Journal of Heredity, 2026, **117**, 699–717
https://doi.org/10.1093/jhered/esag004
Advance access publication 26 January 2026
Original Article

American Genetic Association

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Admixture and environment shape population genetic and phytochemical variation across a conifer hybrid zone (*Juniperus*, Cupressaceae)

Kathryn A. Uckele[1,*], Casey S. Philbin[2], Lora A. Richards[2,3,4], Lee A. Dyer[2,3,4], Joshua P. Jahner[5,6], Thomas L. Parchman[3,4,*]

[1]Division of Biological Sciences, University of Montana, Missoula, MT 59812, United States, [2]Hitchcock Center for Chemical Ecology, University of Nevada, Reno, NV 89557, United States, [3]Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV 89557, United States, [4]Department of Biology, University of Nevada, Reno, NV 89557, United States, [5]Department of Botany, University of Wyoming, Laramie, WY 82071, United States, [6]Department of Biology, New Mexico Institute of Mining and Technology, Socorro, NM 87801, United States

*Corresponding author: Kathryn Uckele, Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA.
Email: kathrynuckele@gmail.com; Thomas Parchman, Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, NV 89557, USA. Email: tparchman@unr.edu

Abstract

Ancestry variation in hybrid zones can reflect the causes and genetic basis of reproductive isolation and result in novel phenotypic variation with the potential for extended ecological effects. Junipers (*Juniperus*) are foundational tree species in many semi-arid landscapes of western North America and often hybridize in zones of secondary contact. Such hybridization can be ecologically significant in foundational tree species, due to the strong genetic control and ecological consequences of plant chemistry. We generated genetic and phytochemical data to analyze hybridization among *Juniperus grandis*, *Juniperus occidentalis*, and *Juniperus osteosperma* in western Nevada and the impact of hybridization on plant chemistry. We used population genomic data [9,125 single-nucleotide polymorphisms (SNPs), 326 individuals, and 25 populations] to quantify patterns of genetic variation across populations and species and to characterize ancestry variation in hybrids. Although populations within species showed little genetic differentiation, the parental species formed distinct, monophyletic lineages with clear phenotypic and ecological differences. Hybrids occupied intermediate environments, contained ancestry from all three parents, and were mainly F_1 or backcross hybrids. Phytochemical data (gas chromatography–mass spectrometry; 163 terpenoid compounds) were likewise analyzed to understand the consequences of hybridization for plant chemistry. The parental species and hybrids displayed distinct phytochemical profiles; hybrids had higher chemical diversity overall, and hybrid terpenoid concentrations were often intermediate or exceeded the range of all the parental species. Our results illustrate that geography and environment shape hybrid ancestry for a syngameon involving three *Juniperus* species, and that admixture generates novel phytochemical variation likely to have ecological consequences.

Key words: forest tree, hybridization, *Juniperus*, phytochemistry, population genetics, secondary contact, terpenoid

Introduction

Genome-scale sequencing has increasingly uncovered signatures of hybridization across diverse taxa, revealing key roles in diversification (Soltis et al. 2015; Tank et al. 2015; Alix et al. 2017), domestication (Arnold 2004), and the evolution of invasive species (Ellstrand and Schierenbeck 2000). The proximate and ultimate outcomes of secondary contact depend on stochasticity, ecological context, and reproductive barriers (Baack and Rieseberg 2007; Mandeville et al. 2017; McFarlane et al. 2024). If reproductive isolation is nearly complete, F_1 hybrids may have reduced fitness, causing F_2 and backcross hybrids to be rare (Burke and Arnold 2001; Burton et al. 2013). Alternatively, without strong barriers, recombinant hybrids may form, allowing introgression among parental species, and offering insights into the genetic basis of speciation and complex trait genetics (Buerkle and Lexer 2008; Gompert et al. 2017). Hybridization may also contribute to adaptation and diversification by way of leading to adaptive introgression and generating novel phenotypic variation in hybrids (Rieseberg et al. 1999, 2003, 2007; Kagawa and Takimoto 2018).

Admixture among plant species can dramatically shape phenotypic variation, with important ecological and evolutionary consequences. Biologically active mixtures of plant specialized metabolites, a key phenotypic axis, mediate species interactions (Wimp et al. 2005), structure ecological communities (Abrahamson et al. 2003; Poelman et al. 2009), and regulate the flow of resources through ecosystems (Schweitzer et al. 2008). Plant hybridization often generates novel phytochemical variation with the potential to shape interactions and community dynamics (Bresadola et al. 2019). Hybrids are often more chemically diverse than parental individuals (Orians 2000; Cheng et al. 2011), as they may combine enzymes and substrates from parental lineages to produce novel compounds or express metabolites at concentrations that exceed parental ranges (Rieseberg and Carney 1998).

Received on 31 March 2025; revised on 1 December 2025; accepted on 9 January 2026
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The genetic basis of this novelty varies across generations. First-generation (F_1) hybrids often exhibit chemical profiles that are intermediate or more similar to one parent than the other, but may also express enhanced compound production consistent with heterosis (Lisec et al. 2009; de Abreu e Lima et al. 2017). In F_2 and later-generation hybrids, recombination and segregation can lead to transgressive phytochemical trait values that surpass parental limits in either direction, leading to an increase in phytochemical diversity in hybrid zones (Rieseberg et al. 1999, 2003, 2007). Backcrosses may largely resemble one parental species but carry subsets of introgressed chemical traits, creating mosaics of chemical traits that can further expand the range of phytochemical variation (Cheng et al. 2011). By generating more diverse and chemically novel metabolite profiles, hybridization can cascade through ecological networks, reshaping species interactions and influencing community structure (Renoult et al. 2025).

Juniperus is a genus characterized by a high diversity of specialized metabolites in both leaves and cones, including flavonoids, coumarins, lignans, tropolones, and the production of essential oils rich in terpenoids such as α-pinene, sabinene, and cedrol (Schwartz et al. 1980; Keeling and Bohlmann 2006; Seybold et al. 2006; Markó et al. 2011; Pardikes et al. 2019). These compounds likely play significant roles in ecological interactions, but most phytochemical investigations for this genus have focused on applied uses, such as antibacterial properties, effects on livestock grazing, and medicinal potential (Bozyel et al. 2024). Even though Great Basin *Juniperus* species house a rich community of arthropods (Pardikes et al. 2019) that are likely important to vertebrate communities supported by juniper woodlands, there is much to be learned about how the rich chemistry of these trees mediates interactions with arthropods and vertebrates. Simple questions about how metabolomic profiles vary predictably across species and also mirror genetic structure are an obvious starting point for characterizing these chemically mediated interactions in a dominant ecosystem across the western US landscape. Here we quantified genetic and chemical variation across a juniper hybrid zone as a basis for further understanding of how admixture may generate novel trait variation, influence species interactions, and shape broader ecological and evolutionary processes (Volf et al. 2024).

Juniperus trees and shrubs are foundational woody plants in many arid regions of the Northern Hemisphere. The serrate leaf junipers of North America (21 species) diversified into the arid and mountainous regions of the western USA and Mexico over the past ~23 million years (Mao et al. 2010; Uckele et al. 2021). Hybridization is common in this clade (Adams 1994; Adams et al. 2017, 2020) and has been documented among the focal serrate junipers of this study: *Juniperus grandis*, *Juniperus occidentalis*, and *Juniperus osteosperma* (Terry et al. 2000; Terry 2010). *Juniperus grandis* (previously *J. occidentalis* var. *australis*) and *J. occidentalis* (previously *J. occidentalis* var. *occidentalis*) are sister species that diverged ~5 mya (Uckele et al. 2021). *Juniperus grandis* grows on dry rocky slopes within the eastern Sierra Nevada of California, and *J. occidentalis* occurs on dry rocky foothills and mountain slopes in northern California, eastern Oregon, and southern Washington (Fig. 1). Basal to these two species is *J. osteosperma*, whose lineage diverged ~11 mya (Uckele et al. 2021) and currently occurs across much of the Great Basin and Colorado Plateau (Fig. 1; Adams 2014). These species can form large stands in otherwise treeless regions, often coexisting with pinyon pines (*Pinus* subsection *Cembroides*) to create key ecosystems in the western USA and Mexico (Miller and Wigand 1994; Weisberg et al. 2007). Pinyon–juniper woodlands, found in drier climates than many other tree-dominated ecosystems, support a high biodiversity of plants, birds, mammals, and invertebrates (Gottfried et al. 1995; Tonkel et al. 2021).

During the Pleistocene glaciation cycles, the ranges of many North American tree species, including junipers, shifted in response to climate changes (Roberts and Hamann 2015). At the height of the Wisconsin glacial (ca. 25 to 21 Kya), *J. grandis*, *J. occidentalis*, and *J. osteosperma* likely occupied isolated glacial refugia. Analyses of packrat midden macrofossils suggest that *J. grandis* occurred in the mesic western aspect of the central Sierra Nevada range, *J. osteosperma* expanded into areas significantly south of its contemporary range in the current-day Sonoran, Mojave, and Chihuahuan deserts, and *J. occidentalis* occurred, at least temporarily, in the northern Great Basin (Betancourt et al. 1990). As the last glacial period ended (~12 Kya), *J. osteosperma* began migrating north, eventually entering into secondary contact with *J. grandis* and *J. occidentalis* in the Sierra Nevada foothills. The resulting hybrid zone in western Nevada spans the Sierra Nevada–Great Basin ecotone (Vasek 1966), a transitional region where hybrid zones frequently cluster (Remington 1968; Swenson and Howard 2005). Previous studies using morphology, phytochemistry, and genetic markers identified this hybrid zone and detected introgression from *J. occidentalis* into the *J. osteosperma* background but lacked the genetic resolution to analyze hybrid zone composition and fine-scale genetic variation (Vasek 1966; Terry et al. 2000, Terry 2010; Adams 2013a, 2013b). Genomic data stands to clarify the factors shaping reproductive isolation and admixture and provide insights into the phenotypic consequences of ancestry variation in hybrids.

We leveraged genetic, phytochemical, and environmental variation across three juniper species and their hybrids to address four key objectives: (1) resolve the evolutionary history of the parental species, (2) characterize ancestry variation in hybrids, (3) examine the relationship between ancestry and environmental variation, and (4) assess hybridization's impact on phytochemistry. Using genomic and phytochemical data from a large sample of individuals and populations, we found that hybrids, primarily F_1s and backcrosses, possess ancestry from all three parental species, with hybrid ancestry varying along geographic and environmental gradients. The hybrid zone spans an ecotone associated with intermediate climatic conditions, suggesting a role for the environment in shaping ancestry patterns. Additionally, hybrids exhibit distinct phytochemical profiles, with the potential to shape novel community structures and interactions. Our findings contribute to an understanding of the factors that shape admixture and its consequences for phytochemical variation in a foundational tree syngameon and should support future investigations into the ecological consequences of this variation.

Methods

Sampling, library preparation, and DNA sequencing

We collected leaf samples from 386 individuals for genetic and phytochemical analyses. Samples were distributed across three *J. grandis* populations ($n = 37$), five *J. occidentalis* populations ($n = 56$), seven *J. osteosperma* populations ($n = 91$),

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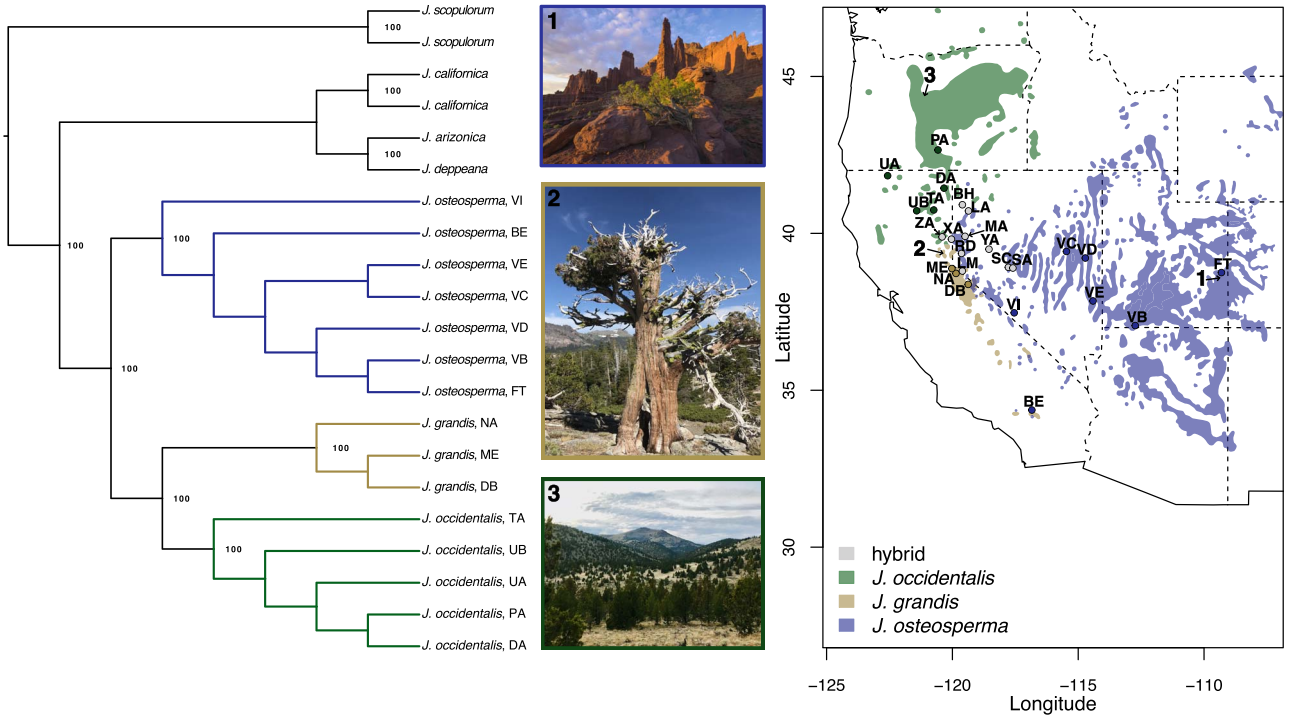

Fig. 1. The phylogenetic tree on the left shows evolutionary relationships among the parental taxa, with outgroup taxa indicated by black tips. Branches and tips of each parental lineage are colored according to the sampling localities on the map to the right. Representative photos of the parental taxa appear between the tree and the map: (1) prostrate *Juniperus osteosperma* at Fisher Towers, UT (photo credit: Floris van Bruegel), (2) *J. grandis* at Donner Lake, CA, and (3) a *J. occidentalis* forest near Smith Rock State Park, OR. The map on the right displays each sampling locality (labeled with its two-letter code), overlaid on colored polygons representing the ranges of the parental species (*J. occidentalis* in green, *J. grandis* in gold, *J. osteosperma* in blue) and hybrid populations in gray. Approximate photo locations are also labeled on the map. Additional locality information is provided in Supplementary Table 1.

and ten hybrid populations ($n = 142$). An additional 60 samples from outgroup taxa (*Juniperus arizonica*, *Juniperus californica*, *Juniperus deppeana*, and *Juniperus scopulorum*) were used for phylogenetic analyses (Supplementary Table 1). Although initial assignment of populations to parental species or hybrids was based on geography, the presence or absence of leaf resin glands, and overall growth form, these characteristics do not reliably distinguish parental and hybrid individuals. Thus, we used inference of ancestry proportions (q) inferred with $K = 3$ to confirm assignments and distinguish hybrid populations that were difficult to assign morphologically (see Methods section "Genetic variation across populations, species, and hybrids"). We considered individuals parental if they had at least 80% ancestry from a single source. This relatively liberal threshold was necessary due to the strong potential for gene flow between *J. grandis* and *J. occidentalis*.

