Annals of Botany **137**: 1094–1114, 2026
https://doi.org/10.1093/aob/mcaf319, available online at www.academic.oup.com/aob

ANNALS OF BOTANY
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ORIGINAL ARTICLE

Phylogenomic analyses of the diverse desert–alpine plant lineage Cistantheae

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Received: 27 August 2025 Returned for revision: 05 December 2025 Accepted: 08 December 2025

• **Background and Aims** Desert and alpine environments, although ecologically distinct, often share similar environmental stressors, such as drought and high radiation. Various plant lineages traverse both biomes, which is often associated with transitions in life-history strategy, whereby annuality is more often associated with drier desert habitats and perenniality is more common in higher elevations. One such lineage is Cistantheae (Montiaceae), a morphologically diverse herbaceous clade in western North and South America. We aimed to infer a robust phylogeny of the clade as a foundation for taxonomic and comparative work.
• **Methods** We used double-digest restriction site-associated DNA sequencing to generate reduced-representation genomic data from >160 samples representing 48 putative species in Cistantheae. Maximum likelihood and coalescent-based phylogenetic methods were used to infer evolutionary relationships across the full clade and within major subclades. We tested for signatures of admixture and introgressive gene flow, and we reconstructed ancestral life history and climatic niche to identify patterns of correlated evolution.
• **Key Results** We inferred a well-resolved phylogeny of Cistantheae, providing strong support for relationships among subclades within Cistantheae. Although many species relationships were clarified, we also found evidence of rampant gene flow and incomplete lineage sorting, particularly within the annual *Cistanthe* clade from the Atacama Desert. Life history is evolutionarily labile across the clade and strongly correlated with temperature and precipitation-related bioclimatic variables: annuals tend to occur in hotter and drier environments, whereas perennials tend to occur in cooler and wetter habitats. Elevational range is also evolutionarily labile, with several species occupying broad elevational gradients.
• **Conclusions** We present the first densely sampled phylogenomic analysis of Cistantheae, providing key insights into species relationships in the clade. Repeated transitions in life history and climatic niche, alongside wide elevational ranges, suggest that many Cistantheae species might be pre-adapted to both arid and montane habitats. This phylogeny will underpin further comparative, taxonomic and phylogenomic studies in this ecologically important lineage.

Key words: phylogenetics, systematics, genomics, life history, arid and semiarid ecosystems, desert, alpine, Cistantheae, Montiaceae.

INTRODUCTION

The dramatic landscapes of western North and South America host a diversity of ecosystems in relatively close proximity to one another, including high-elevation environments, hyper-arid deserts and two of the world's five mediterranean-type climate zones. These montane and xeric systems are noted for their high rates of endemism (Chabot and Billings, 1972; Arroyo *et al.*, 1988; Rundel *et al.*, 1991); at the same time, botanists have also long noticed floristic connections between them (Went,

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1948; Sarmiento, 1975). In general, the colonization of high-elevation or alpine regions and subsequent diversification were speculated to have originated from adjacent lowland or desert ancestors (Stebbins, 1982; Axelrod and Raven, 1985). More recently, phylogenetic studies have confirmed these connections, documenting movements of plant lineages between desert and sub/alpine or alpine ecosystems, including *Linanthus* (Bell and Patterson, 2000; Anghel *et al.*, 2025), *Cirsium* (Kelch and Baldwin, 2003; Siniscalchi *et al.*, 2023), *Oxalis* (Heibl and Renner, 2012) and the Montiaceae (Ogburn and Edwards, 2015). Although desert and alpine environments appear to be distinct, at least in terms of temperature (Chabot and Billings, 1972), there are other factors that might make desert and alpine plants reciprocally pre-adapted to the other environment; both present extreme radiation loads, for example, and many high-elevation environments are also fairly arid (Billings and Mooney, 1968; Ehleringer, 1985; Körner, 2003). Furthermore, there are overlaps in physiological effects of both cold and drought stress (e.g. negative turgor and change in membrane potential at the cellular level; Beck *et al.*, 2007) and the responses by plants to these stressors (e.g. stomatal closure; Agurla *et al.*, 2018).

Multiple studies that documented plant transitions between desert and alpine systems also noted that these shifts are often correlated with changes in life history, with annuals occupying lowland arid areas and perennials more common in the subalpine and alpine regions. It has been long established that higher-elevation areas (associated with lower temperatures) often lack annual plant species (Körner, 2003). Across 32 different angiosperm groups, temperature (specifically the highest temperature of the warmest month) influenced the evolution of annuality (Boyko *et al.*, 2023). Notably, Ogburn and Edwards (2015) found that in Montiaceae, annuals tend to occupy warmer environments and perennials colder. Similar associations have also been observed in other systems; in *Oenothera* (Evans *et al.*, 2005), *Nemesia* (Datson *et al.*, 2008), *Heliophila* (Monroe *et al.*, 2019) and *Veronica* (Wang *et al.*, 2016), shifts to annuality are correlated with increasing temperature, but also with increased aridity or xeric habitats. Globally, annuals have been found to be favoured in dry and hot areas, and a model for biogeographical distribution showed specifically that precipitation and temperature in the driest quarter explains annual plant abundance (Poppenwimer *et al.*, 2023). Conversely, although less frequent, shifts to perenniality are associated with the colonization of montane and alpine habitats in lineages such as *Lupinus* (Drummond *et al.*, 2012) and Arabideae (Karl and Koch, 2013).

The plant family Montiaceae (crown age ~40 Mya; Arakaki *et al.*, 2011; Caryophyllales) comprises ~250 species, widespread and ecologically diverse, inhabiting a range of disparate habitats in the Americas, Australia, New Zealand and Europe. The Montiaceae has been recognized as monophyletic in the process of re-circumscribing Portulacaceae *s.l.* (Nyffeler and Eggli, 2010), with phylogenetic analysis determining two main lineages in Montiaceae (Ogburn and Edwards, 2015). One of these lineages includes recognized genera *Calyptridium* Nutt., *Cistanthe* Spach, *Montiopsis* Kuntze and *Philippiamra* Kuntze (*sensu* Hershkovitz, 2019; previously *Cistanthe* sect. *Philippiamra*; Hershkovitz, 1990*a*, *b*), and monotypic *Lenzia* Phil and *Thingia* Hershk (Hershkovitz, 2019), comprising the Cistantheae clade (Hershkovitz, 2019). Within Cistantheae, *Montiopsis*, *Philippiamra* and *Lenzia* are exclusively South American clades, distributed across Chile, Peru, western Argentina and parts of Bolivia, whereas *Calyptridium* and *Thingia* are North American, predominantly occurring in California and Oregon; *Cistanthe* is predominantly found in South America, but two species are North American (Fig. 1).

The species in the Cistantheae are characterized by having dehiscent valvate capsules as fruit, ranging from one or few to numerous seeds per capsule. Although these herbaceous species exhibit a basic rosette body type (Ogburn and Edwards, 2015), they vary considerably in habit; some are short-lived ephemerals, others are classical herbaceous perennials, while a few become shrubby and woody. Many (although not all) of the species have succulent leaves (Ogburn and Edwards, 2013); we know, for example, that *Cistanthe grandiflora* can plastically increase their succulence (Ogburn and Edwards, 2010). Additionally, multiple succulent species in the Cistantheae can use Crassulacean acid metabolism (CAM) photosynthesis facultatively upon drought (Arroyo *et al.*, 1990; Holtum *et al.*, 2021; Gilman *et al.*, 2023; Chomentowska *et al.*, 2025). Moreover, these species also exhibit substantial diversity in floral morphology, and all investigated species are self-fertile (Hinton, 1976*a*, *b*; Ford, 1992). Ecologically, Cistantheae species are diverse and occupy xeric, mesic/mediterranean and high-elevation montane habitats. The evolutionary transitions between these biomes appear to be correlated with transitions between annual (semelparous) and perennial (iteroparous) life-history strategies (Ogburn and Edwards, 2015). For example, *Philippiamra* species are desert-occupying annuals, surviving as seeds through prolonged drought in the Atacama Desert (Hershkovitz, 2019), whereas some perennial *Montiopsis* and *Cistanthe* species inhabit the Andean mountains ≤4000 m in elevation (Ford, 1992; Peralta and Molina, 2021).

Despite their ecological and morphological diversity, much uncertainty remains in Cistantheae taxonomy. Many of the species now classified in Cistantheae have been moved systematically out of *Calandrinia s.l.* over time (Carolin, 1987, 1993; Peralta, 1988, 1993, 1999; Ford, 1992; Cullen and Peralta, 1994; Peralta and Ford-Werntz, 2008; Hershkovitz, 1990*a*, *b*, 1991, 1993*a*, *b*, 2018, 2019; Peralta and Molina, 2021) after the floristic treatments of the 1800s (including Hooker and Arnott, 1833; Barnéoud, 1847; Philippi, 1860, 1867, 1893; Howell, 1893; Reiche, 1897, 1898). Despite these efforts, decades of confusion persist and have been accompanied by many rounds of synonymizations and splitting of species (Franz, 1908; Pax and Hoffmann, 1934; Añón, 1953; Kelley, 1973; McNeill, 1974; Hinton, 1975; Nyananyo, 1986, 1990; Carolin, 1987, 1993; Peralta, 1988, 1993, 1999; Hershkovitz, 1990*a*, *b*, 1991, 1993*a*, *b*, 2018, 2019; Ford, 1992; Cullen and Peralta, 1994; Ford-Werntz and Peralta, 2002; Peralta and Ford-Werntz, 2008; Guilliams, 2009; Simpson *et al.*, 2010; Guilliams *et al.*, 2011; Guilliams and Miller, 2014; Watson, 2019, 2020; Watson *et al.*, 2020; Peralta and Molina, 2021). The difficulties might be attributable, in part, to the presence of intraspecific variation in morphology (e.g. in *Montiopsis*; Ford, 1992), possibly owing to rampant phenotypic plasticity. This is especially true in the desert taxa, where species are notably hard to identify (Hershkovitz, 2019). Another source contributing to ambiguous species boundaries might be attributable to phenology, when many of the desert species in the Cistantheae will bloom synchronously post-rainfall event; a

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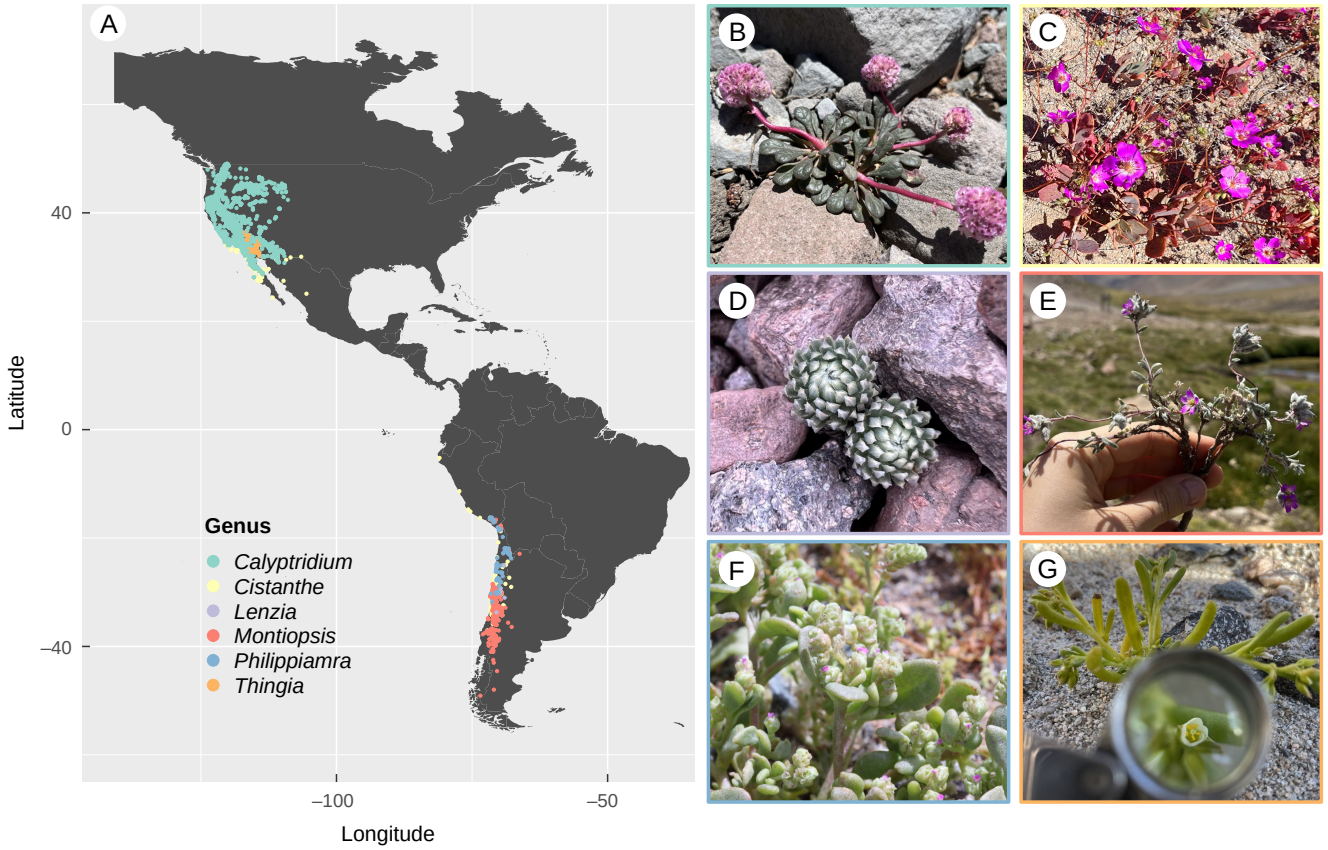

