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## RESEARCH ARTICLE

# Predicting plant species climate niches on the basis of mechanistic traits

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## Abstract

1. Improved estimation of climate niches is critical, given climate change. Plant adaptation to climate depends on their physiological traits and their distributions, yet traits are rarely used to inform the estimation of species climate niches, and the power of a trait-based approach has been controversial, given the many ecological factors and methodological issues that may result in decoupling of species' traits from their native climate.
2. For 107 species across six ecosystems of California, we tested the hypothesis that mechanistic leaf and wood traits can robustly predict the mean of diverse species' climate distributions, when combining methodological improvements from previous studies, including standard trait measurements and sampling plants growing together at few sites. Further, we introduce an approach to quantify species' trait-climate mismatch.
3. We demonstrate a strong power to predict species mean climate from traits. As hypothesized, the prediction of species mean climate is stronger (and mismatch lower) when traits are sampled for individuals closer to species' mean climates.
4. Improved resolution of species' climate niches based on mechanistic traits can importantly inform conservation of vulnerable species under the threat of climatic shifts in upcoming decades.

## KEYWORDS

climatic niche, ecophysiology, functional traits, intraspecific variation, plant climate distributions, trait multifunctionality, trait-climate mismatch

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## 1 | INTRODUCTION

Knowledge of plant climatic preferences (i.e. optimal conditions for establishment, persistence and growth) is critical for species selection for cultivation, for plant conservation and for predicting and mitigating global change impacts (Forestry Commission, 2020; Lancaster & Humphreys, 2020; Peters et al., 2020). The value of new approaches to improve the estimation of climate niches is shown by the use of genomic data to estimate climate preferences of tree ecotypes or crop varieties (Barney & DiTomaso, 2011; Browne et al., 2019; Sang et al., 2022). However, while functional trait-based approaches have gained strong currency in ecology (McGill et al., 2006), to our knowledge, efforts to estimate species' climatic preferences have not included traits, neglecting a potentially critical source of information of species' adaptation to the environment (Pearson & Dawson, 2003; Thuiller et al., 2004; Woodward & Williams, 1987).

