Herbarium specimens reveal a constrained seasonal climate niche despite diverged annual climates across a wildflower clade

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Abstract

Quantifying species' niches across a clade reveals how environmental tolerances evolve, and offers insights into present and future distributions. Niche construction occurs when species select subsets of suitable conditions from those available, and influences niche evolution. We use herbarium specimens to explore climate niche evolution in 14 annual species of the *Streptanthus*/*Caulanthus* clade (Brassicaceae), which originated in deserts and subsequently diversified into cooler, moister areas. We quantify the "lived climate" of specimens from germination, estimated from historical climate records at collection sites, to collection date. We compare these specimen-based, phenologically-specific climate niches to typical annual climate niches and to standardized seasonal niches from the same localities. We also explore the role of spatial microrefugia in shaping lived climate by analyzing field soil samples collected for each species, and by comparing soil texture at collection localities to random locations nearby using soil databases. Specimen-specific climate achieved through niche construction revealed much less clade-wide temperature niche variation than annual and seasonal niches. Species track hotter and drier climates in cooler regions by growing later into the summer, and by inhabiting spatial refugia of drought-prone soils. All climate metrics evolved in a manner consistent with or more constrained than Brownian motion except specimen-specific temperature niches, which showed limited clade-wide variation and no phylogenetic signal. Limited variation in specimen-specific climate niches across the clade underscores how niche construction moderates experienced climate and may impact species' responses to climate change.

Significance statement

Here, we show that species across a clade that appear to have diverged in their climate niches based on annual conditions are actually tracking very similar seasonal climate conditions. This climate similarity is achieved through both the evolution of seasonal phenology and through establishment in suitable spatial refugia. Our results highlight the importance of niche construction in climate adaptation and the diversification of species, as well as the need to consider phenology when assessing and predicting habitat suitability. Restricted climate niches imply that species may be

less adaptable than we expect based on annual climate diversity, and have implications for conservation and management.

Introduction

The distributions of species within a clade reflect how environmental tolerances and niches evolve, and may reveal potential evolutionary constraints on adaptation to changing climates. These insights may be improved by focusing on niche parameters during the temporal window when species are active. Organisms can influence their own growing conditions by adjusting their phenology to restrict activity and life cycle events to a narrower range of environmental conditions than those available to them, and by occupying suitable microhabitats (1–4). Temporal habitat selection modifies the selective regime experienced by organisms, a process defined as niche construction (1, 2, 5). Niche construction may be adaptive; for example, mammals that hibernate during unfavorable winter conditions can occupy environments that would otherwise be too cold in winter (6). Similarly, germination cues used by plants allow them to select seasonal windows of environmental conditions that are favorable for future growth and reproduction (3, 7, 8).

In addition to selecting periods of time that facilitate growth and reproduction, species also sample subsets of space that represent suitable conditions (1, 9, 10). This ability might be obvious in some taxa, for example, many animals can move to occupy favorable temperatures by migrating seasonally (1, 11). However, sessile organisms can also occupy favorable microhabitats in areas of otherwise unsuitable habitat or climate through differential establishment in suitable microrefugia (9, 12–15). Fine-scale spatial variation in the abiotic niche for plants comes from factors including geographic slope and aspect, as well as biotic and abiotic soil attributes (14–17). For instance, tree species adapted to hotter and drier habitats are able to survive on south-facing slopes of less than a kilometer within a matrix of less suitable cooler and wetter habitats (13). Similarly, temperate species that have dispersed southward during glaciations survive in gullies characterized by cooler temperatures in otherwise tropical areas (18). Ultimately, sessile species live in a subset of available conditions by constructing niches that are

temporally narrower than the range of conditions that are broadly available, and by occupying suitable subsets of habitat.

Museum collections offer valuable tools for understanding how species sample available environmental conditions, as these collections are temporally and spatially explicit and often cover broad temporal ranges and geographic space (19). Herbarium specimens are particularly useful as most plants spend their entire lives fixed at the same location. Their label data, coupled with data from climatic and geological databases, can provide detailed estimates of the seasonal growing conditions experienced by the specimen, thereby opening new doors to understanding current distributions as well as trait and niche evolution (4, 20–24). For annual organisms, reconstructing the seasonal climate niche, which only considers the time window when an individual was alive or non-dormant, may allow for a better estimate of the climate factors determining species distributions in space and time than estimates based on annual climate data (23, 25). This level of detail can enhance our ability to characterize niche evolution across clades.

Here, we study the evolution of the seasonal niche in a clade of primarily annual plant species native to the California Floristic Province (CFP), a biodiversity hotspot. The Mediterranean climate that dominates in the CFP consists of a wet season that begins in fall and ends in spring, with no appreciable precipitation during the 3-4 months of hot, dry summer. This Mediterranean climate pattern is relatively recent, originating 2-5 million years ago, and its onset facilitated northward range expansion of southwest desert-adapted species (26). In many groups, northward migration was accompanied by speciation, and these groups constitute what is termed the Madro-Tertiary flora, which comprises 14% of the present day flora of the CFP (26). If climate niches evolved as species diversified from the southwestern and western deserts to northern, more mesic habitats, then we would expect the niches of species that live further north to reflect the cooler, wetter growing seasons in these areas. In contrast, if the seasonal and/or microenvironmental niche has remained relatively constant as species diversified, perhaps indicating some evolutionary constraint, we would expect that life cycle timing and habitat selection would adjust such that species experience similar growing season conditions across the clade, regardless of their geographic location.

One example of the Madro-Tertiary flora is the *Streptanthus*/*Caulanthus* clade in the family Brassicaceae, composed primarily of annual species (27–29). Using an existing phylogeny (28), we assess how the climate niche evolved across the clade as it speciated from the southwest desert to northern or high elevation habitats. We ask: 1) do species' climate niches diverge with speciation into novel annual climates, and 2) to what degree do species maintain niche constancy via temporal niche construction and by occupying a subset of available microhabitats? We use spatially- and temporally-specific information from herbarium specimens, field data, and climate and geological databases to characterize the conditions under which these species grow and reproduce. Using precipitation records and prior experimental data on germination cues, we estimate the germination month for each specimen. Coupled with the collection date, we then estimate the "lived" climate experienced by each specimen (referred to as the "specimen-specific" climate niche). These values could then be compared to those calculated across annual and standardized seasonal ("clade-average") time windows. This approach allows us to consider mechanisms of niche construction as we explore the extent of niche evolution with speciation into new geographic regions.

Results

Phenological variation across the clade

Species varied in which months they grew, with many of the lower-latitude southern species starting their lifespans later and completing them before northern species (Figure 1B, S2, S3). Lower latitude species likely start the growing season slightly later due to substantial rainfall arriving later in these regions (Figure S2, S3A). In general, lower-latitude species have shorter estimated lifespans than high latitude species (Figure S2, S3C). This result is consistent with experimental work in this system, in which low-latitude *Caulanthus* species did not extend their flowering time, even under abundant soil moisture (30).

Evolution of the annual and seasonal climate niche

Annual climate niches were very diverged among species (Figures S4-S6), as might be expected for a group of species that span 3000 m in elevation, nearly 8 degrees of latitude, and occur in diverse habitats (Figures 1, S1). To look at the evolution of the climate niche in more detail, we compared climatic water deficit (CWD), temperature and precipitation niches across annual, clade-average (Oct-April), and specimen-specific seasonal climate intervals, and examined how variation in these niche axes is distributed across the phylogeny.

Annual CWD evolution was significantly more phylogenetically conserved than expected under a Brownian motion model of evolution (31) (Table 1, Figure S4). Annual temperature and precipitation evolution also showed significant phylogenetic signal (Table 1, Figures S5 and S6). Phylogenetic structure in annual climate likely stems in part from climate variation reflecting clade origins, with the Caulanthus clade (*C. coulteri, C. heterophyllus, C. inflatus,* and *C. cooperi*) occupying hotter, drier climates than most other species (Table 1, Figures 2, S4-S6).

Our estimates of the climate niche based on the clade-average seasonal time window (April-October) were highly correlated with the annual climate niche (r >= 0.93, Table 2, Figures S4-S6), indicating that seasonal subsampling without phenological variation among species and specimens does not strongly alter the conditions that species occupy relative to each other, though overall the clade-average time window was lower in temperature and CWD than the annual time window because it does not include the warmest and driest months of the year (Figures S4, S5). All time windows encompassed the vast majority of annual precipitation, so precipitation values were highly correlated and similar across all three time windows (r >= 0.99, Table 2, Figure S6). Patterns of phylogenetic signal for the clade-average niche mirrored those of the annual niche—evolution of the CWD niche was more constrained than expected under Brownian evolution, while temperature and precipitation showed significant signal consistent with Brownian evolution (Table 1).

If species are retaining aspects of their ancestral niche, then we would expect them to be tracking similar growing conditions even as they occupy different geographic regions. Specimen-specific time windows—which span the month of first rain in each

specimen's collection site until the collection month of the specimen—sample temperature and CWD conditions in ways that alter our characterization of species' climate niches (Figure 2). Specimen-specific estimates of the CWD niche were not correlated with estimates of the CWD niche at the clade-average time scale ($r = 0.02$, Table 2), indicating that local phenology is substantially changing the relative CWD conditions these species experience. We found significantly lower variance in CWD in specimen-specific relative to clade-average windows (variance 2991 vs. 12776; Levene's test $F = 10.49$, $p = 0.0033$, Figure 2C) and a narrower range of CWD values calculated over specimen-specific (range: 101-279) vs. clade average time windows (range: 54-366). These results demonstrate that small changes in the timing of the growing season can moderate the climate that these species experience (Figure 2).

