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EVOLUTIONARY ORIGINS OF THREE RARE ALPINE-ENDEMIC SPECIES OF *LOMATIUM* (APIACEAE) IN THE WALLOWA AND ELKHORN MOUNTAINS OF NORTHEASTERN OREGON

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Premise of research. Shared ancestry and convergent/parallel evolution are the two primary causes of morphologically similar species occurring in similar climatic niches. Alpine habitats harbor a unique biodiversity that is often characterized by many convergences in life-forms, such as cushion and rosulate habits. Three species of *Lomatium* (*L. greenmanii*, *L. erythrocarpum*, and *L. oreganum*) are high-alpine specialists endemic to the Wallowa and Elkhorn Mountains of northeastern Oregon. Earlier studies suggested that two of these species might be sister taxa, but because of the prevalence of convergence in alpine habitats and recent studies that have highlighted morphological homoplasy among *Lomatium* species, this hypothesis warrants reconsideration.

Methodology. Phylogenetic analysis of 209 individuals representing 79 taxa belonging to subfamily Apioideae (Apiaceae) was used to investigate the evolutionary origins of three alpine-endemic species of *Lomatium*. A principal components analysis based on BioClim variables was used to further investigate species climatic niches.

Pivotal results. The three alpine-endemic species of *Lomatium* from northeastern Oregon represent three independent origins of alpine adaptations rather than a single or two alpine radiations, as previously suggested.

Conclusions. Convergence and parallelism are especially common in alpine habitats and among *Lomatium* species, a finding confirmed by this study. This study unveils unpredicted phylogenetic diversity in the Wallowa and Elkhorn Mountains, which, therefore, calls for appropriate conservation measures to protect these distinct evolutionary lineages.

Keywords: alpine flora, Apiaceae, climatic niche, convergent evolution, *Lomatium*, phylogenetic diversity, Sanger sequencing.

Online enhancements: supplemental table and figures.

Introduction

Morphological similarity is often the first stage in identifying closely related organisms (Nixon and Wheeler 1990). Morphological similarities, shared phenotypes, and similar environmental niches are frequently the result of common ancestry and allopatric speciation. However, species that originated independently through convergent and/or parallel evolution can also share a similar environmental niche, phenotype, and morphology (Wiens and Graham 2005). Allopatric speciation is thought to be the main mode of speciation in animals, but it may be less common in plants (Lande 1980; Anacker and Strauss 2014); it occurs when a geographic or geologic barrier prevents certain individuals in a population from interbreeding. For example, log perch darters speciated rapidly, following the Gulf Coast pattern of endemism observed in many clades of freshwater fishes; rising sea levels flooded rivers, isolated populations, and cut off gene flow to previously connected watersheds (Near and Benard 2004). In plants, allopatric speciation has occurred in many groups, including, for example, high-elevation endemics in the Iberian Peninsula and Morocco because of interglacial fragmentation during the Quaternary (Martín-Bravo et al. 2010). Subspeciation has been documented in *Campanula thyrsoides* from the European Alps following a glacial pattern similar to that in the Iberian Peninsula (Kuss et al. 2011). In each of these cases, geographic isolation resulted in taxa that are morphologically similar with similar ecological niches. Some authors (Ragionieri et al. 2009; Morin et al. 2015) refer to these speciation patterns as geographic radiations.

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Convergent and parallel evolution can also lead to shared morphology associated with similar ecological niches. The independent origin of similar adaptations in distinct lineages (i.e., not sharing a most recent common ancestor) can lead to confusion regarding evolutionary relationships and even species boundaries (Wake 2003). When convergence occurs in closely related species (e.g., congeners), delimiting taxa and understanding evolutionary relationships can be even more challenging. Convergence of key innovations, such as the similar sensory systems in vertebrates and cephalopods, to solve common problems has been especially well documented (Montgomery and McFall-Ngai 1992; Budelmann 1995). In some cases, convergence occurs in the entire body plan in response to similar selective pressures in the environment. Perhaps the best-known example is the independent origin of stem succulence in both Cactaceae and Euphorbiaceae in response to the desert biomes of the North American and North African deserts, respectively (Alvarado-Cárdenas et al. 2013). Convergence of phenotypic traits at shallower taxonomic scales is less well studied and is frequently referred to as parallel evolution when the sister species share identical characters (Haldane 1932; Schluter et al. 2004). Parallel evolution differs from true convergence because more closely related species share a similar genetic architecture and thus are more likely to evolve similar phenotypes in response to selective pressures (Schluter et al. 2004). This phenomenon has been documented at the molecular pathway level in threespine sticklebacks (Colosimo et al. 2005) and by tracking mutations at the DNA sequence level in the bacteria *Burkholderia* (Lieberman et al. 2011). In practice, detecting the difference between parallel and convergent evolution can be challenging. A near-complete sampling of the clade in question is necessary to know the phenotype of the true sister species. Convergent evolution and parallel evolution are important aspects of replicated speciation (Rosenblum and Harmon 2010; Roquet et al. 2013).

Alpine environments harbor a biodiversity characterized by high degrees of endemism and unique floras (Billings 1974; Wang et al. 2009; Marx et al. 2017). While they are not as species rich as more diverse environments, such as tropical rain forests, alpine habitats can serve as important reservoirs of relictual diversity, where rare but once-common species or genotypes can find refuge after severe range contractions. Despite their importance in maintaining biodiversity, these environments and their biota are especially sensitive to climate change (Klanderud and Totland 2005). Because of their isolation from other similar environments and the geological processes implicit in their formation, the mountains on which alpine habitats are found can be viewed as island-like (Hughes and Atchison 2015). As a consequence of the isolation and common history of montane regions, they can serve as a natural laboratory for testing hypotheses about plant community assemblies, speciation, and convergence (Anthelme and Lavergne 2017). Recent work highlighting this capability includes studies of how increased winter soil temperatures can predict plant community assembly under models of global climate change (Choler 2018), how endemic plant species have diversified in the European Alps (Smyčka et al. 2017), and the convergent development of cushion plants in the western Peruvian Andes (Schittek et al. 2018).

Phenotypic convergence and parallelism are especially pronounced in alpine environments because of the limited number of adaptations that appear to be successful. The alpine environment is characterized by harsh conditions, including a limited growing season, extreme cold and wind, a high degree of solar radiation, and the potential for midseason frosts. The successful adaptations that many plant species have evolved include reduced stature and the ability to flower and set seed in an accelerated time frame (Bliss 1962). These traits are found in nearly all alpine plants, despite the fact that they represent a wide array of plant families (see Flora of North America Editorial Committee 2002). This limited number of potential adaptations increases the likelihood of convergent evolution in alpine environments. The cushion life-form, for example, evolved multiple times in *Androsace* (Primulaceae), a genus distributed across the cordillera of western North America and the Russian Far East (Boucher et al. 2012). *Androsace* demonstrates that convergence occurs not only in deep evolutionary time across disparate taxa but also sometimes in short intervals among closely related species. Within Apiaceae, especially among the early divergent lineages of *Azorella*, independent evolution of similar phenotypes has also occurred, leading to multiple similar life-forms (e.g., cushions, mats, rosettes, and shrubs; Nicolas and Plunkett 2012; Plunkett and Nicolas 2016). In these cases, the choice of morphological characters used to delimit taxa and understand evolution can be unclear. The addition of molecular data can help clarify species relationships and boundaries.

Lomatium is a polyphyletic genus in the larger perennial endemic North American (PENA) clade of Apiaceae, to which ~200 currently recognized species are assigned. Plants in the PENA clade are herbaceous perennials found in a variety of habitats ranging from mesic woodlands to dry, open sagebrush (Hitchcock and Cronquist 1973; Cronquist et al. 1997). Within *Lomatium* and PENA, there are many examples where shared morphologies do not reflect evolutionary history (Feist et al. 2017). As currently understood (George et al. 2014; Feist et al. 2017; Smith et al. 2018), *Lomatium*, *Cymopterus*, and a few smaller closely related genera are polyphyletic. *Intermountain Flora* (Cronquist et al. 1997) and *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1973, 2018) separated the two largest genera (*Lomatium* and *Cymopterus*) on the basis of the presence or absence of membranous wings parallel to the body of the fruit. George et al. (2014) found this morphological character to be unreflective of the evolutionary history of the group, and thus we refer to the various genera as the PENA clade. Other characters traditionally used to delimit taxa, such as root morphology and number of terminal leaflet divisions, have been shown to exhibit a high degree of homoplasy (George et al. 2014). Many common species thought to be “good taxa,” such as the *L. triternatum* species complex (Smith et al. 2018), have been shown to contain cryptic diversity. Feist et al. (2017) made minor taxonomic rearrangements, such as combining the small genus *Orogenia* with *Lomatium*. However, a large-scale taxonomic revision is warranted for the taxonomy to be reflective of evolutionary history, and it is currently underway, utilizing next-generation sequencing data and coalescent-based phylogenetic analyses (Ottenlips 2019). Therefore, the use of molecular data to test the existing classification of different elements within *Lomatium* is a useful approach to assess the roles of parallelism/convergence and inheritance in generating phenotypic similarities in similar habitats.

Three rare alpine-endemic species of *Lomatium* are found in the Wallowa and Elkhorn Mountains of the Blue Mountains ecoregion in northeastern Oregon: *L. erythrocarpum* Meinke & Constance, *L. greenmanii* Math., and *L. oreganum* J.M. Coult. & Rose (fig. 1; Hitchcock and Cronquist 2018). These mountains share a similar recent geological history, and both ranges were once covered by the Wallowa ice cap, until its retreat began about 17 kyBP (1000 yr before present; Licciardi et al. 2004). Each alpine-endemic species exhibits a highly reduced growth form characteristic of many alpine plants (fig. 2; Bliss 1962; Hitchcock and Cronquist 2018), including a rosulate habit with a limited number of leaves, low stature, and a compressed time frame from flower to seed set. *Lomatium erythrocarpum* is listed as endangered by the state of Oregon (Oregon Department of

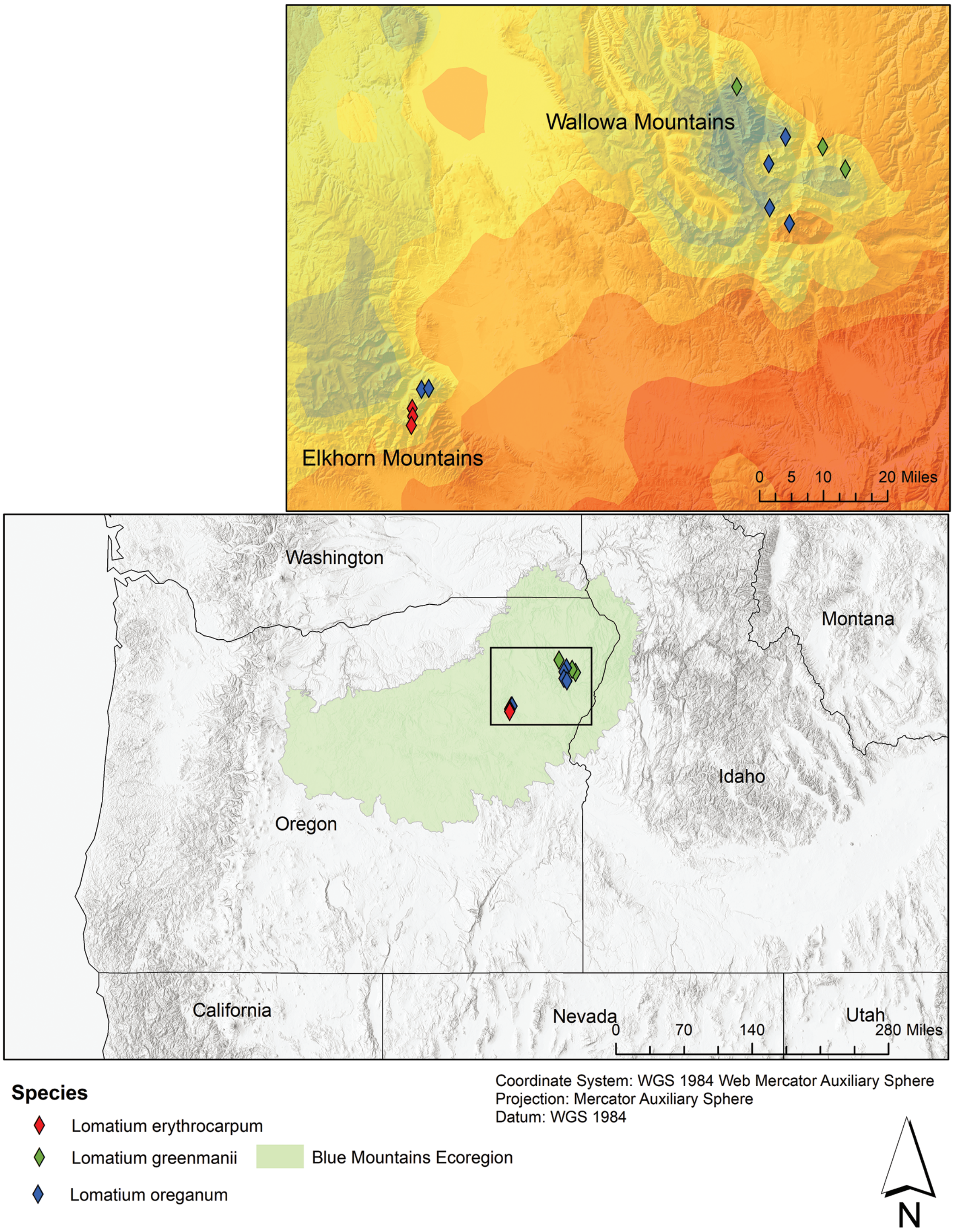

Fig. 1 Map of study area and populations sampled. Similar colors on the base map indicate shared climate space based on kriging interpolation, with warmer colors indicating drier and hotter environments and cooler colors indicating wetter and colder environments.