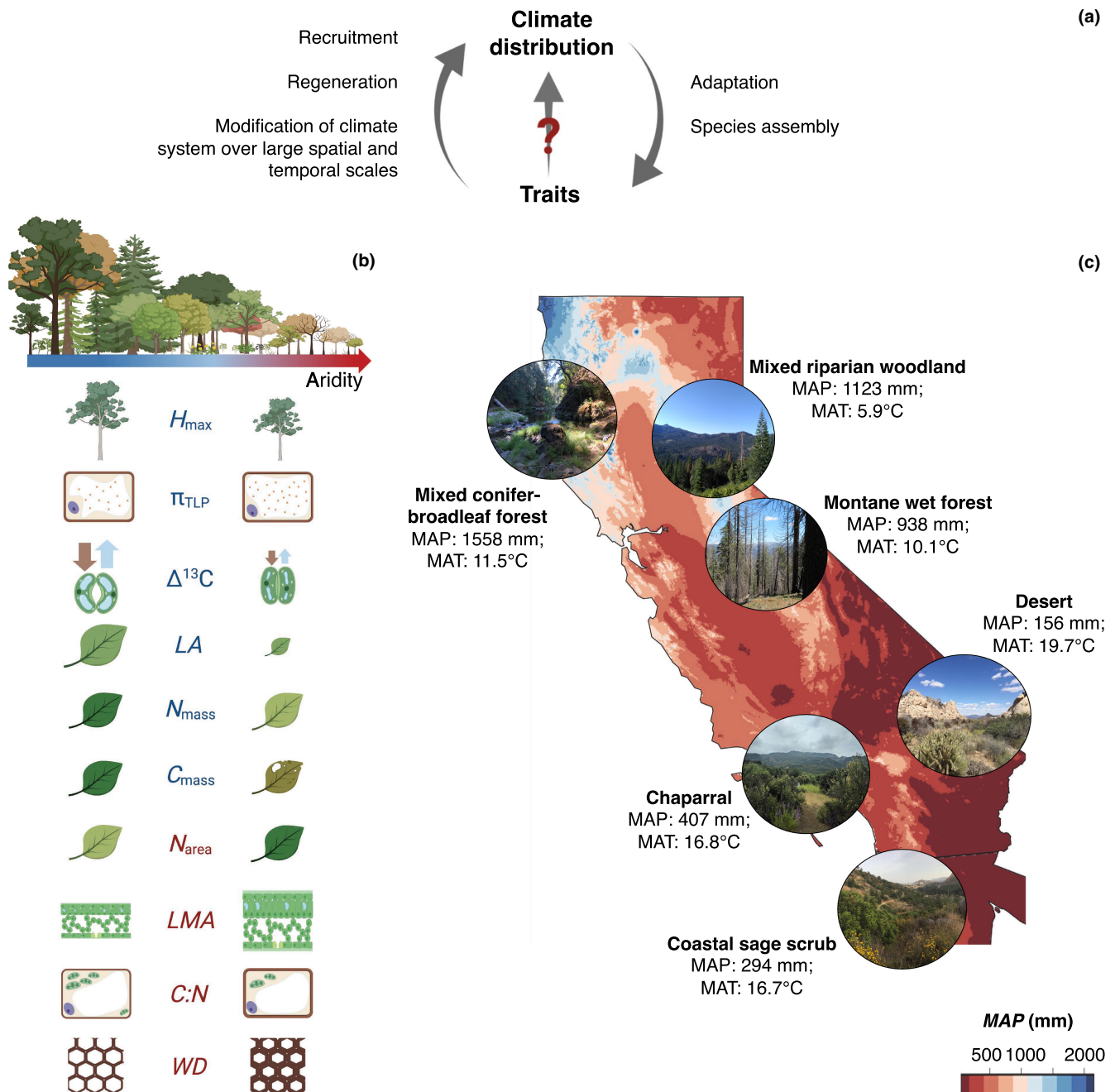
Yet, a rich literature dating back to Ancient Greece (Hort, 1948) describes how numerous phenotypic traits related to growth, reproduction and survival (Adler et al., 2014; Lavorel & Garnier, 2002; Poorter et al., 2008; Violle et al., 2007) may influence plant distributions across environmental conditions (Albert, Thuiller, Yoccoz, Douzet, et al., 2010) and habitat types (Grubb, 1998; Reich et al., 2003; Schimper, 1898; Shipley et al., 2017). Decades of theory has held that plants would optimize their traits to climate (Ackerly, 2003; Enquist et al., 2015). The association of traits with species' climate distributions is due to bidirectional causality (Figure 1a): a species' traits would depend on the climate under which it adapts and its community assembles, and, conversely, the climate into which a species can recruit and regenerate will depend on its traits (Fletcher et al., 2018). Further, over very large spatiotemporal scales, plant traits can influence local and regional climate (Anderegg et al., 2019; Boyce et al., 2009).

However, the generality and strength of trait associations with climatic distributions across diverse species has been controversial

(reviewed by Anderegg, 2023). On one hand, studies have reported cases in which traits were strongly adapted to climate and soil, both for small sets of closely related species within lineages (4–12 species; Cochrane et al., 2016; Fletcher et al., 2018; Ramírez-Valiente et al., 2020), and for the average trait values of communities across climatic gradients (Jager et al., 2015; Kichenin et al., 2013). These trends have been often applied in paleoecological studies aiming to retrodict past climates from community averages of fossil leaf traits (Greenwood, 2007; Peppe et al., 2011; Wolfe, 1978; Yang, Spicer, et al., 2015). On the other hand, relationships across diverse species of traits with climate variables have often been weak and/or highly variable (Costa-Saura et al., 2016; Ordoñez et al., 2009; Wright et al., 2005). For example, depending on the species set, the relationship of leaf nitrogen concentration with mean annual precipitation has been weakly positive (Mitchell et al., 2018), weakly negative (Santiago et al., 2004; Swenson & Weiser, 2010) or not significant (Mitchell et al., 2018; Moles et al., 2014; Wright et al., 2005).