Although the correlation between temperature estimated in specimen-specific and clade-average time windows was fairly high ($r = 0.76$; Table 2), phenological variation among species and individuals somewhat alters the thermal niches that species occupy relative to each other (Figure 2AC, S6). Specimen-specific temperature niches exhibited a narrower range of values than clade-average niches (clade-average range: 7.3-13.2 (5.9°C), specimen-specific range: 8.8-12.4 (3.6°C). In addition, the temperature niche in the specimen-specific time window showed lower variance among species (variance = 0.69) than did estimates in the clade-average time window (variance = 1.94, Figure 2AC), though these variances were not significantly different (Levene's test $F = 1.77$, $p = 0.19$). Unlike other aspects of the climate niche, the specimen-specific temperature niche showed no phylogenetic signal (Table 1), meaning that there was no difference in temperature variation within vs. among subclades (or in other words, that close relatives do not tend to have more similar thermal niches) once specimen-specific timing is taken into account. The variances of the clade-average and specimen-specific time windows were not different for precipitation (Levene's test $F = 0.054$, $p = 0.82$; Figure 2B), as all time windows sample all months with substantial precipitation.

Specimen-specific climate niches also bucked latitudinal climate trends. Surprisingly, specimen-specific CWD in some more northern species (*S. drepanoides, S. breweri, S. polygaloides)* was greater than that exhibited by species with southern

distributions (e.g., *C. heterophyllus, C. simulans, C. inflatus*) whose annual and clade-average climates are hotter and drier (much greater annual CWD) than these northern species (Figure 2A,D). These northern species are constructing a seasonal niche with relatively higher CWD via longer lifespans extending into the hotter, drier months (Figures 1, S2, S3), while more southern species in annually hotter climates are restricting their growing season to cooler months (compare annual, clade-average and specimen-specific CWD in Figures 2AC, S4).

Soil microhabitat across the clade

Aside from constructing niches via the timing of when and how long to grow, species may also occupy spatial refugia in more permeable soils and hotter geographic aspects that result in lower water availability. Using data from soil collected at field sites directly under plants, we find that species that occupy cooler areas tend to grow in substrates with higher fractions of coarse material relative to members of the clade living in warmer areas (Figure 3A; PGLS slope = -6.1, $p = 0.051$; without *C. amplexicaulis*: slope = -11.0, $p = 0.017$). Similarly, we find that species that live in more mesic, low CWD climates occupy soils with greater coarse fractions (Figure 3B; slope = -0.076, $p < 0.001$; without *C. amplexicaulis*: slope = -0.082., $p < 0.001$). Most species (13 of 14) occupy soils with some amount of lower water holding capacity than the surrounding area (Figure S8). In particular, species that occupy cooler and more mesic areas occur in soils with lower water holding capacity than the surrounding area (e.g., Figure S7), while species that occur in warmer and drier areas occupy soils that do not differ as strongly in water holding capacity from the surrounding area (Figure 3CD, PGLS temperature slope = 0.32, $p = 0.10$; CWD slope = 0.0033, $p = 0.037$). Thus differential establishment in suitable spatial microrefugia also contributes to the maintenance of more similar niches than expected based on latitudinal climate gradients.

Discussion

This study shows that niche construction via selection on cues for the timing of germination and reproduction, as well as differential establishment in soils with high

drainage, results in much less realized clade-wide climate niche evolution than expected given the widely divergent environments occupied by annual species in the Streptanthus/Caulanthus clade. We gained this understanding of niche constraint by combining herbarium specimen collection data, climate and soil data, and our knowledge of germination behavior in this clade, which allowed us to estimate specimens' growing seasons. If we had relied only on the annual niche metrics that are typically used in species distribution models and ecological niche models (reviewed in (25)) or even a standard seasonal nice for the clade, we might have concluded that species in this clade exhibit varied climate niches and underwent extensive climate niche evolution as they moved to cooler, moister habitats from ancestral dry ones. However, we show that phenological niche construction, coupled with differential establishment across microhabitats, allows these species to track very similar realized climates, especially temperature and climate water deficit, across divergent habitats. For example, the hotter, drier seasonal niche of species in more mesic habitats is achieved by occupying dry microsites and by growing for a longer time into hot, dry seasons. This longer season may reflect common developmental requirements across the clade, e.g., a longer season may allow species in cooler areas to accumulate the growing degree-days necessary to complete their life cycles. The low variability in growing season CWD and similar trends in temperature experienced by these species across variable environments suggests that there may be strong evolutionary constraints on temperature and moisture tolerance in this clade.

Several other studies have suggested the importance of considering only the months in which species are seasonally active to estimate niche properties (4, 11, 24, 32). In a recent survey, Zurell and colleagues (25) found that very few studies using SDMs explicitly incorporated phenology into SDM estimates, and most of those that did focused on tree species. A few studies have suggested (23) or shown (4, 11, 24, 32) that incorporating the seasonal niche provides better predictions of species' occurrences than annual niche data. For the annual plant *Mollugo verticillata*, species distribution models built from climate records of herbarium specimen collections by month and year were more accurate in predicting spatial occurrences than those using long-term average climate predictors (4). Seasonal models also better predicted

occurrences of invasive mustard *Capsella bursa-pastoris* in the novel range than annual niche models (24). There has been a recent plea to integrate different phenological stages into SDMs even for perennial species because often different life stages exhibit different climatic tolerances (reviewed in (25)). For example, establishment conditions at the seedling stage may be more constrained than those at the adult stage (e.g.,(33)). These studies, and ours, argue that seasonal niche estimation provides a deeper understanding of the environmental tolerances of organisms. Here, we show the power of leveraging museum collections and knowledge of phenological cueing mechanisms (such as, in our case, germination cues) to understand the evolution of the climate niche.

Climate niche similarities across members of a clade that occupy divergent annual environments may indicate strong evolutionary constraint in the conditions tolerated by these species. Cang and colleagues (34) found slow rates of climate niche evolution in 85 largely perennial pairs of sister species across the grass phylogeny, with very small climate niche shifts across sister species pairs, particularly for temperature, similar to our results. Niche shifts in this study were somewhat greater for precipitation, but still much smaller than rates of projected climate change. In a large survey of 266 phylogroups of plants and animals, rates of climate niche evolution were again much lower than the rate of predicted climate change across collection localities (35). Overall, climate niche evolution seems constrained across a large number of taxa, despite the fact that these studies have been conducted across widely different evolutionary scales.

Life history may mediate the extent of niche construction. Our study shows that for many annual species in this clade, the climate niche has remained fairly static with diversification across divergent climatic regions due to changes in the timing of germination and reproduction; however, there are perennial members of this clade that persist aboveground for most or all of the year. Perenniality appears to have evolved multiple times across this clade from annual ancestors, including a subclade of only perennial species (28, 36) that occupy higher elevation habitats with snow (29, 36), suggesting climate niche evolution. Rapid climate niche evolution has been found to be associated with life-history shifts from annuality to perenniality in Montiaceae (37). In our system, all of the perennial species are herbaceous, and the growing season is

relatively short (36). Niche construction via the timing of spring growth and reproduction by perennials could also result in less realized climate niche evolution than one might initially expect based on year-round persistence.

Spatial variation in the environment allows species to occupy areas of suitable conditions (refugia) in surrounding unsuitable habitats. We found that *Streptanthus/Caulanthus* species that had diversified into cooler, more northerly habitats were growing on coarser soils characterized by less water-holding capacity; these species often occur on isolated coarse-soiled serpentine outcrops (38, 39). Field soil collections taken at specimen collection sites revealed that species in annually cooler habitats grow in soils that are coarser with greater water drainage than those in hotter habitats. Moreover, many *Streptanthus/Caulanthus* species are noted to occupy dry serpentine south- or southwest-facing slopes (e.g., six species included here have south-facing slopes in herbarium locality descriptions). Such spatial selectivity in aspect has also been demonstrated for tree species growing in northern California. Species partitioned niches within a very small reserve (<2 km) such that species with higher range-wide CWD occupied open, south-facing slopes and microrefugia that were hotter and drier than surrounding habitat (40). Together, differences in soil texture, topography, precipitation, and temperature determine water availability to plants (represented by CWD), which we found to be significantly less variable across specimen-specific time windows than annual or seasonal ones.

Huey and colleagues (41) suggested that individual plants should have broad tolerance ranges because sessile individuals cannot move to avoid stresses; however, our data and those of others suggest that some plants are subsampling suitable seasonal environments and are constructing relatively constant niches via differential phenology despite their sessile nature. Reproductive traits that facilitate seed dispersal by animal species with specific habitat preferences may also allow plants to track suitable niches through directed dispersal (reviewed in (9, 42)). In these situations, the line between niche construction and passive environmental sampling is blurred. Our results show that plants are subsampling suitable seasonal environments through a variety of means, including 1) by using environmental cues to time seed germination, 2) by slowing or speeding flowering phenology to reproduce under the best conditions, 3)

by using passive or directed dispersal of seed to reach suitable new sites or refugia. Moreover, traits that respond to changing environments are likely both plastic and have an underlying genetic basis that is under selection (e.g., (43)) All of these mechanisms, and arguably many more, suggest that plants are under selection to ameliorate the conditions under which they, or their offspring, grow, and that they may have more constrained environmental tolerances than originally hypothesized (see also (35)).