Fig. 2 Photographs showing *Lomatium greenmanii* (*A*), *L. oreganum* (*B*), and *L. erythrocarpum* (*C*). Images courtesy of Oregon Flora. *A*, © Gerald Carr; *B*, © Bonnie Olson; and C, © Gene Yates.

Agriculture 2018) and is found only within a 3-mi^2 zone in the Elkhorn Mountains. *Lomatium greenmanii* is listed as threatened by the state of Oregon (Oregon Department of Agriculture 2018) and is restricted to the Wallowa Mountains, where it is known only from three alpine localities: Redmont Peak, Mount Howard, and Ruby Peak (Hustafa 2007). *Lomatium oreganum* is found in the alpine zone of both the Wallowa and Elkhorn Mountains. While it is not listed at either the state or the federal level, only six populations are known. Previous studies based on morphological data suggested that *L. greenmanii* might be a glabrous form of *L. oreganum* or potentially its sister species (Meinke and Constance 1982). An unpublished molecular study (Hustafa 2007) based on limited data (sequences only from ITS) and taxon sampling (15 species) corroborated the suggestion of Meinke and Constance (1982) that *L. oreganum* and *L. greenmanii* are sister taxa.

This study proposes to investigate two contrasting hypotheses of the evolution of alpine species in North America using *Lomatium*. By conducting phylogenetic analysis and climate niche inference, we test whether the three alpine species originated in the alpine environment via a geographic radiation (singular alpine adaptation origin) or whether they evolved through convergent/parallel evolution and replicated speciation (multiple alpine adaptation origins). Alpine-adapted forms are relatively uncommon within the PENA clade, known only from the present examples and about a dozen other species (*Cymopterus nivalis*, *C. douglasii*, *C. gilmanii*, *C. davisii*, *C. alpinus*, *L. attenuatum*, *L. cusickii*, *L. minimum*, *Neoparrya lithophila*, *Oreoxis humilis*, and *Podistera* species; Cronquist et al. 1997; Hitchcock and Cronquist 2018). As many alpine PENA species as possible were included in the present analysis. Our study incorporates new samples of alpine *Lomatium* into a phylogeny consisting of previously published (George et al. 2014) and unpublished (M. A. E. Feist and G. M. Plunkett, unpublished data) sequence data of the PENA clade to explain the evolutionary origins of alpine-endemic *Lomatium* in the Wallowa and Elkhorn Mountains.

Material and Methods

Sampling, Extractions, PCR, and Sanger Sequencing

The PENA clade was sampled widely so that the phylogenetic position of the Wallowa and Elkhorn Mountain–endemic *Lomatium* species could be determined. For the three alpine-endemic species under investigation, five individuals of *L. greenmanii*, two individuals of *L. erythrocarpum*, and five individuals of *L. oreganum* were included in the analysis; all were sampled from leaves obtained from herbarium specimens. For the remaining taxa, previously published sequences (George et al. 2014), along with many that are as yet unpublished (M. A. E. Feist and G. M. Plunkett, unpublished data), were used in this analysis, culminating in the broadest sampling of the PENA clade to date. In total, the data set included 209 individuals representing 79 taxa, including outgroups (see app. A).

DNA was extracted with the Qiagen DNeasy Plant Mini Kit (Qiagen, Valencia, CA) following the protocol recommended by the manufacturer with minor modifications according to Smith et al. (2018). Two nuclear ribosomal genes (ETS and ITS) and five chloroplast regions (*rps16* intron, *trnD-trnT*, *ndhA* intron, *trnL*$_{UAG}$, and *psbA-trnH*) were amplified using primers previously published in George et al. (2014) and Smith et al. (2018).

Successful amplifications were determined using UV visualization of ethidium bromide–stained DNA run on 1% agarose gels. ExoSAP-IT (Affymetrix, Cleveland, OH) was used to purify successful amplifications, which were then sent to GENEWIZ (Plainfield, NJ) for Sanger sequencing. Assembly and editing of the raw data from chromatograms were performed in PhyDE (Müller et al. 2010).

Phylogenetic Reconstruction

Each of the seven sequence regions was manually aligned individually in PhyDE (Müller et al. 2010) and then was concatenated with the other regions to construct one supermatrix for downstream phylogenetic analysis. Concatenation of nuclear and plastid markers has been shown to be effective at resolving evolutionary relationships within this group (Sun and Downie 2010; George et al. 2014; Smith et al. 2018). The Python package AMAS (Borowiec 2016) was used to calculate the number of variable sites and the number of parsimony-informative sites.

Three approaches were used to estimate the phylogenetic relationships: maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). MP was performed using PAUP* (Swofford 2002) with 1000 bootstrap replicates, using tree bisection-reconnection and a ratchet input derived from PAUPRat (Müller et al. 2010). ML was performed using RAxML (Stamatakis 2006); bootstrapping was stopped automatically using the default autoMRE.

The Akaike information criterion scores resulting from jModelTest 2 (Darriba et al. 2012) were used to assess the best-fit model of molecular evolution and base pair substitution rate priors for subsequent Bayesian analysis. Two independent runs of MrBayes (Ronquist and Huelsenbeck 2003), each consisting of four chains, a burn-in of 5000 trees, and 10 million generations using the TVM+I+G model and other priors (suggested by following the results of jModelTest 2), were used to conduct the BI analysis. To determine whether the estimated priors had been adequately sampled, we evaluated effective sample size (ESS) values (≥200) using Tracer version 1.7.1 (Rambaut et al. 2018). Trees generated from each MrBayes analysis (minus the burn-in) were imported into MEGA7 (Kumar et al. 2016) to generate majority-rule (50% cutoff) consensus trees in which the consensus percentages represent the posterior probability. All trees were rooted with the outgroup, *Angelica lineariloba*. The Bayesian tree was used as the primary topology from which relationships were inferred and discussed, and support values from the other analyses were imported using TreeGraph 2 (Stöver and Müller 2010).

In addition to the concatenated analysis, separate analyses of chloroplast and nuclear regions were performed. The same BI and ML tree-building techniques described above were used on these data sets. One sample (*L. greenmanii*; WTU 360976) was excluded from the chloroplast analysis because only nuclear ribosomal regions were successfully amplified and sequenced. The CIPRES Science Gateway (Miller et al. 2011) was used to perform all analyses for MrBayes, RAxML, and jModelTest2.

On the basis of the concatenated results, alternative topology tests were used to confirm that the alpine species represented distinct lineages (i.e., were not nested within one another). We constrained each species pair to be sister by manually editing the partitioned Bayesian Newick tree using a text editor. PAUP* (Swofford 2002) was used to determine site log likelihoods for each constraint tree. Approximately unbiased (AU) tests were performed in CONSEL (Shimodaira and Hasegawa 2001) using the site log likelihoods exported for each of the constraint trees by PAUP*.

Climatic Analysis

We obtained geographic information for the alpine endemics by downloading herbarium records from the Consortium of Pacific Northwest Herbaria database (http://www.pnwherbaria.org/index.php). Only one specimen/coordinate set from each known population was retained by comparing localities with all known occurrences of *L. greenmanii* (three) and *L. erythrocarpum* (three) provided by the US Fish and Wildlife Service (USFWS) and US Forest Service (Hustafa 2007). *Lomatium oreganum* is not monitored by any federal or state agency, which makes determining the exact number of populations difficult. Collections of *L. oreganum* with no GPS coordinates were georeferenced first by using township, range, and section and then were refined using label data with information about known geographic markers (such as mountain peaks) on Google Earth Pro (http://www.google.com/earth/). Manual analysis of locations of herbarium records suggests six populations for *L. oreganum*. All localities included in the climatic analysis are represented by herbarium vouchers (table 1).

Spatial data for additional species in Apiaceae were also obtained through herbarium records via the Consortium of Pacific Northwest Herbaria database. We retained only specimens from within the Blue Mountains ecoregion (Omernik 1987) to reduce data complexity and provide a conservative and relevant baseline for comparisons with the alpine-endemic species. We manually filtered records for quality of spatial information by removing points with coordinates outside county boundaries and other obvious georeferencing errors on the basis of a review of label data. To reduce spatial autocorrelation and collection biases, we rarefied points to a radius of 15 km following the methodology of Barga et al. (2018), whereby we performed a spatial principal components analysis (PCA) on BioClim variables (raster data set clipped to Blue Mountains ecoregion) in ArcGIS to reduce the dimensions of the data. A spatial interpolation analysis (kriging) was performed on 3000 random points and PC1, which explained more than 90% of the variance in the BioClim raster data set. Semivariograms were fitted during the kriging analysis so that the extent of spatial autocorrelation in the data set could be uncovered. The range of the semivariogram was analyzed so that the degree of spatial autocorrelation in the data set could be determined. The range of the semivariogram was 13 km, and therefore a conservative rarefaction radius of 15 km was chosen to ensure a lack of collection bias and spatial autocorrelation. Additionally, the kriging analysis shows the climate similarity (fig. 1) between both (Wallowa and Elkhorn Mountains) alpine habitats in the Blue Mountains ecoregion.

BioClim variables were downloaded from the University of California–Davis biogeography repository (http://biogeo.ucdavis.edu/projects.html) and extracted for each set of coordinates (app. B; apps. B–F are available online) with the package raster (Hijmans and van Etten 2014). A PCA (prcomp) was performed in Base R and visualized using ggplot2 (Wickham 2011) and ggfortify (Horikoshi and Tang 2016). Confidence intervals (95%) were calculated for all Apiaceae and *L. oreganum* separately and drawn onto the PCA using the stat_ellipse function of

Table 1

Specimens Used in the Climatic and Morphological Analyses

Species	Collection	Collection date from specimen label	Location	Latitude	Longitude	Herbarium acronym (Thiers 2019) and accession no.
Lomatium greenmanii	Michael Mancuso 3606[b]	June 14, 2010	Redmont Peak, Wallowa Mountains	45.2204	−117.13	ID 163719
L. greenmanii	Jessie Johanson 02-118[a,b]	July 20, 2002	Mount Howard, Wallowa Mountains	45.2557	−117.18	OSC 229580
L. greenmanii	Julie Kierstead 84-33[a]	1984	Ruby Peak, Wallowa Mountains	45.3512	−117.37	OSC 166057
L. greenmanii	Michael R. Hayes 1028					ID 129405
L. greenmanii	Robert J. Meinke 2433					ID 84401
L. greenmanii	Ruth Martin Hansen 4611					HPSU 14885
L. greenmanii	David French 3456					HPSU 14884
L. greenmanii	William C. Cusick 2458					RM 31457
L. oreganum	Rachel Sines s.n.[a,b]	August 1983	Hurwal Divide, Wallowa Mountains	45.2711	−117.26	OSC 160894
L. oreganum	Morton Eaton Peck 18536[a]	July 1934	Summit west of Ice Lake, Wallowa Mountains	45.2286	−117.3	OSC 17765
L. oreganum	Georgia Mason 6489[a]	August 12, 1963	On summit of Eagle Cap, Wallowa Mountains	45.1588	−117.3	OSC 124517
L. oreganum	Peter Zika 10430A[a]	August 1987	Imnaha River headwaters, Wallowa Mountains	45.1336	−117.25	OSC 188525
L. oreganum	Ann Kratz s.n.[a,b]	August 10, 1987	Maxwell Peak, 400°E of summit, Elkhorn Mountains	44.8694	−118.08	ID 77376
L. oreganum	Roy Sines s.n.[a]	August 10, 1982	West side of Hunt Mountain, Elkhorn Mountains	44.8708	−118.07	OSC 159357
L. oreganum	C. L. Hitchcock 21423					WTU 209449
L. oreganum	Jon Titus s.n.					WTU 303772
L. erythrocarpum	Andy Kratz s.n.[a]	August 21, 1982	Cougar Basin, Elkhorn Mountains	44.8389	−118.1	WS 291027
L. erythrocarpum	Robert Meinke 3114[a,b]	August 2, 1983	In saddle between Pine Creek and Cougar Basin, Elkhorn Mountains	44.8262	−118.1	WTU 303772
L. erythrocarpum	Michael Murray s.n.[a]	July 19, 2001	South of Rock Creek Butte, Elkhorn Mountains	44.8117	−118.11	OSC 197364

Note. Specimens examined only for morphology do not include location data.