This frequent weakness of empirical trait-climate associations across diverse species has been ascribed to methodological issues and/or to a range of ecological and evolutionary factors that would result in a mismatch of species' traits from their natural climate distributions (Figure 1a; reviewed in Table 1). These potential sources of mismatch include the use of traits not directly relevant to climate tolerance (Brodribb, 2017; Medeiros et al., 2019), the complexity of the fundamental niche and its divergence from the realized niche (Grubb, 1977; Lee-Yaw et al., 2016; Sheth et al., 2020; Wiens, 2011), indirect relationships between traits and fitness (Laughlin et al., 2020), intraspecific trait variation (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Siefert et al., 2015), trait multi-functionality (Sack & Buckley, 2020), many-to-one mapping of traits to function (Alfaro et al., 2005; Anderegg, 2023; Falster et al., 2017; Marks & Lechowicz, 2006b) and nonequilibrium processes (DeAngelis & Waterhouse, 1987; Dobzhansky, 1950; Ohlemüller et al., 2008).

**FIGURE 1** The potential to predict plant climate distributions from functional traits. (a) Schematic for the bidirectional causal determination of plant traits and climatic distributions. Climate drives the adaptation of plant traits, and filters the species that assemble in a given location (Cornwell & Ackerly, 2009; Cornwell et al., 2006); conversely, traits determine the climatic ranges under which species can recruit and regenerate (Fletcher et al., 2018), and over long periods of time at landscape scale, plant traits can influence local and regional climates (Anderegg et al., 2019; Boyce et al., 2009; Boyce & Lee, 2010; Zarakas et al., 2020). This study tests the ability to predict climate from traits and the question mark represents the possible sources of decoupling explored in Table 1. (b) Multiple traits are adapted and/or plastically adjusted to climatic aridity, from less xeromorphic in cool and wet climates to more xeromorphic in warm and dry climates (see Table 2 for expectations and rationales based on theory and previously published empirical work for each trait). Indeed, traits often adapt in suites due to co-optimization or trade-offs, conferring ensemble advantages in given environments. For example, “economics spectrum” traits tend to be correlated, such that rapidly-growing species of high resource environments have higher foliar nutrient concentrations and photosynthetic rates but shorter lived leaves than slow-growing species of lower-resource conditions (Reich, 2014; Wright et al., 2004). Thus, xeromorphic species are expected to have smaller maximum heights ( $H_{max}$ ), and to have leaves with lower turgor loss point ( $\pi_{tlp}$ ; corresponding to more concentrated cell solutes as depicted) and lower carbon isotope discrimination ( $\Delta^{13}C$ ; corresponding to conservative stomatal opening as depicted), that are smaller in area ( $LA$ ), higher in leaf mass per area ( $LMA$ ; corresponding to denser and/or thicker leaves, as depicted), lower in leaf nitrogen per mass ( $N_{mass}$ ) but higher in nitrogen per area ( $N_{area}$ ; depicted with greenness), lower in leaf carbon per mass ( $C_{mass}$ ; corresponding to greater herbivory, as depicted), and higher in carbon to nitrogen ratio ( $C:N$ ; reflecting greater investment in cell wall relative to chlorophyll as depicted) and higher in wood density ( $WD$ , corresponding to more xylem cell wall tissue per area, as depicted). Created with BioRender.com. (c) Ecosystems distributed across an aridity gradient from Baja California (Mexico) to northern California (US). Photographs show the study ecosystems sampled in the peak of the Spring-early Summer growing season, set in a map of the rainfall gradient.



The potential mismatch between traits and climate might have deterred trait-based estimation of species' climate niches. As discussed above, a great number of previous studies have focused on trait-climate relationships, yet, to our knowledge, only one single previous study directly tested the estimation of diverse species' climate distributions based on traits. That study found that across trees of North America, seed size, maximum plant height and wood density could weakly predict the median and extreme of eight bioclimatic variables, including mean annual temperature, mean annual precipitation and growing degree days (Stahl et al., 2014). The paucity of studies that “flip the axes” to plot climate variables against traits may also be attributed to a lack of motivation for predicting species' climate distributions from traits. If we already have species distribution data, why should we need to estimate climate preferences or climate niches from traits? However,

as climate change hastens, and species' distributions shift, the usefulness of additional lines of information of species' climate niches becomes more evident. As shown by the use of genomic markers to infer climate preferences in tree ecotypes and crop varieties (Barney & DiTomaso, 2011; Browne et al., 2019; Sang et al., 2022), strong climate versus trait relationships would provide useful information to managers seeking to optimize outplantings and conservation area designation (Loiseau et al., 2020), and for the anticipation of the functional responses of species distributions and ecosystem processes to climate change. Indeed, plant and ecosystem process models do implement constraints based on even weak known empirical trait-trait and trait-environment relationships, and thereby project the net effects of trait variation on plant performance under simulated environmental changes (Anderegg, 2023; Henry et al., 2019; Trugman et al., 2019).