Herbarium data have known biases (reviewed in (44)), and we have attempted to address some of these. We added error radius distances for all specimens (as in (24)) and rejected specimens for which location was not recorded accurately enough; our median error radius was less than 0.5 km. We also took care to sample specimens that spanned the geographic range and elevations of the collections and species' ranges, and used only reproductive specimens. For the purposes of our study, biases that are applied similarly to all species (e.g., tendency to collect near roads) may not have large impacts on our conclusions. One potential bias specific to our study is whether species were collected at the same average phenological stage or not. For example, if one species tended to be collected relatively more in fruit, our estimate for lifetime climate niche would be more accurate for that species than for species collected at an earlier phenological stage. Because of botanical etiquette and practice, most herbarium specimens are collected in reproductive stages and another study found that most specimens are collected at peak flowering (45). Moreover, in a separate study, differences in phenological stage, while reducing accuracy, were not great enough to affect overall conclusions (46). While we attempted to be conservative about our estimates of the growing season conditions that specimens experienced, it is possible that differences in phenological stage could affect our estimates of seasonal niche construction. We think it is unlikely to change our overall conclusions, however, due to large differences between annual climate patterns and seasonal niches.

In sum, despite widely divergent annual climates, we find largely similar growing niche conditions among the 14 annual species we sampled across the *Streptanthus*/*Caulanthus* clade. Our results suggest that annual species in this clade are much more constrained in their climatic tolerances than would be predicted by year-round climates of their geographic distributions. Annual climate data are typically

used in SDMs, but we argue these may overestimate the rate and extent of climate niche evolution that has actually occurred in some groups, including our focal clade that diversified from deserts into cooler regions. Our insights of highly constrained niche evolution were gained by reconstructing the climate experienced by herbarium specimens, drawing on extensive historical climate data at fine-scale geographic resolution. This approach can be applied to many more species using museum collections and other online databases that include temporal and spatial observation information. Ultimately, niche constancy achieved through niche construction and establishment in suitable spatial refugia indicates that species have not adapted to divergent climates, but rather have constructed favorable climate niches that are similar across wide geographic regions. Fundamentally narrow climatic tolerances could ultimately lead to an underappreciated climate vulnerability in these species despite the divergent geographic ranges they occupy, especially under rapidly changing climate.

Materials and Methods

We used herbarium specimens to characterize the climate niche of 14 annual species (*Streptanthus* and *Caulanthus* spp., Figure 1) in the Streptanthoid clade (28). We selected these 14 species (which represent about a third of the clade) based on four criteria: 1) sampling across the phylogeny ensuring representation of main subclades, 2) sampling across the latitudinal and elevational breadth that the clade as a whole occupies, 3) sampling species with enough herbarium collections to obtain an adequate sample size (>40 specimens), and 4) limiting our analysis to annual species. We used only annuals for three reasons: 1) we could more precisely estimate their whole lifetime above-ground growing conditions, 2) annuals are a large part of the CFP biodiversity (47), and 3) annuals comprise the large majority of species within this clade. Species in this clade share an affinity for open, bare, rocky (including serpentine outcrops), or sandy habitats (39), encompass a diversity of range sizes, and span 8 degrees of latitude and >3000 m in elevation from desert to montane biomes (Figure 1C; Figure S1); they thus occupy a variety of climates and soil types.

Specimen selection and georeferencing

To build our dataset, we used the extensive digital collection of the Consortium of California Herbaria available through their specimen data portal (cch2.org). In coordination with another trait-focused herbarium project (48), we sampled up to 200 imaged specimens per species. When greater than 200 specimens were available for a species, we subsampled across counties to spread our sampling across the species' geographic range (Figure 1). These efforts resulted in inventories of 53-187 herbarium records per species (average = 141), with specimen years spanning 1898-2016. We used only specimens with reproductive structures present (buds, flowers, or fruits) so that our sample represents only plants that survived long enough to reach the reproductive stage.

Our approach reconstructs the lived climate of each specimen by estimating the start and end of its growing season (see below) and matching that with climate records from the year and location of collection. Geographic data and locality descriptions for each specimen were downloaded from the Consortium of California Herbaria. We checked coordinates and elevations, and added missing ones using Google Earth, complemented by the USGS Historical Topo Map database (49) and information from google searches of description localities. For each specimen, we added error radius distances (as in (13, 24)), estimated as the distance at which the provided description would no longer be logical. Specimens for which we could not determine coordinates with <=5 km error radius were excluded from analyses (though the large majority of specimens had much more precise coordinates, mean = 1.13 km, median = 0.5 km).

Estimating the climate conditions experienced by specimens

To quantify the climate conditions experienced by each specimen, we first estimated when the plant was alive above ground, i.e., the duration of time from when the individual germinated to when it was collected. To estimate germination month, we drew on our prior experiments on germination behavior in this clade with many of the same species (50). In this prior work, we conducted staggered experimental waterings of seed cohorts every two weeks under outdoor conditions from mid-September through December to identify preferred germination conditions (50). We found that most species

had very high or greatest germination fractions at early fall rainfall dates, as has also been found in a number of other desert annual species (51). This result is consistent with adaptation to capitalize on the short winter wet season characteristic of Mediterranean climates. Therefore, using historical weather data, we estimated the germination month for each specimen as the first month in the water year (see below) preceding specimen collection when more than 25 mm of rain fell at the specimen collection site. The threshold rainfall quantity selected was based on results of prior studies finding that more than 25 mm of rain was needed to trigger biological activity in plants living in arid environments (52–54), as well as on field observations in this system (7).

We estimated germination dates at a monthly scale because weather data at a finer temporal grain are not available for the wide range of years in which specimens for this clade were collected. Typically, the water year in the western United States is calculated from October 1-September 30 (e.g. (55)), but we wanted to account for early September rains in some years, so we set our water year from September 1-August 30. We limited plausible germination dates to September through February based on previous studies (7, 50), and to accommodate the possibility of rare late germination events in February. If there were no rain events greater than 25 mm in the months preceding the specimen's collection, we assumed the month with the greatest rainfall preceding March was the germination month; these criteria eliminated 8 specimens for which there was no detected rainfall event prior to March.

Total specimen growing season was estimated as the observed germination month to the month of collection (Figure 1B). Among the specimens we used, ~71% had one or more fruits at the time of collection, so we consider the collection date to be an imperfect but acceptable proxy for the end of life in these annual species. For example, a specimen collected on April 25, 1983, would be estimated to start its growing season during the first month when > 25 mm of rain fell at that specimen's geographic location (September 1982), and end its season in April 1983, at the end of the specimen's collection month. Species-level averages for the end of the season ranged from early April to mid-June (Figure 1B), with 98% of specimens collected in March-July. We extracted monthly values of mean temperature, total precipitation, and total climate

water deficit (CWD) from the California Basin Characterization Model (BCMv65), with a spatial resolution of 270 m (56), for each specimen's location. The Basin Characterization Model estimates CWD based on evapotranspiration, calculated from solar radiation and incorporating aspect (topographic shading), cloudiness, snow and permeability of underlying bedrock (57). Because CWD incorporates temperature, precipitation, physiographic properties and soil permeability (56), it is a very comprehensive metric for sessile plants (58, 59) and especially so for this clade that occupies a large variety of elevations and soil types (39).

We estimated the climate niche for each specimen over three different time windows. In each case, we summed precipitation, summed CWD, and averaged temperature over the selected months. First, we summarized annual climate conditions for each specimen using monthly climate data from September in the year prior to collection until August in the year of collection from the collection site. These annual values are typically used in species distribution and ecological niche models to characterize suitable conditions (25, 60); we refer to these estimates as the "annual climate niche". Second, we estimated the "specimen-specific seasonal climate niche" using only climate data from the estimated month of germination of each specimen until that specimen's collection month; this period circumscribes the lived climate that each specimen experienced. Lastly, we summarized climate data representing the "clade-average seasonal climate niche". For these estimates we used a single temporal window that represents the average start and end of life for all species in this study across the clade. This average window spans October in the year prior to collection through April in the year of collection and allows us to compare climate niches across a common time window that samples only months in the growing season.

Characterizing evolution of the climate niche

Contrasting our specimen-specific seasonal niche estimates with climate niches based on annual data allows us to see the extent to which species are sub-sampling from the annual conditions available in their home sites, and allows us to evaluate the extent to which commonly used annual data are effective in characterizing the niche in these species. Comparing our specimen-specific seasonal niches to the clade-average

seasonal niche allows us to view more precisely how or whether phenological variation among species results in climatic niche construction. Specifically, we test whether the variance in the climate conditions that species occupy differs when considering climate during the clade-average time window vs. the specimen-specific time window. If variance is greater among climate averages that are based on specimen-specific time windows, this indicates that phenological variation acts to increase divergence in the climate niche. If variance is smaller among climate averages that are based on specimen-specific temporal dynamics, this indicates that phenological variation acts to maintain niche constancy across the clade. We test for unequal variances between specimen-specific seasonal climate and clade-average seasonal climate for temperature, precipitation, and CWD using Levene's tests implemented in the R package car (61); values were averaged across specimens to obtain one value of each climate variable per species before analysis.

To understand how the seasonal and annual climate niches have evolved in this clade as it expanded and speciated into more northerly regions and more mesic climates, we visualized mean temperature, precipitation and CWD along the phylogeny using the ggtree package (v.3.6.2) (62). To understand how climate niche traits evolved, we calculated Blomberg's K (63) using phytools v.1.9.16 (64), tested for significant phylogenetic signal, and then tested whether the K estimate significantly differed from what is expected under Brownian evolution, while accounting for standard errors in climate estimates. When we found significant phylogenetic signal in a niche variable, we then asked whether species' niches were significantly more constrained than expected based on a Brownian motion model (K significantly >1) by comparing our estimate of K to a null distribution of K values generated under Brownian motion (31). We also evaluated the extent to which climates in the annual, clade-average, and specimen-specific time windows were correlated. High correlation across time windows indicates that species are subsampling climate in time similarly, e.g., that temporal niche construction is not largely altering the relative climate spaces that these species occupy. Low correlation across time windows indicates that temporal subsampling substantively changes the relative climate spaces that these species occupy. We used correlation tests that account for phylogenetic relationships among species and include standard

errors of estimates; this method assumes trait evolution is given by an Ornstein-Uhlenbeck process (function cor_phylo from the phyr package v.1.1.0) (65).