[a] Georeferenced.

[b] Specimens used for both climate and morphological data.

ggplot2. Confidence intervals could not be calculated for *L. erythrocarpum* and *L. greenmanii* because there were too few points to calculate an ellipse.

All climatic analyses were performed in R version 3.5.1 (Feather Spray; R Core Team 2018) and ArcGIS 10.5 (ESRI 2016). R code for the climatic analysis is available at http://github.com/ottenlipsmv/alpine_lom.

Morphology

We reviewed herbarium specimens (table 1) to investigate overlapping morphological characters. Morphology reviewed includes the presence/absence of the following characters: leaflet margins entire, yellow flowers, caespitose development, dissected leaves, deep taproot, developed involucel, reduced terminal inflorescence, and dorsally flattened fruits. Some of these characters (caespitose development, reduced terminal inflorescence, and developed involucel) could be viewed as adaptations to the alpine environment. All specimens were reviewed via databased images available on the Consortium of Pacific Northwest Herbaria website. Species descriptions (Meinke and Constance 1982), the regional flora (Hitchcock and Cronquist 2018), and USFWS documents (Hustafa 2007) were also consulted so that further observations regarding the morphologies of these three species could be made.

Results

Sampling, Extractions, PCR, and Sanger Sequencing

We successfully extracted and sequenced DNA from a total of 209 samples from the study group (app. A). All seven regions were successfully sequenced for 125 samples, one region was missing for 59 samples, two regions were missing for 15 samples, three regions were missing for seven samples, four regions were missing for two samples, and five regions (all chloroplast markers) were missing for one sample. The final data matrix after alignment and concatenation of all seven DNA regions comprised 7941 characters, of which 1854 (23%) were variable sites and 928 (12%) were potentially parsimony informative.

Phylogenetic Reconstruction

The consensus trees generated from the three phylogenetic reconstruction techniques (MP, ML, BI) were largely congruent with one another, differing only in the placement of a few individuals, none of which involved relationships among the three alpine endemics being studied. The tree resulting from the BI analysis is presented as the base tree in figure 3. MP and ML bootstrap values are plotted alongside the posterior probabilities for shared nodes. MP analysis resulted in 196 most parsimonious trees (length = 4339 steps; consistency index [CI] excluding uninformative positions = 0.4187; retention index = 0.7754; rescaled CI = 0.4187). The ESS values of the two independent runs in MrBayes were 1440 and 1208 in Tracer (well above the threshold of 200), resulting in consensus trees with identical topologies. Trees from all three analyses were congruent in their placement of the three alpine-endemic species of *Lomatium* and strongly supported them as three distinct and monophyletic species in different clades. The AU tests rejected ($P < 0.005$) the possibility of *L. greenmanii* as sister to *L. erythrocarpum*, *L. oreganum* as sister to *L. greenmanii*, and *L. erythrocarpum* as sister to *L. oreganum* (table 2).

While there is a high degree of incongruence between the two data sets, separate analysis of the chloroplast and nuclear regions also supports the conclusion that the three alpine *Lomatium* species endemic to the Blue Mountains ecoregion are distinct monophyletic species. The chloroplast data support the concatenated analysis that the three focal taxa are not sister taxa and are members of distinct clades. In the nuclear data analysis, *L. erythrocarpum* and *L. oreganum* belong to the same polytomy, indicating a possibility that the two may be closely related or sister taxa. However, this tree is generally poorly resolved, and the polytomy (support: BI = 0.82 posterior probability; ML bootstrap value ≤ 50) contains 15 additional taxa. The majority of our results support the conclusion that the three focal taxa are distinct and not sister. These separate chloroplast and nuclear analyses are available in appendixes C–F.

Climatic Analysis

Comparison of BioClim variables for rarefied Apiaceae herbarium collection locations within the Blue Mountains ecoregion with the three alpine species of interest revealed shared climatic niche space among the alpine species, with some overlap with other Apiaceae collections. PC1 explains 88.3% of the variation, and PC2 explains an additional 10.47% of the variation in the data set. Confidence intervals (95%) drawn around *L. oreganum* collections contain all known populations of *L. greenmanii* and *L. erythrocarpum*, confirming that the three alpine endemics of the Wallowa and Elkhorn Mountains occupy similar climates (fig. 4). Furthermore, the spatial interpolation analysis (kriging) highlights shared climates between both mountain ranges independent of specific collection locations (fig. 1). The major loading separating the alpine *Lomatium* from other Apiaceae along PC2 is annual precipitation, followed by two other precipitation variables (precipitation in wettest and coldest quarters), indicating that the amount of annual snowfall is the major climate difference driving the separation between the three focal taxa and other local Apiaceae. PC1 separates the local Apiaceae predominately by annual temperature seasonality.

Morphology

A review of imaged herbarium specimens and the scientific literature reveals a suite of overlapping morphological characters (table 3). All species have caespitose development, thickened dissected leaflets, and reduced terminal inflorescences with similarly shaped umbellets (fig. 2; table 3). *Lomatium greenmanii* and *L. oreganum* can be distinguished by the presence of hirtellous-purbulent hairs on the ultimate segments of the leaves and fruit of *L. oreganum* and by the glabrous or slightly scaberulous leaves and the glabrous fruits of *L. greenmanii*. *Lomatium erythrocarpum* can be easily distinguished from the other two species by its conspicuous red fruits (Hitchcock and Cronquist 2018).

Discussion

Our results indicate that the three alpine-adapted *Lomatium* species endemic to the Wallowa and Elkhorn Mountains of eastern Oregon are distantly related, unique evolutionary lineages. Each species is monophyletic and falls into a unique clade in all molecular analyses, including concatenation (fig. 3) and independent analysis of chloroplast (apps. C, D) and nuclear markers (although *L. erythrocarpum* and *L. oreganum* are part of a polytomy with 15 other species in nuclear DNA alone; apps. E, F). This result supports the hypothesis that replicated speciation and convergence/parallelism have played a key role in the evolution of these species. AU tests further reject the hypothesis of a single independent origin of alpine species of *Lomatium* from the Wallowa and Elkhorn Mountains (table 2). Additionally, the climatic niche analysis confirms the hypothesis that these three species share similar ecological niche space, and a review of the literature and herbarium specimens shows overlap in a variety of morphological characters, including alpine adaptations. The congruence of multiple phylogenetic analyses across markers and methods, in addition to the shared climate niche space and morphological affinities, suggests that these three species are the products of convergent or parallel evolution. A more thorough sampling scheme including greater representation from across the clade would allow us to verify the sister species and determine whether this is a case of convergent or parallel evolution or a combination of the two. Furthermore, the inclusion of more taxa would allow for an accurate ancestral state reconstruction that could determine which clades (if any) have ancestral alpine adaptations to more fully explain the evolution of these adaptations within this group.

Two previous studies (Meinke and Constance 1982; Hustafa 2007) had suggested that *L. oreganum* and *L. greenmanii* might represent sister species. Meinke and Constance (1982) used a traditional taxonomic approach with evidence derived largely from shared morphological characters, such as “caespitose

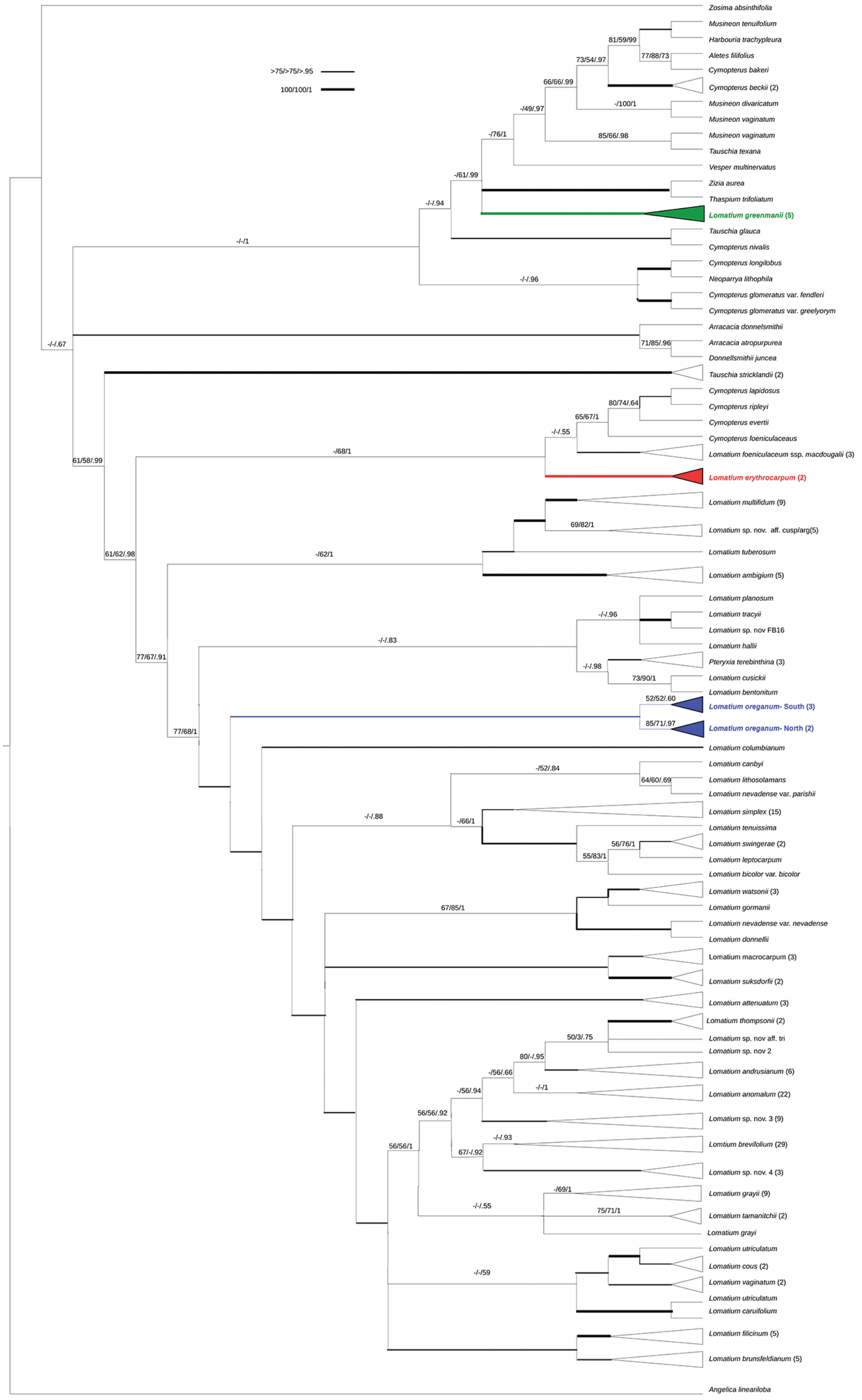

Fig. 3 Phylogenetic tree depicting the relationships between the three alpine-endemic species. *Lomatium greenmanii* branches are colored green, *L. erythrocarpum* red, and *L. oreganum* blue for emphasis. If more than one individual was sampled for a monophyletic species, the branches were collapsed and replaced with a triangle. The number in parentheses after the species name indicates the number of individuals sampled. Support values are maximum parsimony bootstrap (MPBS), maximum likelihood bootstrap (MLBS), and Bayesian inference posterior probabilities (BIPP) in the following format: MPBS/MLBS/BIPP. Values over 75/75/0.95 are indicated with a three-point thickened branch, and maximum support (100/100/1) is indicated by a six-point thickened branch.