FIG. 1. Geographical distribution of Cistantheae and a representative photograph from each clade showing a diversity of growth forms and floral morphologies. (A) Occurrence points on the map are filtered and cleaned data from the Global Biodiversity Information Facility (2025) and colour coded by clade. From the top left: *Calyptridium umbellatum* (B), *Cistanthe* aff. *longiscapa* (C), *Lenzia chamaepitys* (D), *Montiopsis gilliesii* (E), *Philippiamra calycina* (F) and *Thingia ambigua* (G).

phenomenon commonly associated with El Niño years (Vidiella *et al.*, 1999; Jaksic, 2001; Chávez *et al.*, 2019). Given that many of these species live in sympatry, the simultaneous flowering could facilitate easy transfer of pollen between different species and promote interspecific gene flow (Levin and Kerster, 1974), obscuring traits associated with taxonomy or introducing hybrids (Hershkovitz, 2006, 2019).

The result is that the Cistantheae phylogeny, and especially the phylogenetic relationships within the subclade *Cistanthe*, remains essentially unresolved. No previous study has inferred a densely sampled phylogeny (i.e. including multiple specimens per species) for the group. Existing phylogenetic studies including Cistantheae have been either broader (suborder Portulacineae- or Montiaceae-wide) or focused on other Montiaceae clades (Hershkovitz and Zimmer, 2000; Applequist and Wallace, 2001; Applequist *et al.*, 2006; Hershkovitz, 2006; Guilliams, 2009; Nyffeler and Eggli, 2010; Price, 2012; Ogburn and Edwards, 2015; Goolsby *et al.*, 2018; Hancock *et al.*, 2018; Moore *et al.*, 2018; Gilman *et al.*, 2024), and often based on incomplete sampling, limited markers and accumulated GenBank sequences. In all, a robust phylogeny with adequate species representation is essential to clarify relationships in the clade, re-examine the taxonomy and study patterns of trait evolution across Cistantheae.

In this study, we reconstructed the evolutionary history of the desert–alpine lineage Cistantheae using reduced-representation genome sequencing, including both reliably identifiable taxa and morphologically ambiguous specimens. We prioritized sampling species from the field (although our sampling was supplemented by herbarium specimens) and dense sampling within taxa to examine the monophyly of described species. We hoped to improve phylogenetic resolution in the backbone of Cistantheae and at shallow nodes and to identify potential sources of incongruence (e.g. evidence of introgression, incomplete lineage sorting) that might partly explain taxonomic difficulties that persist. From previous phylogenetic work, we expected to find *Calyptridium*, *Philippiamra*, *Thingia* and *Lenzia* to be more closely related to each other than they are to *Montiopsis* and *Cistanthe* (Hershkovitz, 2006; Guilliams, 2009; Ogburn and Edwards, 2015). We also anticipated the annual *Cistanthe* sect. *Rosulate* taxa from the Atacama Desert, a notoriously difficult taxonomic group, to be particularly recalcitrant to phylogenetic resolution.

With our new phylogeny, we re-evaluated the evolutionary correlations between life-history strategy and climate niche. Based on previous results in other lineages and across Montiaceae (Ogburn and Edwards, 2015), we hypothesized that annuality would be associated with warmer, drier and lower-elevation habitats, whereas perennials would be associated with colder, less-dry and higher-elevation environments. We show that this is indeed the case for Cistantheae and theorize why these results hold in so many lineages, based on previous research on resource allocation, morphological traits and life-history theory. But perhaps the most interesting insights from

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Cistantheae are the generally broad elevational tolerance of most species and the apparent facultative nature of annuality and perenniality in select species. We hypothesize that the repeated evolutionary shifts between life-history strategies might have been facilitated by an underlying plasticity and broad temperature tolerance. One environmental variable that is consistent across the Cistantheae is their apparent high-light requirement; they are rarely found under a forest canopy.

Together, these analyses seek to clarify evolutionary relationships in a charismatic desert–alpine clade and provide a well-supported phylogeny as the foundation for current and future taxonomic and comparative research in the Cistantheae. The Cistantheae phylogeny presented here represents a significant step forwards in our efforts to develop the Montiaceae as a model clade (*sensu* Donoghue and Edwards, 2019). We are focusing on one tractable subclade at a time (e.g. Cistantheae in this study; *Parakeelya* in the study by Hancock *et al.*, 2018), working towards a completely sampled species-level phylogeny of Montiaceae.

MATERIALS AND METHODS

Data collection and double-digest restriction site-associated DNA sequencing

We conducted multiple rounds of fieldwork between 2017 and 2023, in Peru, Chile, Argentina and the USA, to collect Cistantheae species (and other Montiaceae species to be used as outgroups). These voucher specimens were deposited at a herbarium in the origin country of the specimens, including UNMSM Herbarium (SMF), Museo Nacional de Historia Natural (SGO), Herbario Ruiz Leal (MERL), Herbario Mendoza (MEN), Clifton Smith Herbarium (SBBG) and the Yale University Herbarium (YU). We also used dried leaf tissue or frozen DNA extractions from previously collected specimens (Arakaki *et al.*, 2011; Ogburn and Edwards, 2015), in addition to herbarium specimens from Steere Herbarium (NY), San Diego State University Herbarium (SDSU) and Sukkulenten-Sammlung Zürich (ZSS). We extracted DNA from dried leaf tissue by first grinding them with TissueLyser III (Qiagen) with 5 mm stainless-steel beads. We used a cetyltrimethylammonium bromide (CTAB)/β-mercaptoethanol-based extraction protocol and cleaned the extractions with Mag-Bind® Total Pure NGS (Omega Bio-tek) on magnetic racks. In all, we collected and extracted DNA from 164 samples (for the full list of specimens sampled, see Supplementary Data File S1).

Double-digest restriction site-associated DNA sequencing (ddRADSeq; Peterson *et al.*, 2012) has been applied successfully in studies spanning population genomic and phylogenomic frameworks (e.g. Jacobs *et al.*, 2021; MacGuigan *et al.*, 2023; Anghel *et al.*, 2025). We prepared ddRAD libraries from our extracted genomic DNA using a combination of PstI (rare cutter) and MspI (common cutter) restriction enzymes, because this enzyme pair yields a high proportion of single-nucleotide polymorphisms (SNPs) from genic and non-repeat regions of the genome in tomatoes (Shirasawa *et al.*, 2016). Custom barcoded adapters were ligated to the digested DNA fragments such that samples could be multiplexed prior to PCR amplification. The amplified fragments were size selected to retain those between 300 and 500 bp. The prepared ddRAD libraries were sequenced at the University of Oregon Genomics and Cell Characterization Core Facility (GC3F) on an Illumina HiSeq 4000 or NovaSeq 6000 machine (100 bp single-end reads).

Double-digest restriction site-associated DNA sequence assemblies

The raw reads from the sequenced ddRAD libraries were demultiplexed and assembled using *ipyrad* v.0.9.81 (Eaton and Overcast, 2020). On average, ddRAD sequencing yielded ∼3 777 063 raw reads per sample. To minimize the risk of erroneously clustering paralogous loci (a worry with *de novo* assemblies), we opted for a reference-based assembly of the ddRAD sequences. Specifically, we implemented two separate assembly methods: one using the full *Cistanthe cachinalensis* genome (Chomentowska *et al.*, 2025) as the reference and another using only the coding sequences from the same *Cistanthe cachinalensis* genome. Assembly parameters from *ipyrad* included strict adapter filtering (filter_adapters = 2) and a maximum of four alleles per site to account for potential polyploidy (max_alleles_consens = 4). Otherwise, we applied slightly more conservative parameter values to reduce the instances of misaligning paralogues and to accommodate potentially messy alignments (e.g. limiting the proportion of shared polymorphic sites per locus with max_shared_Hs_locus = 0.25). Full parameter files and associated *ipyrad* scripts are available at: https://github.com/anriiam/Cistantheae-phylogeny.

For the Cistantheae-wide phylogenetic analyses, we generated a final matrix based on the coding-sequence-referenced assembly (hereafter, CDS-referenced assembly) by subsampling one to five individuals per species (encompassing observed morphological or geographical variation where possible), resulting in a total of 108 samples, including outgroups. The whole-genome-referenced assembly (hereafter, genome-referenced assembly) did not produce sensible phylogenies (i.e. samples coming together as monophyletic where expected) at this broader scale. To balance retention of loci with minimizing missing data, we required that each locus must be present in ≥30 samples in the final output (min_samples_locus = 30). We also produced assemblies for each major subclade (*Philippiamra*, *Calyptridium*, *Montiopsis*, *Cistanthe* sect. *Cistanthe*, and the combined *Cistanthe* sect. *Rosulatae* and sect. *Andinae*), including all sequenced individuals and varying the amount of missing data using the min_samples_locus parameter. Across subclade datasets, the genome-reference assembly yielded an average of ∼15 378 consensus reads (putative loci) per sample (prefiltering across samples with the min_samples_locus parameter), and the CDS-referenced assembly yielded an average of ∼6514 consensus reads per sample. Full assembly statistics are available in Supplementary Data File S2.

Phylogenetic analyses

The final Cistantheae-wide CDS-referenced assembly contained 1412 loci (with an average of 45.1 samples per locus), with 80.18 % missing data across the full sequence matrix of 263 221 sites (with 73.56 % missing in only the SNP matrix containing 19 694 sites, of which 8871 were parsimony informative; Supplementary Data File S2). Using this assembled matrix, we inferred a phylogeny with a maximum-likelihood (ML) approach implemented in *IQ-TREE2* v.2.2.2 (Minh *et al.*,

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2020). According to the *IQ-TREE2* documentation, we modified default parameters (-pers 0.2, -nstop 500) to accommodate the characteristics of our dataset, which contains many short ddRAD sequences. To ensure that our *IQ-TREE2* inferences were comparable across analyses, we used the GTR+I+G model of sequence evolution. We also verified that the resulting topology remained consistent when switching to ModelFinder (the default model selection option) and when varying the starting tree, comparing results obtained using a random starting tree (-t RANDOM) versus a neighbour-joining tree (default settings). Support values were calculated using 1000 ultrafast bootstrap (UFBoot) replicates.

At the subclade level, both the CDS-referenced assemblies and the genome-referenced assemblies were used to infer phylogenies. For phylogenetic inference based on the CDS-referenced alignments, we required that each locus be present in 30 % of the samples within each subclade dataset; these assemblies contained between 43.61 and 58.21 % of missing data. For the genome-referenced assemblies, we required that each locus be present in 90 % of the samples for each subclade, resulting in 34.47–48.03 % missing data. We prioritized inclusion of more data when feasible (which corresponds to more missingness but does not necessarily mean less informative; Eaton *et al.*, 2017). We inferred ML trees using *IQ-TREE2* as described above, and we also inferred coalescent- and quartet-based species trees using the 'tetrad' module implemented in the *ipyrad-analysis* toolkit (https://github.com/eaton-lab/tetrad) with 1000 bootstrap replicates. For each bootstrap replicate, one SNP from every locus was subsampled independently to maximize the number of informative, unlinked SNPs.