Exploring soil microhabitat occupancy across the clade

In addition to temporal selectivity in growing season, the climate that plants experience may be determined by the microhabitats that they occupy, and species may occupy microrefugia within a matrix of unsuitable habitat. To investigate whether *Streptanthus/Caulanthus* species occupy microhabitats that subsample the niche space that is broadly available to them, we used soil texture data from two sources. Soil texture affects water holding capacity and is highly variable at fine spatial scales across the landscape (Figure S7) (58, 66). We first extracted soil available water holding capacity estimates for each specimen locality from the California Soil Resource website at 800m^2 resolution (66). To estimate the soil niches that are broadly available, we also extracted soil water holding capacity from 100 random points within a 20 km buffer radius around each locality. In addition, we leveraged field soil data collections from herbarium specimen sites collected in a previous study (39). In that study, we sampled the top 30 cm of soil underneath 1-3 *Streptanthus* or *Caulanthus* plants per site, with an average of 4.3 localities per species. Field soils were sieved into soil fractions and coarse soil fraction was recorded (see (39) for more details). These two data sources have complementary strengths—the gridded data is available for a large number of localities but with imperfect precision and larger spatial resolution, while the field-collected data are highly specific to exact specimen growing sites, but are available for far fewer sites per species.

To ask whether species living in cooler areas are growing in relatively drier microsites that reflect their drier desert origins, we evaluated the relationship between annual temperature and CWD vs. the coarse soil fraction of field-collected samples using two separate phylogenetic generalized linear models (pgls with branch length transformations at default values of 1 from the caper package v.1.0.2) (67). Both climate data and soil data were averaged across localities to obtain one value per species before analyses. We ran these models with and without *Caulanthus amplexicaulis*, an elevational outlier among our selected species (Figure S1). We use the gridded soil

data to test whether species are differentially occurring in more water permeable (and likely drier) soils relative to what is available. We calculated the difference between the soil water storage capacity in grid cells where specimens occurred to the water storage capacity available in the surrounding area. We represented the water storage capacity of the area surrounding each occurrence by taking the average of our 100 randomly selected grid cells. We calculated the average difference between occurrences and these random points for each species. We then tested whether these differences were related to the average annual temperature or CWD of each species using two separate phylogenetic generalized linear models as described above. We predicted that if species are retaining elements of the ancestral desert niche, species occupying cooler or more mesic climates might establish in areas that are more high-drainage than the surrounding area, that is, with a more negative soil water storage delta.

Acknowledgments

M.W. Schwartz made suggestions that improved the manuscript.

Figures and Tables

Figure 1. Phylogenetic relationships (A.), species-specific seasonal windows (B.), and geographic distributions of specimens (C.) of the 14 annual species from the major subclades in the larger Streptanthus I clade included in this study. The phylogeny in (A.) is from (28), trimmed to our focal species. Shaded tiles in (B.) represent the relative proportion of specimens that were estimated to have germinated (blue) or that were collected (red) in a given month for each species. Point ranges in (B.) represent the average germination month estimate (dark blue) and collection date (dark red) for each species. Map polygons represent locations of herbarium specimens for each species that were used in this study (most specimens were located in California, USA). The color of the species' name on the phylogeny matches the color of points and polygons on the map.

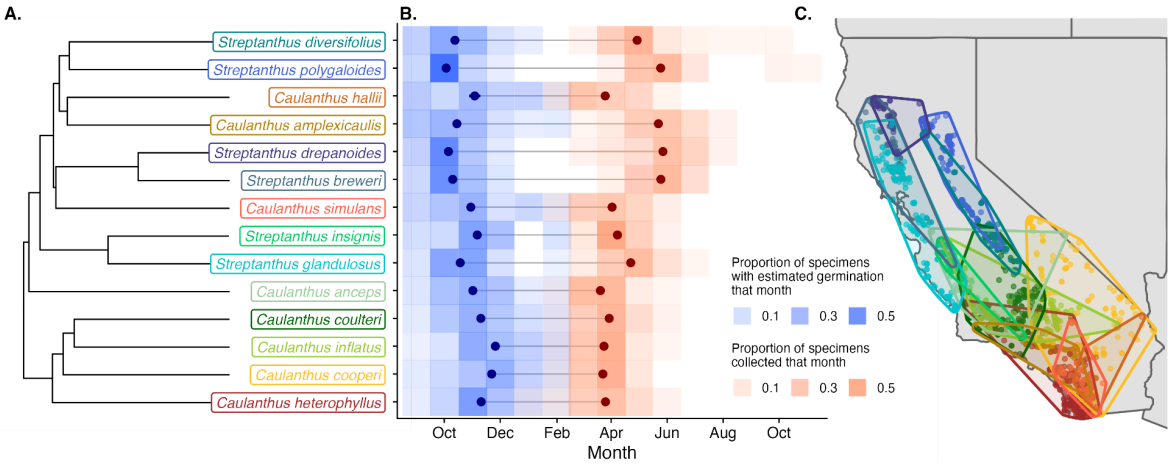


Figure 2. (A.) Visual comparisons of the specimen-specific seasonal climate niche (climate spanning germination month to collection month, averaged over specimens) and average clade-wide seasonal climate niche (Oct-Apr of the collection year) plotted alongside the phylogeny. The three climate variables are total precipitation (mm), average temperature (°C), and total climate water deficit (CWD). Panels (B.), (C.), and (D.) compare average clade-wide and specimen-specific niches for each of the three climate variables. The variances of the average clade-wide and specimen-specific time windows were not different for precipitation (B.) or temperature (C.), but did significantly differ for CWD (D.), with lower variance when CWD was summarized over specimen-specific time windows.

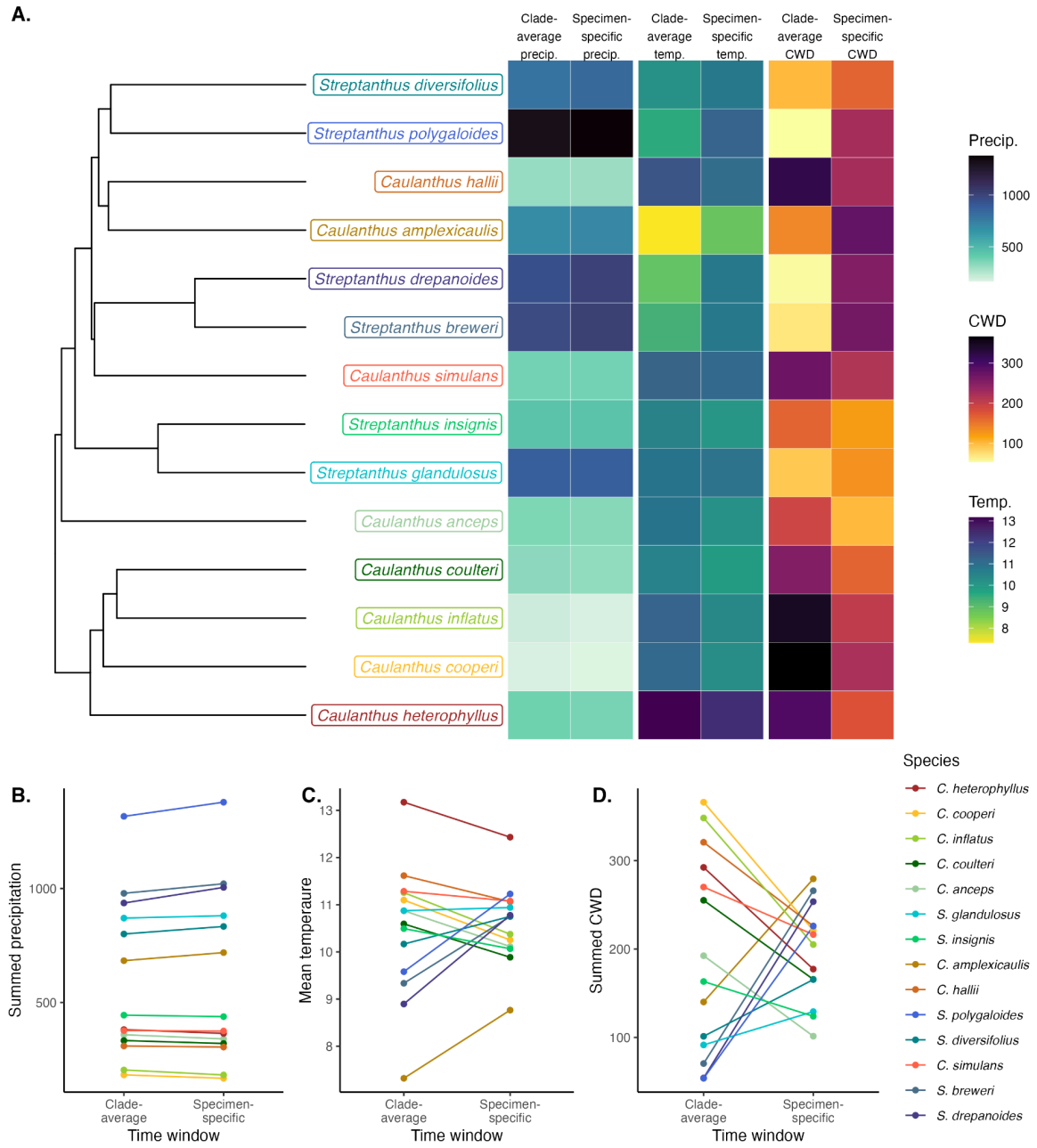


Figure 3. (A.) Species occurring in cooler areas (lower annual average temperature) occur in soils with greater fractions of coarse material. Line is the regression slope from a PGLS model (slope = -6.1, p = 0.051). When *Caulanthus amplexicaulis*, a high elevation species, is omitted the relationship becomes significant (slope = -11.0, p = 0.017). Coarse soil fraction was measured from field soil sampled from the rhizosphere of *Streptanthus* or *Caulanthus* individuals in an average of 4.3 sites per species. (B.) Species occurring in more mesic areas (lower annual climatic water deficit; CWD) occur in soils with greater fractions of coarse material. Line is the regression slope from a PGLS model (slope = -0.076, p < 0.001). (C.) Species occurring in cooler areas tend to occupy grid cells that have lower water holding capacity (WHC) than the surrounding area, while those in warmer areas occupy sites more similar to the surrounding areas, but this trend is only marginally significant (slope from a PGLS model = 0.32, p = 0.10). (D.) Species occurring in more mesic areas (low CWD) occupy grid cells that have lower water holding capacity than the surrounding area, while those in more arid areas (high CWD) occupy sites more similar to the surrounding areas. Line is the regression slope from a PGLS model (slope = 0.0033, p = 0.037).