**TABLE 1** Many factors, not mutually exclusive, that would potentially impede trait-based prediction of the climate distribution of species and ecosystems, including methodological issues and ecological and evolutionary processes that would contribute to the mismatch of species' traits from their optimal climate, with supporting references.

Sources of mismatch	Rationale	Methodological approach to partially reduce mismatch
Study methodology	<p><i>Traits with a limited direct mechanistic role</i></p> <p>Since the publication of the leaf economics spectrum (Wright et al., 2004), ecologists have often focused on the relationships among a core set of 5–8 traits and climate. However, these traits may not always be mechanistically adaptive for given climate variables (Bartlett, Scoffoni, &amp; Sack, 2012; Buckley et al., 1980).</p> <p><i>Large variation in traits compiled from global databases</i></p> <p>The frequent use of measurements compiled in databases from disparate locations, collected with different methods and with uncertainty in trait mean estimation may contribute to weakness in the reported trait–climate associations (Moles et al., 2014; Šimová et al., 2018; van der Plas et al., 2020; Veski et al., 2020; Violle et al., 2015).</p> <p><i>Missing data in global databases</i></p> <p>The relationship between given traits and climate variables might be weakened or missed due to many missing data points for species with restricted distributions and/or small populations, and for traits that are more measurement intensive (Taugourdeau et al., 2014).</p> <p><i>Lack of phylogenetic structure</i></p> <p>As species have shared evolutionary histories, they cannot necessarily be considered independent data points, and thus it is recommended that the phylogenetic structure is accounted for to fully resolve adaptive trait–trait and trait–environment relationships across species (Perez &amp; Feeley, 2021).</p> <p><i>Microclimate</i></p> <p>Species climatic ranges are typically calculated from large databases with coarse resolution (usually between 1 and 340 km<sup>2</sup>). While these climatic ranges are effective in characterizing large scale patterns, the strength of trait–climate relationships could be improved if variation in microclimates, that is temperature, water and nutrient availability, irradiance and soil composition, were accounted for (Opedal et al., 2015)</p>	<p>We selected a set of traits known from previous literature to confer adaptation to aridity (Table 2) and measuring them in field-sampled individuals within the native range of distribution of each species, in several cases measuring different populations of the same species. Traits were measured using consistent methodology across ecosystem types and analysed using phylogenetically explicit analytical approaches</p>
Trait plasticity and/or ecotypic differentiation	<p>Trait plasticity, that is shift of phenotype in accordance with growing conditions, is essential for plant species survival in many environments (Valladares et al., 2000). Likewise, populations of given species may adapt to different conditions, leading to ecotypic variation. Both plasticity and ecotypic differentiation would result in intraspecific trait variation across environments.</p> <p>If species are collected at sites distant from the mean climate of their range, then plastic and ecotypic trait adjustment might weaken the association of measured traits with mean climate, as species' sampled trait values would reflect the sampled climate rather than the mean climate of the species' native range (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Fyllas et al., 2020; Stiefert et al., 2015; Violle et al., 2012)</p>	<p>We sampled a subset of species in two or more sites with contrasting environmental conditions to test for intraspecific trait variation in relation to climate. Further, we developed novel tests of whether intraspecific trait variation contributed to trait–climate mismatch</p>
Trait multifunctionality and many-to-one mapping of traits to function	<p>Individual traits may be multifunctional and thus optimized in evolution and plasticity to multiple environmental factors (e.g. a trait may shift with herbivory, nutrient availability and aridity) and thus may be far from optimal for individual environmental factors, such as single climate variables (Sack &amp; Buckley, 2020). Additionally, adaptation to environmental conditions may be achieved through multiple alternative combinations of traits, such that individual traits would be weakly associated with environmental conditions (Alfaro et al., 2005; Marks &amp; Lechowicz, 2006b)</p>	<p>We measured multiple traits that represent different plant tissues and considered multiple climate variables. Then, we conducted principal component analyses to resolve adaptive and predictive relationships across the multiple traits and climate variables</p>

TABLE 1 (Continued)