DNA was extracted with Qiagen DNeasy Plant Mini Kits (Qiagen Inc., Valencia, CA, USA) and quantified with a QIAxpert microfluidic analyzer (Qiagen Inc., Valencia, CA, USA). Sequencing libraries were prepared following the ddRAD-seq protocol described by Parchman et al. (2012). Briefly, DNA was digested with *Eco*RI and *Mse*I restriction enzymes, custom oligos with Illumina adapters were ligated to fragment ends, and fragments were PCR-amplified using a high-fidelity proofreading polymerase (Iproof polymerase, Bio-Rad Inc., Hercules, CA, USA) before being pooled for sequencing. Libraries were size-selected (350 to 450 bp) using the Pippin Prep System (Sage Sciences, Beverly, MA, USA) at the University of Texas Genome Sequencing and Analysis Facility (Austin, TX, USA). Four lanes of single-end 100 bp sequencing were performed on an Illumina HiSeq 2500 platform at the University of Wisconsin-Madison Biotechnology Center (Madison, WI, USA). Contaminant reads (Illumina adapters, primers, PhiX, and *Escherichia coli*) were removed using a filtering pipeline (https://github.com/ncgr/tapioca), and demultiplexing was performed with custom scripts. The sequencing data are available on the NCBI Sequence Read Archive under BioProject ID PRJNA1037072.

Genetic variation across populations, species, and hybrids

A de novo reference assembly of 160,256 contigs was generated by clustering unique reads present in at least four samples with `cdhit` (v. 4.6; Li and Godzik 2006; Fu et al. 2012) according to a similarity threshold of 80%. Reads were then aligned to this reference using the `aln` and `samse` algorithms in `bwa` (v. 0.7.5a; Li and Durbin 2009). We performed variant calling using `samtools` (v. 1.3; Li and Durbin 2009) and `bcftools` (v. 1.3; Li 2011; Danecek et al. 2021). First, we generated genotype likelihoods for each sample using `samtools mpileup` (v. 1.3; Li and Durbin 2009), specifying a maximum depth of 100 reads per site (`--max-depth 100`), a minimum mapping quality of 20 (`--min-MQ 20`), minimum base quality of 20 (`--min-BQ 20`), a maximum adjusted mapping quality threshold of 50 (`--adjust-MQ 50`), and excluding indels (`--skip-indels`). Variants were then called using `bcftools call` (v. 1.3; Li 2011; Danecek et al. 2021) in multiallelic calling mode (`-m`). We

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applied quality filters using `bcftools filter`, setting genotypes to missing where the site quality was below 20 (QUAL $\leq$19) or genotype quality was below 10 (GQ $\leq$ 9). Finally, we retained only biallelic SNPs passing all quality filters (`-m 2 -M 2 --apply-filter 'PASS'`) using `bcftools view`. To filter for paralogs, we used the `HDplot` pipeline (McKinney et al. 2017) in `Python` and `R` to remove putatively paralogous loci based on the expected proportion of heterozygous individuals within a population and allelic ratios in heterozygous individuals. Separate variant calling procedures were conducted for (1) all 386 samples (including outgroups), (2) 326 samples comprising the parental species and hybrids (excluding outgroups), and (3) subsets corresponding to each parental species. For each dataset, we used `vcftools` (Danecek et al. 2011) to thin SNPs (`--thin 90`) to randomly select one SNP per locus to minimize linkage disequilibrium and removed sites with minor allele frequencies below 5% (`--maf 0.05`). Each dataset was filtered to different levels of missingness to balance missingness levels with SNP yield. SNPs present in $\geq$60% of samples (`--max-missing 0.6`) were retained for the full dataset (8,319 SNPs) and parental/hybrid subset (9,125 SNPs). For *J. occidentalis* and *J. osteosperma* subsets, we retained SNPs present in $\geq$70% of samples (`--max-missing 0.7`), yielding 9,120 and 9,765 SNPs, respectively. For the *J. grandis* subset, SNPs present in $\geq$65% of samples (`--max-missing 0.65`) were retained, resulting in 8,554 SNPs.

Due to the constraints of marker density provided by this data, we focus on genome-wide, rather than locus-specific, parameters and analyses in order to generally understand the factors shaping ancestry variation and its phytochemical consequences across the landscape. Individual ancestry proportions were inferred with `entropy` (Gompert et al. 2014; Shastry et al. 2021), a Bayesian clustering method analogous to `STRUCTURE` (Pritchard et al. 2000; Falush et al. 2003). `Entropy` leverages genotype likelihoods and population allele frequencies to infer ancestry proportions (q) and genotype probabilities while accounting for uncertainty arising from stochastic variation in coverage depth, as well as sequencing and mapping error (Gompert et al. 2014; Shastry et al. 2021). Incorporating genotype uncertainty is particularly appropriate for low-to-medium-coverage reduced representation data, where maximizing sample sizes rather than sequencing depth yields more precise and less biased parameter estimates (Buerkle and Gompert 2013; Fumagalli et al. 2013). To propagate uncertainty, genotype probabilities inferred by `entropy` were then used as input for downstream analyses based on genotypic variation. For the analysis of all the samples, including outgroups, we set the number of source populations (K) to seven, corresponding to the number of species sampled. For the analysis of parental species and hybrids, K was set to three, reflecting the number of parental species. To facilitate convergence, we initialized the MCMC chains with cluster membership probabilities derived from linear discriminant analysis and K-means clustering of the first five principal components calculated from genotype likelihoods (see Jombart et al. 2010). Four independent chains were run with a burn-in phase of 30,000 iterations, followed by sampling every tenth iteration for 60,000 iterations. Convergence and mixing were assessed visually with `R` (v. 4.1.2; R Core Team 2020).

`Entropy` was also used to estimate interspecific ancestry, defined as the proportion of an individual's genome where alleles were inherited from different source populations (Shastry et al. 2021). By comparing individual ancestry proportions (q) to interspecific ancestry proportions (Q), it is possible to distinguish ancestry classes, such as F_1, F_2, backcrosses, and later-generation hybrids. For example, both F_1, F_2, and later-generation hybrids are expected to have individual ancestry proportions of 0.5. However, F_1 individuals have Q values of one because each copy of their genome is inherited from a different parental species, whereas later-generation hybrids have Q values less than one due to recombination breaking up long tracts of high interspecific ancestry (Gompert et al. 2014; Shastry et al. 2021). For K values greater than two, the interpretation of ancestry classes becomes more complex due to the increased number of possible interspecific ancestry combinations. To address this, we treated *J. grandis* and *J. occidentalis* as a single ancestral population (i.e. the western parental taxa) given their much lower divergence from one another compared with their combined divergence from *J. osteosperma* (i.e. the eastern parental taxon).

To visualize genetic structure across populations and species, principal component analysis (PCA) was performed on the genotype probabilities. PCA was conducted using the *prcomp* function in `R` with centering but no scaling. To mitigate the effects of unbalanced sampling of species, we randomly selected 15 individuals from each species for the analysis of all samples. To quantify genetic differentiation among populations, Nei's D (Nei 1972) and Hudson's F_{ST} (Hudson et al. 1992) were calculated from population allele frequencies with custom scripts in `R`. A neighbor-joining tree was constructed from Nei's D values using the *nj* function (`ape` package; Paradis and Schliep 2019). Mantel tests (`vegan` package; Oksanen et al. 2020) using Spearman correlations and complete permutation enumeration assessed the relationship between genetic (Nei's D) and geographic distances for *J. osteosperma* and *J. occidentalis* (*J. grandis* was excluded due to insufficient population sampling). Geographic distances between populations were calculated from geographic coordinates (Supplementary Table 1) using the *earth.dist* function (`fossil` package; Vavrek 2011).

We calculated two estimates of genome-wide genetic diversity—Θ_π (the average number of polymorphisms per pairwise sequence comparison; Tajima 1983) and Θ_w (the number of segregating sites; Watterson 1975)—for each population using methods that account for genotype uncertainty, as implemented in `ANGSD` (v. 0.923; Korneliussen et al. 2014). First, we estimated the site allele frequency (SAF) likelihood from the BAM files and de novo reference assembly using the *-doSaf* option. We then used the `realSFS` utility (Nielsen et al. 2012) to estimate the folded site frequency spectrum (SFS) from the SAF and calculated Θ_π and Θ_w for each site using the *saf2theta* option. To evaluate whether the populations are evolving neutrally and conforming to mutation–drift balance, we calculated Tajima's D (Tajima 1989) for each site using the `thetaStat` utility and the *doStat* option (Korneliussen et al. 2013).

Phylogenetic analyses

To clarify the evolutionary relationships among the parental species, phylogenetic inference was performed on parental and outgroup samples. To maximize the amount of data available for clustering loci across samples, we selected the sample with the largest FASTQ file size from each population. Reads were de novo assembled and filtered with `iPyRAD`

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(v.0.7.19; Eaton and Overcast 2020) (detailed methods are provided in the online supplementary materials). Phylogenetic analysis was conducted with TETRAD (Eaton et al. 2017), which implements the SVDquartets algorithm. In brief, SVDquartets applies the multispecies coalescent model to estimate a probability distribution over site patterns at the tips of a species tree, which is then used to score quartets and infer their most likely relationships (Chifman and Kubatko 2014, 2015). These inferred quartet topologies—either for all possible quartets or a selected subset—are then assembled into a full species tree using a quartet amalgamation algorithm (here, QMC v2.10; Snir and Rao 2012). All possible species quartets were analyzed to infer the unrooted species tree, which was manually rooted with the *J. scopulorum* outgroup. Node support values were estimated based on 100 bootstrap replicates.

Ecological divergence among parental taxa and hybrids

To assess divergence in the contemporary climate envelopes of each parental species range and the hybrid zone, we analyzed range-wide climate data with discriminant analysis of principal components (DAPC; Jombart et al. 2010). For each parental species, 200 geographic coordinates were randomly selected from plot observations in the US Forest Service Forest Inventory and Analysis (USFIA) database (USDA Forest Service 2019). Because hybrids were not specifically identified in the database, we classified all the *J. osteosperma* plot observations west of 118° W longitude as hybrids, based on the geographic distribution of hybrid ancestry (see Results section "Phylogenetic analyses"). For each geographic coordinate, 25 climate variables were extracted at 30-arcsec (approximately 800 m) resolution from PRISM (PRISM Climate Group 2014) and the Climate Water Deficit Toolbox (Dilts and Yang 2015), based on 64-year average climate data (1950 to 2014) derived from monthly temperature and precipitation values. Using species and hybrid assignments as a priori groups, we retained 10 principal components of scaled climate data and performed linear discriminant analysis with the *dapc* function (*adegenet* package; Jombart 2008) in R.

To assess the extent to which climate predicts ancestry variation across our sampled populations, we used random forest models. For each parental and hybrid population, we extracted 30 climate variables from their geographic coordinates using the same method as the range-wide analysis described above. The model assigned each individual to an ancestry group (*J. grandis*, *J. occidentalis*, *J. osteosperma*, or hybrid) based on the climate data associated with their population of origin. The classification model, implemented with the randomForest package in R (Liaw and Wiener 2002), was trained on 70% of the individuals and tested by predicting group membership for the remaining 30%. We developed a second random forest model using the H2O framework in R (LeDell and Poirier 2020) to predict hybrid ancestry proportions (q) from 30 climate and 2 geographic predictors (latitude and longitude). The dataset was randomly split into 80% training and 20% test sets, and hyperparameters were optimized using a random grid search with leave-one-out cross-validation. The best model, selected based on the lowest cross-validated mean squared error, was evaluated using root mean squared error (RMSE), mean absolute error (MAE), and R^2 on both cross-validation and test sets.

To assess the relationship between genetic variation and climate variation, we performed redundancy analysis (RDA; Legendre and Legendre 2012; Capblancq and Forester 2021) using genotype probabilities as the response matrix. Because our objective was to explore how genome-wide allele frequency differences among the three species and hybrids corresponded to climatic variation, we did not condition the analysis on neutral genetic structure (e.g. ancestry coefficients). As a result, the identified climate associations reflect both historical divergence among species and potential adaptive differentiation. To minimize multicollinearity among predictor variables, we sequentially removed climate variables with the highest mean correlations until all the remaining variables had correlations below 0.7. The resulting set of seven climate variables was then scaled and used as multivariate predictors. The final set of variables included the fraction of actual evapotranspiration derived from monthly precipitation rather than soil water (pdAET-SWB), maximum winter temperature, the ratio of potential evapotranspiration to actual evapotranspiration (PET:AET), minimum winter temperature, minimum annual temperature, cumulative water supply (cumlWS), and precipitation seasonality (pcseas) (Table 1). RDA was conducted with the *rda* function (vegan package) in R.

Phytochemical variation across species and hybrids

We quantified specialized metabolite profiles for 314 of 326 focal individuals, based on the availability of sufficient leaf material after DNA extraction. Silica-dried leaf samples were lysed using a Qiagen TissueLyser II (Qiagen Inc., Valencia, CA, USA), and 20 mg of tissue was extracted with 1 mL hexanes containing an internal standard of *n*-eicosane (0.25 mM). After vortexing, samples were sonicated in ice water for 15 min, centrifuged, and chilled at −20°C to minimize evaporation before transfer to gas chromatography–mass spectrometry (GC–MS) autosampler vials. Extracts (1 μL) were injected onto an Agilent 7890A gas chromatograph coupled to an Agilent 5975C quadrupole mass spectrometer with an Agilent HP-5MS capillary column (Agilent Technologies Inc., Santa Clara, CA, USA). Full GC–MS protocol and data processing details are in the online supplementary materials. The final phytochemical dataset included concentrations for 163 terpenoid compounds, 56 of which (34%) were annotated using a National Institute of Standards and Technology (NIST) match (score > 60) against the Adams GCMS library (Adams 2007). When a compound matched multiple peaks, the peak with the closest retention index was annotated as that compound, and the other peaks were categorized as structural analogues.

PCA was performed to examine variation in terpenoid compound profiles. Due to strong positive skew in the GC–MS data, a log2 transformation was applied before analysis. Preliminary PCA identified 14 outliers from the ZA population (*J. grandis* × *J. occidentalis* hybrids) that dominated variance in PCs 1 and 2; these were excluded in subsequent analyses, leaving 300 samples. PCA was conducted using the *prcomp* function in R with centering but no scaling. To assess whether terpenoid variation could classify individuals into ancestry groups, we performed a random forest analysis using terpenoid data with the randomForest package (Liaw and Wiener 2002) in R. The model was trained on 70% of the data and evaluated on the remaining 30%.