Genetic structure and introgression

For analyses of genetic structure across all individuals in each subclade, we initially filtered the VCF files from the subclade-level *ipyrad* assemblies (min_samples_locus = 30 %) using *VCFtools* v.0.1.16 (Danecek *et al.*, 2011). This included filtering out non-biallelic sites, in addition to sites with minor allele frequencies of <0.05 (–maf 0.05). Additionally, we thinned out the matrix by retaining one site per locus to limit linkage among SNPs. We also filtered out genotypes with high missingness (–max-missing), requiring that 70–95 % of individuals have a genotype called at a given SNP, while still retaining >1000 SNPs per assembly.

These filtered assemblies were loaded into R v.4.4.0 (R Core Team, 2024), where we assessed genetic structure and potential admixture by estimating ancestry coefficients using sparse non-negative matrix factorization (sNMF), implemented in the package *LEA* v.3.16.0 (Frichot and François, 2015); sNMF does not assume an evolutionary model, hence this was chosen above other popular methods, such as STRUCTURE (Pritchard *et al.*, 2000). To determine the optimal number of genetic clusters (K), we used a cross-entropy criterion after testing K values from 2 to 20 (or 10, for smaller datasets; Supplementary Data Fig. S1) for each subclade. We used a regularization parameter $\alpha = 100$ for smaller datasets and ran each analysis with 100 replicates.

Furthermore, we wanted to detect instances of introgression using the 'baba' module in the *ipyrad-analysis* toolkit, which calculates *D*-statistics (ABBA-BABA tests) from the .loci file outputs from *ipyrad* (min_samples_locus = 30 %). For each subclade-level analysis, we used either the subclade-level ML or Tetrad trees to draw four-taxon trees including one outgroup and three ingroups (P3, P2 and P1), where each group could contain one or more samples. To generate tests, the outgroup and P3 were held constant, and all possible combinations of P2 and P1 were evaluated to produce the full set of trees for each analysis. Each test in a given analysis consisted of 1000 repetitions (where loci were resampled with replacement), which could be used to calculate the mean *D*-statistic and 95 % confidence interval. A positive *D*-statistic indicates excess allele sharing between P3 and P2 taxa (an 'ABBA' allelic pattern, where A = ancestral and B = derived), whereas a negative value indicates excess allele sharing between P3 and P1 (Durand *et al.*, 2011). We focused these analyses particularly on samples that showed mixed ancestry in the sNMF results, changed position across different tree inferences or were suspected of hybrid origin owing to morphology (following recommendations in how these tests should be performed and interpreted by Eaton *et al.*, 2015). Statistical significance was determined using z-scores calculated for each test, with $|z| > 3$ considered significant.

Trait evolution and correlation

In order to assign a life-history strategy to each species (annual or perennial), we used a combination of expert knowledge and descriptions from protologues and floras. To obtain geographical ranges and construct species climate envelopes, we downloaded and filtered occurrence data from the Global Biodiversity Information Facility (GBIF.Org, 2025); these occurrence points were used to extract 19 bioclimatic variables and elevation from WorldClim v.2 (Fick and Hijmans, 2017), which were then averaged for each species. The number of GBIF occurrence records per species ranged from 2 (*Philippiamra pachyphylla*) to 1354 (*Calyptridium monandrum*), with an average of 91.2 specimens per species. To estimate the elevational range for each species, we calculated the interquartile range (IQR), which ignores outliers; we used linear models to test whether mean elevation predicts elevational range within annual and perennial species separately, and whether the relationship differs between the two life-history strategies.

We trimmed the Cistantheae-wide phylogeny to include one sample per species. For instances where a species was nested within another, both taxa were kept for this analysis (effectively reflecting a sister relationship between those species). We did, however, opt to collapse the *Cistanthe longiscapa* complex, where there was no phylogenetic resolution among samples (see Results), to one tip (*Cistanthe longiscapa*; this includes individuals we had assigned morphologically to *Cistanthe litoralis* and *Cistanthe cymosa*). We time-calibrated the trimmed tree using secondary calibrations from Arakaki *et al.* (2011). This was done using the R package *phytools* v.2.6.5 (Revell, 2024), specifically the chronos() function, which uses penalized likelihood. We calibrated three nodes (the Montiaceae crown, the node where *Calandrinia* + *Lewisiopsis* and Cistantheae diverge, and the node where *Cistanthe paniculata* and the rest of *Cistanthe* sect. *Cistanthe* diverge) and estimated divergence times for all other nodes using ten discrete rate categories under a molecular clock (model = 'discrete') with a smoothing parameter (lambda = 0.1; Supplementary Data Fig. S2).

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We conducted a series of phylogenetic comparative analyses to test the correlation between life-history strategy and climate variation across Cistantheae. To explore the difference in climatic niche between annuals and perennials, we first conducted a principal components analysis using the PCA() function in the *FactoMineR* v.2.11 package (Lê *et al.*, 2008). To infer the ancestral states of life-history strategies, we used the ancr() function implemented in *phytools* (Revell, 2024). We fitted both the equal-rates (ER) and the all-rates-different (ARD; effectively an asymmetric model with a binary trait) models via the fitMk() function, and we estimated ancestral states as weighted averages (using an ANOVA-based model comparison) between the two models. For continuous climate variables and elevation, we used the fastAnc() function in *phytools* to reconstruct ancestral states under a Brownian motion model. Specifically for elevation, we visualized raw GBIF occurrence points using ridge plots with the R package ggridges (Wilke, 2024), retaining only the portion of each density curve above a minimum relative height of 0.01.

Finally, we calculated trait correlations between life history and each continuous climate variable using multiple approaches. First, we performed phylogenetic generalized least squares (PGLS) regression using pgls() from the *caper* v.1.0.3 R package (Orme *et al.*, 2023), treating life history as a binary predictor (0 = annual, 1 = perennial) and each climate or elevation variable as the response. To account for the independent comparisons of multiple traits, we applied a false-discovery rate correction (Benjamini and Hochberg, 1995) to the *P*-values. We also used PGLS to test whether elevational range differs significantly between annual and perennial species. Second, we used the phylolm() function from the *phylolm* package (Ho and Ane, 2014) to fit an Ornstein–Uhlenbeck (OU) model of trait evolution (model = 'OUfixedRoot'). For each trait, we compared the fits of the OU and Brownian motion models using the Akaike information criterion (AIC) and extracted the regression coefficients from the preferred model. Third, we used the threshold model implemented in the threshBayes() function in *phytools* (Revell, 2024) to model jointly the evolution of life-history liability and continuous climate variables under Brownian motion. The liability of a binary trait (in our case, life-history strategy) can be interpreted as the underlying/unobserved continuous values that determine whether a species is more likely to be an annual or perennial, given a threshold value (Felsenstein, 2005, 2012). We ran Markov chain Monte Carlo chains for 1 million generations, discarding the first 10 % as burn-in. Convergence was assessed by examining the posterior density plots and calculating the effective sample size (ESS). We used the posterior distributions to estimate the evolutionary correlation (posterior sample mean) between life history and a given climate variable (deemed significant if the 95 % highest posterior density interval excluded zero).

RESULTS

Phylogenetic inference of Cistantheae

The representative ddRAD phylogeny of the Cistantheae contained 108 specimens, which included 7 outgroup species and 48 Cistantheae species, which represent ~63 % of the described Cistantheae taxa. Of these, 10 are *Calyptridium*, 5 are *Philippiamra*, 14 are *Montiopsis*, and 17 are *Cistanthe*, in addition to the monotypic *Lenzia chamaepitys* and *Thingia ambigua*. The resulting Cistantheae ML phylogeny shows well-supported relationships among the major subclades (Fig. 2).

The topology places *Cistanthe* as sister to the rest of the clade, contrary to previous inferences, which placed *Cistanthe* and *Montiopsis* as sister lineages (Ogburn and Edwards, 2015). Instead, *Montiopsis* appears more closely related to the Calyptridinae Hershk. (which includes *Philippiamra*, *Lenzia*, *Thingia* and *Calyptridium*) than to *Cistanthe* (also inferred by Hancock *et al.*, 2018). The monotypic *Lenzia* is sister to the *Thingia* + *Calyptridium* clade, and *Philippiamra* the rest of Calyptridinae (Fig. 2). The only nodes along the backbone with <100 % UFBoot support are the split between *Lenzia* and the *Thingia* + *Calyptridium* clade (UFBoot = 97) and the split between *Thingia* and *Calyptridium* (UFBoot = 98). Because of the limitation to interpreting ultrafast bootstrap values on concatenated phylogenomic datasets, these two splits should be considered only weakly supported.

This tree also supports at least two long-distance, amphitropical dispersal events in Cistantheae (Fig. 2). The first occurs along the branch leading to the *Thingia* + *Calyptridium* clade, which is composed of North American species and is sister to the perennial, high-elevation Andean *Lenzia*, which, as stated before, are all sister to *Philippiamra*, a clade made entirely up of arid-adapted annuals. The second instance involves *Cistanthe maritima*, a North American desert species that is sister to the rest of *Cistanthe* sect. *Cistanthe*, which are all South American.

Subclade-level phylogenetic analyses

Subclade-level analyses provided greater resolution and support for certain species relationships across datasets and inference methods, in comparison to the broader Cistantheae-wide tree. Although some taxa were problematic, there was no consistent pattern that could explain differences in topology between datasets that exclude and include non-coding regions, or between concatenation and species-tree approaches.

Calyptridium. This clade is well sampled and includes 10 of 11 described taxa (minimum-rank). The relationships among the North American pussypaws (*Calyptridium*) are also mostly resolved. Across both the Cistantheae-wide and subclade-level phylogenies, the *Calyptridium umbellatum* complex (including perennial *Calyptridium umbellatum*, perennial *Calyptridium monospermum* and annual *Calyptridium pulchellum*; *sensu* Hinton, 1975; Guilliams, 2009) forms a clearly distinct, independently evolving lineage, while the remaining *Calyptridium* species (all annual) form a separate clade (Figs 2, 3A and 4A; Supplementary Data Figs S3 and S4).

We should note, however, that neither *Calyptridium umbellatum* nor *Calyptridium monospermum* is monophyletic in the more densely sampled subclade-level phylogenies. Furthermore, the relationships among the samples of these two species differ between the whole-genome-referenced and CDS-referenced trees (Figs 3A and 4A; Supplementary Data Figs S3 and S4). There is strong evidence of introgression between three of the *Calyptridium monospermum* samples

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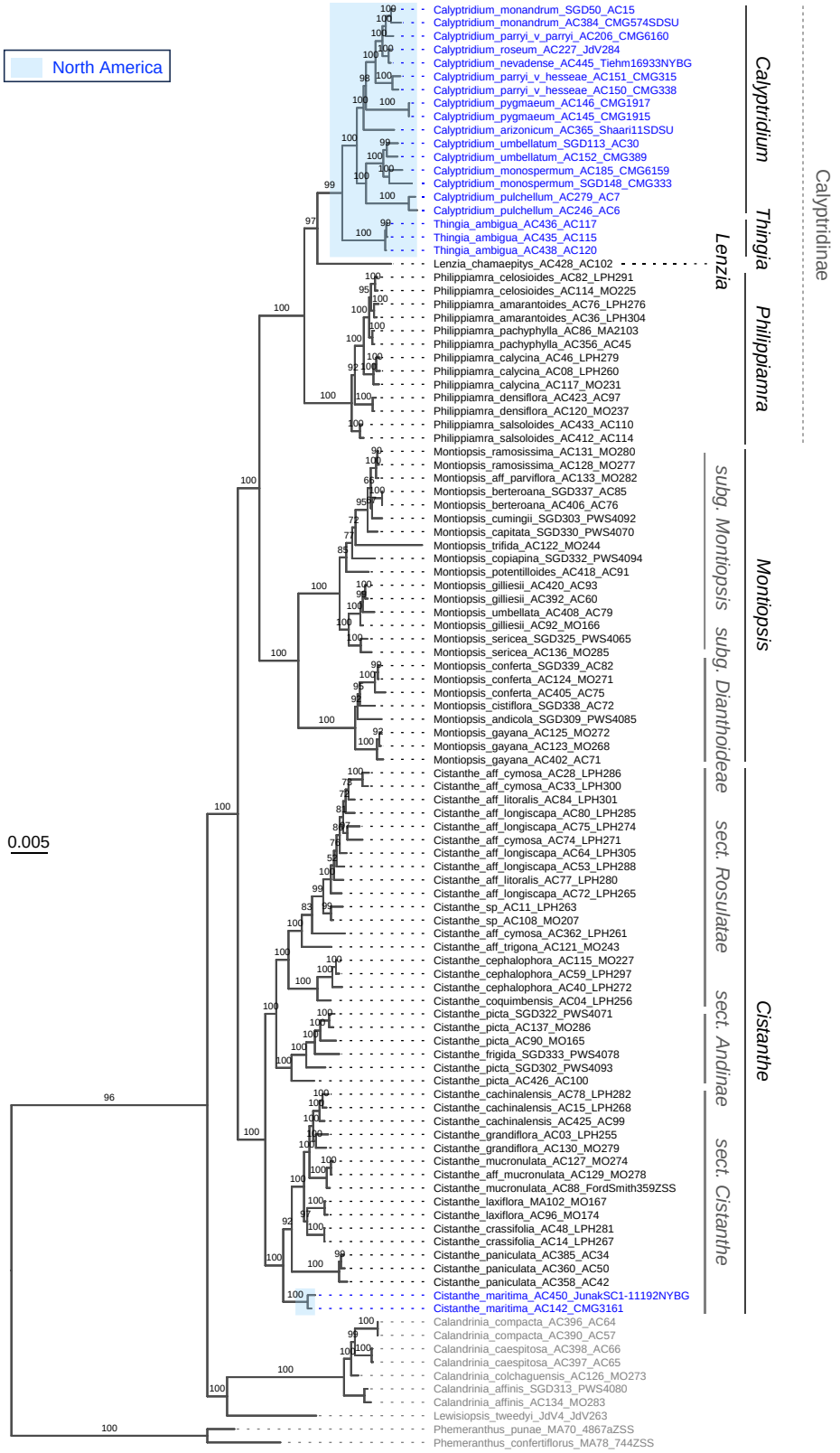