Table 2

Results from the Approximately Unbiased (AU) Test Performed in CONSEL

Topology	Rank	AU score
Maximum parsimony tree	1	1
(*Lomatium greenmanii*, *L. erythrocarpum*)	3	3.00E-05
(*L. oreganum*, *L. greenmanii*)	4	6.00E-07
(*L. erythrocarpum*, *L. oreganum*)	2	4.00E-06

Note. P values <0.05 were considered significant. The results reject the possibility of the alpine endemics being sister to each other.

development from a fibrous multicipital caudex surmounting a deep taproot, oblong to lanceolate pinnately dissected leaves, reduction of the inflorescence to a solitary terminal umbel with only 1–3 fertile umbellets, each bearing 1–6(–8) short-pedicellate fruits, yellow flowers, and dorsally flattened fruits" (Meinke and Constance 1982, p. 14). However, the authors also admitted that the observed similarity between these two taxa and other alpine Apiaceae "perhaps . . . means only that most alpine Umbelliferae tend to resemble one another" (Meinke and Constance 1982, p. 17), indicating that the contrasting hypotheses of a singular or multiple origins of alpine adaptations of *Lomatium* in the Elkhorn Mountains set forth in the present study have been under consideration for at least 40 years. The study by Hustafa (2007) was a candidate conservation agreement prepared for USFWS to determine whether *L. greenmanii* met the criteria to be added to the federal endangered species list. That study more confidently asserted that *L. greenmanii* and *L. oreganum* were sister species. As part of the assessment, they performed a phylogenetic analysis using a regional sampling of *Lomatium* species that attempted (but failed) to include all potential sister taxa of *L. greenmanii*. Hustafa (2007) used MP to analyze DNA sequence data from the ITS region and corroborated one suggestion by Meinke and Constance (1982) that *L. oreganum* and *L. greenmanii* are sisters. However, this study relied on a much more limited taxon sampling (15 species) compared with the present study and was based on only a single DNA sequence region.

Moreover, the analysis provided no measure of clade support; the samples were not vouchered and are therefore of unknown origin; and, to our knowledge, the data were not deposited in any publicly accessible database, such as GenBank. Our study encompassed a much wider sampling scheme (209 individuals spread across 79 taxa), more sophisticated phylogenetic reconstruction techniques (BI as well as ML and MP), and six additional molecular markers (including chloroplast regions). Finally, we attempted to recreate the results of Hustafa (2007) by limiting our taxon sampling, data (including using only nuclear markers and the ITS region), and methodologies to those employed in that study (MP), but we did not obtain the same phylogenetic tree (M. V. Ottenlips, M. A. E. Feist, D. H. Mansfield, G. M. Plunkett, S. Buerki, and J. F. Smith, unpublished data). Therefore, we conclude that the results of Hustafa (2007) are not reliable and that *L. greenmani* and *L. oreganum* are not sister species and in fact are only very distantly related (i.e., within the larger PENA clade). More broadly, we conclude that alpine species of Apiaceae frequently share morphologies despite lacking a most recent common ancestor, as Meinke and Constance (1982) additionally speculated.

Data from the original species descriptions by Meinke and Constance (1982) and from herbarium material (table 3) show many morphological and ecological similarities among all three taxa, including a low stature, compressed life cycle (from flowering to seed set), thickened rootstock, and preference for similar substrate (fig. 1; see also Hitchcock and Cronquist 2018). Many of these morphological similarities are common adaptations found among alpine plants originating from a variety of lineages (Billings 1974).

Climatic analysis using BioClim variables indicates that *L. greenmanii*, *L. oreganum*, and *L. erythrocarpum* share a similar environmental niche (fig. 4). We did not further model or project the climatic niche of these species because all known populations were included in the analysis. The commonly employed *D* and *I* statistics (Warren et al. 2008) lack statistical power at low sample sizes and are designed for use in distribution modeling scenarios. Schulz and Matthews (2007) created species distribution models (SDMs) for *L. greenmanii* in an attempt to locate new populations. Using their models as guides, they were able to locate one new population of *L. greenmanii*. The combination of these SDMs and associated fieldwork, along with the restricted habitat type, overall rarity, and ongoing monitoring of these species by the USFWS (Hustafa 2007), increases our confidence that there are no (or few) additional populations that have not been included in this analysis, and thus no further modeling or projection of potential distribution is warranted. The similar climatic niche and morphological overlap of these species, considering their phylogenetic position, further support our claim that these three alpine endemics represent replicated speciation within the PENA clade.

In addition to highlighting the importance of parallelism/convergence in the evolution of these three species, our study provides insights into parallelism/convergence within closely related lineages, the biogeography of the flora of the Wallowa and Elkhorn Mountains, rare plant conservation, and the molecular systematics of the PENA clade. Convergent evolution and parallel evolution are thought to be especially common in alpine communities because of the limited number of feasible adaptations plants can evolve to survive in such a stressful environment (Billings and Mooney 1968). While the independent evolution of similar adaptations is oftentimes viewed as one of the leading lines of evidence for natural selection, others have proposed that it is simply the result of structural limitations inherent in an organism's body plan (Wake 2003). Both hypotheses share degrees of validity, and the biological reality is likely a combination of both aspects. The harsh environment of alpine habitats in combination with the physical limits to adaptations in plant architecture may lead to a flora frequently characterized by distantly related species that share similar adaptations (Billings and Mooney 1968; Chabot and Billings 1972; Mansfield 2000). In studying the alpine flora of the French Alps, Marx et al. (2017) found that species-neutral processes, such as colonization and extirpation, can also play a role in shaping alpine plant communities. The independent origins of alpine adaptations observed in this study suggest that extreme selective pressure and colonization are both factors in the formation of the plant communities in the Wallowa and Elkhorn Mountains.

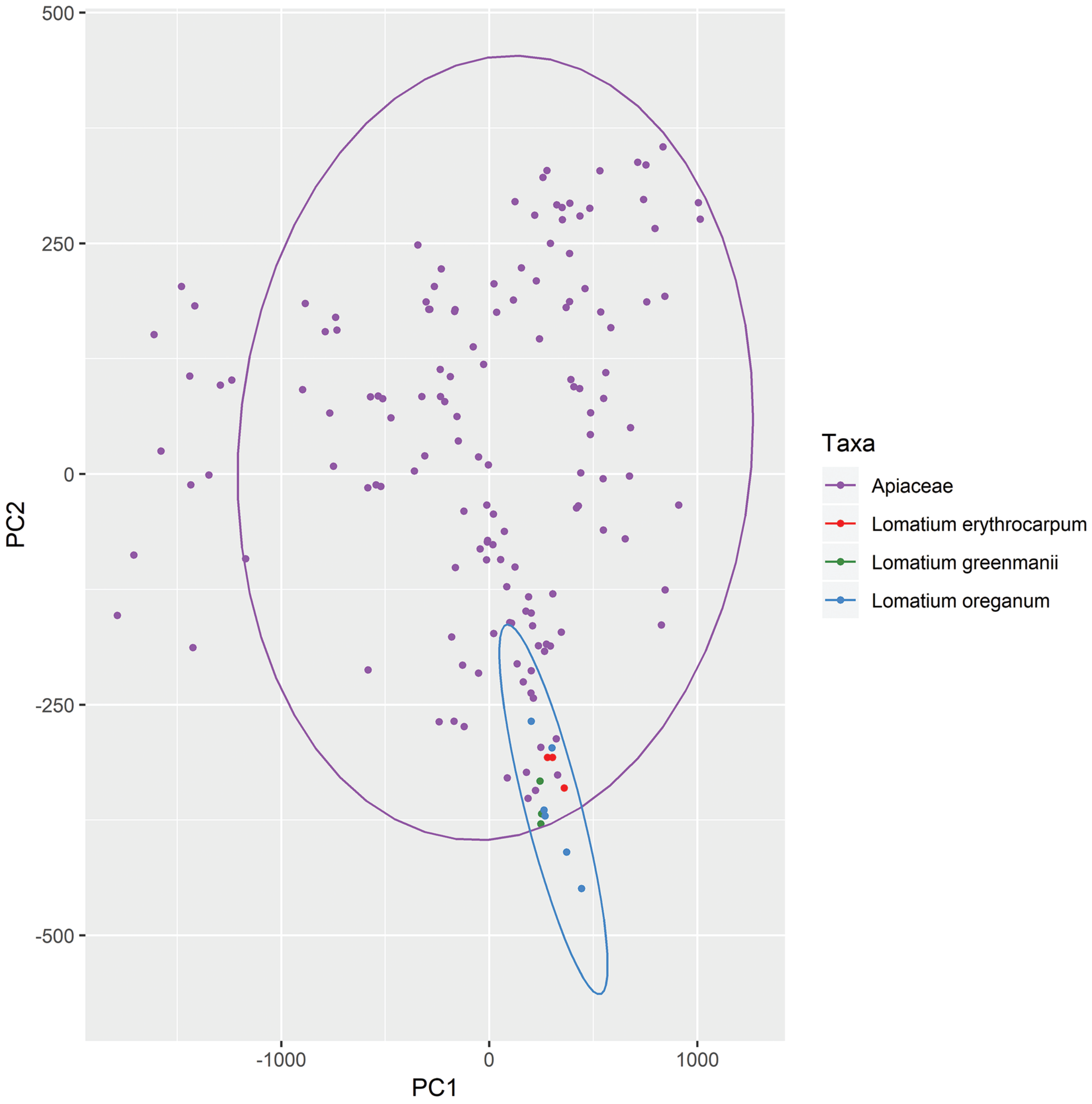

Fig. 4 Principal components analysis (PCA) depicting the similar climatic niche space of the three *Lomatium* species. PCA was performed on noncorrelated, centered, and scale BioClim variables extracted at the 30–arc second resolution. All known populations of the alpine-endemic *Lomatium* within this resolution are included in the analysis. The Apiaceae found in the Blue Mountains ecoregion are represented by spatially rarefied points based on herbarium records downloaded from the Consortium of Pacific Northwest Herbaria. Confidence intervals of 95% were drawn in R to highlight the shared climate niche space in comparison with the rest of the Apiaceae found in the Blue Mountains ecoregion.

Convergent evolution can occur across both shallow and deep evolutionary timescales. Some of the most well-known and exciting examples of convergence, such as the independent origin of pitcher traps in *Nepenthes* and the Sarraceniaceae, have occurred across great phylogenetic distance (Thorogood et al. 2018). Deep convergence also plays a unique role in shaping alpine floras, where most taxa share a specialized suite of traits that makes them uniquely adapted to their alpine environment (Billings 1974). Convergence among closely related species (in some instances referred to as parallel evolution) is less well studied (Schluter et al. 2004). This phenomenon has also been observed in other alpine plant groups outside the PENA clade, such as with the multiple independent origins of the cushion life-form in *Androsace* (Boucher et al. 2012).

Table 3

Comparison of Morphological Similarities among Three Alpine Species of *Lomatium*

Character	*L. greenmanii*	*L. oreganum*	*L. erythrocarpum*	Reference(s)
Leaflet margins entire	Yes	No	Yes	Hitchcock and Cronquist 2018
Yellow flowers	Yes	Yes	No	Meinke and Constance 1982
Caespitose development	Yes	Yes	Yes	Meinke and Constance 1982; Hitchcock and Cronquist 2018
Dissected leaves	Yes	Yes	Yes	Hitchcock and Cronquist 2018
Deep taproot	Yes	Yes	Yes	Hitchcock and Cronquist 2018
Developed involucel	Yes	Yes	Yes	Hitchcock and Cronquist 2018
Reduced terminal inflorescence	Yes	Yes	No	Meinke and Constance 1982
Dorsally flattened fruits	Yes	Yes	No	Meinke and Constance 1982

Our study lends support to the importance of shallow-scale (within genera) independent evolution of similar traits in the evolution of alpine plant community assembly. However, further study including the sampling of more species to uncover sister taxa and ancestral state reconstruction is needed to allow us to determine whether these alpine adaptations arose from ancestors with similar characters, indicating parallel evolution, or dissimilar characters, indicating convergence.