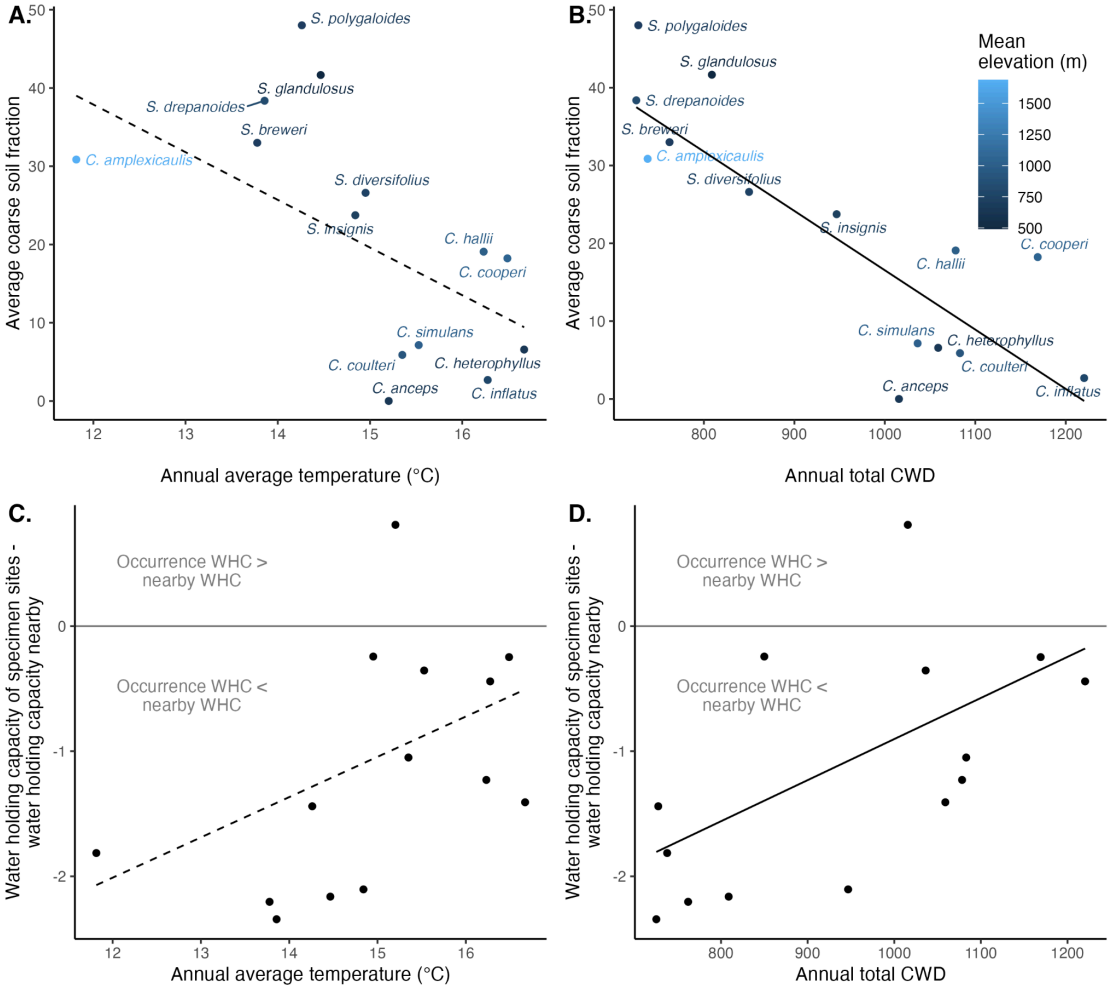


Table 1. Evaluation of phylogenetic signal (Blomberg's K), for each of the climate variables for each time window. The three climate variables were total precipitation (mm), average temperature (°C), and total climate water deficit (CWD). Climate values used in these analyses were species' averages of data from each specimen. When K > 1, p_{bm} refers to the significance of the test for whether there is phylogenetic signal consistent with a Brownian motion model of evolutionary change through time (significant if $p_{bm} < 0.05$). When K > 1 and $p_{bm} < 0.05$, we tested whether K significantly differed from 1; p_{gt1} represents a test for whether K is significantly greater than 1, which indicates that trait evolution is more constrained than expected under Brownian motion (significant if $p_{gt1} < 0.05$). Note that there is no phylogenetic signal in the specimen-specific temperature niche, in contrast to other climate variables.

	Annual climate niche	Average clade-wide seasonal climate niche	Specimen-specific seasonal climate niche
Total precipitation	K = 1.22 **p_{bm} = 0.0099** p_{gt1} = 0.062	K = 1.20 **p_{bm} = 0.013** p_{gt1} = 0.074	K = 1.22 **p_{bm} = 0.010** p_{gt1} = 0.055
Average temperature	K = 1.16 **p_{bm} = 0.017** p_{gt1} = 0.11	K = 1.12 **p_{bm} = 0.034** p_{gt1} = 0.17	K = 0.91 p_{bm} = 0.65
Total CWD	K = 1.35 **p_{bm} = 0.0029** **p_{gt1} = 0.017**	K = 1.30, **p_{bm} = 0.0052,** **p_{gt1} = 0.026**	K = 1.22 **p_{bm} = 0.013** p_{gt1} = 0.060

Table 2. Correlations between climate variables summarized across each of the three time windows. Phylogenetic structure in each climate variable is accounted for when estimating these correlations. Also presented are bootstrapped 95% confidence intervals based on 1000 replicates.

Climate variable	Annual vs. clade-average	Annual vs. specimen-specific	Clade-average vs. specimen-specific
Temperature	r = 0.93 [0.79-0.99]	r = 0.65 [0.25-0.97]	r = 0.76 [0.37-0.94]
Precipitation	r = 1.00 [0.99-1.00]	r = 1.00 [0.99-1.00]	r = 0.99 [0.99-1.00]
Climatic water deficit	r = 0.94 [0.84-0.99]	r = -0.24 [-0.73-0.37]	r = 0.02 [-0.55-0.61]

Supplementary Figures and Tables

Figure S1. Distributions of specimen elevations (m) for each species. Heights of ridges reflect densities of elevation data scaled within each species. Species are ordered based on the phylogeny plot in Figure 1.