FIG. 2. Maximum-likelihood phylogeny of Cistantheae using coding-sequence-referenced ddRAD assembly. The subclades are annotated on the right. The tree was inferred using *IQ-TREE2* with 1000 ultrafast bootstraps (support values on branches) and includes 108 samples. Outgroup taxa are indicated by grey tip labels. In the ingroup, the North American clades are emphasized with blue tip labels and with a light blue highlight around the clades on the phylogeny. Otherwise, all the rest are Peruvian, Chilean and/or Argentinean taxa.

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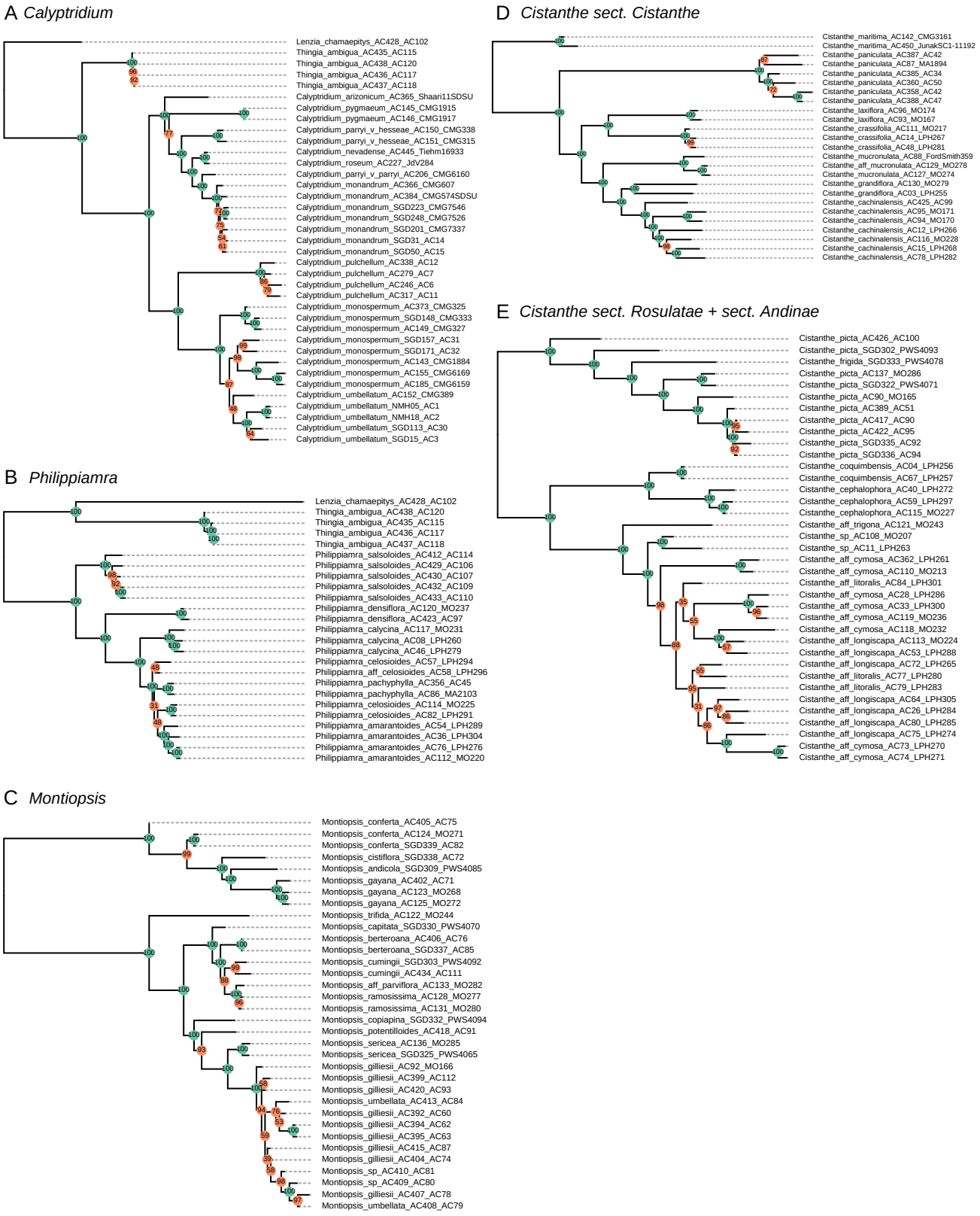

FIG. 3. Maximum-likelihood (ML) phylogenies using whole-genome-referenced ddRAD assemblies in *Calyptridium* (A), *Philippiamra* (B), *Montiopsis* (C), *Cistanthe* sect. *Cistanthe* (D) and *Cistanthe* sect. *Rosulatae* and sect. *Andinae* (E). The trees were inferred using *IQ-TREE2* with 1000 ultrafast bootstraps, with support values on nodes (support = 100 in green; support < 100 in orange). Subclade-level ML phylogenies using coding sequence-referenced ddRAD loci are available in the Supplementary Data S3.

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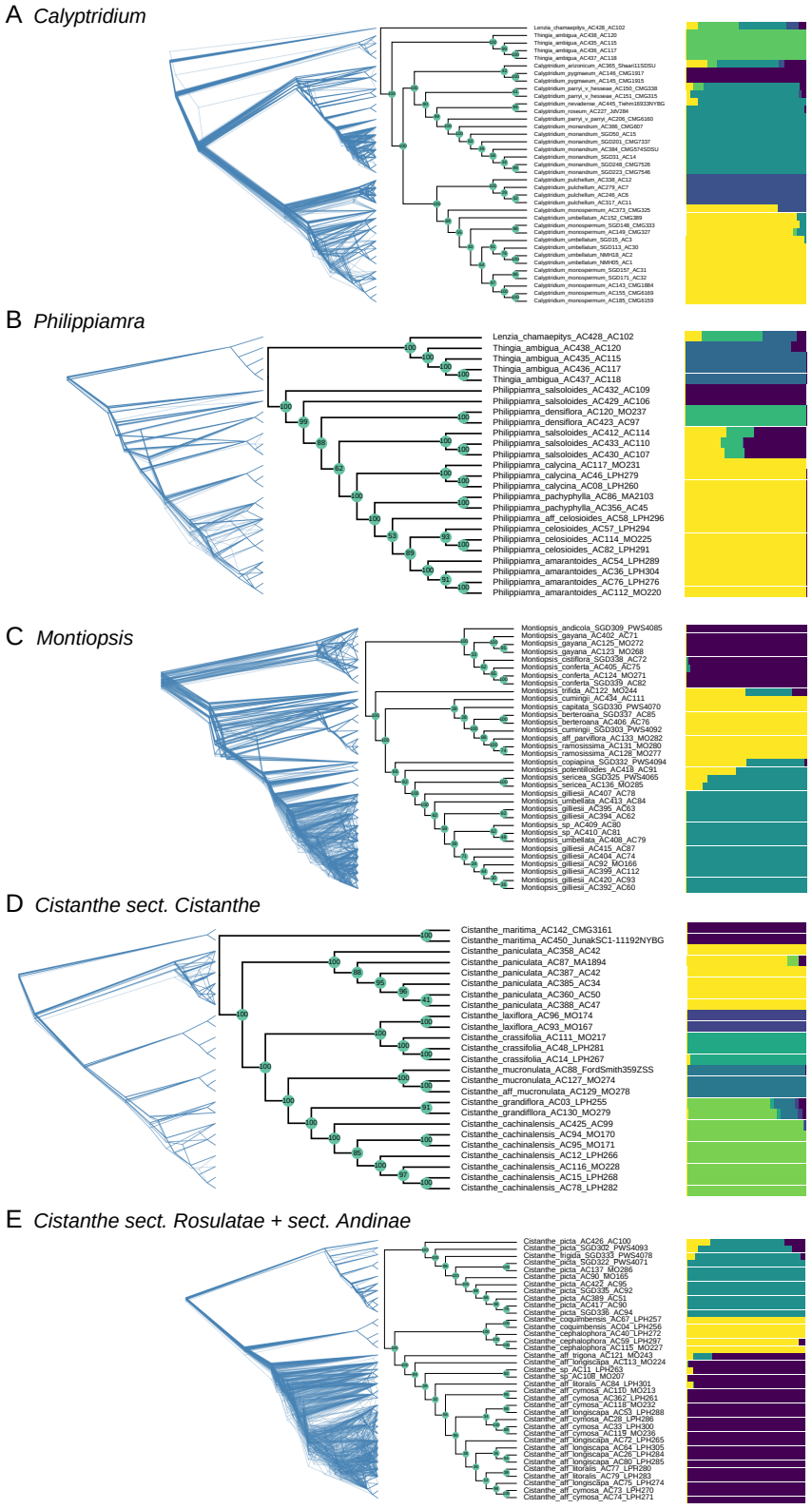

FIG. 4. Tetrad phylogenies (coalescent-based quartet trees) and genomic structure using whole- genome-referenced ddRAD assemblies in *Calyptridium* (A), *Philippiamra* (B), *Montiopsis* (C), *Cistanthe* sect. *Cistanthe* (D) and *Cistanthe* sect. *Rosulatae* and sect. *Andinae* (E). For each subclade panel, the leftmost tree shows a sample of 100 out of 1000 quartet-based bootstrap replicates, and the middle tree shows the consensus Tetrad phylogeny. The rightmost graph shows genetic clustering for each subclade, as inferred by ancestry coefficients estimated with sparse non-negative matrix factorization (sNMF). The colours represent the optimal number of genetic clusters (*K*) for each subclade (Supplementary Data Fig. S1). Each horizontal bar represents an individual sample (in the same order as the tips on the phylogenies), and the proportions within each bar correspond to the estimated ancestry coefficients. Same analyses using coding-sequence-referenced ddRAD assemblies for each subclade are available in the Supplementary Data S4.