Sources of mismatch	Rationale	Methodological approach to partially reduce mismatch
Complexity of the fundamental niche and divergence from the realized niche	A species' "fundamental niche" is complex, including the habitat niche, life form niche, phenological niche and regeneration niche, and each of these depend on the set of abiotic environmental conditions in which species is able to persist, as determined by its traits and physiological limits (Brown, 1984; Grubb, 1977; Hanski et al., 1993; Lee-Yaw et al., 2016; Peterson et al., 2012; Wiens, 2011). The climate niche refers specifically to the set of environmental conditions (e.g. temperature and precipitation) where a given species can occur, and thus would contribute, among other processes, to the fundamental niche (Bonetti & Wiens, 2014). Yet, the realized niche may differ from the fundamental niche due to other factors such as dispersal limitation, disturbance and biotic interactions including competition which can alter distributions in the field (Pérez-Ramos et al., 2019; Sheth et al., 2020; Walter, 1979)	NA
Traits and fitness are not directly related	Functional traits are frequently used as a metric for fitness, and assumed to influence success in a given environment, but this equivalence is not always straightforward, as functional traits are related to fitness through vital rates, and thus they might not predict fitness in many systems (Laughlin et al., 2020)	NA
Nonequilibrium processes	Species' distributions relate to dynamic processes including immigration, competition, evolution, and extinction under changing climates, and thus species' traits may not necessarily match their current distributions, and might better relate to their distribution under historical climates (DeAngelis & Waterhouse, 1987; Dobzhansky, 1950; Ohlemüller et al., 2008; Sheth et al., 2020; Stevens, 1989)	NA

Here, we tested the hypothesis that traits can robustly predict diverse species' current mean climate distributions. Across California, a biodiversity hotspot, we sampled a set of 107 diverse species within six ecosystems across a strong precipitation gradient (Figure 1c; see Table S1 in Supporting Information) to test trait-based prediction of species' climate niches. We implemented methods designed to effectively resolve trait-climate relationships. First, we sampled a strong climate gradient, to provide power to discern trait-climate relationships (Mooney & Dunn, 1970). Second, by sampling species growing together at few sites, we reduced the effects of plasticity and ecotypic variation (Ackerly & Cornwell, 2007; Lepš et al., 2011; Pellegrini et al., 2023), which we also estimated for a set of species that occurred at multiple sites. Third, we focused on 10 structural, hydraulic and economic traits that would contribute mechanistically to tolerance of climate stress (Bartlett, Scoffoni, & Sack, 2012; Greenwood et al., 2017; Liang et al., 2021; Rosas et al., 2019; Rowland et al., 2021; detailed in Figure 1b; Tables 2 and S1). Fourth, traits were measured using standard protocols, rather than compiled from databases (He et al., 2020; Li et al., 2022). Finally, we incorporated phylogenetic structure (Felsenstein, 1985; Opedal et al., 2015; Sanchez-Martinez et al., 2020; Skelton et al., 2021). Previous studies have incorporated these individual approaches extensively and rigorously, and a novel aspect of this study is our simultaneously applying all of them. Further, we clarified species' trait-climate mismatch, quantified as their deviation from the all-species climate-trait relationship (Figure 7a; Table 3). We expected that trait-climate mismatch would arise in part from intraspecific trait variation arising from plasticity and ecotypic adaptation. Thus, we hypothesized that trait-climate mismatch would be greater for species sampled for trait measurements further from the mean climate of their native ranges (Browne et al., 2019), that is, measured with a greater "climate sampling bias" (Figure 2b; Table 3).

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

We focused on six contrasting ecosystem types representing the range of biogeographic conditions in the California and Desert floristic provinces (CAFP, DFP; Figure 1c; Table S1). Together, the six sites contain vegetation of types that represent >247,000 km<sup>2</sup> of California, or 70% of its the terrestrial land area (Thorne et al., 2017). The sampling locations were distributed across a gradient of climatic aridity, including desert (Sweeney Granite Mountains Desert Research Center, part of the University of California Natural Reserve System, UCNRS), coastal sage scrub (Centro de Investigación Científica y de Educación Superior de Ensenada and Cañon de Doña Petra, Baja California), chaparral (Stunt Ranch Santa Monica Mountains Reserve, UCNRS), montane wet forest (Yosemite Forest Dynamics Plot, part of the ForestGEO network [Anderson-Teixeira et al., 2015]), mixed riparian woodland (Onion Creek, near the Chickering American River Reserve, UCNRS) and mixed conifer-broadleaf forest

**TABLE 2** Traits sampled for 107 California native woody species from six ecosystems distributed across a range of precipitation from Baja California (MX) to northern California (US), including symbols, units, and hypotheses for adaptation to climatic aridity (i.e. low precipitation, high temperature and high soil pH), based on previously published studies on a range of species, with references; a negative trend (indicated by “-”) indicates the trait would decrease from the mixed conifer-broadleaf forest to the desert, and a positive trend (indicated by “+”), indicates the trait would increase (Figure 1).