To categorize terpenoid compounds as parent-like, intermediate, or extreme in the hybrids relative to the parental species,

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Table 1. Climate variables used in various analyses. Discriminant analysis of principal components (DAPC) was performed on range-wide climate data from 200 populations across the hybrid zone and parental ranges. In contrast, redundancy analyses (RDA) and random forest models (RF_a and RF_b) utilized data from the parental and hybrid populations (Fig. 1). The table displays variable contributions for DAPC and variable importance for RF_a and RF_b, with the five most influential variables for each model highlighted in bold. Asterisks in the first column denote variables used as predictors in the RDA model (Fig. 5c and d). RF_a employed a random forest classification approach to predict ancestry class, whereas RF_b used a random forest regression approach to predict hybrid admixture proportions. Variables not included in certain models are indicated as NA.

Variable	Definition	DAPC	RF_a	RF_b
cumlPET	Cumulative PET; amount of water that would be evapo-transpired if enough water were available	0.0075	**5.6**	0.33
cumlAET	Cumulative AET; actual amount of water that is evapo-transpired; proxy for productivity	0.0195	2.29	0.11
cumlSWB	Cumulative SWB; quantity of water stored in the soil from one month to the next	0.0043	2.54	0.12
cumlWS*	Cumulative WS	0.0023	3.82	0.01
cumlCWD	Cumulative CWD; proxy for drought stress	0.0003	**4.07**	0.09
SWB:AET	Ratio of SWB to AET; values > 1 indicate more stored soil water than used in AET	0.0011	2.29	**6.82**
WS:AET	Ratio of WS to AET; values > 1 indicate more water for soil water storage, runoff, or deep percolation than used in AET	NA	4.07	**7.99**
AET:CWD	Ratio of AET to CWD; values > 1 indicate mesic climate, values < 1 indicate xeric climate	0.0042	4.83	0.28
PET:AET*	Ratio of PET to AET; relative drought indicator; values > 1 indicate an unmet demand for water	0.0031	3.56	0.02
pdAET-SWB*	Positive difference between AET and SWB; fraction of AET derived from monthly precipitation rather than soil water	**0.1246**	**7.12**	0.1
pdWS-AETorSWB	Positive difference between WS and the greater of AET or SWB; cumulative water available for runoff or deep percolation	0.0134	1.27	**21.32**
WS:AETorSWB	Spring ratio of WS and the greater of AET or SWB; values > 1 indicate spring water available for runoff or deep percolation	0.0031	3.56	0.27
Monsoon	Monsoonality; pattern of pronounced precipitation during summer months	**0.2903**	**4.83**	**10.64**
pcseas	Precipitation seasonality	**0.1317**	3.05	0.24
prcpann	Annual precipitation	0.0009	2.04	0.003
prcpspr	Spring precipitation	0.0029	2.04	1.05
prcpsum	Summer precipitation	NA	**7.38**	1.02
prcpfal	Fall precipitation	0.0053	1.27	0.07
prcpwin	Winter precipitation	NA	2.04	0.34
mintemp	Minimum temperature	**0.0635**	6.87	0.16
maxtemp	Maximum temperature	0.0048	3.82	0.006
temprang	Temperature range	0.0539	2.8	0.05
mntmpspr	Minimum spring temperature	0.0185	2.54	0.09
mxtmpspr	Maximum spring temperature	NA	1.53	0.71
mntmpsum	Minimum summer temperature	**0.1283**	1.78	0.1
mxtmpsum	Maximum summer temperature	NA	2.04	0.36
mntmpfal	Minimum fall temperature	0.0355	3.56	0.01
mxtmpfal	Maximum fall temperature	0.0034	2.04	1.64
mntmpwin*	Minimum winter temperature	0.0435	3.31	0.11
mxtmpwin*	Maximum winter temperature	0.0338	2.54	0.61
Latitude		NA	NA	0.94
Longitude		NA	NA	**6.74**

Abbreviations: AET, actual evapotranspiration; CWD, climate water deficit; PET, potential evapotranspiration; SWB, soil water balance; WS, water supply. The five most influential variables for the RFa and RFb are bolded. Asterisks denote variables used as predictors in the RDA model.

we used pairwise Wilcoxon rank-sum tests with the Holm–Bonferroni correction (*pairwise.wilcox.test* in `R`). Due to positive skew, we present the nonparametric test results, though one-way analysis of variance (ANOVA) with Tukey's Honestly Significant Difference (HSD) produced similar results. Compounds were classified as parent-like if the hybrid group was significantly different from at least one parental species but not all. Intermediate compounds were those where the hybrid group differed from both parental species but had concentrations within the parental range. Transgressive compounds were those where the hybrid group differed significantly from all the parental species, with mean concentrations outside the parental range. We repeated this analysis after separating F_1 and backcross hybrids (as identified in the ancestry analysis) to assess whether the absence of recombination in the F_1 generation leads to distinct trait patterns. We also quantified the number of transgressive hybrids exceeding parental ranges and calculated total terpenoid concentrations by summing all compounds, assessing group differences with pairwise Wilcoxon tests.

To disentangle genetic, geographic, and environmental influences on phytochemical variation, we performed variance partitioning using partial redundancy analysis (pRDA). The response matrix included terpenoid concentrations and the predictor matrix included (1) the first two principal components from PCA of climate data (explaining 73.74% of variance), (2) the first two principal components from PCA of genotype probabilities (50.56% of variance), and (3)

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geographic coordinates (latitude and longitude). A standard RDA was first conducted to estimate total constrained variance. Three pRDAs were then performed, conditioning on two predictor sets at a time, to isolate the unique contributions of climate, genetics, and geography. Results were consistent with variance partitioning using the *varpart* function (`vegan` package) in `R`.

To examine terpenoid diversity and variation within and among ancestry groups, we used diversity indices and distance-based analyses. To account for uneven sample sizes, we rarefied the data by randomly selecting six samples per population for *J. osteosperma* (for a total of 36 samples), seven per population for *J. occidentalis* (for a total of 35 samples), and four per hybrid population (for a total of 40 samples). All 36 available samples for *J. grandis* were included. For comparisons among hybrid classes, we used all the available samples for F_1 ($N = 34$) and for backcrosses to the western parental taxa (*J. grandis*/*J. occidentalis*; $N = 35$) and rarefied backcrosses to the eastern parental taxon (*J. osteosperma*) to $N = 35$ (random without replacement; available $N = 62$) to mitigate sample-size imbalance. Alpha diversity (per sample) and gamma diversity (pooled within ancestry group), expressed as the effective number of compounds, were calculated by exponentiating the Shannon diversity index (`vegan` package) separately for terpenoid concentration data and presence/absence data. A generalized linear model with a Gaussian distribution was used to test differences in mean alpha diversity among ancestry groups, followed by post hoc Tukey's HSD tests (`multcomp` package; Hothorn et al. 2008). Additive beta diversity was also calculated across individuals for each ancestry group, with detailed methods provided in the online supplementary materials.

We employed two distance-based analyses to evaluate beta diversity within and between ancestry groups: Permutational Multivariate Analysis of Variance (PERMANOVA) to test for differences in terpenoid composition and a multivariate analogue of Levene's test to assess the homogeneity of variances. Because PERMANOVA is sensitive to variance differences, testing for multivariate homogeneity of variances ensured consistent variances across groups while providing additional insight into beta diversity. To reduce the influence of large peaks, data were log2-transformed. Both quantitative (terpenoid concentrations) and qualitative (presence/absence) variations were analyzed using Manhattan and Jaccard distances, respectively, calculated with the *vegdist* function (`vegan` package). Pairwise comparisons of ancestry groups were conducted with the *pairwise.adonis* wrapper (*pairwiseAdonis* package; Martinez Arbizu 2020), using 999 permutations for significance testing. The *betadisper* function was used to calculate Euclidean distances to group spatial medians with principal coordinate analysis (PCoA). Variance differences were tested with ANOVA, followed by Tukey's post hoc comparisons, and patterns were visualized by plotting the first three principal coordinate axes.

Results

Genetic variation across populations, species, and hybrids

Sequencing generated 930.7 million raw reads, reduced to 738.6 million reads after filtering. The mean number of assembled reads per individual was 359,245. After stringent filtering, 8,319 SNPs were retained for all the samples and 9,125 SNPs for the subset of parental and hybrid (ingroup) individuals. The average sequencing coverage depth per locus per individual was 5.0× (SD 1.7) for all the samples and 4.1× (SD 1.3) for the ingroup subset on which most population genetic analyses were conducted. The PCA of all the species (Fig. 2A) showed clear separation between ingroup and outgroup taxa along PC1 (30.8% variance explained). PC2 (15.5% variance explained) distinguished the three major outgroup lineages that were resolved by the phylogenetic analysis (Fig. 1): (1) *J. scopulorum*, (2) *J. californica*, and (3) *J. arizonica*/*J. deppeana*. For parental and hybrid samples, PC1 (50.6% variance explained) separated the three parental species, with *J. grandis* and *J. occidentalis* closer on PC1 but differentiated along PC2 (3.4% variance explained) (Fig. 2B). Hybrids formed a diffuse cluster between parental species clusters. PCAs within each parental species explained less variance and showed limited clustering (Fig. 2C to E). Geographic and genetic distances were not significantly correlated in *J. osteosperma* ($r = -0.54$, P-value = 0.89) or *J. occidentalis* ($r = 0.55$, P-value = 0.2), suggesting a lack of isolation by distance. *Juniperus grandis* was excluded from this analysis due to insufficient population sampling. Geographic distances between populations ranged from 72 to 859 km in *J. osteosperma*, 58 to 250 km in *J. occidentalis*, and 20 to 77 km in *J. grandis* (Fig. 2F to H).

Overall, F_{ST} values were low; however, interspecific F_{ST} values (mean $F_{ST} = 0.091$) were approximately 4.5 times higher than intraspecific values (mean $F_{ST} = 0.02$) (Fig. 3). Genetic diversity measures (Θ_π and Θ_w) were generally high and correlated with one another across populations ($r = 0.89$). Hybrids exhibited higher diversity than parental species (Supplementary Tables 2 and 3). Tajima's D was negative for all populations except UA, suggesting an excess of rare alleles consistent with population expansion (Supplementary Table 3).

A neighbor-joining tree based on Nei's D (Fig. 4A) mirrored the phylogeny (Fig. 1) and PCA (Fig. 2B), resolving hybrids as an evolutionary grade between *J. osteosperma* and the *J. grandis*–*J. occidentalis* clade, except for population ZA, which grouped between *J. grandis* and *J. occidentalis*. The $K = 3$ Bayesian clustering model identified the three parental species as ancestral populations. Parental individuals were rare in the hybrid zone, consistent with previous observations (Adams 2013a, 2013b). Most hybrids exhibited ancestry from all three species, but hybrid population ZA displayed primarily *J. grandis* and *J. occidentalis* ancestry (Fig. 4A). Ancestry proportions varied geographically across the hybrid zone: western hybrids possessed more equal proportions of parental ancestry, *J. osteosperma* ancestry increased with increasing longitude, and northern and southern hybrids showed higher *J. occidentalis* or *J. grandis* ancestry, respectively (Fig. 4B). In the $K = 2$ Bayesian clustering model, sister species *J. occidentalis* and *J. grandis* (hereafter referred to as "the western parentals") were identified as a single source population and *J. osteosperma* was identified as the other source population. Plotting admixture proportions (q) against interspecific ancestry (Q) revealed a predominance of F_1 and backcross hybrids, with few late-generation hybrids (3%, Fig. 4C). Based on q values from the three-parent model ($K = 3$) and Q values from the two-parent model ($K = 2$), we classified 37% of the hybrids as backcrossed to *J. osteosperma*, 25% as backcrossed to the western parentals, 24% as F_1 hybrids, and 11% as

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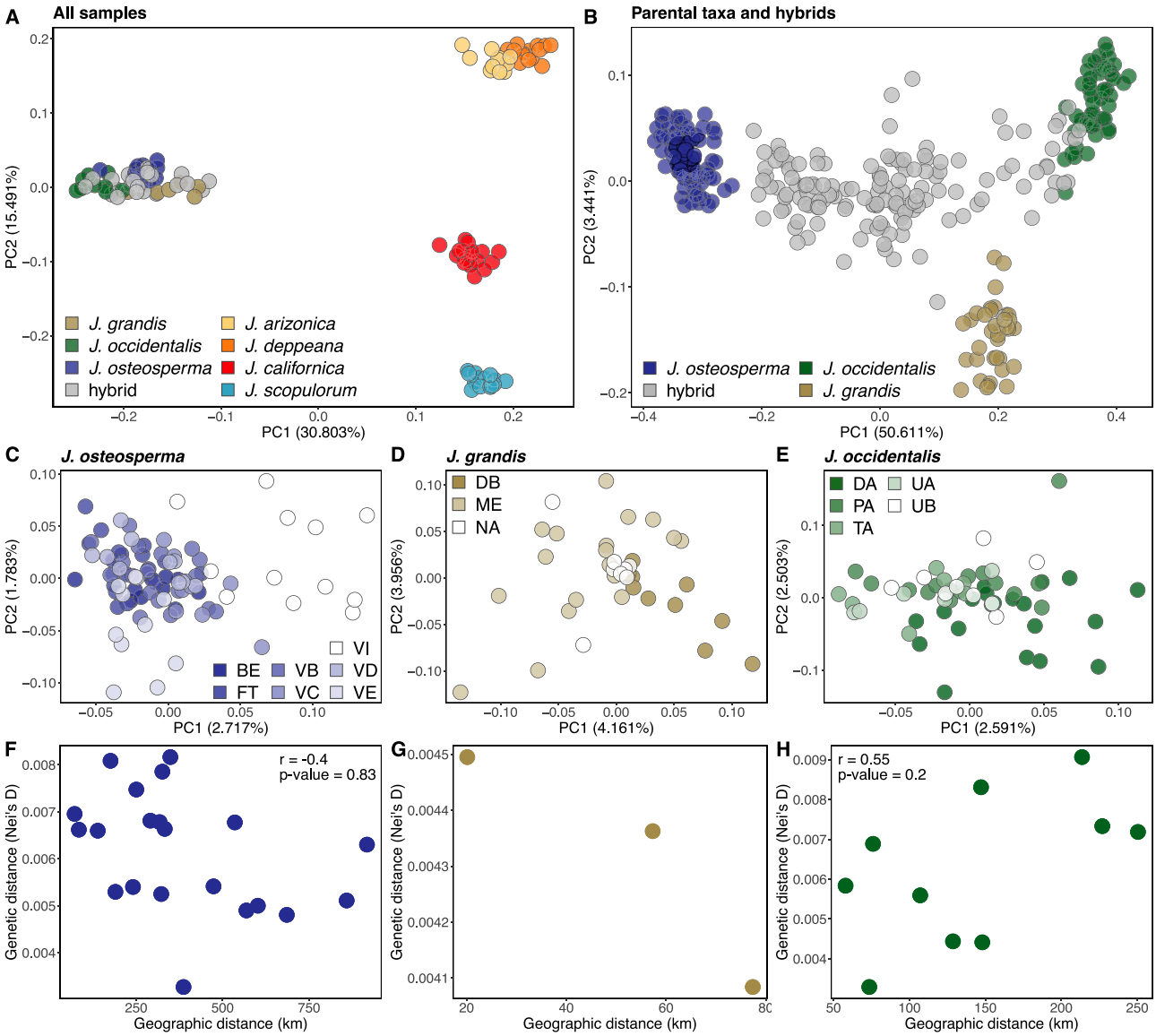

Fig. 2. Genetic variation is strongly structured by species and hybrid status, yet intraspecific differentiation among populations is minimal. Genotype probabilities estimated with `entropy` were analyzed via PCA for (A) ingroup and outgroup individuals and (B) parental species and hybrids, with points colored by species. Separate PCAs were then performed for each parental species (C–E), with points shaded by population. Finally, geographic versus genetic distance relationships are shown for each parental species (F–H). No significant relationship was found for *J. osteosperma* and *J. occidentalis*, and *J. grandis* could not be tested due to limited sampling localities.