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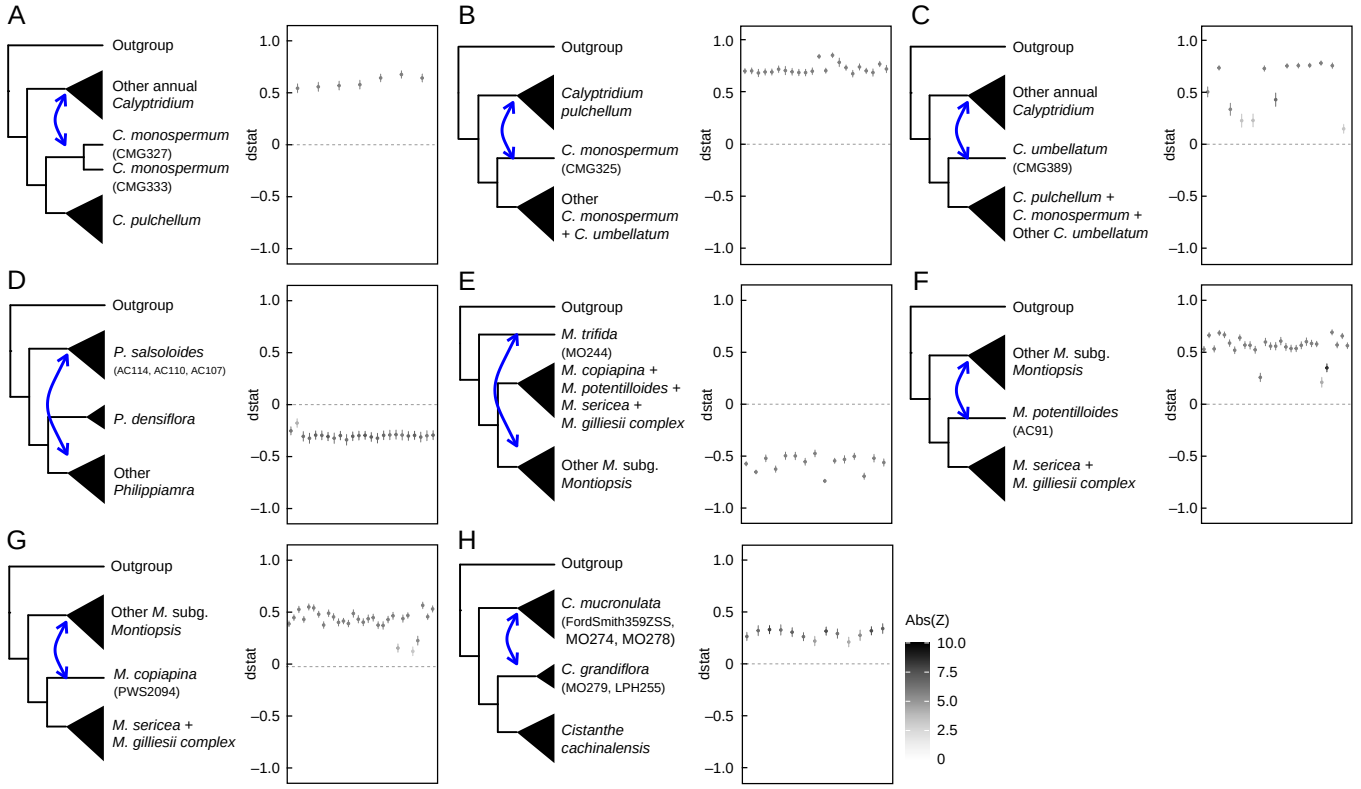

FIG. 5. Results from ABBA-BABA tests using the whole-genome reference loci. In each panel, the cladograms on the left indicate the test set-up; in Newick format, the test follows the topology (outgroup (P3 (P2, P1))), where tips can represent individual samples or clades. Each point in the graphs on the right side of the panels represents the mean *D*-statistic from 100 repetitions per test, with 95% confidence intervals shown. The test consists of every possible permutation of the P2 and P1 taxa. Positive *D*-statistics indicate excess allele sharing between the P3 and P2 taxa, whereas negative values indicate excess sharing between P3 and P1 (as indicated by the blue arrows on the cladograms). All *D*-statistic values shown here are statitistically significant ($|z| > 3$), and the colour intensity of each point corresponds to the magnitude of $|z|$. Shown are ABBA-BABA tests in *Calyptridium*, (A–C), *Philippiamra* (D), *Montiopsis* (E–G) and *Cistanthe* (H).

(CMG325, CMG327 and CMG333) and other *Calyptridium* species: specifically, CMG327/CMG333 with the other annual *Calyptridium* samples (Fig. 5A) and CMG325 with *Calyptridium pulchellum* (Fig. 5B). CMG325 is particularly noteworthy, because the sample represents a herbarium specimen collected from a *Calyptridium monospermum* population found outside of its typical range. In the CDS-referenced ML tree and both Tetrad trees, one *Calyptridium umbellatum* sample (CMG389) falls outside of the otherwise monophyletic *Calyptridium umbellatum* samples. CMG389 also shows evidence of introgression with the annual *Calyptridium* species (Fig. 5C).

Within the annual *Calyptridium* clade, all minimum-rank taxa are monophyletic, except for *Calyptridium parryi*; however, it is worth noting that several of these annual species are currently represented by only a single sample (Figs 3A and 4A). The non-monophyly of the previously described *Calyptridium parryi* varieties is consistent with results from a previous five-gene phylogeny (Guilliams, 2009). These consistent results support the relatively new combination of *Calyptridium hesseae* (J.T. Thomas) Hershk. and *Calyptridium nevadense* (J.T. Thomas) Hershk. as their own separate species instead of being varieties of *Calyptridium parryi* (Hershkovitz, 2019), although this conclusion would be strengthened with the inclusion of additional samples for each variety. Most importantly, our trees support the conclusions of Simpson *et al.* (2010), which established *Calyptridium arizonicum* as its own species based on morphological differences from *Calyptridium parryi* and other previous varieties. Relationships among these species in the clade are inconsistent with earlier works; specifically, in the studies by both Guilliams (2009) and Ogburn and Edwards (2015), *Calyptridium pygmaeum* and *Calyptridium roseum* are sister taxa. Nevertheless, the phylogenies presented here boast mostly strong support for each split (Figs 2, 3A and 4A; Supplementary Data Figs S3 and S4).

Philippiamra. This clade is well sampled and includes five of seven described species. The phylogenetic relationships among the extremely arid-adapted annuals in *Philippiamra* are relatively straightforward, with little to no incongruence between the full Cistantheae tree (Fig. 2) and the subclade-level trees (Figs 3B and 4B; Supplementary Data Figs S3 and S4). The species relationships are generally well supported and morphologically recognizable. Notably, the Chilean *Philippiamra celosioides* is more closely related to the Chilean *Philippiamra amarantoides* than it is to the Peruvian *P. pachyphylla*, despite past taxonomic treatments that synonymized *P. pachyphylla* with *P. celosioides* (Govaerts *et al.*, 2021).

In the subclade-level analysis, we had two additional samples of *P. celosioides* (LPH294 and LPH296). LPH294, a morphologically distinct and sterile sample, formed a monophyletic

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group with the other two *P. celosioides* samples in the genome-referenced Tetrad tree (Fig. 4B), in addition to the CDS-referenced ML (Supplementary Data Fig. S3) and Tetrad trees (Supplementary Data Fig. S4); LPH296, in contrast, was outside of this three-sample clade. In the genome-referenced ML tree (Supplementary Data Fig. S5B), however, LPH294 and LPH296 were sister to each other and not monophyletic with the other *P. celosioides* samples. The behaviour of LPH296 could be attributable to introgressive gene flow or admixture, for which we found a strong signal with *P. calycina* (Fig. 5D). All of the *P. celosioides* samples do belong in a strongly supported monophyletic group with *P. pachyphylla* and *P. amarantoides* samples; a pattern that was recovered across datasets and inference methods (Figs 3B and 4B; Supplementary Data Figs S3 and S4). However, the support values for the relationship between these species were low across trees. In all, the monophyly of *P. pachyphylla* and *P. celosioides* remain questionable, especially given that *P. amarantoides* appears nested within this group with strong support. Finally, there is some discordance in the two Tetrad trees (Fig. 4; Supplementary Data Fig. S4) where *P. salsoloides* samples are not monophyletic, probably owing to shared derived alleles (via introgression) between three specific *P. salsoloides* samples (AC412, AC433 and AC430) and the *P. calycina*/*P. pachyphylla*/*P. celosioides*/*P. amarantoides* clade (Fig. 5D).

Montiopsis. This clade is well sampled and includes 14 of 19 described species. *Montiopsis* species, many of which occur at higher elevations than most other Cistantheae species, clearly fall into two clades considered as two subgenera: *Montiopsis* subg. *Dianthoideae* and *Montiopsis* subg. *Montiopsis* (Ford, 1992). The former consists of only perennial species, whereas the latter includes both annuals and perennials. Across the different phylogenies, support for species relationships within each of the two clades ranges from strong to weak (Figs 2, 3C and 4C; Supplementary Data Figs S3 and S4). However, sampling remains limited in some of these species, several of which are represented by only one sample.

In the full Cistantheae tree, *Montiopsis gayana* is sister to the rest of the species in subg. *Dianthoideae*, although the relationships among the three remaining species are weakly supported (Fig. 2). In contrast, the subclade-level ML trees show a well-supported topology: *M. gayana* is instead sister to *Montiopsis andicola*, which are together sister to *Montiopsis cistiflora*, which are all nested within a non-monophyletic *Montiopsis conferta* (Fig. 3C; Supplementary Data Fig. S3). Furthermore, there was no evidence of introgression among these samples, suggesting that the observed incongruences are likely to stem from incomplete lineage sorting across the subclade (Goulet *et al.*, 2017). Morphologically, species in subg. *Dianthoideae* have tricolpate pollen, whereas the species in subg. *Montiopsis* have pantoporate pollen, complex barbellate trichomes and three-toothed sepals (Ford, 1992; Peralta and Molina, 2021).

In contrast, there is much less resolution among species in subg. *Montiopsis*, particularly in the Cistantheae-wide tree (Fig. 2). Nonetheless, the sister relationship between the perennial *Montiopsis sericea* and the perennial *Montiopsis gilliesii* complex is well supported. We found that *Montiopsis umbellata* samples were non-monophyletic and instead nested among *M. gilliesii* samples, leading us to treat this as a species complex. This complex includes *Montiopsis* sp. AC410 and AC409, which we suspected were hybrids of *M. gilliesii* and *M. umbellata* in the field based on their morphology. Removing these 'hybrid' samples did not change the non-monophyly of *M. gilliesii* and *M. umbellata*. The two other perennial species, *Montiopsis potentilloides* and *Montiopsis copiapina*, subtend the annuals in subg. *Montiopsis* with minimal support. There is low support for species relationships among the annuals in the Cistantheae-wide tree (Fig. 2). Moreover, *M. potentilloides*, *M. copiapina* and *Montiopsis trifida* exhibit mixed ancestry across genetic clusters (Fig. 4C) and might have experienced recent introgressive gene flow (Fig. 5E–G).

The relationships within subg. *Montiopsis* are better resolved in the CDS-referenced subclade tree (Supplementary Data Fig. S5), which is largely consistent with the Cistantheae-wide tree topology, with the exception of the strongly supported sister relationship between *M. trifida* and *M. capitata*. However, the topology shifts considerably in the genome-sequence-referenced subclade tree, where *M. trifida* is inferred as sister to the rest of subg. *Montiopsis* species, and where *M. potentilloides* and *M. copiapina* are sister to the other perennials (*M. sericeae* and the *M. gilliesii* complex; Fig. 3C). Together, the evidence of mixed ancestry and topological discordance point to a complex evolutionary history that has probably shaped the diversification of subg. *Montiopsis*.

Cistanthe. *Cistanthe* is the most species-rich clade in Cistantheae and also the group in most need of taxonomic work. We sampled only 17 of 37 described species. In the Cistantheae-wide phylogeny, *Cistanthe* species form three subclades: one with species that have mostly been assigned to *Cistanthe* sect. *Cistanthe* Reiche (with the exception of *Cistanthe maritima*), one with perennials in *Cistanthe* sect. *Andinae* Reiche, and one with desert annuals included in *Cistanthe* sect. *Rosulatae* Hershk. (Hershkovitz, 2019). We inferred *Cistanthe maritima*, a North American species, as sister to the rest of *Cistanthe* sect. *Cistanthe* (composed entirely of South American species) with strong support. Within the South American clade, *Cistanthe paniculata* (a Peruvian species) is sister to the rest; a relationship that has weak support in the Cistantheae-wide tree (Fig. 2) but strong support in the subclade-level trees (Figs 3D and 4D; Supplementary Data Figs S3 and S4). This is consistent with previous inferences by Smith *et al.* (2018) and Hancock *et al.* (2018). Moreover, the inferred sister-species relationship between *Cistanthe crassifolia* and *Cistanthe laxiflora* has strong support in the subclade-level trees (Fig. 3D and 4D; Supplementary Data Figs S3 and S4). The relationships among the remaining *Cistanthe* sect. *Cistanthe* species are strongly supported in both the broader (Fig. 2) and subclade-level phylogenies (Figs 3D and 4D; Supplementary Data Figs S3 and S4). All the species in this subclade are perennial except for two: *Cistanthe maritima*, subtending the rest of sect. *Cistanthe*, and *Cistanthe cachinalensis*, nested well within the group. Additionally, we found evidence of introgressive gene flow between *Cistanthe mucronulata* and *Cistanthe grandiflora* (Fig. 5H).