These results also highlight the importance of rare plant conservation and research. Previous workers (Meinke and Constance 1982; Hustafa 2007) entertained the possibility that two of these taxa might represent a monophyletic group and therefore a single alpine-adapted lineage. *Lomatium greenmanii* falls out in a broader PENA clade that does not include any other species of *Lomatium*, whereas the other two species are placed in two other distantly (relatively) related clades (*L. erythrocarpum* with *L. foeniculaceum* ssp. *macdougalii* and several species of *Cymopterus* and *L. oreganum* with the remaining species of *Lomatium*). Therefore, the phylogenetic diversity of this montane area of Oregon is higher than would have been thought on the basis of the traditional taxonomic treatment of these taxa in the most common reference for the region, *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1973, 2018). While the state and federal agencies responsible for protecting plant species do not directly take phylogenetic diversity into account, they do prioritize conservation of threatened/endangered taxa from monotypic and smaller genera. Additionally, one of the three known populations of *L. greenmanii* is located at the top of the Wallowa Lake tramline, a public gondola that brings tourists to the summit of Mount Howard in the summer months. This population is sensitive to trampling and other anthropogenic disturbances caused by summer visitors (Hustafa 2007).

Conclusions

This study sampled widely from across the PENA clade, including 209 individuals representing 79 taxa, and provided higher resolution than any previously published study of the clade. In addition to the phenotypic similarities among the three alpine species from different clades investigated here, there are many other cases of convergent/parallel evolution represented in the PENA clade (George et al. 2014), including similarities in leaflet morphology between *L. simplex* and the *L. triternatum* species complex (Smith et al. 2018). The three alpine taxa studied here do not share the same most recent common ancestor, and moreover, they are from different phylogenetic positions within the PENA clade. These rare taxa represent unique evolutionary lineages and thus warrant increased conservation measures, especially in the face of anthropogenic disturbance and climate change. A wide sampling scheme and molecular data were instrumental in uncovering the three independent origins of these species. In addition to improving our understanding of the evolutionary history of the PENA clade, our results provide insights into alpine plant phylogenetic community assembly, convergence/parallelism in closely related lineages, and the biogeographical history of alpine *Lomatium* associated with the Wallowa and Elkhorn Mountains.

Acknowledgments

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Appendix A

Voucher and Gene Accession Information

***Aletes filifolius* Mathias, Constance & W.L. Theob.**, R. C. Sivinski 4561 (RM), Socorro, New Mexico, MN995839, MN995903, X, MN996021, MN996072, X, MN996175

***Angelica lineariloba* A. Gray**, A. Thiehm 11344 (NY), Esmeralda, Nevada, MN995840, MN995904, MN995966, X, MN996073, MN996132, MN996176

***Arracacia atropurpurea* (Lehm.) Hemsl**, A. Ventura 479 (NY), Tepeapulco, Mexico, MN995841, MN995905, MN995967, X, MN996074, MN996133, MN996177

***Arracacia donnell-smithii* J.M. Coult. & Rose**, D. E. Breedlove 22815 (NY), Chiapas, Mexico, MN995842, MN995906, MN995968, X, MN996075, MN996134, MN996178

***Cymopterus bakeri* (J.M. Coult. & Rose)**, M. E. Jones, B. Franklin 3947 (RM), San Juan, Utah, MN995850, MN995914, MN995975, MN996028, MN996083, X, MN996186

***Cymopterus beckii* S.L. Welsh & Goodrich**, J. Anderson 87-149, D. Atwood and B. Thompson (RM), San Juan, MN995845, MN995909, MN995971, MN996024, MN996078, X, MN996181

***Cymopterus evertii* R.L. Hartm. & R.S. Kirkp.**, H. Marriott 10806 (RM), Park, Wyoming, MN995846, MN995910, MN995972, MN996025, MN996079, X, MN996182

***Cymopterus glomeratus* var. *fendleri* (A. Gray) R.L. Hartm**, C. E. Hinchliff 1314 (CIC), Mesa, Colorado, KF619882, X, KF619745, KF620018, X, X, X

***Cymopterus glomeratus* var. *greeleyorum* (J.W. Grimes & P.L. Packard) R.L. Hartm**, E. George 087 (CIC), Malheur, Oregon, MN995847, MN995911, MN995973, MN996026, MN996080, MN996136, MN996183

***Cymopterus lapidosus* (M.E. Jones) M.E. Jones**, B. E. Nelson 35207 (RM), Uinta, Wyoming, MN995848, MN995912, MN995974, MN996027, MN996081, MN996137, MN996184

***Cymopterus longilobus* (Rydb.) W.A. Weber**, B. Ertter 22416 (SRP), Teton, Wyoming, MN995843, MN995907, MN995969, MN996022, MN996076, MN996135, MN996179

***Cymopterus nivalis* S. Watson**, C E. Hinchliff 1348 (CIC), Beaverhead, Montana, MN995849, MN995913, X, X, MN996082, MN996138, MN996185

***Cymopterus ripleyi* Barneby**, C. E. Hinchliff 1310 (SRP), Lincoln, Nevada, KF619616, X, KF619894, KF619757, X, X, X

***Cymopterus* sp. nov.**, D. Roth 1380 (NAVA), Navajo, Arizona, MN995844, MN995908, MN995970, MN996023, MN996077, X, MN996180

***Donnellsmithia juncea* (Humb. & Bonpl. ex Spreng.) Mathias & Constance**, T. R. VanDevender 98-999 (NY), Sonora, Mexico, MN995851, MN995915, X, X, MN996084, X, MN996187

***Harbouria trachypleura* (A. Gray) J.M. Coult. & Rose**, K. Marlow 113 (CIC), Boulder, Colorado, MN995852, MN995916, MN995976, MN996029, MN996085, MN996139, MN996188

***Lomatium ambiguum* (Nutt.) J.M. Coult. & Rose**, B. Ertter 22278 (SRP), British Columbia, Canada, MH131697, MH131898, MH132102, MH132294, MH132480, MH132647, MH132843, C. E. Hinchliff 1273 (CIC), Idaho, Idaho, KF619621, X, KF619895, KF619758, X, X, X, J. F. Smith 9561 (SRP), Gem, Idaho, KF619622, X, KF619896, KF619759, X, X, X, J. F. Smith 9720 (SRP), Adams, Idaho, MN995853, MN995917, MN995977, MN996030, MN996086, MN996140, MN996189, Frank H. Rose 1536 (MONTU), Missoula, Montana, MN995854, MN995918, X, MN996031, MN996087, MN996141, MN996190

***Lomatium andrusianum* McK. Stevens & Mansfield**, B. Ertter 20719 (CIC), Ada, Idaho, MH131826, MH132031, MH132230, MH132416, MH132589, MH132778, MH132915, B. Ertter 20748 (CIC), Ada, Idaho, MH131827, MH132032, MH132231, MH132417, MH132590, MH132779, MH132976, D. Johnson & T. Day 026-1 (CIC), Gem, Idaho, MH131836, MH132040, MH132240, MH132426, MH132599, MH132788, MH132978, D. Johnson & T. Day 026-2 (CIC), Gem, Idaho, MH131837, MH132041, MH132241, MH132427, MH132600, MH132789, MH132979, D. Mansfield 16004 (CIC), Payette, Idaho, MH131828, MH132033, MH132232, MH132418, MH132591, MH132780, MH132916, J. F. Smith et al. 11580 (SRP), Boise, Idaho, MH131831, MH132035, MH132235, MH132421, MH132594, MH132783, MH132977

***Lomatium anomalum* M.E. Jones ex J.M. Coult. & Rose**, J. T. Duncan 05 (CIC), Jackson, Oregon, MN995889, MN995952, MN996008, MN996060, X, MN996164, MN996215, J. Benca 08-62 (WTU), Granite, Montana, MN995890, MN995953, MN996009, MN996061, MN996120, MN996165, MN996216, D. Mansfield 15-001 (CIC), Washington, Idaho, MN995883, MN995946, MN996002, MN996054, MN996113, MN996159, MN996211, D. Mansfield 15-088 (SRP), Owyhee, Idaho, MN995882, MN995945, MN996001, MN996053, MN996112, MN996158, MN996210, M. Darrach 645 (CIC), Grant, Oregon, MH131719, MH131922, MH132126, MH132315, MH132503, MH132671, MH132861, M. Darrach 656 (CIC), Asotin, Washington, MH131720, MH131923, MH132316, MH132316, MH132504, MH132672, MH132862, D. Mansfield 07-011 (CIC), Malheur, Oregon, X, MH131905, MH132109, MH132299, MH132487, MH132654, MH132848, D. Mansfield 07-055 (CIC), Washington, Idaho, MH131708, MH131911, MH132115, MH132305, MH132493, MH132660, MH132852, D. Mansfield 15-001 (CIC), Malheur, Oregon, MH131703, MH131906, MH132110, MH132300, MH132488, MH132655, MH132849, D. Mansfield 15-152 (CIC), Owyhee, Idaho, MH131705, MH131908, MH132112, MH132302, MH132490, MH132657, MH132851, E. George & J. Reichel 058 (CIC), Malheur, Oregon, KF619689, MH131912, KF619961, KF619824, MH132494, MH132661, MH132853, E. George & J. Reichel 066 (CIC), Washington, Idaho, MH131710, MH131913, MH132117, MH132307, MH132495, MH132662, MH132854, E. George & D. Mansfield 091 (CIC), Malheur, Oregon, KF619690, MH131915, KF619962, KF619825, MH132497, MH132664, MH132856, E. George 102 (CIC), Idaho, Idaho, MH131711, MH131914, MH132118, MH132308, MH132496, MH132663, MH132855, C. E. Hinchliff 1252 (SRP), Morrow, Oregon, MH131700, MH131902, MH132106, MH132297, MH132484, MH132651, MH132846, C. L. Hitchcock 23492 (WTU), Asotin, Washington, MH131701, MH131903, MH132107, X, MH132485, MH132652, X, P. Lesica 10794 (CIC), Idaho, Idaho, MH131724, MH131927, MH132131, MH132320, MH132508, MH132676, MH132866, X, P. Lesica 10798 (CIC), Idaho, Idaho, MH131725, MH131928, MH132132, MH132321, MH132509, MH132677, MH132867, C. V. Piper s.n. (WTU:88603), Whitman, Washington, MH131702, MH131904, MH132108, MH132298, MH132486, MH132653, MH132847, L. Polito et al. 002 (CIC), Owyhee, Idaho, MH131715, MH131918, MH132122, MH132312, MH132500, MH132667, MH132858, L. Polito et al. 003 (CIC), Owyhee, Idaho, MH131716, MH131919, MH132123, MH132313, MH132501, MH132668, MH132859, L. Polito et al. 004 (CIC), Owyhee, Idaho, MH131717, MH131920, MH132124, MH132314, MH132502, MH132669, MH132860, J. F. Smith et al. 10748 (SRP), Nez Perce, Idaho, MH131713, MH131916, MH132120, MH132310, MH132498, MH132665, MH132857, A. Truksa & S. Truksa 38 (CIC), Malheur, Oregon, MH131726, MH131929, MH132133, MH132322, MH132510, MH132678, MH132868

Lomatium attenuatum **Evert**, E. Evert 16359 (RM), Park, Wyoming, KF619624, X, KF619897, KF619761, X, X, X, C. E. Hinchhliff 1349 (SRP), Beaverhead, Montana, KF619623, X, KF619898, KF619760, X, X, X

Lomatium basalticum **Mansfield & M. Stevens**, C. E. Hinchliff 891 (CIC), Baker, Oregon, MH131727, MH131930, MH132134, MH132323, MH132511, MH132679, MH132869, L. Polito et al. 043 (CIC), Adams, Idaho, MH131728, MH131931, MH132135, MH132324, MH132512, MH132680, MH132870, L. Polito et al. 044 (CIC), Adams, Idaho, MH131729, MH131932, MH132136, MH132325, MH132513, MH132681, MH132871, L. Polito et al. 045 (CIC), Adams, Idaho, MH131730, MH131933, MH132137, MH132326, MH132514, MH132682, MH132872, M. Darrach 1115 (CIC), Wallowa, Oregon, MH131731, MH131934, MH132138, MH132327, MH132515, MH132683, MH132873

Lomatium bentonitum **K. Carlson & D. Mansfield**, E. George & D. Mansfield 089 (CIC), Malheur, Oregon, KF619625, MH131935, KF619899, KF619762, MH132516, MH132684, MH132874

Lomatium bicolor **(S. Watson) J.M. Coult. & Rose var.** ***bicolor***, B. Moseley 1768 (ID), Franklin, Idaho, KF619626, MH131936, KF619900, KF619763, MH132517, MH132685, MH132875

Lomatium bicolor **(S. Watson) J.M. Coult. & Rose var.** ***leptocarpum*** **(Torr. & A. Gray) Schlessman**, E. George & J. Reichel 064 (CIC), Washington, Idaho, KF619629, MH131937, KF619903, KF619766, MH132518, MH132686, X, MH132876