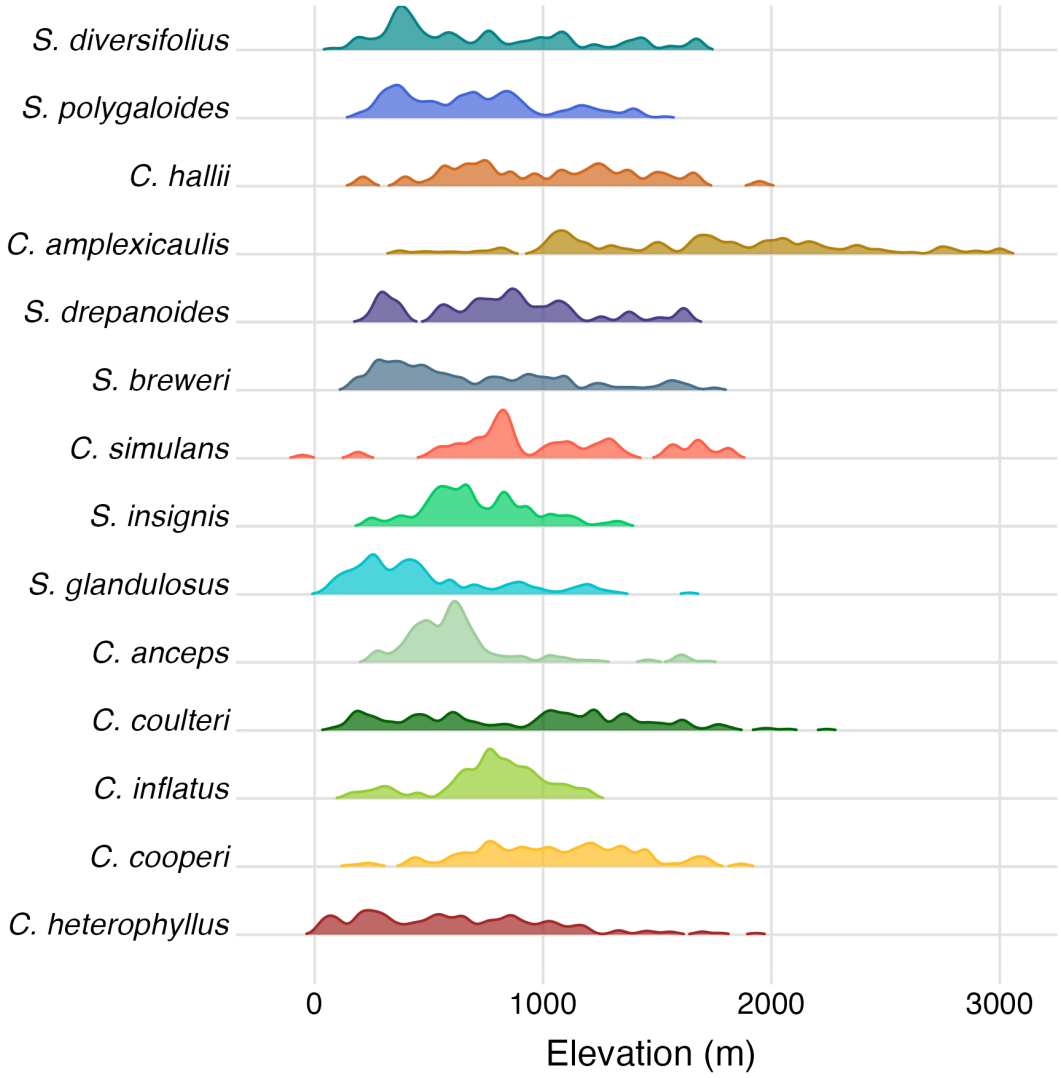


Figure S2. Differences in growing season among the species arranged by latitude (these data are also shown in Figure 1B). Shaded tiles represent the relative proportion of specimens that were estimated to have germinated (blue) or that were collected (red) in a given month for each species. Start month of the growing season was estimated for each specimen as the first month in the fall prior to collection, starting in September, with greater than 25 mm of precipitation. End month of the growing season was the month of collection of each specimen. Specimen-level values were then averaged for species-level estimates of start month and end month, these are depicted with the darker point ranges. *C. amplexicaulis* grows at higher elevations than other species, which may contribute to its deviation from a latitudinal trend in growing season length (Figure S1).

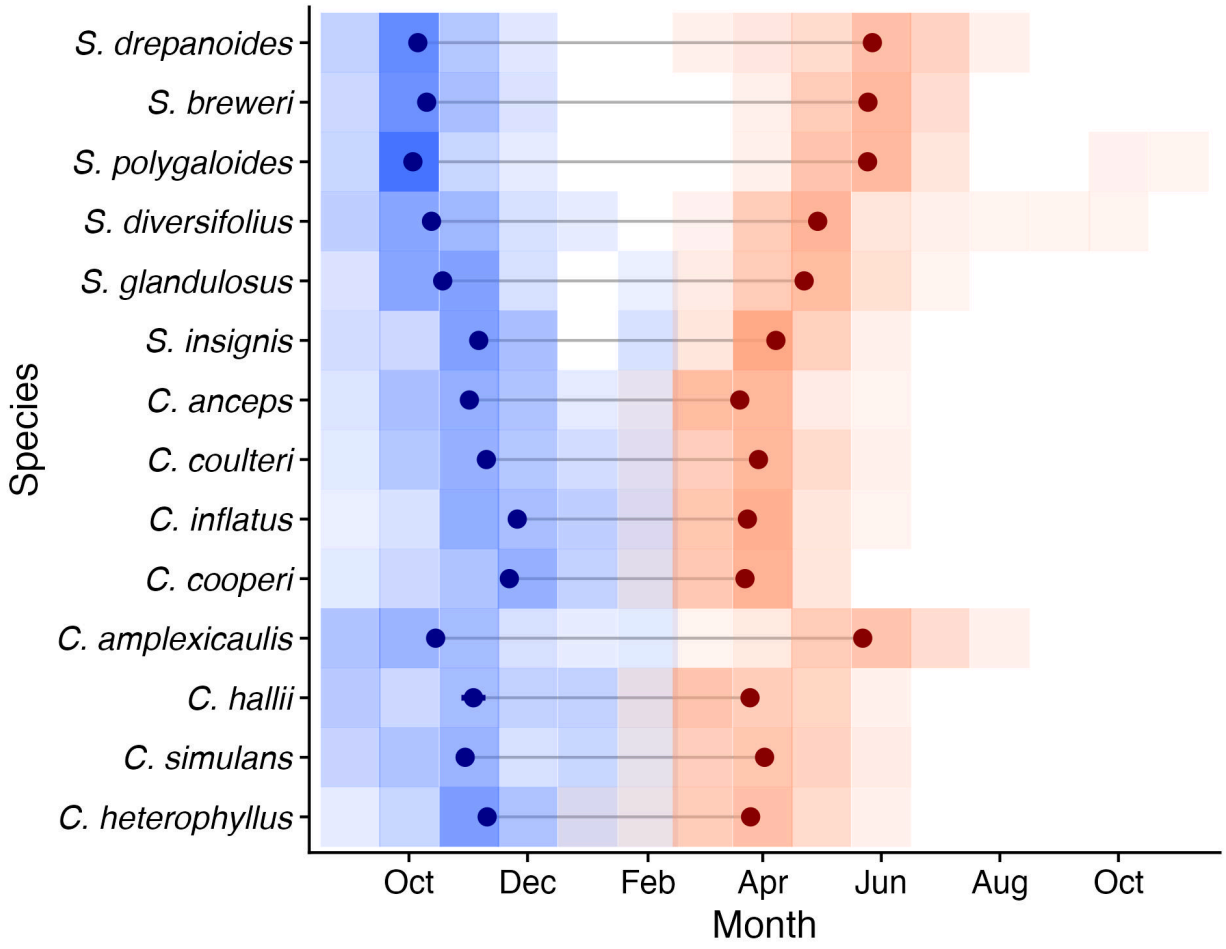


Figure S3. Phenological metrics plotted against latitude. In each panel, trends for individual species are shown with colored lines and the clade-wide pattern is shown with the thick black line. (A.) Species at high latitudes tend to get a first large rain event earlier in the year than those at lower latitudes. (B.) Species at high latitudes tend to be collected later in the year than those at lower latitudes. (C.) Species at high latitudes tend to have longer estimated lifespans than those at low latitudes. Note that trend lines are from linear regressions that do not consider phylogeny and are meant as visual aids rather than statistical estimates.

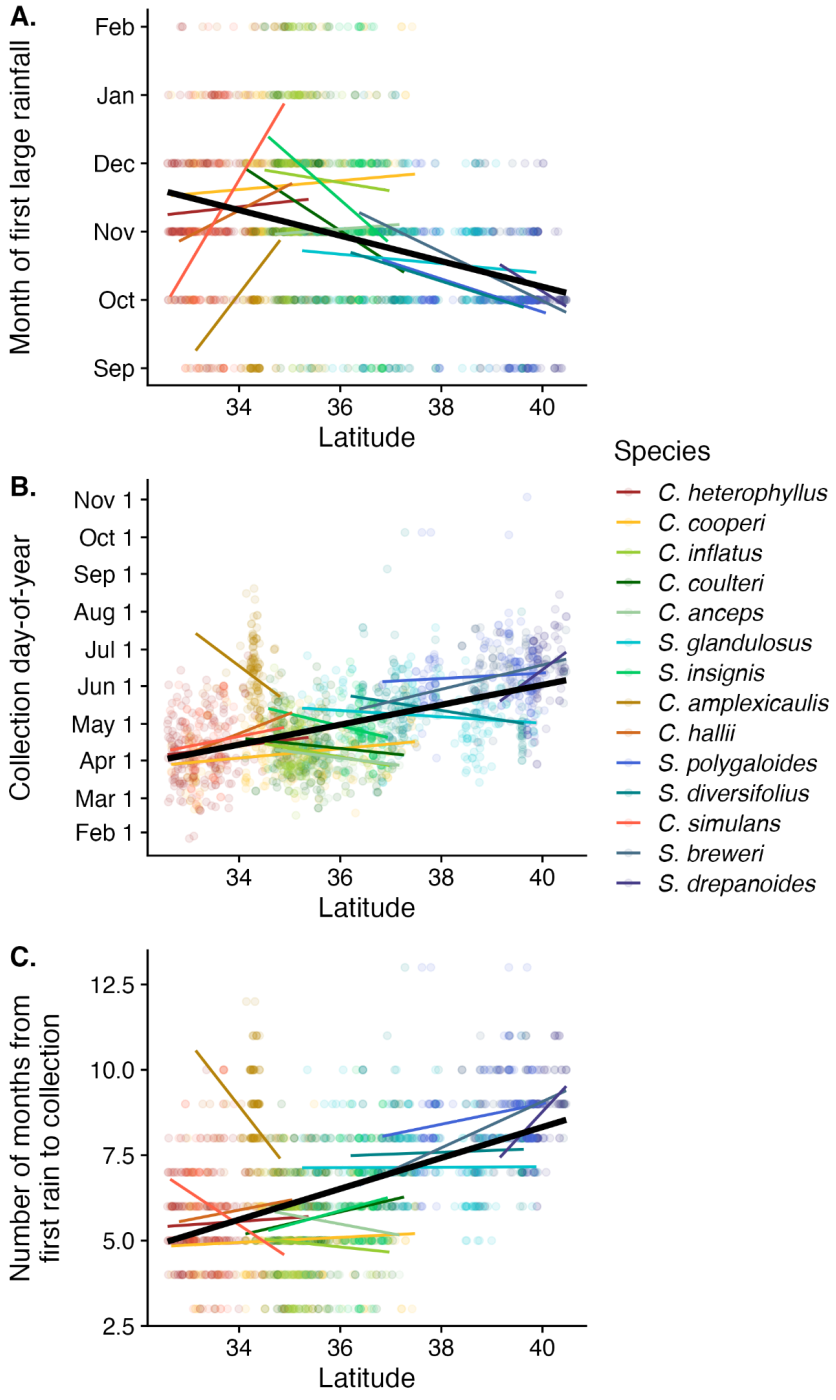


Figure S4. (A.) Climate water deficit (CWD), which estimates water stress from precipitation, temperature, aspect and soil properties) for annual, average clade-wide seasonal, and specimen-specific seasonal time windows plotted alongside the phylogeny. The same color scale is used for all three time windows. (B.) An alternate visualization of the same annual, average clade-wide seasonal, and specimen-specific seasonal CWD; this panel highlights the variation within species and the magnitude of differences between the three time windows. Species are in the same order as branch tips in (A.)