In contrast, the phylogenetic inference in the rest of *Cistanthe* is far less straightforward. *Cistanthe* sect. *Andinae*, which is

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represented by the high-elevation perennial species *Cistanthe picta* and *Cistanthe frigida* in this phylogeny, is sister to the rest of the desert annuals, with 100 % UFBoot support in the Cistantheae-wide tree (Fig. 2). Furthermore, *Cistanthe frigida* (a species found at some of the highest elevations within the Cistantheae) is nested within *Cistanthe picta*. Notably, our *Cistanthe picta* sampling straddles the Chile–Argentina border, on either slope of the western Cordillera of the Andes. In all the subclade-level trees (Fig. 3E and 4E; Supplementary Data Figs S3 and S4), the Chilean *Cistanthe picta* samples form a gradient (including *Cistanthe frigida*) before the monophyly of the Argentinian *Cistanthe picta* samples (MO165, AC51, AC90, AC95, AC92 and AC94), suggesting some geographical structure to the topology.

After the divergence of the *Cistanthe picta* clade, a well-supported clade of *Cistanthe coquimbensis* and *Cistanthe cephalophora* is inferred as sister to the rest of *Cistanthe* sect. *Rosulate* (across all the phylogenies; Figs 2, 3E and 4E; Supplementary Data Figs S3 and S4). This clade corresponds to the taxonomic group 'subsect. *Thyrsoideae*' from Hershkovitz (2019). The rest of sect. *Rosulate* is poorly resolved, and we will refer to it here as the '*Cistanthe longiscapa* complex'. All the specimens in this clade are united by conspicuous shiny petals, although within the clade no morphologically delineated species appear to be monophyletic. *Cistanthe longiscapa* is the iconic species known for painting the Atacama Desert magenta pink during 'superblooms'.

In the *Cistanthe longiscapa* complex, *Cistanthe* aff. *trigona* (MO243) is consistently inferred as sister to the rest of the samples in the group, which forms a comb-like topology in the Cistantheae-wide tree (Fig. 2). Nonetheless, the subclade-level tree from CDS-referenced loci shows stronger support and some emerging patterns (Supplementary Data Figs S3 and S4). Two *Cistanthe* sp. samples (MO207 and LPH263) resemble the vegetative morphology of *Cistanthe arenaria* (but are clearly annuals with smooth seeds) and diverge from the rest of the complex with strong support. Although they were collected many years apart and by different collectors, they are geographically close and might represent two individuals of the same population. Within the remainder of the complex, we then see a split between two subgroups. Both of the subgroups include samples with *Cistanthe cymosa*-like inflorescence morphology and samples with *Cistanthe longiscapa*-like traits (Supplementary Data Fig. S5). According to previous descriptions, *Cistanthe* aff. *cymosa* samples (as defined by the inflorescence morphology) should have smooth seeds, whereas *Cistanthe* aff. *longiscapa* samples should have pusticulate-tomentose seed morphology (Kelley, 1973). However, we found both morphotypes with both seed types. There are *Cistanthe* aff. *cymosa* and *Cistanthe* aff. *longiscapa* samples with smooth seeds (the latter, therefore, might be referred to more appropriately as *Cistanthe* aff. *litoralis*; Hershkovitz, 2022*a*, *b*) and *Cistanthe* aff. *cymosa* and *Cistanthe* aff. *longiscapa* samples with pusticulate-tomentose seeds (Supplementary Data Fig. S5). One sample, LPH305, even exhibited hairy seeds reminiscent of *Cistanthe cachinalensis*. The overall topology of the complex is broadly similar in the genome-referenced tree at the subclade level, although the support values are starkly lower (Figs 3E and 4E). An interactive map of the specimens in the sect. *Rosulatae* tree alongside the genome-referenced Tetrad phylogeny demonstrates the relationship of specimen clustering and geography: https://camayal.info/wa/treetom/?id=5Z1rykPR29ChQAG8QzSj (via TreeTOM; Maya-Lastra, 2020). The distribution of the samples does not suggest that different morphologies in the complex could be explained by geography; for example, *Cistanthe* aff. *litoralis* localities span Parque Nacional Llanos de Challe to the city of Taltal, with various *Cistanthe* aff. *longiscapa* and *Cistanthe* aff. *cymosa* specimens found in between. Geography does explain many of the phylogenetic groupings and sister relationships between specimens but cannot completely explain them either; for example, *Cistanthe* aff. *cymosa* MO213 and LPH261 are from different sites.

Evolutionary correlation between life history and environmental variables

We found that life history is evolutionarily labile across the Cistantheae (Fig. 6A). Ancestral state reconstruction using the ancr() function from *phytools* suggests that the ancestral life history state is ambiguous, although a perennial ancestor has a higher marginal probability. However, this result might be biased by the fact that all the sampled outgroup taxa in the tree happen to be perennial. Using a threshold model to estimate the liability across ancestral nodes yielded a similar result; the estimated liability of the Cistantheae ancestor was close to zero (i.e. near the threshold). This suggests uncertainty in the ancestral life-history state, although with a slight preference for perenniality based on the posterior distribution. Assuming a perennial ancestor, annuality appears to have evolved independently at least five times within the clade. We also infer two subsequent shifts from annual to perennial: once along the *Lenzia* branch, and again in the lineage leading to *Calyptridium umbellatum* and *Calyptridium monospermum*.

We also found bioclimatic variables to be fairly labile across the phylogeny (Supplementary Data Fig. S6). A principal components analysis of climate values (averaged per species) showed moderate separation between annuals and perennials, albeit with some overlap (Supplementary Data Fig. S7). Patterns of trait correlations between these climate variables and life history were largely consistent with our expectations: across the phylogeny, perennials are associated with colder, wetter and higher-elevation environments, whereas annuals tend to occupy hotter, drier and lower-elevation habitats (Table 1; Fig. 6A, B; Supplementary Data Fig. S7). Furthermore, there was no significant difference in elevation IQR between life-history strategies (Fig. 6C). However, a linear regression of mean elevation versus elevation IQR showed a significant positive relationship in annuals ($P = 0.0011$), with no corresponding trend in perennials (Fig. 6C); these two slopes were significantly different ($P = 0.0077$). Moreover, the number of specimens per species is not a significant predictor of elevation IQR ($P = 0.879$), indicating that sampling effort does not bias our estimates of elevational range. Across all traits, OU models consistently fit the data better than Brownian motion models, based on ΔAIC values from *phylolm* (Table 1).

Specific temperature-related variables were significantly and strongly correlated with life-history strategy across the phylogeny. Based on PGLS (using the pgls function in *caper*) and phylogenetic linear models assuming an OU process (*phylolm*, model = 'OUfixedRoot'), the strongest signals were found among Bio11 (mean temperature of coldest quarter), Bio1

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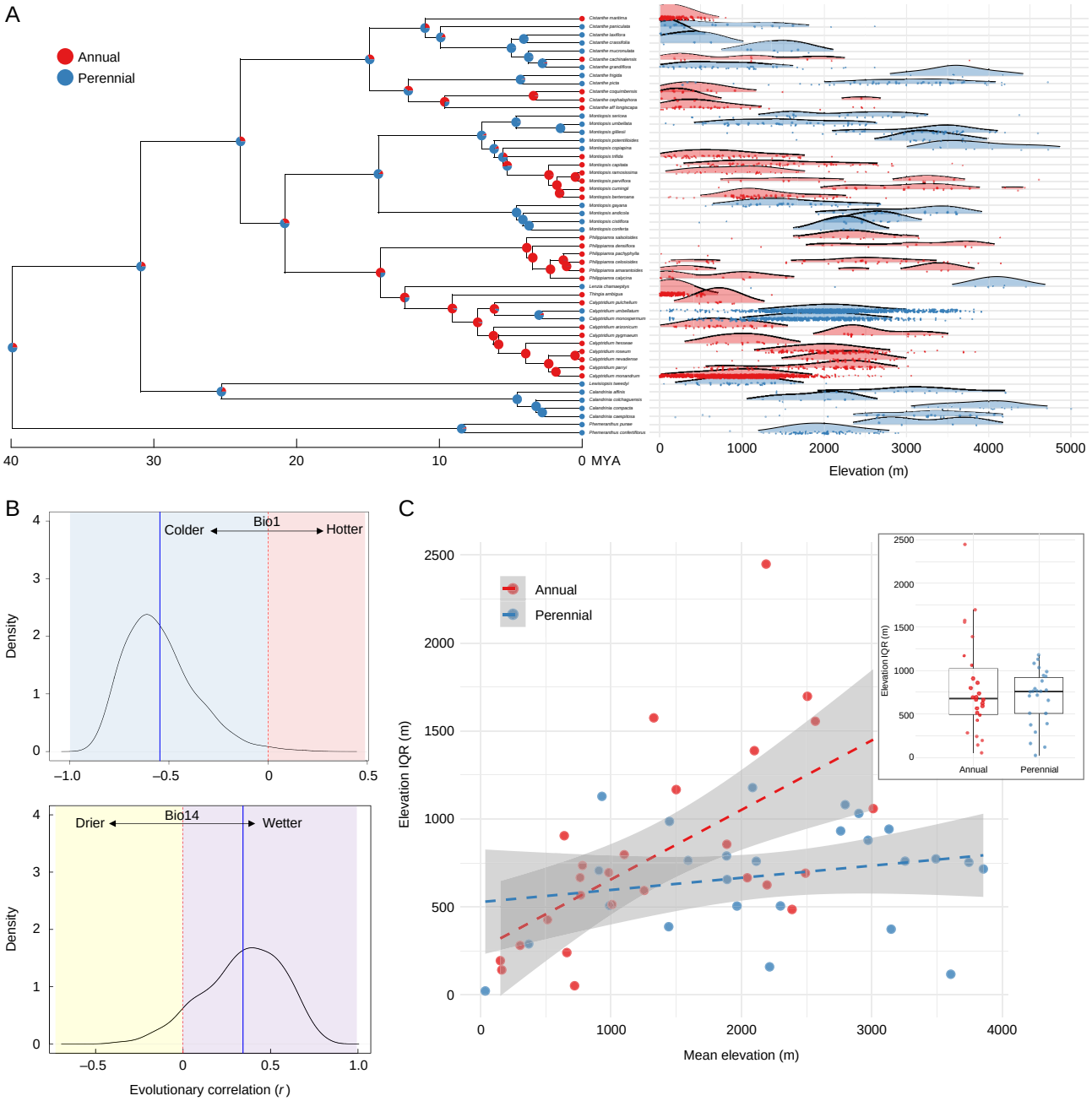

FIG. 6. Life history and climatic niche evolution across Cistantheae. (A) Ancestral state reconstructions of life-history strategy and corresponding species-level elevation distributions. The phylogeny shown (left) is time calibrated and trimmed to one sample per species (see Supplementary Data Fig S2). Tip colours indicate life-history strategy: red for annual species and blue for perennials. Pie charts at internal nodes represent the inferred likelihood of each ancestral state (annual vs. perennial), following the same colour scheme. Elevation ridge plots (right) use the same colour scheme, with each point representing an occurrence record from cleaned Global Biodiversity Information Facility (2025) data. Density curves were visualized with the minimum relative height of 0.01. (B) Posterior density distributions of evolutionary correlations (r) between life history and two climate variables: Bio1 (mean annual temperature, top panel) and Bio14 (precipitation of driest month, bottom panel). Vertical red dashed lines denote $r = 0$; solid blue lines denote the posterior mean. Positive correlations indicate that perennials tend to occur in colder (Bio1) and wetter (Bio14) environments. (C) Linear regression of mean elevation versus elevation IQR by life-history strategy. Each point represents a species; red and blue points represent annuals and perennials, respectively. A significantly positive relationship in annuals indicates that annual species with higher mean elevations tend to have broader elevational ranges ($P = 0.0011$). This slope differs significantly from the perennial slope ($P = 0.0077$). The boxplot inset (top right) comparing IQR between annuals and perennials shows no statistically significant differences in elevational range between life-history strategies.

