dryad.4qrfj6q8v), along with associated alpine species taxonomy.

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