J. grandis × *J. occidentalis* hybrids. A longitudinal cline in admixture proportions showed a sharp transition to admixed ancestry between 123°W and 119.5°W, followed by a more gradual shift toward *J. osteosperma* ancestry eastward of ~119.5°W. Hybrid ancestry was most variable at the inflection point (~119.5°W), where F_1, western parental backcrosses, and late-generation hybrids occurred across a range of latitudes. East of this inflection point, backcross hybrids to *J. osteosperma* occur across a larger range of longitudes, extending into central Nevada (Fig. 4D and Supplementary Fig. 1).

Phylogenetic analyses

Assembly and filtering with `iPyRAD` yielded 66,280 SNPs for phylogenetic analysis. On average, 19,858 loci were recovered per sample, with more than half present in only four or five individuals. All the ingroup and outgroup species were resolved as monophyletic with 100% bootstrap support. The ingroup (*J. grandis*, *J. occidentalis*, and *J. osteosperma*) and the broader serrate leaf juniper clade (ingroup species + *J. arizonica*, *J. californica*, and *J. deppeana*) were each monophyletic. Consistent with Uckele et al. (2021), *J. osteosperma* was basal to sister species *J. grandis* and *J. occidentalis* (Fig. 1).

Ecological divergence among parental taxa and hybrids

Climate variables were highly correlated with one another (Supplementary Figs 2 and 3). The DAPC of range-wide climate data revealed distinct contemporary climates for the parental species, with hybrids occupying intermediate climatic environments (Fig. 5B). Key variables differentiating species included monsoonality, minimum summer temperature, pre-

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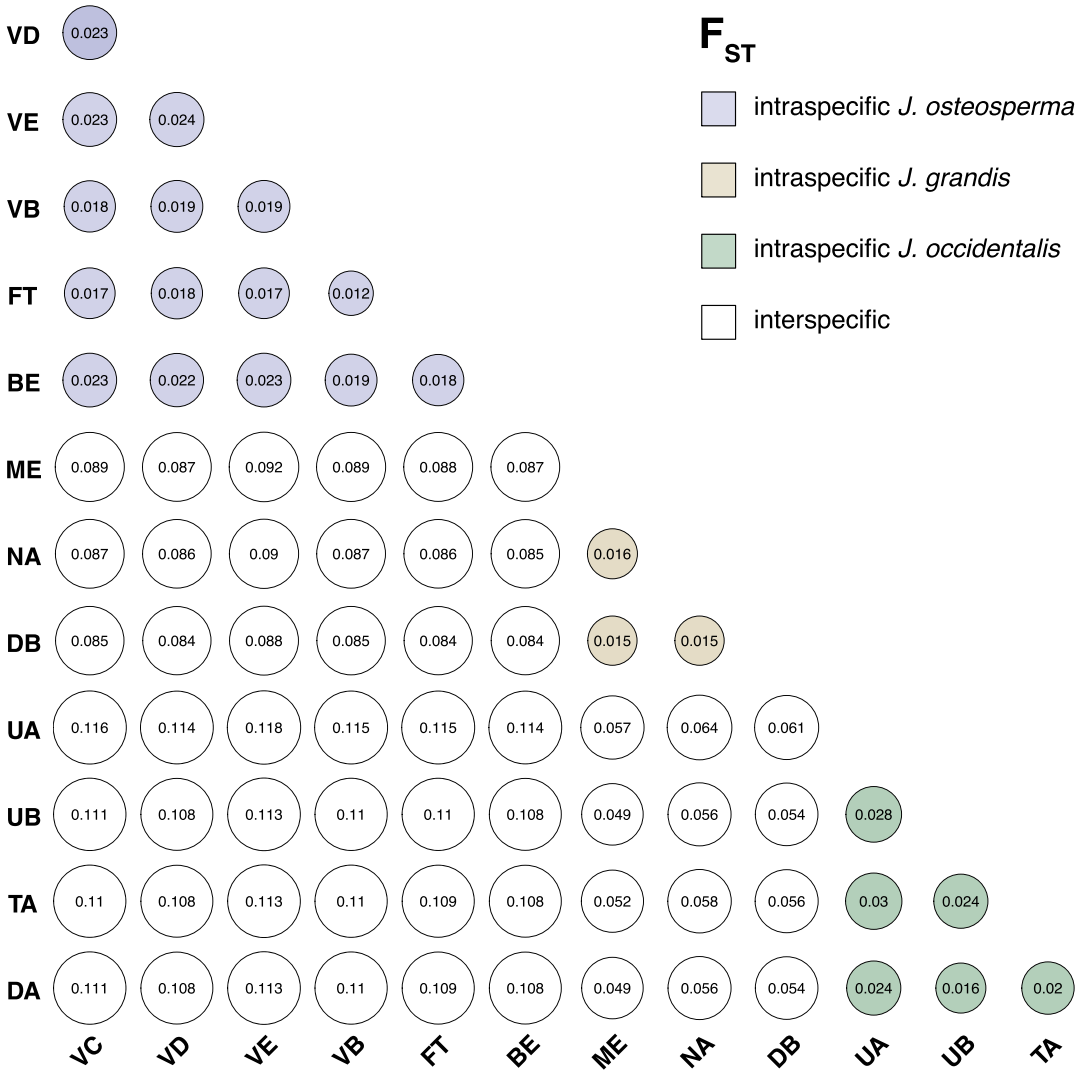

Fig. 3. Genome-wide F_{ST} estimates are depicted in a bubble plot, where bubble size corresponds to the F_{ST} value. All pairwise estimates among parental populations are shown; additional population details can be found in Fig. 1 and Supplementary Table 1. Unfilled bubbles represent interspecific F_{ST} estimates, while filled bubbles indicate intraspecific F_{ST}.

cipitation seasonality, and the fraction of actual evapotranspiration derived from monthly precipitation rather than from soil water (pdAET-SWB) (Table 1).

The random forest classification model accurately predicted ancestry class (95% CI: 96.5% to 100%) using climate data alone. The five most important variables, ranked by mean decrease in accuracy, were summer precipitation, pdAET-SWB, cumulative potential evapotranspiration, monsoonality, and cumulative climate water deficit (Table 1). A second random forest regression model was developed to predict hybrid ancestry proportions using climate and geographic variables (latitude and longitude). The model achieved a test set MAE of 0.04 and RMSE of 0.05, consistent with cross-validated MAE (0.05) and RMSE (0.07). The R^2 values for cross-validation (0.77) and the test set (0.88) indicate strong predictive performance and generalization. Variable importance analysis highlighted cumulative water available for runoff or deep percolation (pdWS-AETorSWB) (21.3%) as the most influential predictor (Table 1).

The first three axes of the RDA with seven climate variables as predictors explained approximately 12% of genetic variance (Fig. 5). The first two RDA axes separated the parental species into distinct clusters, with hybrids positioned between them. *Juniperus grandis* and *J. occidentalis* were associated with higher values of cumulative water supply and precipitation seasonality, whereas *J. osteosperma* was linked to higher values of pdAET-SWB, which was strongly correlated with summer precipitation ($r = 0.71$) and monsoonality ($r = 0.79$) (Fig. 5C). The third RDA axis separated hybrids from parental individuals, with hybrids associated with higher values of unmet demand for water and maximum winter temperature (Fig. 5D).

Phytochemical variation across species and hybrids

GC–MS analysis identified 163 terpenoid compounds, 55 of which were matched to known molecules, including 1 aliphatic, 1 phenylpropanoid, 15 monoterpenes, 19 diterpenes (2 bicyclic, 17 tricyclic), and 19 sesquiterpenes (6 monocyclic, 11 bicyclic, and 2 tricyclic) (Supplementary Table 4). Hybrids produced no novel terpenoids but did synthesize all 163, whereas each parental species produced only a subset (Supplementary Fig. 4). Hybrids differed significantly from

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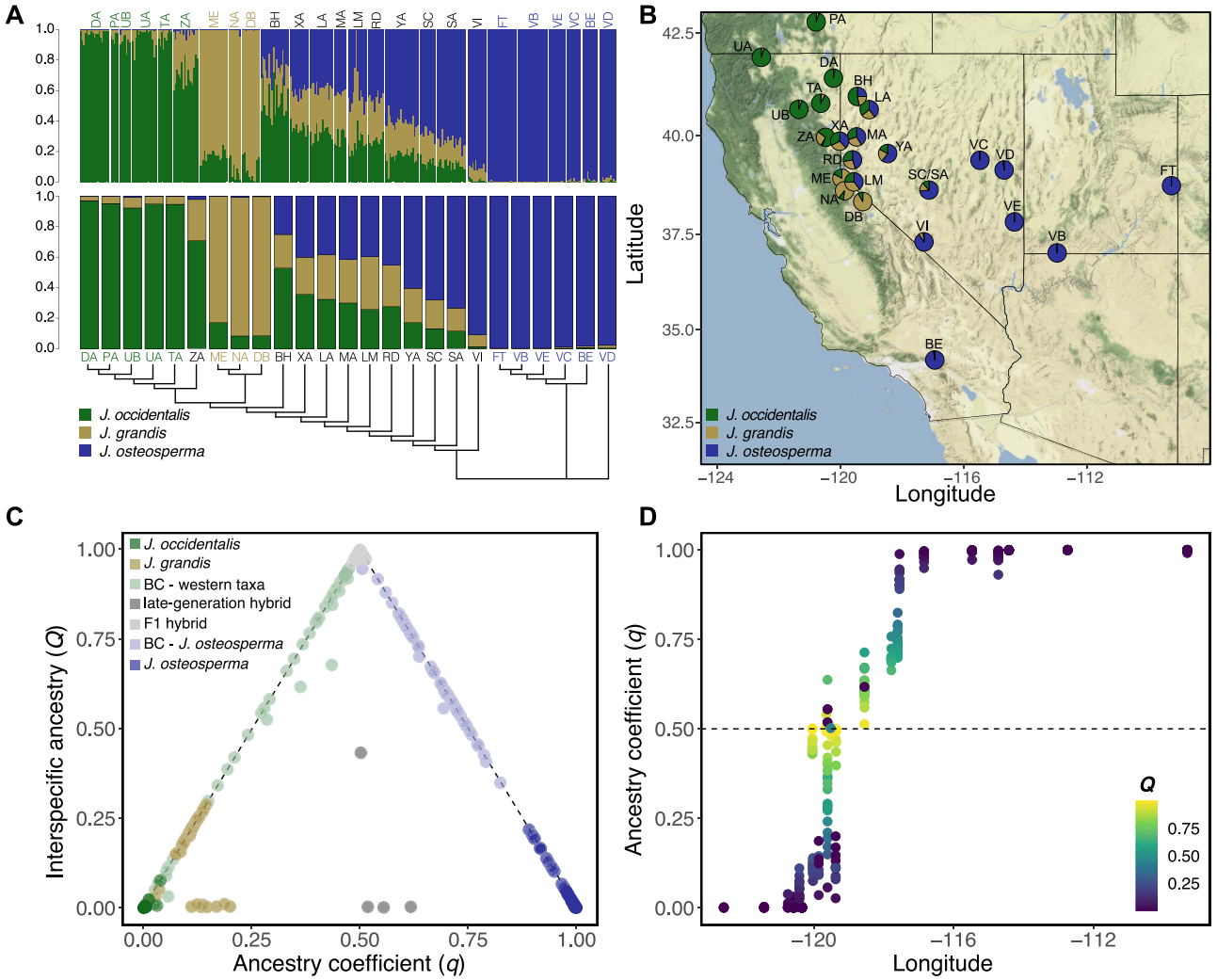

Fig. 4. (A) The admixture model of `entropy` was set with three ancestry sources ($K = 3$), resulting in parental populations with complete or nearly complete ancestry from one of the three lineages (color-coded) and hybrid populations with mixed ancestry from two or three lineages. Individual ancestries (q) are shown in the upper barplot, while population mean ancestries are depicted in the lower barplot. Below the barplots, a neighbor-joining tree based on Nei's D genetic distances illustrates the evolutionary relationships among populations. Population labels are color-coded based on majority ancestry, with hybrid populations shown in black. (B) Population mean ancestries for each sampling locality are also depicted as pie charts overlaid on a geographic map. (C) The ancestry complement model of `entropy` was set with two ancestry sources ($K = 2$) for ease of interpretation, treating sister taxa *J. grandis* and *J. occidentalis* as a single ancestral source population (see Methods). This model estimates interspecific ancestry (Q), i.e., the proportion of an individual's genome with alleles inherited from different source populations. Interspecific ancestries (Q) are plotted against individual ancestries (q) for each parental and hybrid individual to distinguish hybrid classes (e.g. backcrosses, F_1, F_2, F_N). (D) Individual ancestries (q) are plotted against longitude, with a color ramp indicating the corresponding interspecific ancestries (Q).

one or more parental groups for 96 compounds (59%), with 68 (71%) classified as parent-like, 14 (15%) as intermediate, 14 (15%) as significantly higher, and none as significantly lower. Among the parent-like compounds, 17 (25%) were *J. grandis*-like, 17 (25%) were both *J. grandis*- and *J. occidentalis*-like, 12 (18%) were both *J. grandis*- and *J. osteosperma*-like, 11 (16%) were *J. osteosperma*-like, 9 (13%) were both *J. osteosperma*- and *J. occidentalis*-like, and 2 (3%) were *J. occidentalis*-like. Results partitioned by hybrid class (F_1 vs. backcross) are available in the online supplementary materials. For 99 compounds (61% of those measured), there was at least one hybrid that exhibited a higher value than any of the parents. Total terpenoid concentrations were also higher in hybrids than in any parent (Supplementary Fig. 5).