Lomatium brevifolium **(J.M. Coult. & Rose) J.M. Coult. & Rose**, B. Legler 2616 (WTU), Yakima, Washington, MN995858, MN995922, MN995981, MN996034, MN996091, MN996145, MN996194, D. French 2759 (WTU), Klickitat, Washington, X, MH131944, MH132147, MH132337, X, MH132694, MH132883, M. Darrach 1056 (CIC), Klickitat, Washington, MH131759, MH131963, MH132163, MH132351, MH132531, MH132711, MH132903, B. Ertter 7572 (WTU), Klickitat, Washington, MH131736, MH132711, X, MH132331, MH132519, MH132878, X, B. Legler 1798 (WTU), Kittitas, Washington, MH131737, MH131940, MH132142, MH132332, MH132520, MH132689, MH132879, G. N. Jones 1554 (WTU), Yakima, Washington, MH131745, MH131949, MH132150, MH132341, X, MH132699, MH132889, C. E. Hinchliff 1267 (SRP), Klickitat, Washington, MH131739, MH131942, MH132144, MH132334, MH132522, MH132691, MH132881, S. Gage & S. Rodman 227 (WTU), Yakima, Washington, MH131766, MH131970, MH132170, MH132356, X, MH132718, MH132909, C. L. Hitchcock 20278 (WTU), Kittitas, Washington, MH131740, X, MH132145, MH132335, MH132523, MH132692, MH132882, J. G. Smith 152 (WTU), Kittitas, Washington, MH131751, MH131955, X, MH132156, MH132529, MH132705, MH132895, J. W. Thompson 11577 (WTU), Kittitas, Washington, MH131754, MH131958, MH132159, MH132347, X, MH132707, MH132897, M. A. Schlessman 211 (WTU), Kittitas, Washington, MH131758, MH131962, MH132162, MH132350, X, MH132710, MH132902, D. Mansfield 11-491 (CIC), Kittitas, Washington, MH131741, MH131945, MH132148, MH132338, MH132524, MH132695, MH132884, F. A. Warren 1562 (WTU), Pierce, Washington, MH131742, MH131946, MH132149, MH132339, X, MH132696, MH132886, F. A. Warren 1609 (WTU), Pierce, Washington, MH131743, MH131947, X, MH132340, X, MH132697, MH132887, J. W. Thompson 12577a (WTU), Pierce, Washington, MH131752, MH131956, MH132157, MH132346, MH132530, MH132706, MH132898, K. A. Beck 200101 (WTU), Klickitat, Washington, MH131757, MH131961, MH132160, MH132349, X, MH132709, MH132901, P. F. Zika 24419 (SRP), Klickitat, Washington, MH131763, MH131967, MH132167, MH132354, MH132535, MH132715, MH132906, M. Darrach 304 (SRP), Klickitat, Washington, MH131760, MH131964, MH132164, X, MH132532, MH132712, X, D. H. French 1883 (CIC), Wasco, Oregon, X, MH131943, MH132146, MH132336, X, MH132693, MH132885, I. C. Otis 1903 (WTU), Thurston, Washington, MH131746, MH131950, MH132151, X, X, MH132700, MH132890, P. P. Lowry 712 (WTU), Skamania, Washington, MH131764, MH131968, MH132168, MH132355, X, MH132716, MH132907

Lomatium brunsfeldianum **Kemper & R.P. McNeill**, C. R. Bjork 6481 (ID), Kootenai, Idaho, KF619633, MH131971, KF619906, KF619769, MH132537, MH132719, MH132910, T. Kemper 93 (CIC), Idaho, Idaho, MH131772, MH131976, MH132176, MH132362, MH132542, MH132724, MH132925, P. Brunsfeld et al. 6426 (ID), Shoshone, Idaho, MH131770, MH131974, MH132174, MH132360, MH132540, MH132722, MH132926, S. Walker 218 (ID), Idaho, Idaho, KF619634, MH131975, KF619907, KF619770, MH132541, MH132723, X, T. Spribille 14241 (ID), Shoshone, Idaho, X, MH131977, MH132177, MH132363, MH132543, MH132725, MH132927

Lomatium canbyi **(J.M. Coult. & Rose) J.M. Coult. & Rose**, E. George & D. Mansfield 086 (CIC), Malheur, Oregon, KF619639, MH131978, KF619911, KF619775, MH132544, MH132726, MH132928

Lomatium caruifolium **(Hook. & Arn.) J.M. Coult. & Rose**, R. McNeill s.n. (CIC), Madera, California, MN995859, MN995923, MN995982, MN996035, MN996092, MN996146, MN996195

***Lomatium columbianum* Mathias & Constance**, C. E. Hinchliff 1265 (SRP), Klickitat, Washington, KF619642, MH131979, KF619915, KF619778, MH132545, MH132727, X

***Lomatium cous* (S. Watson) J.M. Coult. & Rose**, D. Mansfield 11-010 (CIC), Umatilla, Oregon, KF619647, MH131980, KF619920, KF619783, MH132546, MH132728, MH132929, C. Johnson 7260 (WTU), Wallowa, Oregon, MN995878, MN995942, MN995998, MN996050, MN996109, MN996155, MN996208

***Lomatium cusickii* (S. Watson) J.M. Coult. & Rose**, B. E. Nelson 50572 (CIC), Idaho, Idaho, KF619648, X, KF619921, KF619784, X, X, X

***Lomatium cuspidatum* Mathias & Constance**, G. Patrick s.n. (WTU), Chelan, Washington, MN995861, MN995925, MN995984, MN996037, MN996094, X, MN996197, P. Elvaneter 1000 (WTU), Kittitas, Washington, MN995862, MN995926, MN995985, MN996038, MN996095, X, MN996198, G. Patrick s.n. (WTU), Chelan, Washington, MN995860, MN995924, MN995983, MN996036, MN996093, X, MN996196

***Lomatium dissectum* (Nutt.) Mathias & Constance**, R. Helliwell 3957 (CIC), Douglas, Oregon, KF619654, X, KF619927, KF619790, X, X, X, J. T. Duncan 11 (CIC), Jackson, Oregon, KF619652, X, KF619925, KF619788, X, X, X

***Lomatium donnellii* (J.M. Coult. & Rose) J.M. Coult. & Rose**, C. E. Hinchliff 1258 (CIC), Jefferson, Oregon, KF619656, MH131983, KF619929, KF619792, MH132549, MH132731, MH132932

***Lomatium erythrocarpum* Meinke & Constance**, Michael Murray s.n. (OSC), Baker, Oregon, MN995868, MN995932, MN995989, MN996041, MN996100, MN996152, X, Meinke 3201 (OSC), Baker, Oregon, MN995867, MN995931, MN995988, X, X, MN996151, X

***Lomatium foeniculaceum* var. *fimbriatum* (W.L. Theob.) B. Boivin**, K. Carlson 002 (CIC), Malheur, Oregon, HQ426076, X, HQ426127, HQ426102, X, X, X, C. E. Hinchliff 1306 (SRP), Lincoln, Nevada, KF619659, X, KF619932, KF619795, X, X, X, D. Mansfield 07001 (CIC), Canyon, Idaho, KF619660, X, KF619933, KF619796, X, X, X

***Lomatium gormanii* (Howell) J.M. Coult. & Rose**, C. E. Hinchliff 1212 (CIC), Walla Walla, Washington, KF619664, MH131984, KF619937, KF619800, MH132550, MH132732, MH132933

***Lomatium grayi* (J.M. Coult. & Rose) J.M. Coult. & Rose**, M. Stevens 016 (SRP), Boise, Idaho, MN995869, MN995933, MN995990, MN996042, MN996101, MN996153, MN996203, C. E. Hinchliff 1240 (CIC), Yakima, Washington, KF619670, MH131986, KF619943, KF619806, MH132552, MH132734, MH132935, C. E. Hinchliff 1264 (SRP), Klickitat, Washington, MH131782, MH131987, MH132187, MH132373, MH132553, MH132735, MH132936, D. Mansfield et al. 12-444 (CIC), Owyhee, Idaho, MH131785, MH131990, MH132190, MH132376, X, MH132738, MH132939, D. Mansfield 15-155 (CIC), Owyhee, Idaho, MH131784, MH131989, MH132189, MH132375, MH132555, MH132737, MH132938, J. F. Smith et al. 10766 (SRP), Nez Perce, Idaho, MH131786, MH131991, MH132191, MH132377, X, MH132739, MH132940, J. F. Smith et al. 11591 (SRP), Gem, Idaho, MH131787, MH131992, MH132192, MH132378, MH132556, MH132740, MH132941, M. Stevens & J. Avitia 067 (CIC), Washington, Idaho, MH131789, MH131994, MH132194, MH132380, MH132558, MH132742, MH132943, Brill s.n. (WTU), Yakima, Washington, MH131780, MH131985, MH132185, MH132371, MH132551, MH132733, MH132371

***Lomatium greenmanii* Mathias**, R. D. Kratz & R. Sines s.n. (WTU), Wallowa, Oregon, MN995872, MN995936, MN995993, MN996045, MN996103, MN996154, X, Jessie Johanson 02-118 (WTU), Wallowa, Oregon, MN995871, MN995937, X, MN996044, MN996102, X, X, Jessie Johanson 02-118 (OSC), Wallowa, Oregon, MN995873, MN995935, MN995992, X, MN996104, X, X, G. D. Carr 1565 (OSC), Wallowa, Oregon, MN995870, MN995934, MN995991, MN996043, X, X, X, Jessie Johanson 02-112 (WTU), Wallowa, Oregon, MN995874, MN995938, MN995994, MN996046, MN996105, X, MN996204

***Lomatium hallii* (S. Watson) J.M. Coult. & Rose**, Porter P. Lowry II 569 (WTU), Multnomah, Oregon, MN995875, MN995939, MN995995, MN996047, MN996106, X, MN996205

***Lomatium lithosolamans* J.F. Sm. & M.A. Feist**, C. E. Hinchliff 1237 (CIC), Yakima, Washington, KF619737, MH131995, KF620011, KF619874, X, MH132743, MH132944

***Lomatium macrocarpum* (Hook. & Arn.) J.M. Coult. & Rose**, D. Mansfield 07-329 (CIC), Harney, Oregon, MH131791, MH131996, X, MH132382, MH132559, MH132744, MH132945, E. George 101 (CIC), Nez Perce, Idaho, MH131792, MH131997, MH132196, MH132383, MH132560, MH132745, MH132946, R. Helliwell 3952 (CIC), Josephine, Oregon, MH131798, MH132003, MH132202, MH132389, MH132566, MH132751, MH132952

***Lomatium multifidum* (Nutt.) R.P. McNeill & Darrach**, C. E. Hinchhliff 1249 (SRP), Asotin, Washington, KF619650, X, KF619926, KF619789, X, X, X, C. E. Hinchhliff 1296 (SRP), Coconino, Arizona, KF619651, X, KF619924, KF619787, X, X, X, D. Mansfield 7048c (CIC), Elmore, Idaho, MN995864, MN995928, X, MN996039, MN996097, MN996148, MN996200, D. Mansfield 07391 (CIC), Malheur, Oregon, MN995863, X, MN995986, X, MN996096, MN996147, MN996199, E. George 059 (CIC), Washington, Idaho, KF619653, X, KF619926, KF619789, X, X, X, Emma George 100 (CIC), Nez Perce, Idaho, MN995865, X, X, X, MN996098, MN996149, MN996201, B. Chavez 028 (CIC), Owyhee, Idaho, MN995866, MN995930, MN995987, MN996040, MN996099, MN996150, MN996202

Lomatium nevadense* (S. Watson) J.M. Coult. & Rose var. *nevadense, D. Mansfield 11-081 (CIC), Elko, Nevada, KF619682, MH132005, KF619954, KF619817, MH132568, MH132753, MH132953

***Lomatium nevadense* (S. Watson) J.M. Coult. & Rose var. *parishii* (J.M. Coult. & Rose) Jeps.**, C. E. Hinchliff 1283 (CIC), Apache, Arizona, KF619681, MH132006, KF619953, KF619816, X, MH132754, MH132954