Trait	Symbol	Units	Hypothesized relationship with climatic aridity	Trends across species/ecosystems
Maximum plant height	$H_{max}$	m	-; when resources are abundant a greater height would enable stronger competition, and when resources are limited and temperatures high, lower stature would enable greater allocation below ground and reduced hydraulic pathlength susceptible to tension-driven embolism (King et al., 2006; Koch et al., 2004)	Liu et al. (2019) and Moles et al. (2009)
Osmotic potential at turgor loss (absolute)	$\pi_{tip}$	MPa	+; higher absolute $\pi_{tip}$ (or wilting point) indicates greater capacity to maintain cell volume and turgor pressure, and to maintain open stomata during dehydration. It is strongly correlated with drought tolerance within and across species, that is more tolerant species tend to have larger $\pi_{tip}$ and to withstand lower soil water potentials (Bartlett, Scoffoni, & Sack, 2012)	Fletcher et al. (2018), Griffin-Nolan et al. (2019)/Bartlett, Scoffoni, and Sack (2012)
Carbon isotope discrimination	$\Delta^{13}C$	‰	-; in $C_3$ photosynthetic species, higher $\Delta^{13}C$ values tend to correspond to high stomatal conductance integrated over leaf lifetimes, and may indicate higher $CO_2$ assimilation rates, whereas lower values tend to correspond to higher water use efficiency (i.e. assimilation relative to transpiratory water loss) integrated over the leaf lifetime (Farquhar et al., 1989)	Hu et al. (2009)
Leaf area	LA	cm <sup>2</sup>	-; smaller leaves have thinner boundary layers enabling leaves to avoid dangerous overheating on hot days and chilling on cool nights, and potentially to achieve higher gas exchange rates when soil is moist and temperatures are moderate (Gibson, 1998). Additionally, smaller leaves have smaller major veins and xylem conduits, and higher major vein densities, which can provide greater hydraulic safety during dehydration (Sack et al., 2012; Wright et al., 2017)	Wright et al. (2017)
Leaf mass per area	LMA	g m <sup>-2</sup>	+; higher LMA tends to confer longer leaf lifetimes and thus a conservative resource allocation that is adaptive for leaves that persist through multiple droughts and for species on low fertility soils. A high LMA may also correspond to higher elastic modulus which may enable greater water retention in leaves with lower wilting points (Evans, 1973; John et al., 2017; Westoby & Wright, 2006; Wright et al., 2004). Additionally, a high LMA may enable lower cuticular transpiration rates after stomata close due to lower surface area-to-volume ratio	de la Riva et al. (2016), He et al. (2006), Lamont et al. (2002) and Wright et al. (2005)
Nitrogen per mass	$N_{mass}$	mg g <sup>-1</sup>	-/+; higher $N_{mass}$ tends to correspond to higher light-saturated photosynthetic rates per leaf mass, typical of species native to high resource availability (Wright et al., 2004). Higher $N_{mass}$ can also provide drought adaptation by promoting both higher pulse-driven growth in periods of high water availability and a higher water use efficiency during moderate drought (Santiago et al., 2004; Wright et al., 2001; Wright & Westoby, 2002)	Field and Mooney (1986), Reich and Oleksyn (2004) and Wright et al. (2005)
Nitrogen per area	$N_{area}$	g m <sup>-2</sup>	+; higher $N_{area}$ can also provide drought adaptation by promoting both higher pulse-driven growth in periods of high water availability and a higher water use efficiency during moderate drought (Cunningham et al., 1999; Wright et al., 2001)	He et al. (2006) and Wright et al. (2005)
Carbon per mass	$C_{mass}$	mg g <sup>-1</sup>	-; higher $C_{mass}$ is linked with higher lignin concentration, which may protect leaves against herbivory. Adaptive for leaves that persist through multiple droughts and for species on low fertility soils	Ma et al. (2018)
Carbon to nitrogen ratio	C:N	-	+; higher C:N ratio reflects investment in structural support relative to photosynthesis, and thus thicker, sturdier cell walls adaptive for leaves that persist through multiple droughts and for species on low fertility soils (Fang et al., 2019)	Fang et al. (2019)
Wood density	WD	g cm <sup>-3</sup>	+; higher WD is associated with longer wood lifetimes and with a conservative resource allocation strategy that is adaptive for species that persist through multiple droughts and for species on low fertility soils. In addition, higher WD can correspond to lower vulnerability to xylem embolism and survival during drought (Chave et al., 2009; Gleason et al., 2016; Hacke et al., 2001; Liang et al., 2021)	Preston et al. (2006) and Thomas et al. (2007)