PCA of terpenoid data separated ancestry groups along PC1 (12.7% variance) and PC2 (8.2%), driven largely by tricyclic diterpenes (Fig. 6A and Supplementary Table 4). Hybrids were differentiated from the parental groups along PC1, and intermediate to *J. osteosperma* and *J. occidentalis* along PC2 (Fig. 6A). The random forest model predicting ancestry class based on terpenoid data was highly accurate (95% CI: 85.3% to 97%). RDA-based variance partitioning revealed that genetics, geography, and environment explained 11.9% of the terpenoid variation, with genetic variation contributing the most (3.3%), followed by geography (2.8%) and environment (1.3%). The remaining 4.6% was confounded, indicating that the effects of genetics, geography, and climate could not be fully separated (Table 2).

Alpha and gamma diversity, whether based on concentrations or presence/absence data, was highest in hybrids (Supplementary Table 5 and Supplementary Fig. 6). The results of the additive beta diversity analyses are presented in the online supplementary materials (Supplementary Results and Supplementary Fig. 7). We also used distance-based

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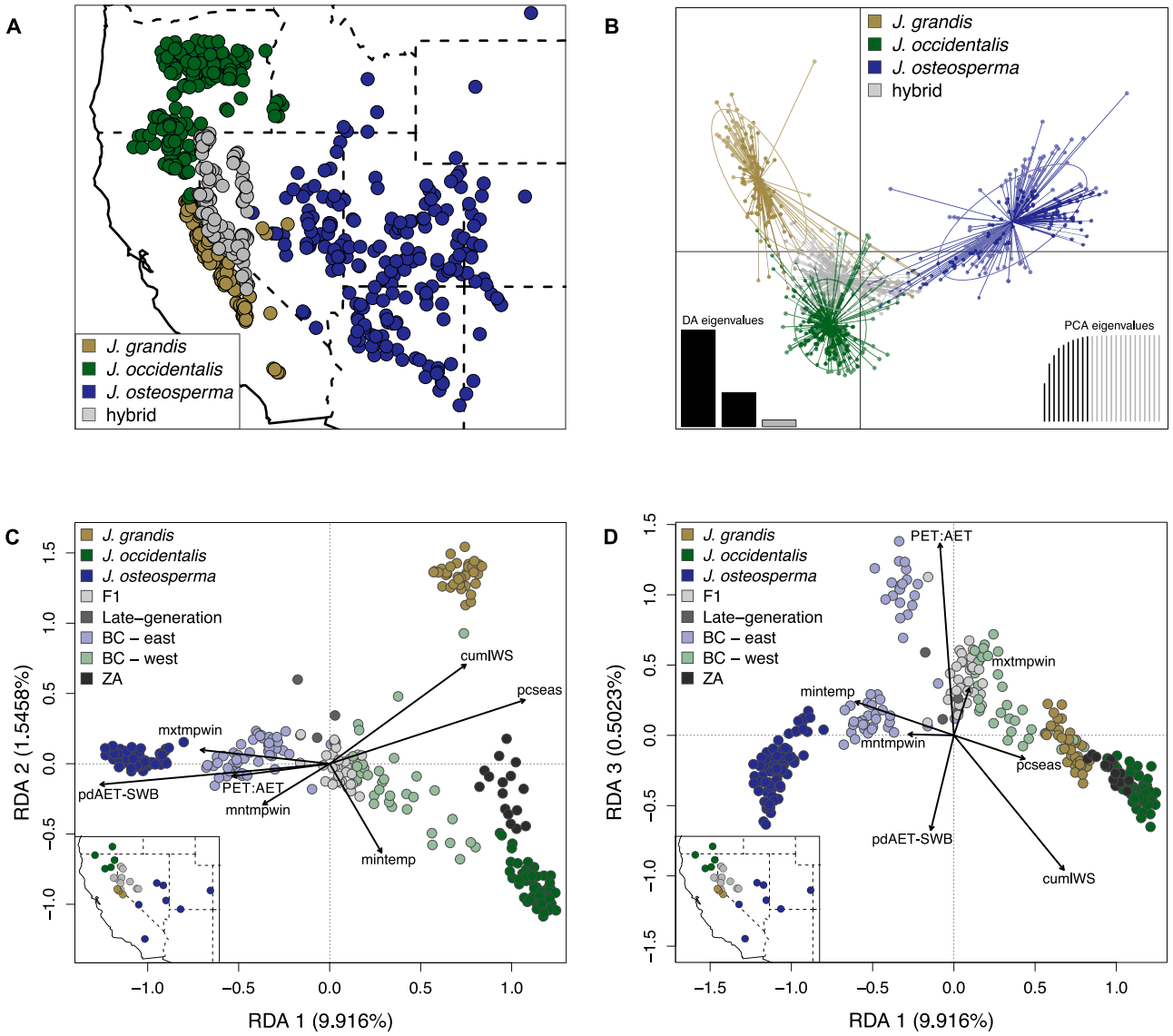

Fig. 5. Climate variation differs among parental species and hybrids, with hybrid populations occupying environments intermediate to the parentals. (A) Two hundred geographic coordinates were randomly sampled across the ranges of each parental species and the hybrid zone. All the *Juniperus osteosperma* observations west of −118° longitude were classified as hybrids based on population genetic analyses (Fig. 4). (B) Climate data for each locality in panel (A) were analyzed using discriminant analysis of principal components (DAPC) with the first ten principal components. (C and D) Redundancy analyses (RDA) were conducted to illustrate how climate variables explain genetic variation across the hybrid zone. Unlike the DAPC in panel (B), these RDAs used genotype probabilities and climate data from the 25 sampled populations (map insets, lower left). In the RDA biplots, the proximity of points (representing individuals) indicates similar genetic responses to climate predictors. Right-angle projections of points onto vectors represent variable values: Smaller projections indicate larger values for a given variable, and vice versa. RDA axes 1 and 2 are shown in panel (C), and axes 1 and 3 in panel (D). Descriptions of climate variables are provided in Table 1.

Table 2. Variance partitioning results from redundancy analysis (RDA) and partial redundancy analysis (pRDA), elucidating the contributions of genetic, geographic, and environmental factors to phytochemical variation.

Models	Inertia	R^2	P (>F)	Proportion of explainable variance	Proportion of total variance
Full model: *chem.* (Euclidean) ~ *clim.* + *genet.* + *geo.*	19.430	0.119	0.001	1	0.119
Pure climate: *chem.* (Euclidean) ~ *clim.* | (*genet.* + *geo.*)	2.086	0.013	0.001	0.107	0.013
Pure genetic: *chem.* (Euclidean) ~ *genet.* | (*clim.* + *geo.*)	5.350	0.033	0.001	0.275	0.033
Pure geographic: *chem.* (Euclidean) ~ *geo.* | (*clim.* + *genet.*)	4.519	0.028	0.001	0.233	0.028
Confounded climate/genetic/geography	7.476			0.385	0.046

Abbreviations: chem, chemical variation; genet, genetic variation; clim, climatic variation; geo, geographical variation

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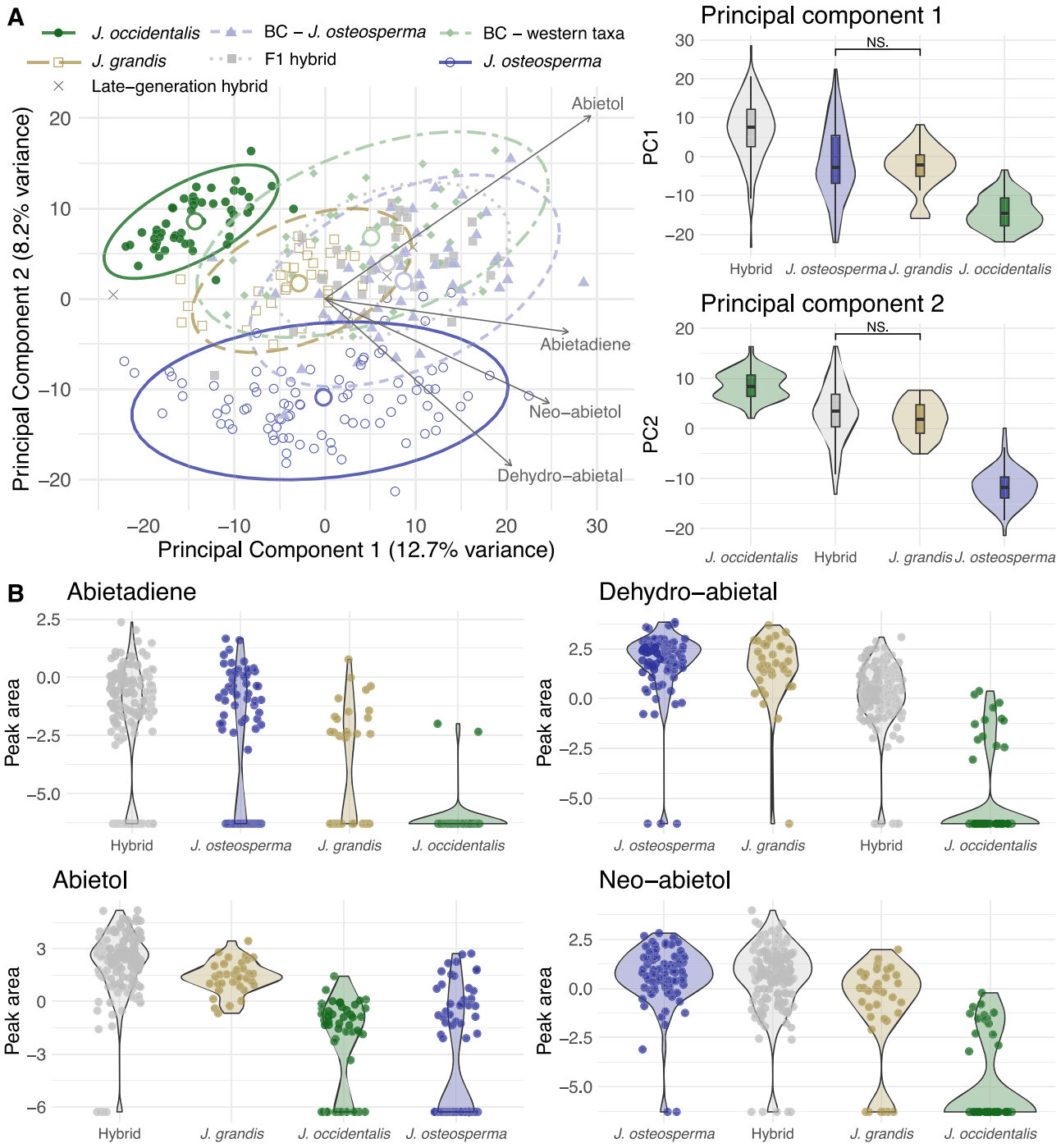

Fig. 6. (A) Principal component analysis (PCA) of terpenoid profiles for *Juniperus* species and hybrids. Each point represents an individual sample, color-coded by ancestry and hybrid group. Ellipses represent the 95% confidence intervals for each group, and larger open points indicate group centroids. Gray arrows illustrate the loadings of key terpenoid compounds highlighted in panel (B) and the Discussion. To the right of the PCA, violin plots display the distributions of PC1 and PC2 scores for each ancestry group, with hybrid groups pooled, ordered by their mean PC scores from highest to lowest. All the pairwise comparisons of group means are significant except those indicated with brackets. (B) Violin plots showing the distributions of $\log_2$-transformed peak areas for four key abietane diterpenoids that significantly load onto PC1 and PC2. Ancestry groups are ordered by their group mean from highest to lowest. Jittered points within the violins represent individual sample values, highlighting variations in compound concentrations across species and hybrid groups.

approaches to assess differences in terpenoid variability and composition across ancestry groups. The hybrid group showed the highest variance in terpenoid concentrations, while the *J. occidentalis* group exhibited the most variance in terpenoid presence/absence. PCoA of terpenoid data separated ancestry groups along the first three principal coordinates axes (Supplementary Fig. 8). Additional results from the distance-based analyses are presented in the online supplementary materials.

Discussion

We leveraged genetic and phytochemical data to describe patterns of hybridization and its consequences in a group

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of ecologically significant *Juniperus* species of the arid west, revealing clear genetic differentiation among the parental species despite extensive hybridization in an environmentally intermediate secondary contact zone. Environmental factors predicted both hybrid occurrence and ancestry variation, suggesting that environment plays an important role in shaping patterns of hybrid admixture. An abundance of backcrosses, and a paucity of late-generation hybrids, indicates that gene flow across species boundaries is a factor further shaping genetic variation in this clade despite the maintenance of divergence among parental species. This syngameon structure not only connects and expands the environments and distributions where these species occur but also likely buffers their evolutionary potential amid rapid environmental change (Cannon and Petit 2020; Touchette et al. 2024). By coupling landscape genomic analyses with untargeted metabolomic data, we further characterized distinct phytochemical profiles between parental species and hybrids. Hybrids exhibited novel variation, including increased chemical diversity and higher concentrations for key defensive specialized metabolites, illustrating how hybridization can generate new genetic and functional variation with extended ecological consequences.

Genetic variation across populations, species, and hybrids

Hybridization significantly shapes evolutionary histories and often complicates phylogenetic reconstructions in plants (Rieseberg and Soltis 1991; Folk et al. 2017). In *Juniperus*, phylogenetic analyses have been particularly challenging due to reticulation. For instance, chloroplast DNA analyses (Adams et al. 2006; Adams and Schwarzbach 2013) positioned *J. grandis* and *J. osteosperma* as sister species, conflicting with morphological evidence supporting a sister relationship between *J. grandis* and *J. occidentalis*. In contrast, our analysis of thousands of nuclear loci resolved these relationships with 100% bootstrap support, confirming *J. grandis* and *J. occidentalis* as sister species (Fig. 1; see also Uckele et al. 2021).

Forest trees commonly exhibit low genetic differentiation across broad geographic ranges, even over vast distances (Petit and Hampe 2006; Neale 2007). Populations within each of the parental *Juniperus* species displayed low population genetic differentiation and no isolation by distance (Fig. 2F to H), even among *J. osteosperma* populations separated by nearly 1,000 km (Fig. 2F). Despite this, clear genetic differentiation among species is maintained, indicating reproductive barriers (Fig. 3). Similar to other North American conifers (Menon et al. 2018; Acosta et al. 2019; Haselhorst et al. 2019), genetic diversity was high within parental and hybrid populations (Supplementary Table 2). Standing genetic variation, a key predictor of adaptive potential, may be particularly important for long-lived, sessile trees facing climate change (Barnosky 1987; De Carvalho et al. 2010). Hybrids and *J. osteosperma* showed the highest genetic diversity (Supplementary Table 2), suggesting roles for admixture and large population sizes, respectively, in maintaining diversity.