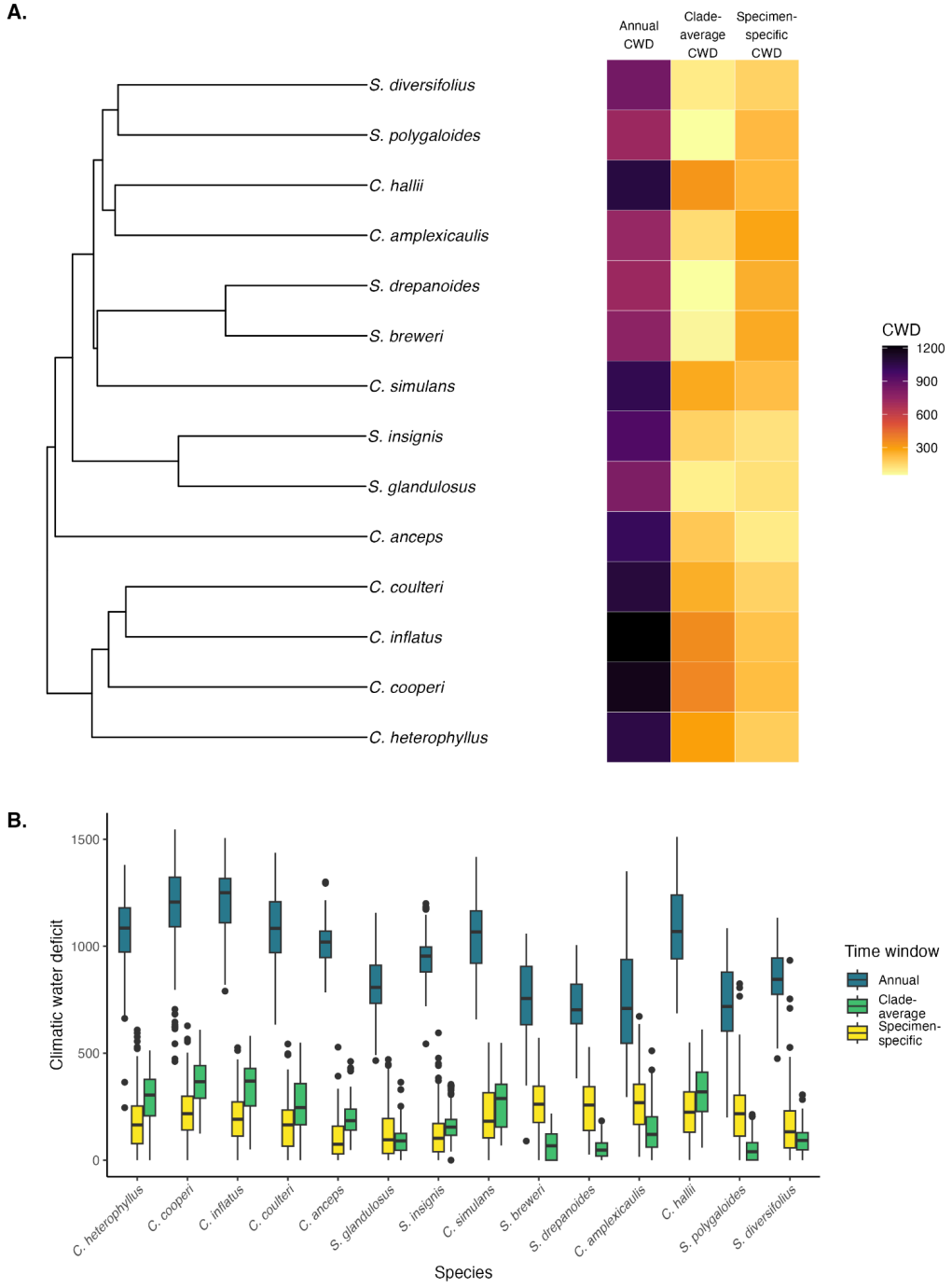


Figure S5. (A.) Average temperature (°C) for the annual, average clade-wide seasonal, and specimen-specific seasonal time windows displayed alongside the phylogeny. The same color scale is used for all time windows to display the differences in average temperature. (B.) An alternate visualization of the same annual, average clade-wide seasonal, and specimen-specific seasonal temperature; this panel highlights the variation within species and the magnitude of differences between the three time windows.. Species are in the same order as branch tips in (A.).

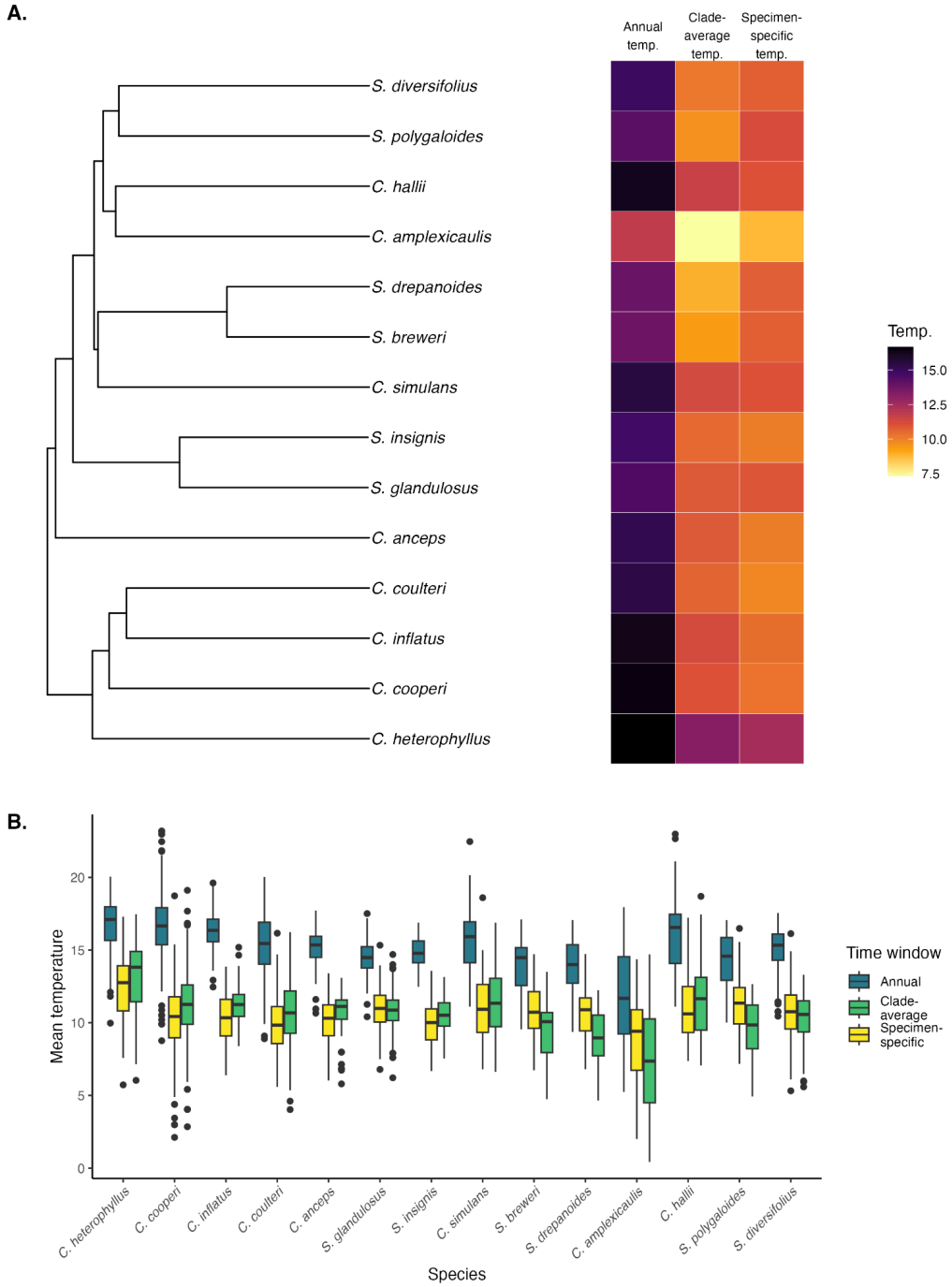


Figure S6. (A.) Summed precipitation (mm) for the annual, average clade-wide seasonal, and specimen-specific seasonal time windows displayed alongside the phylogeny. The same color scale is used for all time windows. (B.) An alternate visualization of the same annual, average clade-wide seasonal, and specimen-specific seasonal precipitation; this panel highlights the variation within species and the magnitude of differences between the three time windows. Species are in the same order as branch tips in (A.)