TABLE 3 Indices of variation presented in the study, including definition, calculation and references.

Term	Definition	Calculation
Trait-climate mismatch	The mismatch between the trait values measured for individuals occurring in the field and the trait values expected given the overall relationship of species' traits to their climatic distributions. The trait-climate mismatch represents the degree that a species' traits do not conform to expectations based on adaptation to its current climate distribution	Calculated as the residuals from the all-species' trait vs. climate relationship (Gelman & Hill, 2007). In this study, species' scores in principal component axes of climate variables were used, and scaled such that higher trait-climate mismatch represents traits more putatively adapted to aridity than expected, that is "hyperxeromorphic". $\text{trait} - \text{climate mismatch}_i = \text{obs Traits PC}_{1,i} - \text{pred Traits PC}_{1,i}$ , where obs Traits PC <sub>1,i</sub> is the measured Traits-PC1 score and pred Traits PC <sub>1,i</sub> is the Traits-PC1 score predicted from Climate-PC1 for each species
Climate sampling bias	The difference between the climate of the site where a species was sampled and the mean of its climatic distribution, calculated from current occurrences	climate sampling bias <sub>j</sub> = climate <sub>j</sub> - climate <sub>i</sub> , where climate <sub>j</sub> is the mean climate of the site j where species i was sampled from and climate <sub>i</sub> is the mean climate of its distribution. Based on (Browne et al., 2019)
Intraspecific trait and climate variation	Indices of variation in values for trait and climate variables of a given species sampled from multiple sites, a measure of the intra-specific variation (see Table 1). While based on the plasticity index (Valladares et al., 2000), ITV does not quantify species' phenotypic plasticity, which can only be measured from controlled experiments, but rather a combination of genetic and plastic variation	ITV or ICV <sub>j</sub> = $\frac{(\text{max}_j - \text{min}_j)}{\text{max}_j}$ , where max <sub>j</sub> is the maximum and min <sub>j</sub> is the minimum value of a given trait or climate variable for species i. Based on (Valladares et al., 2000)

(Angelo Coast Range Reserve, UCNRS). Permits were obtained for work in the UCNRS sites through direct communication with the reserve directors and for the Yosemite Forest Dynamics Plot through the United States Department of the Interior National Park Service (Permit #YOSE-2017-SCI-0009).

To test predictions of species' climate-trait relationships, we sampled single representative ecosystems of widespread types. This is a common approach in ecophysiological studies comparing communities (Baltzer et al., 2008; Blackman et al., 2014; Markesteijn et al., 2010; Zhu et al., 2013) and enables rigorous tests of species' trait relationships to climate. While statistical differences between single specific ecosystems in trait means are not necessarily generalizable to the ecosystem type, they highlight hypotheses to be tested in future studies using replicate ecosystems of each type.