***Lomatium oreganum* (J.M. Coult. & Rose) J.M. Coult. & Rose**, C. Johnson s.n. (WTU), Wallowa, Oregon, MN995879, MN995943, MN995999, MN996051, MN996110, MN996156, MN996209, B. Bafus 402 (WTU), Baker, Oregon, MN995877, MN995941, MN995997, MN996049, MN996108, X, MN996207, Rachel Sines s.n. (OSC), Wallowa, Oregon, MN995880, X, MN996000, MN996052, MN996111, X, X, Roy Sines s.n. (OSC), Baker, Oregon, MN995881, MN995944, X, X, X, X, X, Ann Kratz s.n. (WTU), Baker, Oregon, MN995876, MN995940, MN995996, MN996048, MN996107, MN996157, MN996206

Lomatium peckianum **Mathias & Constance**, Forman and Butts 73573 (WTU), Lake, Oregon, MN995884, MN995947, MN996003, MN996055, MN996114, X, MN996212

Lomatium planosum **(Oster.) Mansfield & S. R. Downie**, C. E. Hinchliff 1322 (SRP), Delta, Colorado, KF619617, X, KF619891, KF619754, X, X, X

Lomatium roneorum **Darrach**, D. Mansfield 11493 (CIC), Kittitas, Washington, MN995855, MN995919, MN995978, MN996032, MN996088, MN996142, MN996191, M. Darrach 649 (CIC), Chelan, Washington, MN995856, MN995920, MN995979, MN996033, MN996089, MN996143, MN996192

Lomatium simplex **(Nutt. ex S. Watson) J.F. Macbr.**, B. Ertter 21062 & A. DiNicola (CIC), Adams, Idaho, MH131808, MH132013, MH132212, MH132399, MH132575, MH132761, MH132961, B. Ertter 22285 (SRP), British Columbia, Canada, MH131806, MH132011, MH132210, MH132397, MH132573, MH132759, MH132959, B. Ertter 22286 (SRP), British Columbia, Canada, MH131807, MH132012, MH132211, MH132398, MH132574, MH132760, MH132960, D. Giblin 5208 (WTU), Kittitas, Washington, MH131812, MH132017, MH132216, MH132403, MH132576, MH132764, MH132964, C. A. Morrow s.n. (WTU), Gallatin, Montana, MH131809, MH132014, MH132213, MH132400, X, MH132762, MH132962, J. F. Smith 5428 (SRP), Blaine, Idaho, MH131822, MH132027, MH132226, MH132413, MH132586, MH132774, MH132973, D. Mansfield 11-007 (CIC), Harney, Oregon, KF619715, MH132021, KF619988, KF619851, MH132580, MH132768, MH132968, D. Mansfield et al. 14-009 (CIC), Ada, Idaho, MH131813, MH132018, MH132217, MH132404, MH132577, MH132765, MH132965, D. Mansfield et al. 14-110 (CIC), Ada, Idaho, MH131814, MH132019, MH132218, MH132405, MH132578, MH132766, MH132966, R. Goff 99-18 (WTU), Ferry, Washington, MH131824, MH132029, MH132228, X, X, MH132776, MH132975, C. E. Hinchliff 1345 (SRP), Lemhi, Idaho, MH131810, MH132015, MH132214, MH132401, X, MH132763, MH132963, C. L. Hitchcock 9288 (WTU), Lemhi, Idaho, MH131811, MH132016, MH132215, MH132402, X, X, MH133032

Lomatium **sp. nov.**, J. W. Thompson 9763.5 (WTU), Kittitas, Washington, MN995885, MN995948, MN996004, MN996056, MN996115, MN996160, X

Lomatium **sp. nov. 2**, M. Darrach 627 (CIC), Morrow, Oregon, MH131838, MH132042, MH132242, MH132428, MH132601, MH132790, MH132980

Lomatium **sp. nov. 3**, C. L. Hitchcock 8397 (WTU), Latah, Idaho, MH131841, MH132079, MH132273, MH132457, X, MH132821, X, C. L. Hitchcock 17794 (WTU), Lake, Montana, MH131840, MH132044, MH132244, MH132430, MH132603, MH132792, MH132981, P. Lesica 10541 (CIC), Sanders, Montana, MH131857, MH132060, MH132256, MH132439, MH132611, MH132804, MH132992, P. Lesica 10552 (CIC), Lake, Montana, MH131858, MH132061, MH132257, MH132440, MH132612, MH132805, MH132993, I. C. Otis 1940 (WTU: second sheet), Whitman, Washington, MH131849, MH132052, MH132250, X, X, MH132797, MH133033, J. W. Oppe 71 (WTU), Latah, Idaho, MH131851, MH132054, MH132251, MH132436, MH132608, MH132798, X, M. A. Schlessman 423 (WTU), Whitman, Washington, MH131853, MH132056, MH132253, MH132437, MH132609, MH132800, MH132990, M. A. Schlessman 589 (WTU), Nez Perce, Idaho, MH131853, MH132056, MH132253, MH132437, MH132609, MH132800, MH132990, M. A. Schlessman 651 (WTU), Nez Perce, Idaho, MH131856, MH132059, MH132255, MH132438, MH132610, MH132803, MH132991, L. M. Umbach 425 (WTU), Yakima, Washington, MH131852, MH132055, MH132252, X, X, MH132799, X

Lomatium **sp. nov. 4**, R. G. Olmstead 096-55 (WTU), Lake, Oregon, MH131871, MH132073, MH132267, MH132451, MH132621, MH132815, MH133004, M. Friend s.n. (SRP), Plumas, California, MH131870, MH132072, MH132266, MH132450, X, MH132814, X

Lomatium **sp. nov. 5**, R. Helliwell 3953 (CIC), Josephine, Oregon, MH131876, MH132078, MH132272, MH132456, MH132626, MH132820, MH133009, A. R. Kruckeberg 1891 (WTU), Josephine, Oregon, MH131872, MH132074, MH132268, MH132452, MH132622, MH132816, MH133005, M. F. Denton 2433 (ID), Josephine, Oregon, MH131875, MH132077, MH132271, MH132455, MH132625, MH132819, MH133008

Lomatium suksdorfii **(S. Watson) J.M. Coult. & Rose**, M. Darrach 900 (CIC), Wasco, Oregon, MH131878, MH132081, MH132275, MH132459, MH132628, MH132823, MH133011, C. E. Hinchliff 1363 (SRP), Klickitat, Washington, MH131877, MH132080, MH132274, MH132458, MH132627, MH132822, MH133010

Lomatium swingerae **R.P. McNeill**, R. P. McNeill s.n. (CIC), Idaho, Idaho, MH131879, MH132082, X, MH132460, MH132629, MH132824, MH133012, R. P. McNeill s.n. (CIC), Idaho, Idaho, MH131880, MH132083, X, MH132461, MH132630, MH132825, MH133013

Lomatium tamanitchii **Darrach & Thie**, M. Darrach 624 (CIC), Klickitat, Washington, MH131881, MH132085, MH132277, MH132463, MH132632, MH132827, MH133015, C. E. Hinchliff 1268 (SRP), Klickitat, Washington, X, MH132084, MH132276, MH132462, MH132631, MH132826, MH133014

Lomatium tenuissimum **(Geyer ex Hook.) Feist & G.M. Plunkett**, C. E. Hinchliff 1272 (SRP), Shoshone, Idaho, KF619738, MH132086, KF620012, KF619875, MH132633, MH132828, MH133016

Lomatium thompsonii **(Mathias) C.L. Hitchc.**, D. French 2513 (CIC), Chelan, Washington, MH131884, MH132088, MH132280, MH132466, MH132635, MH132830, MH133018, C. E. Hinchliff 1355 (CIC), Kittitas, Washington, KF619711, MH132087, KF619984, KF619087, MH132634, MH132829, MH133017

Lomatium tracyi **Mathias & Constance**, J. Duncan 2013-4 (CIC), Curry, Oregon, MN995888, MN995951, MN996007, MN996059, MN996118, MN996163, X

Lomatium triternatum **(Pursh) J.M. Coult. & Rose**, K. Carlson & E. Valdes 097 (CIC), Owyhee, Idaho, MH131886, MH132090, MH132282, MH132468, MH132637, MH132832, MH133020

Lomatium tuberosum **Hoover**, C. E. Hinchliff 1270 (WS), Yakima, Washington, KF619716, MH132091, KF619989, KF619852, MH132638, MH132833, MH133021

Lomatium utriculatum **(Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose**, R. P. McNeill s.n., Kern, California, MH131888, MH132092, MH132284, MH132470, MH132639, X, MH133023

Lomatium vaginatum **J.M. Coult. & Rose**, R. Helliwell 3956 (CIC), Douglas, Oregon, MH131892, MH132096, MH132288, MH132474, X, MH132837, MH133022, D. Mansfield 11-005 (CIC), Harney, Oregon, KF619717, MH132093, KF619990, KF619853, MH132640, MH132834, MH133024, D. Mansfield 11-006 (CIC), Harney, Oregon, KF619719, MH132094, KF619992, KF619855, MH132641, MH132835, MH133025

Lomatium watsonii **(J.M. Coult. & Rose) J.M. Coult. & Rose**, B. Legler 13650 (WTU), Yakima, Washington, MN995886, MN995949, MN996005, MN996056, MN996116, MN996161, MN996213, C. E. Hinchliff 1269 (CIC), Klickitat, Washington, KF619720, MH132097, KF619993, KF619856, MH132643, MH132838, MH133027, B. Legler 13650b (WTU), Yakima, Washington, MN995887, MN995950, MN996006, MN996057, MN996117, MN996162, MN996214

Musineon divaricatum **(Pursh) Nutt.**, P. Lesica 11295 (CIC), Granite, Montana, MN995891, MN995954, MN996010, MN996062, MN996121, MN996166, MN996217

Musineon glaucescens **Lesica**, P. Lesica 11308 (CIC), Lewis and Clark, Montana, MN995894, MN995956, MN996012, MN996064, MN996123, MN996167, MN996219

Musineon tenuifolium **Nutt. ex Torr. & A. Gray**, B. E. Nelson 25258 (RM), Niobrara, Wyoming, MN995892, MN995955, MN996011, MN996063, MN996122, X, MN996218

Musineon vaginatum **Rybd.**, P. Lesica 11285 (CIC), Missoula, Montana, MN995893, MN995957, MN996013, MN996065, MN996124, MN996168, MN996220

Neoparrya lithophila **Mathias**, C. E. Hinchliff 1275, Taos, New Mexico, KF619725, X, KF619998, KF619861, X, X, X

Pteryxia terebinthina **var. *terebinthina*** **(Hook.) J.M. Coult. & Rose**, B. Ertter 22298 (SRP), Grant, Washington, MH131894, MH132101, MH132293, MH132479, MH132646, MH132842, MH133031, C. E. Hinchliff 1271 (CIC), Grant, Washington, KF619733, MH132098, KF620007, KF619870, X, MH132839, MH133028, L. Polito 038 (CIC), Boise, Idaho, MH131897, MH132100, MH132292, MH132478, MH132645, MH132841, MH133030, J. F. Smith 11038 (SRP), Blaine, Idaho, MH131896, MH132099, MH132291, MH132477, MH132644, MH132840, MH133029

Tauschia glauca **(J.M. Coult. & Rose) Mathias & Constance**, R. Spellenberg 10254 (ID), Trinity, California, MN995895, MN995958, MN996014, MN996066, MN996125, MN996169, MN996221

Tauschia stricklandii **(J.M. Coult. & Rose) Mathias & Constance**, B. Legler 3597 (WTU), Pierce, Washington, MN995896, MN995959, MN996015, MN996067, MN996126, X, MN996222, David Giglin 5362 (WTU), Yakima, Washington, MN995897, MN995960, MN996016, MN996068, MN996127, MN996170, MN996223

Tauschia texana **A. Gray**, F. R. Barrie 1435 (RM), Gonzalez, Texas, MN995898, MN995961, MN996017, MN996069, MN996128, MN996171, X

Thaspium trifoliatum **(L.) A. Gray**, R.B. Clarkson 2474 (RM), Burnet, Texas, MN995899, MN995962, X, X, X, X, MN996224

Vesper constancei **(R.L. Hartm.) R.L. Hartm. & G.L. Nesom**, C. E. Hinchliff 1224 (CIC), Bernalillo, New Mexico, MN995857, MN995921, MN995980, X, MN996090, MN996144, MN996193

Vesper multinervatus **(J.M. Coult. & Rose) R.L. Hartm. & G.L. Nesom**, M. Darrach 622 (CIC), Clark, Nevada, MN995900, MN995963, MN996018, MN996070, MN996129, MN996172, MN996225

Zizia aurea **(L.) W.D.J. Koch**, R. L. McGregor 32892 (RM), Cherokee, Kansas, MN995901, MN995964, MN996019, MN996071, MN996130, MN996173, MN996226

Zosima absinthifolia **Link**, C. Davidson 12429 (SRP), Republic of Georgia, MN995902, MN995965, MN996020, X, MN996131, MN996174, X

Literature Cited

Alvarado-Cárdenas LO, E Martínez-Meyer, TP Feria, LE Eguiarte, HM Hernández, G Midgley, ME Olson 2013 To converge or not to converge in environmental space: testing for similar environments between analogous succulent plants of North America and Africa. Ann Bot 111:1125–1138.