(mean annual temperature), Bio6 (minimum temperature of coldest month) and Bio10 (mean temperature of warmest quarter). Large negative regression coefficients were consistently recovered across both analyses (Table 1; Supplementary Data Table S1). For example, Bio11 (in degrees Celsius × 100) had a coefficient of −61.26 ($P = 0.0008$) based on the PGLS analysis, and a coefficient of −63.91 ($P = 0.0002$) in the OU phylogenetic linear model (Table 1). Such regression-based results

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TABLE 1. Phylogenetic correlations between environmental variables and life history in the Cistantheae.

Variable	Description	PGLS coefficient	PGLS adjusted *P*-value	Phylolm coefficient (OU)	Phylolm adjusted *P*-value	threshBayes mean correlation (95 % CI)	threshBayes ESS
Bio_1	Mean annual temperature	−57.28	0.0008	−59.24	0.0009	−0.546 (−0.810, −0.139)	307.0
Bio_{11}	Mean temperature of coldest quarter	−61.26	0.0008	−63.91	0.0009	−0.569 (−0.825, −0.135)	160.7
Bio_{12}	Annual precipitation	+242.6	0.0142	+229.9	0.0197	+0.313 (−0.092, +0.662)	80.96
Bio_{13}	Precipitation of wettest month	+46.97	0.0062	+46.81	0.0071	+0.355 (−0.148, +0.757)	124.4
Bio_{14}	Precipitation of driest month	+5.329	0.0062	+5.691	0.0030	+0.363 (−0.123, +0.738)	169.4
Elevation	–	+938.8	0.0062	+854.4	0.0037	–	–

Abbreviations: CI, credible interval; ESS, effective sample size; OU, Ornstein–Uhlenbeck; PGLS, phylogenetic generalized least squares; Phylolm, phylogenetic linear models.

were also supported by Bayesian threshold model analyses using threshBayes from *phytools*. The estimated posterior mean correlations were also consistent with the direction of regression coefficients from PGLS and phylolm analyses (Table 1). For example, Bio1 had a posterior mean evolutionary correlation coefficient of −0.546 (95 % credible interval between −0.810 and −0.139) with an ESS of 307.8, which confirms convergence (Fig. 6B). Taken together, these analyses suggest that perennials were more associated with lower temperatures across the tree.

Precipitation-related variables were also correlated with life-history strategy across the tree, although the associations were generally weaker. For example, Bio12 (annual precipitation; measured in millimetres), Bio13 (precipitation of wettest month) and Bio14 (precipitation of driest month) were positively correlated with perenniality in the PGLS analyses (Bio12 coefficient = +242.6, $P = 0.00922$; Bio13 coefficient = +46.97, $P = 0.00277$; Bio14 coefficient = +5.329, $P = 0.00261$; Table 1), suggesting that perennials tend to occur in wetter environments. These results were consistent in both direction and magnitude with results from OU phylogenetic linear models (Table 1). The threshBayes analyses showed similar directional trends in the correlation coefficient, supporting the association of wetter habitats with perenniality. However, for these precipitation-related variables, such as Bio 14 (ESS = 420.9; Fig. 6B), the 95 % credible intervals included zero, which means that the correlation coefficients were not statistically significant even if the directionalities were consistent (Supplementary Data Fig. S8). Elevation also showed a moderate positive correlation with life history across the tree (PGLS coefficient = +911, $P = 0.0018$; phylolm coefficient = +876, $P = 0.0015$), suggesting that perennials tend to occupy higher elevations than annuals.

DISCUSSION

In many ways, the Cistantheae represent much of the ecological and morphological diversity that is found in the Montiaceae more broadly. Ecologically, many of these species have an affinity to montane and high-elevation environments, whereas other xeric species will flower synchronously in the Atacama 'superblooms' to paint the desert magenta pink (Chávez *et al.*, 2019). Physiologically, both perennial and annual *Cistanthe* species in the clade can upregulate CAM photosynthesis facultatively, which is an adaptation to drought that confers increased water-use efficiency, when subjected to drought conditions (Holtum *et al.*, 2021; Chomentowska *et al.*, 2025). Cistantheae species also present a gradient of leaf succulence (Ogburn and Edwards, 2013), a trait that is related to the expression of CAM (Gilman *et al.*, 2024). Biogeographically, we found at least two independent long-distance dispersal events in the Cistantheae, which are both examples of an American amphitropical disjunct dispersal pattern; this adds to the 237 American amphitropical disjunct divergence events that fit this amphitropic pattern of distribution found so far in vascular plants (Simpson *et al.*, 2017).

Phylogenetic analyses of Cistantheae

Overall, our efforts have clarified the backbone of Cistantheae, providing strong support for the major clades and relationships between them (Fig. 2). There has been substantial taxonomic work in this group over the last 50 years, including Kelley (1973); Carolin (1987, 1993); Hershkovitz (1990*a*, *b*, 1991, *1993a*, *b*, 2018, 2019); Peralta (1993, 1999); Ford (1992); Ford-Werntz and Peralta (2002); Peralta and Ford-Werntz (2008); Guilliams (2009); Simpson *et al.* (2010); Guilliams and Miller (2014); and Peralta and Molina (2021). These studies are good progress from the treatments of the late 1800s (Hooker and Arnott, 1833; Barnéoud, 1847; Philippi, 1860, 1867, 1893; Howell, 1893; Reiche, 1897, 1898), but they were largely undertaken without a strongly supported molecular phylogeny.

The overall topology of the Cistantheae phylogeny highlights *Montiopsis* as a particularly interesting clade. In the study by Ogburn and Edwards (2015), *Montiopsis* was inferred as sister to *Cistanthe* (based on five markers). Hancock *et al.* (2018), in contrast, inferred different relationships depending on marker sampling: *Montiopsis* was sister to *Cistanthe* in the 115-loci tree, whereas *Montiopsis* was sister to Calyptridinae in the 297-loci tree. Our phylogeny infers the latter relationship (Fig. 2). These topological differences might reflect conflicting

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evolutionary histories among different genes or ancient introgression at the origin of *Montiopsis*. Furthermore, our phylogeny places *Lenzia* sister to *Thingia* + *Calyptridium*, all of which are then most closely related to *Philippiamra*, which matched our expectations (Fig. 2). However, this topology should be confirmed in future work, specifically because the support is low in the node that unites *Lenzia* with the *Thingia* + *Calyptridium* clade.

Within each of these clades, the relationships between recognized taxonomic groups were also clarified. By and large, the taxonomic assignments of species were supported by the phylogeny (making up subclades), and the relationships between these subclades were also generally well supported. For example, *Montiopsis* consists of subclades that correspond to subgenera *Montiopsis* and subgenera *Dianthoideae*; *Cistanthe* includes sections *Cistanthe*, *Rosulatae* and *Andinae*, with the latter two subclades as sister (Fig. 2). However, within each of these subclades there is persistent uncertainty about many species relationships and species delineation, highlighting the need for further investigation.

Cistanthe longiscapa *complex and evolution in the desert*

Although a taxonomic revision of the *Cistanthe longiscapa* complex is clearly needed, defining species boundaries might prove difficult in these types of complexes with potentially rampant gene flow, incomplete lineage sorting (Fig. 4E) and phenotypic plasticity. Our results also suggest that the vegetative, inflorescence and seed morphology characters often used to distinguish species in this complex might not be reliable taxonomic indicators.

Moreover, the complexity of phenology in the Atacama Desert must be taken into account when considering the evolution of this clade. The desert species, particularly those in the *Cistanthe longiscapa* complex, are often associated with 'superblooms' during El Niño years, which are characterized by above-average precipitation. Although this association is generally true, these species can also flower in drier years, although germination and growth are patchy across the landscape. Even in years with substantial rainfall, blooms can remain patchy and unpredictable; the same site may be completely barren in one El Niño year despite having been in full bloom during another, while a field nearby may show the opposite pattern. What are the consequences of such patchiness and episodic reproduction on the rate of evolution and patterns of gene flow? Although no single model currently captures all the interacting forces that shape diversification in desert plants, there are relevant empirical studies that relate to individual components. For example, Falahati-Anbaran *et al.* (2014) found that gene flow through time (i.e. many generations of seeds germinating simultaneously) can counteract genetic variability introduced to a population via dispersal from another population in *Arabidopsis thaliana*.

It appears that in the *Cistanthe longiscapa* complex, putative species can easily reproduce with each other, and interspecific gene flow is rampant, which further muddies morphological differentiation (and taxonomic resolution). With the addition of the temporal and geographical separation of flowering and stochastic gene flow between populations, the complex has not sorted into independently evolving lineages that we can easily define as species. What might be more helpful in understanding how evolution works in this group is a population-level view into how SNPs, geography, phenology and morphology interact. Assigning species to organize or categorize diversity between populations is useful (Levin, 1979), but it also might not be appropriate in certain population biology settings, especially in plants (Raven, 1976). Although we aim eventually to sample all described species in *Cistanthe*, we predict that many will fall into the *Cistanthe longiscapa* complex and warrant a careful taxonomic revision.

Future work in the Calyptridium umbellatum *complex*

Another area for future work lies in the underexplored diversity of the *Calyptridium umbellatum* complex, particularly in the perennial species. In the subclade-level analyses with all the voucher specimens that were available, the perennial *Calyptridium umbellatum* is nested within *Calyptridium monospermum* (the other perennial in *Calyptridium*). Although the two species overlap in range, *Calyptridium umbellatum* also occurs at higher latitudes. We might find genetic or morphological differentiation that corresponds to appropriate species boundaries within the current circumscriptions of *Calyptridium monospermum* or the wider *Calyptridium umbellatum* complex; more so if we collect from populations at higher latitude, where we were unable to sample for this study. It might be worthwhile to revisit the varietal designations in the *Calyptridium umbellatum* complex from Hinton (1975) based on morphology. Additionally, applying multispecies coalescent models (Jackson *et al.*, 2017; Leaché *et al.*, 2019) might be helpful for species delimitation in this complex.

Implications of current gaps in taxon sampling

As previously discussed, our phylogeny includes only a single sample of *Lenzia*, and its placement remains uncertain. Although we recovered the relationship where *Lenzia* is sister to the *Thingia* + *Calyptridium* clade, support for this node is low, and its long branch might be driving spurious relationships via long-branch attraction. A denser sampling of *Lenzia* (although they are rare plants, with a small geographical range in high-elevation Andes, making it a hard species to collect) and the use of whole-genome sequencing might help to clarify its phylogenetic position. It is also imperative to include *Hectorella* and *Lyallia*, two monospecific taxa currently not classified in the Cistantheae (but rather as Hectorelleae Appleq., Nepokr. & W.L. Wagner; Hershkovitz, 2019) but with some morphological similarity to *Lenzia* with wildly disjunct distributions in the Kerguelen Islands and New Zealand, respectively. It is possible that *Lenzia* is sister to the rest of Calyptridinae (as inferred by previous studies by only a handful of markers and with weak support; Hershkovitz, 2006; Ogburn and Edwards, 2015).

In addition, several other key taxa remain unsampled in our present phylogeny. For example, the North American *Cistanthe guadalupensis* was excluded owing to poor DNA extraction quality. This species is most likely to be sister to *Cistanthe maritima* (*Cistanthe guadalupensis* has been shown or hypothesized to be sister to species in *Cistanthe* sect. *Cistanthe*; Applequist and Wallace, 2001; Hershkovitz, 2019), although we cannot currently rule out the possibility of yet another independent amphitropical dispersal event. Otherwise,

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the species relationships within the rest of *Cistanthe* sect. *Cistanthe* (to which, we found, *Cistanthe maritima* is sister) are well resolved and strongly supported. In *Cistanthe* sect. *Rosulate*, however, we are missing notable perennials, such as *Cistanthe arenaria* and *Cistanthe fenzlii*, which are likely to be close relatives of the annual *Cistanthe longiscapa* complex (Hershkovitz, 2022*b*). Including these taxa might reveal an additional transition between annual and perennial life-history strategies. Lastly, there are several described species in the *Cistanthe longiscapa* complex that were not included in our analyses; future work will determine whether these additional morphological varieties are embedded within the complex or represent independently evolving lineages (*sensu* De Queiroz, 2007).