Juniperus osteosperma occupies the largest geographic range of the three parental species. Fossil evidence indicates that during the last glacial maximum, *J. osteosperma* maintained a stable range in the Great Basin Desert and expanded southward into the Mojave Desert, southern Sierras, Central Valley, and Sonoran Desert (Thompson 1990; Nowak et al. 1994). In contrast, *J. grandis* and *J. occidentalis* reached their current ranges in the early Holocene, experiencing greater displacement and range contraction due to ice-age climate shifts (Cole 1983; Nowak et al. 1994). Juniper woodlands declined until the late Holocene, when wetter conditions during the neoglaciation period spurred population growth and downslope expansion (Wigand et al. 1995). This history may explain the negative genome-wide Tajima's *D* values observed in nearly all the populations, with significantly lower values in *J. osteosperma* (Table 3), suggesting recent population expansion.

Patterns of admixture in a secondary contact zone

Contemporary hybrid zones and evidence of ancient reticulation suggest admixture has played an important role in *Juniperus* (Adams 1994, 2016; Adams et al. 2016, 2017, 2018, 2020; Farhat et al. 2020). Our study expands this understanding by documenting ancestry variation across a hybrid zone formed by admixture among three closely related species. These species underwent recurrent cycles of allopatry and secondary contact during the Quaternary, with the latest secondary contact likely beginning after the last glacial retreat in the early Holocene (~11,700 years ago), as milder climates enabled downslope expansion (Cole 1983; Nowak et al. 1994).

The hybrid zone lacked late-generation hybrids (e.g. F_2s, F_Ns, etc.) despite the prevalence of F_1s, suggesting strongly asymmetric gene flow from parental populations (Barton and Hewitt 1985) or some degree of hybrid breakdown (Burke and Arnold 2001). An abundance of backcrosses indicates permeable but strongly maintained species boundaries among the three *Juniperus* species, typical of a syngameon, where networks of closely related species hybridize with consequences for the evolutionary dynamics of the group. Syngameons have been observed in many woody plants, including pinyon pines (Buck et al. 2023), oaks (Cronk and Suarez-Gonzalez 2018), poplars (Chhatre et al. 2018), birches (Touchette et al. 2024), and *Eucalyptus* spp. (Flores-Rentería et al. 2017). These networks of admixture may enhance resilience to environmental change by increasing effective population sizes, maintaining genetic diversity, creating novel genomic combinations, facilitating adaptive introgression, and increasing the geographic extent of occupied habitat (Cannon and Petit 2020; Buck et al. 2023; Massatti et al. 2025).

Our results provide evidence for bidirectional backcrossing, with gene flow into the western parental genomic background confined to the California–Nevada border, and gene flow into *J. osteosperma* extending east into central Nevada (Fig. 4B and D). This pattern mirrors dominant, west-to-east wind patterns in western Nevada (the westerlies), which can shape genetic structure in wind-pollinated trees (Kling and Ackerly 2021). The transition from western parental to *J. osteosperma* ancestry forms a longitudinal cline along the ecotone between the Cascade–Sierra ranges and the Great Basin Desert (Fig. 4D). Hybridization often occurs in ecotones, where transitional zones provide contact opportunities for diverged ecotypes and reduced parental fitness favors hybrids (Barton and Hewitt 1985; Harrison 1993; Abbott 2017). Consistent with this pattern, our results suggest that the juniper parental species occupy distinct climatic zones, whereas hybrids are found in intermediate climates. Climate

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was indeed a strong predictor of ancestry variation across the hybrid zone, aligning with findings from other tree hybrid systems (Cullingham et al. 2012; Hamilton et al. 2013; De La Torre et al. 2014; Menon et al. 2018). Random forest analyses identified climate variables, particularly cumulative water available for runoff or deep percolation, as stronger predictors of hybrid ancestry proportions than geography. Due to low marker density in our current data, and because hybrids generally contain three parental ancestries, we did not apply genomic cline analyses (e.g. bgc; Gompert and Buerkle 2011; Gompert et al. 2024) here, but future work with denser genomic and geographic sampling could apply such methods to identify loci with exceptional introgression or associated with reproductive isolation.

Although conservation and restoration are not a current concern for these juniper species, our results indicate that hybrids, which occur in intermediate environments and often exhibit novel phytochemical profiles, could represent important sources of genetic and ecological variation across both past and future climate shifts. Hybridization in intermediate environments is common in conifers (Hamilton et al. 2015; Menon et al. 2018; Haselhorst et al. 2019; Buck et al. 2023) and widespread shrub species across western North America (Faske et al. 2024; Massatti et al. 2025). In such situations, hybridization may augment genetic variation underlying evolution to changing climates and increase distributional continuity via niche expansion into intermediate environments (Buck et al. 2022; Massatti et al. 2025). Although we lack a functional understanding of the consequences of phytochemical variation in hybrids (but see below), an understanding of the association of parental and hybrid ancestry with environment could help to prevent genetic–environment mismatches in conservation or restoration actions in response to changing climate (Hamilton and Miller 2016).

Phytochemical variation across species and hybrids

Known ecological functions of plant specialized metabolites include defense, signaling, and protection from environmental stress (Pichersky and Raguso 2018). In conifers, terpenoids are central to these roles, forming the primary constituents of oleoresin, a viscous resin found throughout the plant that contains mixtures of monoterpenes, sesquiterpenes, and diterpenoid resin acids (Celedon and Bohlmann 2019). The exudation and hardening of oleoresin in response to wounding, as well as its antimicrobial and antiherbivore properties, make it a primary defense in conifers. Here we quantified foliar terpenoid variation across a conifer hybrid zone encompassing a large range of genetic and environmental variation. Genetic variation explained the most variance in terpenoid concentrations (3.3%), followed by geography (2.8%) and environment (1.3%). The high accuracy of the random forest model and clustering by ancestry in the PCA revealed distinct chemotypes for each ancestry group, highlighting a strong genetic basis for terpenoid biosynthesis, with additional unmeasured influences that may be attributed to phenology, ontogeny, and biotic and abiotic factors (Moore et al. 2014).

Variation in terpenoid profiles among species and hybrids arises from differences in presence/absence of individual compounds (qualitative) and concentration of those compounds (quantitative). Our results show that both contribute to the unique profiles observed. Although hybrids did not express novel terpenoids, their profiles were more chemically rich than those of the parental species. This richness resulted from complementarity, with hybrids expressing the full spectrum of parental terpenoids, whereas each parent expressed a subset. Such patterns are common in plant hybrids and align with Mendelian inheritance with dominance (Orians 2000). Hybrids were not only more chemically rich but also more variable in their terpenoid concentrations. Higher variation, often documented in plant hybrids, is likely driven by additive inheritance of compound concentrations and a broad spectrum of hybrid ancestries from backcrossing (Cheng et al. 2011). For most compounds, at least one hybrid exceeded the parental range, and for 8.6% of the compounds, the concentrations in the hybrid group significantly exceeded the ranges of the parents. Extreme values in F_1s likely reflect heterosis from dominance, overdominance, favorable epistasis, and dosage balance, whereas extremes in backcrosses may result from segregation and recombination generating novel multilocus combinations that increase metabolite concentrations (Hochholdinger and Yu 2025). Although hybrids are generally as susceptible or more to herbivores than their parents, some studies show greater resistance, both of which could provide novel ecological outcomes even if such trait variation is unlikely to introgress widely (Cheng et al. 2011). In juniper hybrids, the elevated expression of two biosynthetic precursors of abietic acid, abietadiene and abietol (Fig. 6B), points to potential ecological consequences given the central role of abietic acid in conifer defense (Keeling and Bohlmann 2006; Oh et al. 2017). Although we could not directly assess abietic acid expression in the hybrids, the elevated expression of its precursors highlights the need to quantify resin acids in natural juniper hybrids and to evaluate whether such differences translate into altered herbivore resistance.

Although phytochemical variation in hybrids is well documented (Rieseberg et al. 1993; Orians 2000; Cheng et al. 2011; Caseys et al. 2015), its ecological and evolutionary consequences in foundational tree hybrid zones remain largely unexplored, limiting our understanding of which aspects of hybrid phytochemistry influence communities and ecosystems (Wetzel and Whitehead 2020; Volf et al. 2024). Theory and empirical studies suggest phytochemical diversity can affect herbivorous insect diversity in contrasting ways (Jones and Lawton 1991). For instance, higher phytochemical richness in Protieae species was associated with lower herbivore diversity, likely due to increased challenges for herbivores (Salazar et al. 2018). Alternatively, higher chemical diversity may facilitate host shifts or provide enemy-free space, potentially increasing herbivore diversity, as observed in *Piper* species (Richards et al. 2015). However, no studies have specifically examined this relationship in hybrid zones. Although tree hybrid zones frequently host more diverse arthropod communities than parental populations (Whitham et al. 1994), the role of phytochemistry in shaping this diversity remains uncertain. Investigating patterns of arthropod diversity in this juniper hybrid zone, and its relationship to different dimensions of phytochemical diversity, could provide insights into the ecological impacts of hybridization in foundational trees.

Acknowledgments

Library size selection was conducted by the Genomic Sequencing and Analysis Facility at UT Austin's Center for Biomedical Research Support (RRID#: SCR_021713). We extend our gratitude to Oren Shelef for his assistance with population sampling and to Thomas Dilts and Sarah Barga for their support in obtaining climate data for this study.

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Additionally, we thank Genalynn Joy Lapira, Regina Gojar, and Brianna Jones for their help with chemical extractions.

Author contributions

Kathryn Uckele (Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing), Casey Philbin (Investigation, Methodology, Resources, Writing—original draft, Writing—review & editing), Lora Richards (Conceptualization, Resources, Supervision, Writing—review & editing), Lee Dyer (Conceptualization, Supervision, Writing—original draft, Writing—review & editing), Joshua Peter Jahner (Supervision, Writing—review & editing), and Thomas L. Parchman (Conceptualization, Funding acquisition, Resources, Supervision, Writing—original draft, Writing—review & editing).

Supplementary material

Supplementary material is available at *Journal of Heredity* online.

Funding

This work was supported by the American Genetic Association EECG award to KAU, who was also supported by the National Science Foundation Graduate Research Award (award no. 1650114) and the Hitchcock Center for Chemical Ecology Fellowship. JPJ received support from the Modelscape Consortium through NSF funding (award no. OIA-2019528).

Data availability

We have deposited the primary data underlying these analyses in public repositories as follows:

- Environmental data, terpenoid concentration data, and ddRADseq genotype probability matrix: available on Dryad (https://doi.org/10.5061/dryad.0vt4b8h91).
- Raw DNA sequence reads: accessible via NCBI SRA under Bioproject PRJNA1037072.

References

Abbott RJ. Plant speciation across environmental gradients and the occurrence and nature of hybrid zones. *J Syst Evol*. 2017;**55**:238–258. https://doi.org/10.1111/jse.12267

Abrahamson WG, Hunter MD, Melika G, Price PW. Cynipid gall-wasp communities correlate with oak chemistry. *J Chem Ecol*. 2003;**29**:209–223. https://doi.org/10.1023/A:1021993017237

Acosta JJ, Fahrenkrog AM, Neves LG, Resende MF, Dervinis C, Davis JM, Holliday JA, Kirst M. Exome resequencing reveals evolutionary history, genomic diversity, and targets of selection in the conifers *Pinus taeda* and *Pinus elliottii*. *Genome Biol Evol*. 2019;**11**:508–520. https://doi.org/10.1093/gbe/evz016

Adams RP. Geographic variation and systematics of monospermous *Juniperus* (Cupressaceae) from the Chihuahua Desert based on RAPDs and terpenes. *Biochem Syst Ecol*. 1994;**22**:699–710. https://doi.org/10.1016/0305-1978(94)90056-6

Adams RP. *Identification of essential oil components by gas chromatography/mass spectrometry*. Vol. **456**. Carol Stream: Allured Publishing Corporation; 2007:544–545.

Adams RP. Hybridization between *Juniperus grandis*, *J. occidentalis* and *J. osteosperma* in northwest Nevada I: terpenes, leviathan mine, Nevada. *Phytologia*. 2013a;**95**:58–69.

Adams RP. Hybridization between *Juniperus grandis*, *J. occidentalis* and *J. osteosperma* in northwest Nevada II: terpenes, Buffalo Hills, northwestern Nevada. *Phytologia*. 2013b;**95**:107–114.

Adams RP. *Junipers of the world: the genus Juniperus*. Bloomington, Indiana: Trafford Publishing; 2014.

Adams RP. Two new cases of chloroplast capture in incongruent topologies in the *Juniperus excelsa* complex: *J. excelsa* var. *turcomanica* comb. nov. and *J. excelsa* var. *seravschanica* comb. nov. *Phytologia*. 2016;**98**:219–231.

Adams RP, Johnson S, Coombes AJ, Caamaño L, González-Elizondo MS. Preliminary examination of hybridization and introgression between *Juniperus flaccida* and *J. poblana*: nrDNA and cpDNA sequence data. *Phytologia*. 2018;**100**:145–152.

Adams RP, Johnson ST, Schwarzbach AE. Long distance gene flow facilitated by bird-dispersed seeds in wind-pollinated species: a story of hybridization and introgression between *Juniperus ashei* and *J. ovata* told by nrDNA and cpDNA. *Phytologia*. 2020;**102**:55–74.

Adams RP, Nguyen S, Morris JA, Schwarzbach AE. Re-examination of the taxonomy of the one-seeded, serrate leaf *Juniperus* of southwestern United States and northern Mexico (Cupressaceae). *Phytologia*. 2006;**88**:299–309. https://doi.org/10.5962/bhl.part.10457

Adams RP, Schwarzbach AE. Taxonomy of the serrate leaf *Juniperus* of North America: phylogenetic analyses using nrDNA and four cpDNA regions. *Phytologia*. 2013;**95**:172–178.

Adams RP, Schwarzbach AE, Tashev AN. Chloroplast capture in *Juniperus sabina* var. *balkanensis* RP Adams and AN Tashev, from the Balkan peninsula: a new variety with a history of hybridization with *J. thurifera*. *Phytologia*. 2016;**98**:219–231.

Adams RP, Socorro G-EM, González-Elizondo M, Ramirez ND, Schwarzbach AE. DNA sequencing and taxonomy of unusual serrate *Juniperus* from Mexico: chloroplast capture and incomplete lineage sorting in *J. coahuilensis* and allied taxa. *Phytologia*. 2017;**99**:62–73.

Alix K, Gérard PR, Schwarzacher T, Heslop-Harrison JS. Polyploidy and interspecific hybridization: partners for adaptation, speciation and evolution in plants. *Ann Bot*. 2017;**120**:183–194. https://doi.org/10.1093/aob/mcx079

Arnold ML. Natural hybridization and the evolution of domesticated, pest and disease organisms. *Mol Ecol*. 2004;**13**:997–1007. https://doi.org/10.1111/j.1365-294X.2004.02145.x

Baack EJ, Rieseberg LH. A genomic view of introgression and hybrid speciation. *Curr Opin Genet Dev*. 2007;**17**:513–518. https://doi.org/10.1016/j.gde.2007.09.001

Barnosky CW. Response of vegetation to climate changes of different duration in the late Neogene. *Trends Ecol Evol*. 1987;**2**:247–250. https://doi.org/10.1016/0169-5347(87)90007-3

Barton NH, Hewitt GM. Analysis of hybrid zones. *Annu Rev Ecol Syst*. 1985;**16**:113–148. https://doi.org/10.1146/annurev.es.16.110185.000553

Betancourt JL, Van Devender TR, Martin PS. *Packrat middens: the last 40,000 years of biotic change*. Tucson, AZ: University of Arizona Press; 1990.