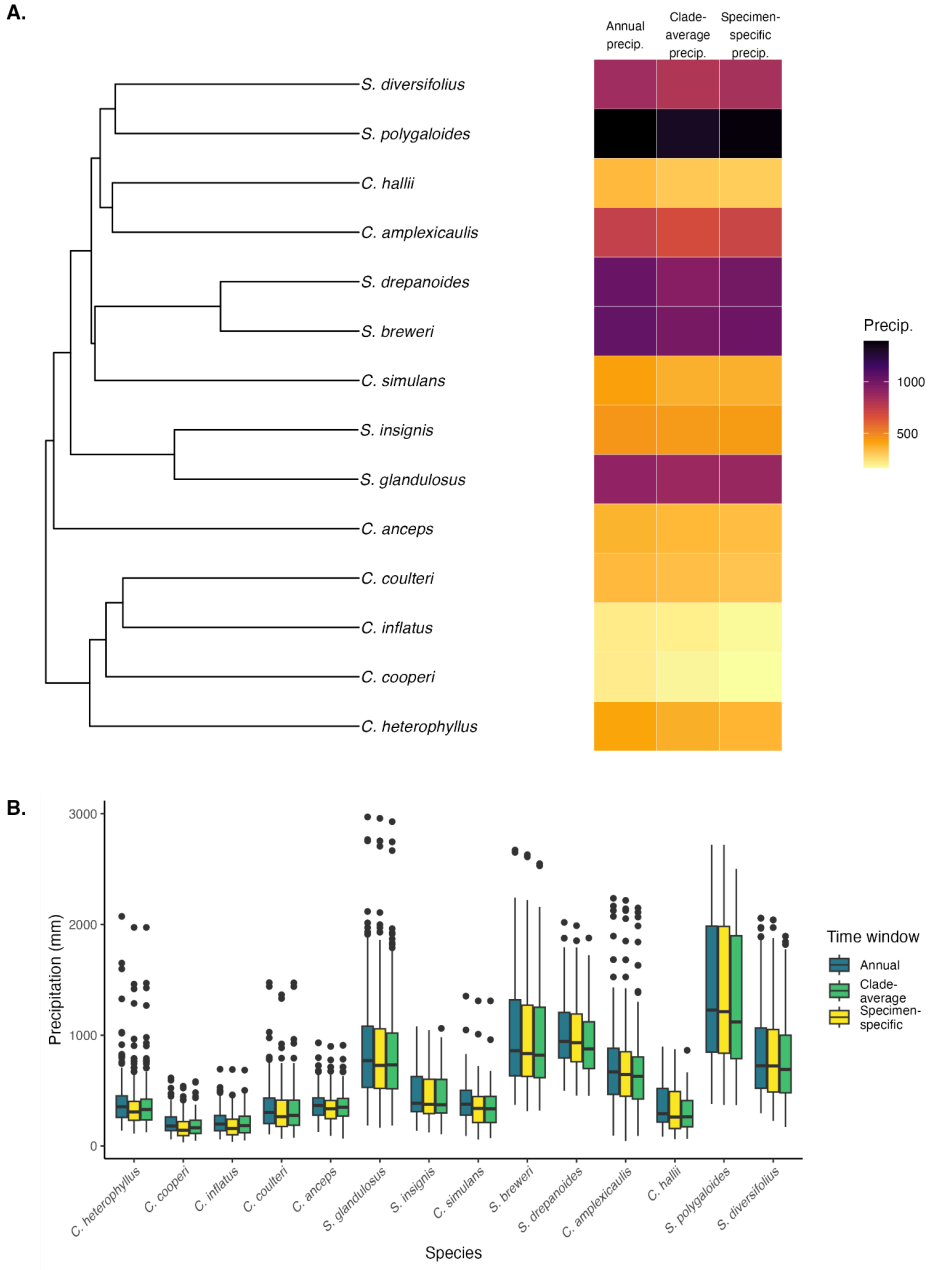
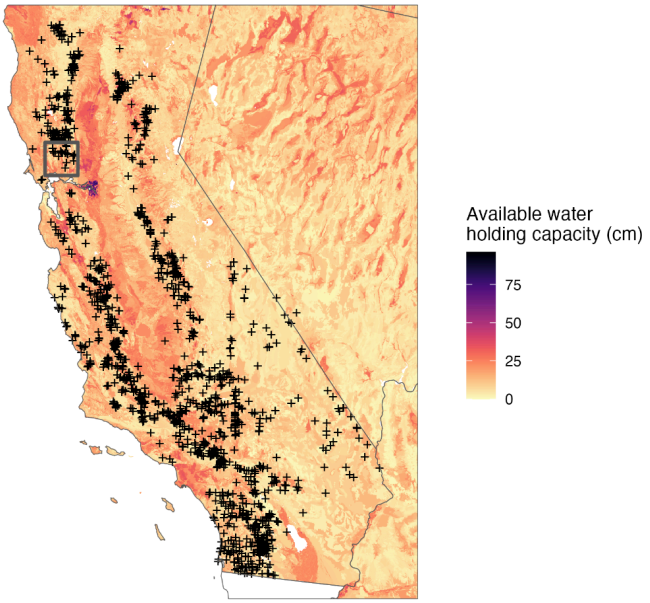


Figure S7. (A.) USDA-NCSS soil survey data within 800 m grid cells illustrating spatial variation in water holding capacity (66). Symbols represent locations of specimens used in this study. (B.) Zoomed in view of the area in the grey square in (A.) showing how specimen occurrences in northern parts of the range are in grid cells with lower water holding capacity than the surrounding areas. Note that color scales differ between the two panels.

A.



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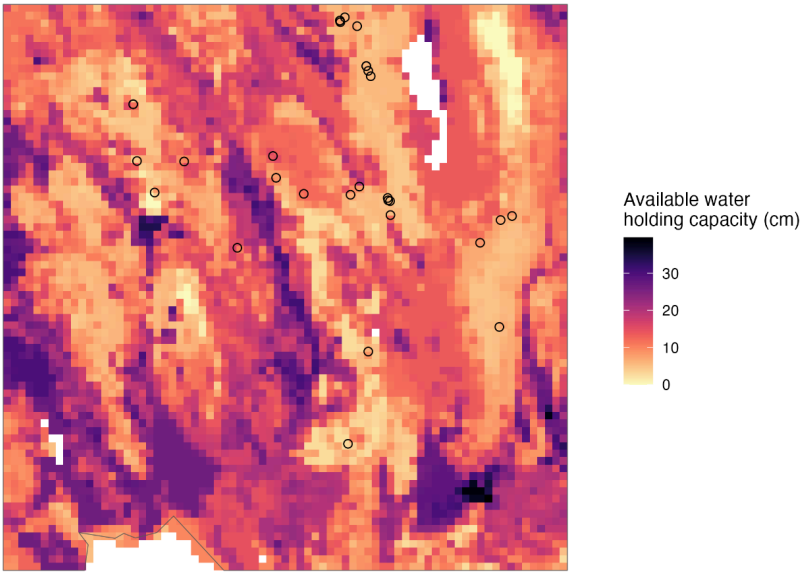
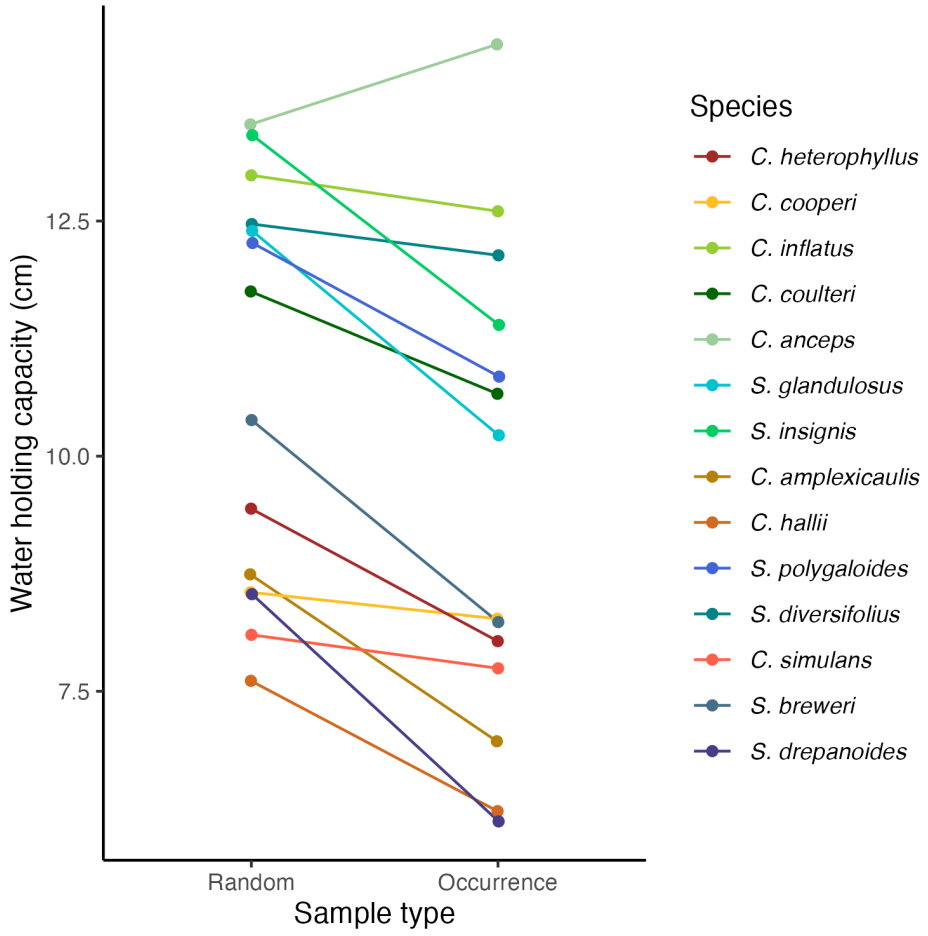


Figure S8. Water holding capacity from occurrence points and from 100 randomly placed points within 20 km of each occurrence. Values were averaged for each species (i.e., averaged across all occurrences for a species, and averaged across the 100 random values x the number of occurrences for each species). Species-averages from occurrence points tend to have lower water holding capacity than the surrounding areas.



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