Double-digest RAD sequencing: its advantages and limitations

Double-digest RAD sequencing (ddRADSeq) has remained popular over the past decade for good reason: it is a cost-effective method of generating many non-random genomic fragments across many individuals (Peterson *et al.*, 2012). One of the strengths of ddRADSeq is its sequencing depth-to-cost ratio, allowing application at both phylogenomic and population-genomic scales (e.g. Lavretsky *et al.*, 2021; Psonis *et al.*, 2021; Anghel *et al.*, 2025). However, our study also encountered the limitations of ddRADSeq for phylogenetic inference. As with many reduced-representation approaches, missing data were substantial, and very few loci were supporting certain splits. Rodewald *et al.* (2025) additionally found that fewer loci are shared with increasing phylogenetic distance, which contributes to deeper splits having a limited number of loci that underlie them. Such ddRAD loci dropout might be attributable to the loss of cut sites through evolutionary time, or shared additional cut sites, among descendent lineages (Eaton *et al.*, 2017). Our findings suggest that we might be approaching the upper limit of the utility of ddRADSeq for deeper divergences in fast-evolving herbaceous lineages (as opposed to slower-evolving woody clades, but see Vargas *et al.*, 2017). Furthermore, large datasets, such as ours, can yield strong support across the phylogeny that might conceal discordance (owing to incomplete lineage sorting, ancient hybridization or other sources of conflict; e.g. Morales-Briones *et al.*, 2021). This might be reflected in the disagreement in the placement of *Montiopsis* between the phylogeny in this study, in the study by Ogburn and Edwards (2015), and in the two trees in the study by Hancock *et al.* (2018). In contrast, ddRADSeq had more power (in the form of more loci and more complete matrices) in discerning species-level relationships in the subclade analyses. Even then, coalescent-based inferences showed considerable discordance among ddRAD loci, which explains, in part, why there is little phylogenetic resolution in certain areas, such as the *Cistanthe longiscapa* complex (Fig. 4E). We also detected evidence of introgression and admixture, which might be contributing to the taxonomic uncertainty and phylogenetic conflict in this clade.

Life-history evolution in Cistantheae

Beyond clarifying subclade and species relationships, this Cistantheae phylogeny in its present form is also useful in exploring patterns of trait evolution. Particularly, we examined how life-history strategy might be related to climatic variables. Unlike previous studies, which relied on one sample to represent a given species and few molecular markers, our phylogeny is based on many newly collected and sequenced specimens per species and thousands of loci. Our results were broadly consistent with patterns identified across Montiaceae (Ogburn and Edwards, 2015): perennial species tend to occupy colder climates, whereas annuals tend to occupy warmer climates (Table 1). This suggests that evolutionary correlations between life-history strategy and temperature niche persist across phylogenetic scales. We also found a weaker, but still notable, association between life history and precipitation, whereby perennials tend to be occupying wetter habitats. These results align with those from other plant lineages, highlighting the potential roles that temperature and aridity play in shaping life-history evolution (Evans *et al.*, 2005; Datson *et al.*, 2008; Wang *et al.*, 2016; Monroe *et al.*, 2019; Boyko *et al.*, 2023).

Why might life-history strategies be strongly correlated with environmental variables, across diverse lineages and phylogenetic scales? One possibility is that the life-history strategies represent different ways in which plants might allocate resources and biomass under specific environmental constraints. In deserts, where precipitation is sporadic and drought stress is imminent, high seedling survival is more advantageous than low adult mortality (Charnov and Schaffer, 1973; Stearns, 1992). Based on these trade-offs, annuals should be favoured in more unpredictable and harsher climates (Stearns, 1976). However, similarly ‘harsh’ alpine or high-elevation habitats rarely host annual plants, probably owing to shorter growing seasons and lower temperatures (relative to deserts) that limit the ability of a plant to complete its life cycle (Körner and Larcher, 1988; Körner, 2003). In these conditions, low adult mortality and perenniality might instead be more advantageous. Moreover, different morphological and physiological traits are also related to plant life-history strategies (Roumet *et al.*, 2006; Lundgren and Des Marais, 2020). For example, high allocation to below-ground biomass might be considered a part of a perennial ‘syndrome’, a trait especially important for surviving in higher elevations and its associated climate (Lundgren and Des Marais, 2020). These traits associated with life-history strategies evolve repeatedly and correlatively (composing ‘life-history syndromes’) with environmental niche, with perennial species being more common in colder, wetter and higher-elevation environments, whereas annuals are favoured in warmer, drier and low-elevation habitats (Hjertaas *et al.*, 2023).

It is the exceptions to these patterns that are especially interesting. Both annual and perennial *Cistanthe* species exist in desert environments, often in sympatry; the same is true for the annual and perennial *Montiopsis* species in mid-elevational bands in the Andes. Interestingly, the architecture of desert perennials is more diverse than alpine/high-elevation perennial *Cistanthe*, which are herbaceous perennials with extensive below-ground woody root systems. This growth form also exists in the desert (*Cistanthe arenaria*, *Cistanthe fenzlii* and *Cistanthe grandiflora*), but there are also species with persistent above-ground tissue, becoming soft-wooded shrubs (*Cistanthe laxiflora* and relatives). In Eriogonoideae, Kostikova *et al.* (2013) found that perennials had broader niche breadth than annual species, even while occurring at higher mean elevations. In contrast, climatic niches tend to evolve more rapidly in herbaceous lineages than in woody ones (Smith and Beaulieu,

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2009), and faster molecular evolution in annuals might also facilitate this adaptability (Yue *et al.*, 2010).

The Cistantheae thus provide an excellent system to explore evolutionary shifts in life history, particularly in relationship to species that occupy narrow niche space versus those that span broad climatic and elevational gradients (i.e. an 'ecological generalist'). Such ecological flexibility might be key to evolution of certain traits; for example, a study of pollination syndromes in *Roscoela* has found that generalized pollinators, rather than only specialized pollinators, are important for the evolution of pollinator-related traits in flowers (Paudel *et al.*, 2019). In Cistantheae, the prevalence of ecological generalists supports the idea that these species are reciprocally predisposed to adapt to both alpine and desert environments. Across the phylogeny, many Cistantheae species exhibit broad elevational niches that might exemplify adaptability in both directions (Fig. 6A). This is perhaps facilitated by climatic overlaps between these environments, such as similarly low relative humidity (Billings and Mooney, 1968; Ehleringer, 1985; Körner, 2003). Although perennials tend to occur at higher elevations and annuals at lower, some sister species with the same life-history strategy show little overlap in their elevational ranges (Fig. 6A). In general, elevational niche appears to be evolutionarily labile across the Cistantheae phylogeny. Although there is no significant difference in the elevation IQR between life-history strategies, the species with the broadest elevational ranges are annuals, potentially reflecting greater ecological plasticity or dispersal potential in these species (Fig. 6C). Significantly, annuals exhibit a significant positive relationship between mean elevation and elevation IQR; annuals with higher mean elevations tend to occupy broader elevational niches. In general, Cistantheae species demonstrate broad elevational tolerances, which would provide a diversity of ecological selection pressures that might, in turn, facilitate repeated evolutionary shifts between life-history strategies.

Lastly, there is a continuum between annual and perennial life-history strategies, which introduces further complexity in the discussion of life-history evolution. Some annuals are facultatively perennial in favourable environmental conditions; conversely, some perennials can behave as annuals under disturbance or water limitation (Friedman, 2020). In the Cistantheae, *Cistanthe cachinalensis* has been categorized as an annual but has also been described as a biennial (Philippi, 1860; Reiche, 1898). In our experience of growing *Cistanthe cachinalensis* in the growth chamber, they can become somewhat woody at the base of the rosette when grown in well-watered conditions; interestingly, some genotypes have multiple bouts of reproduction, suggesting that the genes underlying perenniality might be partly intact, whereas others clearly senesce after one round of flowering. This species belongs to an otherwise perennial *Cistanthe* sect. *Cistanthe* lineage, representing a recent transition from perenniality to annuality (Fig. 6A). Therefore, it is perhaps unsurprising that *Cistanthe cachinalensis* could behave variably as a facultative perennial. In contrast, perenniality has recently (re-)evolved in *Calyptridium monospermum* and *Calyptridium umbellatum* in an otherwise annual *Calyptridium* lineage, another subclade suited for further investigation. We are starting to understand differences in the genetic mechanisms underlying investment into flowering versus vegetative growth between annuals and perennials (e.g. in *Mimulus*, Gould *et al.*, 2017; or Brassicaceae, Albani and Coupland, 2010; Kiefer *et al.*, 2017). Furthermore, many such genes are likely to be pleiotropic (Friedman, 2020). Future research could combine target analyses of candidate genes with comparative methods to explore the evolution of life-history strategies in Cistantheae.

Conclusion

This study presents the first densely sampled phylogenomic analysis of Cistantheae. We clarify key phylogenetic relationships and identify long-distance dispersal events, abundant instances of admixture, and new species complexes that warrant further attention. Comparative analyses reveal a consistent association between life-history strategies and environmental variables: annuals are associated with hotter, drier and lower-elevation environments, whereas perennials were associated with cooler, wetter climates. Nonetheless, the most compelling insights come from the exceptions to these trends, including broad ecological ranges and facultative behaviours, which accompany the evolutionary lability of life-history strategies. Rather than representing fixed sets of traits and characteristics, annuality and perenniality appear to encompass complex and dynamic syndromes in Cistantheae, and perhaps other plant lineages, which merit further investigations.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. Figure S1: cross-entropy estimates from sparse non-negative matrix factorization (sNMF) analyses for each subclade. Figure S2: time-calibrated phylogeny of representative Cistantheae species. Figure S3: subclade-level maximum-likelihood (ML) phylogenies using coding sequence-referenced ddRAD assemblies. Figure S4: subclade-level Tetrad phylogenies (coalescent-based quartet trees) and genomic structure using coding sequence-referenced ddRAD assemblies. Figure S5: distribution of morphological characters in the *Cistanthe longiscapa* complex. Figure S6: ancestral state reconstructions of bioclimatic variables across Cistantheae. Figure S7: principal components analysis of bioclimatic variables. Figure S8: posterior density distributions of evolutionary correlations between life history and climate variables across Cistantheae. Table S1: summary statistics from phylogenetic generalized least squares (PGLS) and Ornstein–Uhlenbeck phylogenetic linear models (phylolm) between life history and bioclimatic variables. File S1: list of vouchers and specimens sampled for phylogenetic analyses. File S2: assembly statistics from ddRAD assemblies.

FUNDING

Funding for this project was provided by the US National Science Foundation Division of Environmental Biology grant No. 2327957, and the Sussex Fund through the Yale Peabody Museum.

ACKNOWLEDGEMENTS

We would like to thank and acknowledge Thomas Near, Carlos Maya-Lastra, Jose Moreno-Villena, Karolina Heyduk, Edgar Benavides, Morgan Moeglein, Ava Ghezelayagh, Liam Taylor and Alison Carranza for training, help and advice on sequencing

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and analyses. We also thank Samantha O'Brien and Sarah Teichman for substantial help in the field. We would also like to thank Michael Donoghue, Susan Mazer and Ian Gilman for valuable insights on the overall project. A special thank you to UNMSM Herbarium, Museo Nacional de Historia Natural, Herbario Ruiz Leal, Clifton Smith Herbarium, Yale University Herbarium, Steere Herbarium, San Diego State University Herbarium and Sukkulenten-Sammlung Zürich for their collaboration and assistance.

DATA AVAILABILITY

All raw, demultiplexed sequencing data are available on NCBI Sequence Read Archive (SRA) under BioProject PRJNA1368686. Alignment files, tree files, character and climate matrices, and scripts used for analyses are available at https://github.com/anriiam/Cistantheae-phylogeny.

COMPETING INTERESTS

None declared.

AUTHOR CONTRIBUTIONS

A.C., A.M.-M., C.M.G., E.J.E., I.E.P., J.A.M.H., L.G., L.P.H., N.H., P.W.S., R.M.O. and S.G.D. conducted fieldwork and collected plant specimens and tissues. A.C., N.H. and S.G.D. extracted DNA, and A.C. prepared genomic libraries. A.C. assembled the ddRADSeq data, inferred phylogenies and conducted downstream analyses. A.M.-M., C.M.G., E.J.E., I.E.P. and P.W.S. provided essential taxonomic expertise. A.C. and E.J.E. prepared the manuscript, while all authors edited or reviewed and approved the manuscript.

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