Anacker BL, SY Strauss 2014 The geography and ecology of plant speciation: range overlap and niche divergence in sister species. Proc R Soc B 281:2013–2980.

Anthelme F, S Lavergne 2017 Alpine and arctic plant communities: a worldwide perspective. Perspect Plant Ecol 30:1–5.

Barga SC, TE Dilts, EA Leger 2018 Contrasting climate niches among co-occurring subdominant forbs of the sagebrush steppe. Divers Distrib 24:1291–1307.

Billings WD 1974 Adaptations and origins of alpine plants. Arct Antarct Alp Res 6:129–142.

Billings WD, HA Mooney 1968 The ecology of arctic and alpine plants. Biol Rev 43:481–529.

Bliss LC 1962 Adaptations of arctic and alpine plants to environmental conditions. Arctic 15:117–144.

Borowiec ML 2016 AMAS: a fast tool for alignment manipulation and computing of summary statistics. PeerJ 4:1660.

Boucher F, W Thuiller, C Roquet, R Douzet, S Aubert, N Alvarez, S Lavergne 2012 Reconstructing the origins of high-alpine niches and cushion life form in the genus *Androsace* s.l. (Primulaceae). Evolution 66:1255–1268.

Budelmann BU 1995 Cephalopod sense organs, nerves and the brain: adaptations for high performance and life style. Mar Freshw Behav Physiol 25:13–33.

Chabot BF, WD Billings 1972 Origins and ecology of the Sierran alpine flora and vegetation. Ecol Monogr 42:163–199.

Choler P 2018 Winter soil temperature dependence of alpine plant distribution: implications for anticipating vegetation changes under a warming climate. Perspect Plant Ecol 30:6–15.

Colosimo PF, KE Hosemann, S Balabhadra, G Villarreal, M Dickson, J Grimwood, DM Kingsley 2005 Widespread parallel evolution in sticklebacks by repeated fixation of ectodysplasin alleles. Science 307:1928–1933.

Cronquist AJ, NH Holmgren, PK Holmgren 1997 Intermountain flora: vascular plants of the intermountain West, USA: subclass Rosidae (except Fabales). Vol 3, pt A. New York Botanical Garden, New York.

Darriba D, GL Taboada, R Doallo, D Posada 2012 jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9:772.

ESRI (Environmental Systems Research Institute) 2016 ArcGIS desktop: release 10.5. ESRI, Redlands, CA.

Feist MAE, JF Smith, DH Mansfield, M Darrach, RP McNeill, SR Downie, BL Wilson 2017 New combinations in *Lomatium* (Apiaceae, subfamily Apioideae). Phytotaxa 316:95–98.

Flora of North America Editorial Committee 2002 Flora of North America. Oxford University Press, Oxford.

George EE, DH Mansfield, JF Smith, RL Hartman, SR Downie, CE Hinchliff 2014 Phylogenetic analysis reveals multiple cases of morphological parallelism and taxonomic polyphyly in *Lomatium* (Apiaceae). Syst Bot 36:662–675.

Haldane JBS 1932 The causes of evolution. Longman, London.

Hijmans RJ, J van Etten 2014 raster: geographic data analysis and modeling (R package). http://cran.r-project.org/web/packages/raster/index.html.

Hitchcock CL, A Cronquist 1973 Flora of the Pacific Northwest: an illustrated manual. University of Washington Press, Seattle.

——— 2018 Flora of the Pacific Northwest: an illustrated manual. University of Washington Press, Seattle.

Horikoshi M, Y Tang 2016 ggfortify: data visualization tools for statistical analysis results (R package). http://cran.r-project.org/package=ggfortify.

Hughes CE, GW Atchison 2015 The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. New Phytol 207:275–282.

Hustafa J 2007 Candidate conservation agreement for *Lomatium greenmanii* Greenman's desert parsley. USDA Forest Service, Eagle Cap Ranger District, Enterprise, OR, and Wallowa-Whitman National Forest, Baker City, OR/US Fish and Wildlife Service, La Grande Field Office, La Grande, OR, and Oregon Fish and Wildlife Office, Portland, OR. http://www.fws.gov/oregonfwo/species/data/greenmansdesertparsley/documents/ca-greenman07.pdf.

Klanderud K, Ø Totland 2005 Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. Ecology 86:2047–2054.

Kumar S, G Stecher, K Tamura 2016 MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol Biol Evol 33:1870–1874.

Kuss P, GFJ Armbruster, HH Ægisdóttir, JF Scheepens, J Stöcklin 2011 Spatial genetic structure of *Campanula thyrsoides* across the European Alps: indications for glaciation-driven allopatric subspeciation. Perspect Plant Ecol 13:101–110.

Lande R 1980 Genetic variation and phenotypic evolution during allopatric speciation. Am Nat 116:463–479.

Licciardi JM, PU Clark, EJ Brook, D Elmore, P Sharma 2004 Variable responses of western US glaciers during the last deglaciation. Geology 35:81–84.

Lieberman TD, JB Michel, M Aingaran, G Potter-Bynoe, D Roux, MR Davis Jr, AJ McAdam 2011 Parallel bacterial evolution within multiple patients identifies candidate pathogenicity genes. Nat Genet 43:1275.

Mansfield DH 2000 Flora of Steens Mountain. Oregon State University Press, Corvallis.

Martín-Bravo S, V Valcárcel, P Vargas, M Luceño 2010 Geographical speciation related to Pleistocene range shifts in the western Mediterranean mountains (*Reseda* sect. *Glaucoreseda*, Resedaceae). Taxon 59:466–482.

Marx HE, C Dentant, J Renaud, R Delunel, DC Tank, S Lavergne 2017 Riders in the sky (islands): using a mega-phylogenetic approach to understand plant species distribution and coexistence at the altitudinal limits of angiosperm plant life. J Biogeogr 44:2618–2630.

Meinke RJ, L Constance 1982 *Lomatium oreganum* and *L. greenmanii* (Umbelliferae), two little known alpine endemics from northeastern Oregon. Madrono 29:13–18.

Miller MA, W Pfeiffer, T Schwartz 2011 The CIPRES Science Gateway: a community resource for phylogenetic analyses. Pages 1–8 *in* Proceedings of the 2011 TeraGrid Conference: Extreme Digital Discovery, Salt Lake City, UT, July 18–21. Gateway, New Orleans.

Montgomery MK, MJ McFall-Ngai 1992 The muscle-derived lens of a squid bioluminescent organ is biochemically convergent with the ocular lens: evidence for recruitment of aldehyde dehydrogenase as a predominant structural protein. J Biol Chem 267:20999–21003.

Morin PA, KM Parsons, FI Archer, MC Ávila-Arcos, LG Barrett-Lennard, L Dalla Rosa, JK Ford 2015 Geographic and temporal dynamics of a global radiation and diversification in the killer whale. Mol Ecol 24:3964–3979.

Müller J, K Müller, D Quandt, C Neinhuis 2010 PhyDE: phylogenetic data editor, version 0.995. http://phyde.de.

Near TJ, MF Benard 2004 Rapid allopatric speciation in logperch darters (Percidae: *Percina*). Evolution 58:2798–2808.

Nicolas AN, GM Plunkett 2012 Untangling generic limits in *Azorella*, *Lareitia*, and *Mulinum* (Apiaceae: Azorelloideae): insights from phylogenetics and biogeography. Taxon 61:826–840.

Nixon KC, QD Wheeler 1990 An amplification of the phylogenetic species concept. Cladistics 6:211–223.

Omernik JM 1987 Ecoregions of the conterminous United States. Ann Assoc Am Geogr 77:118–125.

Oregon Department of Agriculture 2018 Oregon's threatened, endangered, and candidate plants. Oregon Department of Agriculture, Salem. http://oregon.gov/oda/programs/plantconservation/pages/aboutplants.aspx.

Ottenlips M 2019 Convergent evolution and species boundaries in *Lomatium* species (Apiaceae). MS thesis. Boise State University, ID.

Plunkett GM, AN Nicolas 2016 Assessing *Azorella* (Apiaceae) and its allies: phylogenetics and a new classification. Brittonia 69:31–61.

Ragionieri L, S Fratini, M Vannini, CD Schubart 2009 Phylogenetic and morphometric differentiation reveal geographic radiation and pseudo-cryptic speciation in a mangrove crab from the Indo-West Pacific. Mol Phylogenet Evol 52:825–834.

Rambaut A, AJ Drummond, D Xie, G Baele, MA Suchard 2018 Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst Biol 67:901–904.

R Core Team 2018 R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ronquist F, JP Huelsenbeck 2003 MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

Roquet C, FC Boucher, W Thuiller, S Lavergne 2013 Replicated radiations of the alpine genus *Androsace* (Primulaceae) driven by range expansion and convergent key innovations. J Biogeogr 40:1874–1886.

Rosenblum EB, LJ Harmon 2010 "Same same but different": replicated ecological speciation at White Sands. Evolution 65:946–960.

Schittek KM, D Forbriger, J Berg, F Hence, F Schaebitz, B Eitel 2018 Last millennial environmental dynamics in the western Peruvian Andes inferred from the development of a cushion-plant peat hillock. Perspect Plant Ecol 30:115–124.

Schluter D, EA Clifford, M Nemethy, JS McKinnon 2004 Parallel evolution and inheritance of quantitative traits. Am Nat 16:809–822.

Schulz J, J Matthews 2007 Appendix D: research, monitoring and predictive habitat modeling. Pages 1–26 *in* J Hustafa, ed. Candidate conservation agreement for *Lomatium greenmanii* Greenman's desert parsley. USDA Forest Service, Eagle Cap Ranger District Enterprise, OR, and Wallowa-Whitman National Forest, Baker City, OR/US Fish and Wildlife Service, La Grande Field Office, La Grande, OR, and Oregon Fish and Wildlife Office, Portland, OR.

Shimodaira H, M Hasegawa 2001 CONSEL: for assessing the confidence of phylogenetic tree selection. Bioinformatics 17:1246–1247.

Smith JF, DH Mansfield, M Stevens, E Sosa, MAE Feist, SR Downie, GM Plunkett, M Darrach 2018 Try Tri again? resolving species boundaries in the *Lomatium triternatum* (Apiaceae) complex. J Syst Evol 56:218–230.

Smyčka J, C Roquet, J Renaud, W Thuiller, NE Zimmermann, S Lavergne 2017 Disentangling drivers of plant endemism and diversification in the European Alps: a phylogenetic and spatially explicit approach. Perspect Plant Ecol 28:19–27.

Stamatakis A 2006 RAxML-VI-HPC: maximum likelihood–based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690.

Stöver BC, KF Müller 2010 TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. BMC Bioinformatics 11:7.

Sun FJ, SR Downie 2010 Phylogenetic analyses of morphological and molecular data reveal major clades within the perennial, endemic western North American Apiaceae subfamily Apioideae. J Torrey Bot Soc 137:133–156.

Swofford DL 2002 PAUP*: phylogenetic analysis using parsimony (*and other methods): version 4 b10. Sinauer, Sunderland, MA.

Thiers B 2019 Index herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden, Bronx, NY. http://sweetgum.nybg.org/ih/.

Thorogood CJ, U Bauer, SJ Hiscock 2018 Convergent and divergent evolution in carnivorous pitcher plant traps. New Phytol 217:1035–1041.

Wake DB 2003 Homology and homoplasy. Pages 191–201 *in* BK Hall, WM Olson, eds. Keywords and concepts in evolutionary developmental biology. Harvard University Press, Cambridge, MA.

Wang L, RJ Abbott, WEI Zheng, P Chen, Y Wang, J Liu 2009 History and evolution of alpine plants endemic to the Qinghai-Tibetan Plateau: *Aconitum gymnandrum* (Ranunculaceae). Mol Ecol 18:709–721.

Warren DL, RE Glor, M Turelli 2008 Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883.

Wickham H 2011 ggplot2. WIREs Comput Stat 3:180–185.

Wiens JJ, CH Graham 2005 Niche conservatism: integrating evolution, ecology, and conservation biology. Annu Rev Ecol Evol Syst 36:519–539.