Bozyel ME, Turu D, Benek A, Merdamert-Bozyel E, Canli K. Bioactivities, pharmacological properties, and ethnomedicinal uses of Juniper berries (genus *Juniperus*). In: *Ethnomedicinal plants for drug discovery: current developments*. Singapore: Springer Nature Singapore; 2024:205–216.

Bresadola L, Caseys C, Castiglione S, Buerkle CA, Wegmann D, Lexer C. Admixture mapping in interspecific *Populus* hybrids identifies classes of genomic architectures for phytochemical, morphological and growth traits. *New Phytol*. 2019;**223**:2076–2089. https://doi.org/10.1111/nph.15930

Buck R, Ortega-Del Vecchyo D, Gehring C, Michelson R, Flores-Rentería D, Klein B, Whipple AV, Flores-Rentería L. Sequential hybridization may have facilitated ecological transitions in the Southwestern pinyon pine syngameon. *New Phytol*. 2023;**237**:2435–2449. https://doi.org/10.1111/nph.18543

Buerkle CA, Gompert Z. Population genomics based on low coverage sequencing: how low should we go? *Mol. Ecol*. 2013;**22**:3028–3035. https://doi.org/10.1111/mec.12105

Downloaded from https://academic.oup.com/jhered/article/117/4/699/8440983 by AGA Member Access user on 06 July 2026

Buerkle CA, Lexer C. Admixture as the basis for genetic mapping. *Trends Ecol Evol*. 2008;**23**:686–694. https://doi.org/10.1016/j.tree.2008.07.008

Burke JM, Arnold ML. Genetics and the fitness of hybrids. *Annu Rev Genet*. 2001;**35**:31–52. https://doi.org/10.1146/annurev.genet.35.102401.085719

Burton RS, Pereira RJ, Barreto FS. Cytonuclear genomic interactions and hybrid breakdown. *Annu Rev Ecol Evol Syst*. 2013;**44**:281–302. https://doi.org/10.1146/annurev-ecolsys-110512-135758

Cannon CH, Petit RJ. The oak syngameon: more than the sum of its parts. *New Phytol*. 2020;**226**:978–983. https://doi.org/10.1111/nph.16091

Capblancq T, Forester BR. Redundancy analysis: a Swiss Army knife for landscape genomics. *Methods Ecol Evol*. 2021;**12**:2298–2309. https://doi.org/10.1111/2041-210X.13722

Caseys C, Stritt C, Glauser G, Blanchard T, Lexer C. Effects of hybridization and evolutionary constraints on secondary metabolites: the genetic architecture of phenylpropanoids in European *Populus* species. *PLoS One*. 2015;**10**:e0128200. https://doi.org/10.1371/journal.pone.0128200

Celedon JM, Bohlmann J. Oleoresin defenses in conifers: chemical diversity, terpene synthases and limitations of oleoresin defense under climate change. *New Phytol*. 2019;**224**:1444–1463. https://doi.org/10.1111/nph.15984

Cheng D, Vrieling K, Klinkhamer PG. The effect of hybridization on secondary metabolites and herbivore resistance: implications for the evolution of chemical diversity in plants. *Phytochem Rev*. 2011;**10**:107–117. https://doi.org/10.1007/s11101-010-9194-9

Chhatre VE, Evans LM, DiFazio SP, Keller SR. Adaptive introgression and maintenance of a trispecies hybrid complex in range-edge populations of *Populus*. *Mol Ecol*. 2018;**27**:4820–4838. https://doi.org/10.1111/mec.14820

Chifman J, Kubatko L. Quartet inference from SNP data under the coalescent model. *Bioinformatics*. 2014;**30**:3317–3324. https://doi.org/10.1093/bioinformatics/btu530

Chifman J, Kubatko L. Identifiability of the unrooted species tree topology under the coalescent model with time-reversible substitution processes, site-specific rate variation, and invariable sites. *J Theor Biol*. 2015;**374**:35–47. https://doi.org/10.1016/j.jtbi.2015.03.006

Cole K. Late Pleistocene vegetation of Kings Canyon, Sierra Nevada, California. *Quat Res*. 1983;**19**:117–129. https://doi.org/10.1016/0033-5894(83)90031-5

Cronk QC, Suarez-Gonzalez A. The role of interspecific hybridization in adaptive potential at range margins. *Mol Ecol*. 2018;**27**:4653–4656. https://doi.org/10.1111/mec.14927

Cullingham CI, James PM, Cooke JE, Coltman DW. Characterizing the physical and genetic structure of the lodgepole pine × jack pine hybrid zone: mosaic structure and differential introgression. *Evol Appl*. 2012;**5**:879–891. https://doi.org/10.1111/j.1752-4571.2012.00266.x

Danecek P, Auton A, Abecasis G, Albers CA, Banks E, DePristo MA, Handsaker RE, Lunter G, Marth GT, Sherry ST, et al. The variant call format and VCFtools. *Bioinformatics*. 2011;**27**:2156–2158. https://doi.org/10.1093/bioinformatics/btr330

Danecek P, Bonfield JK, Liddle J, Marshall J, Ohan V, Pollard MO, Whitwham A, Keane T, McCarthy SA, Davies RM, et al. Twelve years of SAMtools and BCFtools. *Gigascience*. 2021;**10**:giab008. https://doi.org/10.1093/gigascience/giab008

de Abreu e Lima F, Westhues M, Cuadros-Inostroza Á, Willmitzer L, Melchinger AE, Nikoloski Z. Metabolic robustness in young roots underpins a predictive model of maize hybrid performance in the field. *Plant J*. 2017;**90**:319–329. https://doi.org/10.1111/tpj.13495

De Carvalho D, Ingvarsson PK, Joseph J, Suter L, Sedivy C, Macaya-Sanz D, Cottrell J, Heinze B, Schanzer I, Lexer C. Admixture facilitates adaptation from standing variation in the European aspen (*Populus tremula* L.), a widespread forest tree. *Mol Ecol*. 2010;**19**:1638–1650. https://doi.org/10.1111/j.1365-294X.2010.04595.x

De La Torre AR, Wang T, Jaquish B, Aitken SN. Adaptation and exogenous selection in a *Picea glauca* × *Picea engelmannii* hybrid zone: implications for forest management under climate change. *New Phytol*. 2014;**201**:687–699. https://doi.org/10.1111/nph.12540

Dilts TE, Yang J. *Climate water deficit toolbox for ArcGIS 10.1*. Reno (NV): University of Nevada; 2015.

Eaton DA, Overcast I. ipyrad: interactive assembly and analysis of RADseq datasets. *Bioinformatics*. 2020;**36**:2592–2594. https://doi.org/10.1093/bioinformatics/btz966

Eaton DA, Spriggs EL, Park B, Donoghue MJ. Misconceptions on missing data in RAD-seq phylogenetics with a deep-scale example from flowering plants. *Syst Biol*. 2017;**66**:399–412. https://doi.org/10.1093/sysbio/syw092

Ellstrand NC, Schierenbeck KA. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc Natl Acad Sci U S A*. 2000;**97**:7043–7050. https://doi.org/10.1073/pnas.97.13.7043

Falush D, Stephens M, Pritchard JK. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics*. 2003;**164**:1567–1587. https://doi.org/10.1093/genetics/164.4.1567

Farhat P, Takvorian N, Avramidou M, Garraud L, Adams RP, Siljak-Yakovlev S, Kharrat MBD, Robert T. First evidence for allotriploid hybrids between *Juniperus thurifera* and *J. sabina* in a sympatric area in the French Alps. *Ann For Sci*. 2020;**77**:1–17. https://doi.org/10.1007/s13595-020-00969-7

Faske TM, Agneray AC, Jahner JP, Osuna-Mascaró C, Sheta LM, Richardson BA, Leger EA, Parchman TL. Environment predicts the maintenance of reproductive isolation in a mosaic hybrid zone of rubber rabbitbrush. *Evolution*. 2024;**78**:300–314. https://doi.org/10.1093/evolut/qpad207

Flores-Rentería L, Rymer PD, Riegler M. Unpacking boxes: integration of molecular, morphological and ecological approaches reveals extensive patterns of reticulate evolution in box eucalypts. *Mol Phylogenet Evol*. 2017;**108**:70–87. https://doi.org/10.1016/j.ympev.2017.01.019

Folk RA, Mandel JR, Freudenstein JV. Ancestral gene flow and parallel organellar genome capture result in extreme phylogenomic discord in a lineage of angiosperms. *Syst Biol*. 2017;**66**:320–337. https://doi.org/10.1093/sysbio/syw083

Fu L, Niu B, Zhu Z, Wu S, Li W. CD-HIT: accelerated for clustering the next-generation sequencing data. *Bioinformatics*. 2012;**28**:3150–3152. https://doi.org/10.1093/bioinformatics/bts565

Fumagalli M, Vieira FG, Korneliussen TS, Linderoth T, Huerta-Sánchez E, Albrechtsen A, Nielsen R. Quantifying population genetic differentiation from next-generation sequencing data. *Genetics*. 2013;**195**:979–992. https://doi.org/10.1534/genetics.113.154740

Gompert Z, Buerkle CA. Bayesian estimation of genomic clines. *Mol Ecol*. 2011;**20**:2111–2127. https://doi.org/10.1111/j.1365-294X.2011.05074.x

Gompert Z, DeRaad DA, Buerkle CA. A next generation of hierarchical Bayesian analyses of hybrid zones enables model-based quantification of variation in introgression in R. *Ecol Evol*. 2024;**14**:e70548. https://doi.org/10.1002/ece3.70548

Gompert Z, Lucas LK, Buerkle CA, Forister ML, Fordyce JA, Nice CC. Admixture and the organization of genetic diversity in a butterfly species complex revealed through common and rare genetic variants. *Mol Ecol*. 2014;**23**:4555–4573. https://doi.org/10.1111/mec.12811

Gompert Z, Mandeville EG, Buerkle CA. Analysis of population genomic data from hybrid zones. *Annu Rev Ecol Evol Syst*. 2017;**48**:207–229. https://doi.org/10.1146/annurev-ecolsys-110316-022652

Gottfried GJ, Swetnam TW, Allen CD, Betancourt JL, Chung-MacCoubrey AL. Pinyon-juniper woodlands. *United States Department of Agriculture Forest Service General Technical Report RM*. Fort Collins, CO. 1995;95–132.

Hamilton JA, De la Torre AR, Aitken SN. Fine-scale environmental variation contributes to introgression in a three-species spruce hybrid complex. *Tree Genet Genomes*. 2015;**11**:817. https://doi.org/10.1007/s11295-014-0817-y

Downloaded from https://academic.oup.com/jhered/article/117/4/699/8440983 by AGA Member Access user on 06 July 2026

Hamilton JA, Lexer C, Aitken SN. Differential introgression reveals candidate genes for selection across a spruce (*Picea sitchensis* × *P. glauca*) hybrid zone. *New Phytol*. 2013;**197**:927–938. https://doi.org/10.1111/nph.12055

Hamilton JA, Miller JM. Adaptive introgression as a resource for management and genetic conservation in a changing climate. *Conserv Biol*. 2016;**30**:33–41. https://doi.org/10.1111/cobi.12574

Harrison RG, ed. *Hybrid zones and the evolutionary process*. New York: Oxford University Press; 1993.

Haselhorst MS, Parchman TL, Buerkle CA. Genetic evidence for species cohesion, substructure and hybrids in spruce. *Mol Ecol*. 2019;**28**:2029–2045. https://doi.org/10.1111/mec.15056

Hochholdinger F, Yu P. Molecular concepts to explain heterosis in crops. *Trends Plant Sci*. 2025;**30**:95–104. https://doi.org/10.1016/j.tplants.2024.07.018

Hothorn T, Bretz F, Westfall P. Simultaneous inference in general parametric models. *Biom J*. 2008;**50**:346–363. https://doi.org/10.1002/bimj.200810425

Hudson RR, Slatkin M, Maddison WP. Estimation of levels of gene flow from DNA sequence data. *Genetics*. 1992;**132**:583–589. https://doi.org/10.1093/genetics/132.2.583

Jombart T. adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics*. 2008;**24**:1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Jombart T, Devillard S, Balloux F. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genet*. 2010;**11**:94. https://doi.org/10.1186/1471-2156-11-94

Jones CG, Lawton JH. Plant chemistry and insect species richness of British umbellifers. *J Anim Ecol*. 1991;**60**:767–777. https://doi.org/10.2307/5413

Kagawa K, Takimoto G. Hybridization can promote adaptive radiation by means of transgressive segregation. *Ecol Lett*. 2018;**21**:264–274. https://doi.org/10.1111/ele.12891

Keeling CI, Bohlmann J. Diterpene resin acids in conifers. *Phytochemistry*. 2006;**67**:2415–2423. https://doi.org/10.1016/j.phytochem.2006.08.019

Kling MM, Ackerly DD. Global wind patterns shape genetic differentiation, asymmetric gene flow, and genetic diversity in trees. *Proc Natl Acad Sci U S A*. 2021;**118**:e2017317118. https://doi.org/10.1073/pnas.2017317118

Korneliussen TS, Albrechtsen A, Nielsen R. ANGSD: analysis of next generation sequencing data. *BMC Bioinformatics*. 2014;**15**:1–13. https://doi.org/10.1186/s12859-014-0356-4

Korneliussen TS, Moltke I, Albrechtsen A, Nielsen R. Calculation of Tajima's D and other neutrality test statistics from low depth next-generation sequencing data. *BMC Bioinformatics*. 2013;**14**:1–14. https://doi.org/10.1186/1471-2105-14-289

LeDell E, Poirier S. H2o automl: Scalable automatic machine learning. In: *Proceedings of the AutoML Workshop at ICML*. 2020, 2020.

Legendre P, Legendre L. *Numerical ecology*. Vol. **24**. Elsevier; 2012.

Li H. A statistical framework for SNP calling, mutation discovery, association mapping and population genetical parameter estimation from sequencing data. *Bioinformatics*. 2011;**27**:2987–2993. https://doi.org/10.1093/bioinformatics/btr509

Li H, Durbin R. Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics*. 2009;**25**:1754–1760. https://doi.org/10.1093/bioinformatics/btp324

Li W, Godzik A. Cd-hit: a fast program for clustering and comparing large sets of protein or nucleotide sequences. *Bioinformatics*. 2006;**22**:1658–1659. https://doi.org/10.1093/bioinformatics/btl158

Liaw A, Wiener M. Classification and regression by randomForest. *R news*. 2002;**2**:18–22.

Lisec J, Steinfath M, Meyer RC, Selbig J, Melchinger AE, Willmitzer L, Altmann T. Identification of heterotic metabolite QTL in *Arabidopsis thaliana* RIL and IL populations. *Plant J*. 2009;**59**:777–788. https://doi.org/10.1111/j.1365-313X.2009.03910.x

Mandeville EG, Parchman TL, Thompson KG, Compton RI, Gelwicks KR, Song SJ, Buerkle CA. Inconsistent reproductive isolation revealed by interactions between *Catostomus* fish species. *Evol Lett*. 2017;**1**:255–268. https://doi.org/10.1002/evl3.29

Mao K, Hao G, Liu J, Adams RP, Milne RI. Diversification and biogeography of *Juniperus* (Cupressaceae): variable diversification rates and multiple intercontinental dispersals. *New Phytol*. 2010;**188**:254–272. https://doi.org/10.1111/j.1469-8137.2010.03351.x

Markó G, Novák I, Bernáth J, Altbäcker V. Both gas chromatography and an electronic nose reflect chemical polymorphism of juniper shrubs browsed or avoided by sheep. *J Chem Ecol*. 2011;**37**:705–713. https://doi.org/10.1007/s10886-011-9974-8

Martinez Arbizu P. pairwiseAdonis: pairwise multilevel comparison using adonis. *R package version 0.4, 1* 2020.

Massatti R, Faske TM, Barnes IM, Leger EA, Parchman TL, Richardson BA, Knowles LL. Suturing fragmented landscapes: mosaic hybrid zones in plants may facilitate ecosystem resiliency. *Proc Natl Acad Sci U S A*. 2025;**122**:e2410941122. https://doi.org/10.1073/pnas.2410941122

McFarlane SE, Jahner JP, Lindtke D, Buerkle CA, Mandeville EG. Selection leads to remarkable variability in the outcomes of hybridisation across replicate hybrid zones. *Mol Ecol*. 2024;**33**:e17359. https://doi.org/10.1111/mec.17359

McKinney GJ, Waples RK, Seeb LW, Seeb JE. Paralogs are revealed by proportion of heterozygotes and deviations in read ratios in genotyping-by-sequencing data from natural populations. *Mol Ecol Resour*. 2017;**17**:656–669. https://doi.org/10.1111/1755-0998.12613

Menon M, Bagley JC, Friedline CJ, Whipple AV, Schoettle AW, Leal-Sàenz A, Wehenkel C, Molina-Freaner F, Flores-Rentería L, Gonzalez-Elizondo MS, et al. The role of hybridization during ecological divergence of southwestern white pine (*Pinus strobiformis*) and limber pine (*P. flexilis*). *Mol Ecol*. 2018;**27**:1245–1260. https://doi.org/10.1111/mec.14505

Miller RF, Wigand PE. Holocene changes in semiarid pinyon-juniper woodlands: response to climate, fire, and human activities in the US Great Basin. *BioScience*. 1994;**44**:465–474. https://doi.org/10.2307/1312298

Moore BD, Andrew RL, Külheim C, Foley WJ. Explaining intraspecific diversity in plant secondary metabolites in an ecological context. *New Phytol*. 2014;**201**:733–750. https://doi.org/10.1111/nph.12526

Neale DB. Genomics to tree breeding and forest health. *Curr Opin Genet Dev*. 2007;**17**:539–544. https://doi.org/10.1016/j.gde.2007.10.002

Nei M. Genetic distance between populations. *Am Nat*. 1972;**106**:283–292. https://doi.org/10.1086/282771

Nielsen R, Korneliussen T, Albrechtsen A, Li Y, Wang J. SNP calling, genotype calling, and sample allele frequency estimation from new-generation sequencing data. *PLoS One*. 2012;**7**:e37558. https://doi.org/10.1371/journal.pone.0037558

Nowak CL, Nowak RS, Tausch RJ, Wigand PE. Tree and shrub dynamics in northwestern Great Basin woodland and shrub steppe during the Late-Pleistocene and Holocene. *Am J Bot*. 1994;**81**:265–277. https://doi.org/10.1002/j.1537-2197.1994.tb15443.x

Oh HW, Yun CS, Jeon JH, Kim JA, Park DS, Ryu HW, Oh SR, Song HH, Shin Y, Jung CS, et al. Conifer diterpene resin acids disrupt juvenile hormone-mediated endocrine regulation in the Indian meal moth *Plodia interpunctella*. *J Chem Ecol*. 2017;**43**:703–711. https://doi.org/10.1007/s10886-017-0861-9

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, et al. *Vegan: community ecology package. R package version 2.5-6. 2019*. 2020.

Orians CM. The effects of hybridization in plants on secondary chemistry: implications for the ecology and evolution of plant–herbivore interactions. *Am J Bot*. 2000;**87**:1749–1756.

Paradis E, Schliep K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*. 2019;**35**:526–528. https://doi.org/10.1093/bioinformatics/bty633

Downloaded from https://academic.oup.com/jhered/article/117/4/699/8440983 by AGA Member Access user on 06 July 2026

Parchman TL, Gompert Z, Mudge J, Schilkey FD, Benkman CW, Buerkle CA. Genome-wide association genetics of an adaptive trait in lodgepole pine. *Mol Ecol*. 2012;**21**:2991–3005. https://doi.org/10.1111/j.1365-294X.2012.05513.x

Pardikes NA, Forister ML, Dyer LA. Preference and performance of Lepidoptera varies with tree age in juniper woodlands. *Ecol Entomol*. 2019;**44**:140–150. https://doi.org/10.1111/een.12682

Petit RJ, Hampe A. Some evolutionary consequences of being a tree. *Annu Rev Ecol Evol Syst*. 2006;**37**:187–214. https://doi.org/10.1146/annurev.ecolsys.37.091305.110215

Pichersky E, Raguso RA. Why do plants produce so many terpenoid compounds? *New Phytol*. 2018;**220**:692–702. https://doi.org/10.1111/nph.14178

Poelman EH, Dam NM, Loon JJA, Vet LE, Dicke M. Chemical diversity in *Brassica oleracea* affects biodiversity of insect herbivores. *Ecology*. 2009;**90**:1863–1877. https://doi.org/10.1890/08-0977.1

PRISM Climate Group. *PRISM climate data*. Corvallis, Oregon, USA: Oregon State University; 2014: Available at https://www.prism.oregonstate.edu; accessed Apr. 11, 2018.

Pritchard JK, Stephens M, Donnelly P. Inference of population structure using multilocus genotype data. *Genetics*. 2000;**155**:945–959. https://doi.org/10.1093/genetics/155.2.945

R Core Team. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing; 2020: Available at https://www.R-project.org/.

Remington CL. Suture-zones of hybrid interaction between recently joined biotas. In: *Evolutionary biology*. Boston (MA): Springer; 1968:321–428.

Renoult SA, Leong JV, Mezzomo P, Sebek P, Koutecký P, Kukla J, Nguyen P, Moos M, Pokorny V, Wagner ND, et al. Effects of hybridization on chemical diversity and plant–insect herbivore interactions in *Salix alba* × *fragilis*. *J Exp Bot*. 2025;**76**:6974–6986. https://doi.org/10.1093/jxb/eraf296

Richards LA, Dyer LA, Forister ML, Smilanich AM, Dodson CD, Leonard MD, Jeffrey CS. Phytochemical diversity drives plant–insect community diversity. *Proc Natl Acad Sci U S A*. 2015;**112**:10973–10978. https://doi.org/10.1073/pnas.1504977112

Rieseberg LH, Archer MA, Wayne RK. Transgressive segregation, adaptation and speciation. *Heredity*. 1999;**83**:363–372. https://doi.org/10.1038/sj.hdy.6886170

Rieseberg LH, Carney SE. Plant hybridization. *New Phytol*. 1998;**140**:599–624. https://doi.org/10.1046/j.1469-8137.1998.00315.x

Rieseberg LH, Ellstrand NC, Arnold M. What can molecular and morphological markers tell us about plant hybridization? *Crit Rev Plant Sci*. 1993;**12**:213–241. https://doi.org/10.1080/07352689309701902

Rieseberg LH, Kim SC, Randell RA, Whitney KD, Gross BL, Lexer C, Clay K. Hybridization and the colonization of novel habitats by annual sunflowers. *Genetica*. 2007;**129**:149–165. https://doi.org/10.1007/s10709-006-9011-y

Rieseberg LH, Soltis DE. Phylogenetic consequences of cytoplasmic gene flow in plants. *Evolutionary Trends in Plants*. 1991;**5**:65–84.

Rieseberg LH, Widmer A, Arntz AM, Burke B. The genetic architecture necessary for transgressive segregation is common in both natural and domesticated populations. *Philos Trans R Soc Lond Ser B Biol Sci*. 2003;**358**:1141–1147.

Roberts DR, Hamann A. Glacial refugia and modern genetic diversity of 22 western North American tree species. *Proc R Soc B Biol Sci*. 2015;**282**:20142903

Salazar D, Lokvam J, Mesones I, Vásquez Pilco M, Ayarza Zuñiga JM, de Valpine P, Fine PV. Origin and maintenance of chemical diversity in a species-rich tropical tree lineage. *Nat Ecol Evol*. 2018;**2**:983–990. https://doi.org/10.1038/s41559-018-0552-0

Schwartz CC, Regelin WL, Nagy JG. Deer preference for juniper forage and volatile oil treated foods. *J Wildl Manag*. 1980;**44**:114–120. https://doi.org/10.2307/3808357

Schweitzer JA, Madritch MD, Bailey JK, LeRoy CJ, Fischer DG, Rehill BJ, Lindroth RL, Hagerman AE, Wooley SC, Hart SC, et al. From genes to ecosystems: the genetic basis of condensed tannins and their role in nutrient regulation in a *Populus* model system. *Ecosystems*. 2008;**11**:1005–1020. https://doi.org/10.1007/s10021-008-9173-9

Seybold SJ, Huber DP, Lee JC, Graves AD, Bohlmann J. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. *Phytochem Rev*. 2006;**5**:143–178. https://doi.org/10.1007/s11101-006-9002-8

Shastry V, Adams PE, Lindtke D, Mandeville EG, Parchman TL, Gompert Z, Buerkle CA. Model-based genotype and ancestry estimation for potential hybrids with mixed-ploidy. *Mol Ecol Resour*. 2021;**21**:1434–1451. https://doi.org/10.1111/1755-0998.13330

Snir S, Rao S. Quartet MaxCut: a fast algorithm for amalgamating quartet trees. *Mol Phylogenet Evol*. 2012;**62**:1–8. https://doi.org/10.1016/j.ympev.2011.06.021

Soltis PS, Marchant DB, Van de Peer Y, Soltis DE. Polyploidy and genome evolution in plants. *Curr Opin Genet Dev*. 2015;**35**:119–125. https://doi.org/10.1016/j.gde.2015.11.003

Swenson NG, Howard DJ. Clustering of contact zones, hybrid zones, and phylogeographic breaks in North America. *Am Nat*. 2005;**166**:581–591. https://doi.org/10.1086/491688

Tajima F. Evolutionary relationship of DNA sequences in finite populations. *Genetics*. 1983;**105**:437–460. https://doi.org/10.1093/genetics/105.2.437

Tajima F. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*. 1989;**123**:585–595. https://doi.org/10.1093/genetics/123.3.585

Tank DC, Eastman JM, Pennell MW, Soltis PS, Soltis DE, Hinchliff CE, Brown JW, Sessa EB, Harmon LJ. Nested radiations and the pulse of angiosperm diversification: increased diversification rates often follow whole genome duplications. *New Phytol*. 2015;**207**:454–467. https://doi.org/10.1111/nph.13491

Terry RG. Re-evaluation of morphological and chloroplast DNA variation in *Juniperus osteosperma* Hook and *Juniperus occidentalis* Torr. Little (Cupressaceae) and their putative hybrids. *Biochem Syst Ecol*. 2010;**38**:349–360. https://doi.org/10.1016/j.bse.2010.03.001

Terry RG, Nowak RS, Tausch RJ. Genetic variation in chloroplast and nuclear ribosomal DNA in Utah juniper (*Juniperus osteosperma*, Cupressaceae): evidence for interspecific gene flow. *Am J Bot*. 2000;**87**:250–258. https://doi.org/10.2307/2656913

Thompson RS. *Late Quaternary vegetation and climate. Packrat middens: the last 40,000 years of biotic change*. Tucson, Arizona: University of Arizona Press, 1990:200.

Tonkel KC, Dimitri LA, Longland WS, Kirchoff VS, Rector BG. Parallel paths in a miniature world. *Ecology*. 2021;**102**:e03460. https://doi.org/10.1002/ecy.3460

Touchette L, Godbout J, Lamothe M, Porth I, Isabel N. A cryptic syngameon within *Betula* shrubs revealed: implications for conservation in changing subarctic environments. *Evol Appl*. 2024;**17**:e13689. https://doi.org/10.1111/eva.13689

Uckele KA, Adams RP, Schwarzbach AE, Parchman TL. Genome-wide RAD sequencing resolves the evolutionary history of serrate leaf *Juniperus* and reveals discordance with chloroplast phylogeny. *Mol Phylogenet Evol*. 2021;**156**:107022. https://doi.org/10.1016/j.ympev.2020.107022

USDA Forest Service. *Forest Inventory and Analysis database*. St Paul (MN): USDA Forest Service, Northern Research Station; 2019.

Vasek FC. The distribution and taxonomy of three western junipers. *Brittonia*. 1966;**18**:350–372. https://doi.org/10.2307/2805152

Vavrek MJ. Fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontol Electron*. 2011;**14**:16.

Volf M, Renoult SA, Panthee S, van Dam NM. Quantifying various aspects of chemical diversity in hybrid plants can help understanding ecological consequences of hybridization. *Am J Bot*. 2024;**111**:e16283. https://doi.org/10.1002/ajb2.16283

Watterson GA. On the number of segregating sites in genetical models without recombination. *Theor Popul Biol*. 1975;**7**:256–276. https://doi.org/10.1016/0040-5809(75)90020-9

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Weisberg PJ, Lingua E, Pillai RB. Spatial patterns of pinyon–juniper woodland expansion in central Nevada. *Rangel Ecol Manag*. 2007;**60**:115–124. https://doi.org/10.2111/05-224R2.1

Wetzel WC, Whitehead SR. The many dimensions of phytochemical diversity: linking theory to practice. *Ecol Lett*. 2020;**23**:16–32. https://doi.org/10.1111/ele.13422

Whitham TG, Morrow PA, Potts BM. Plant hybrid zones as centers of biodiversity: the herbivore community of two endemic Tasmanian eucalypts. *Oecologia*. 1994;**97**:481–490. https://doi.org/10.1007/BF00325886

Wigand PE, Hemphill ML, Sharpe SE. *Great Basin semi-arid woodland dynamics during the late Quaternary (No. CONF-9409325-)*. Grand Junction (CO): Rust Geotech, Inc.; 1995.

Wimp GM, Martinsen GD, Floate KD, Bangert RK, Whitham TG. Plant genetic determinants of arthropod community structure and diversity. *Evolution*. 2005;**59**:61–69. https://doi.org/10.1111/j.0014-3820.2005.tb00894.x

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Journal of Heredity, 2026, 117, 699–717
https://doi.org/10.1093/jhered/esag004
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