## 2.2 | Sampling for leaf trait measurements

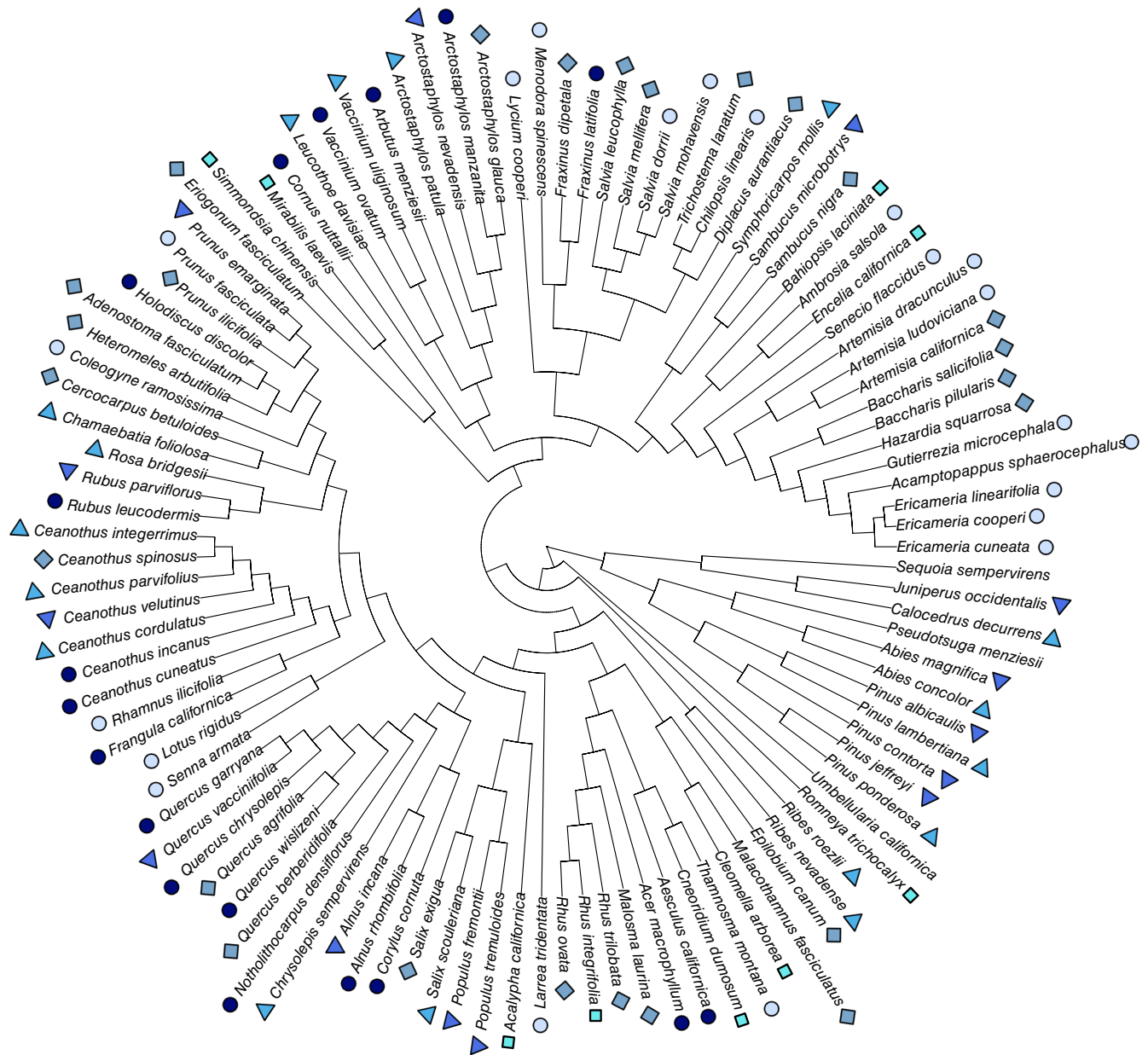
We selected the most abundant species for sampling at each site according to reserve managers and forest inventories. The species included in this study are taxonomically diverse, representing 31 plant families of mostly woody species (with the exception of *Artemisia dracuncululus*, *Epilobium canum* and *Mimulus aurantiacus*) and including many cases of closely related species that occur in contrasting environments (Extended data and Figure 2). Individual trees were sampled across the landscape and we avoided sampling adjacent individuals of the same species; thus, the microclimate of the exact sampling location differs across species and across individuals of the same species. Most species were sampled from a single site, but 15 of the 107 species were among the most common in two ecosystems (and one species, *Eriogonum fasciculatum* in three ecosystems; Table S12), and they were sampled in each location.

For 3–5 individuals of 14 to 26 species per site, we collected a mature, sun-exposed and non-epicormic branch, with no signs of damage or herbivory using pole pruners or a slingshot. Branches were transported to the lab in dark plastic bags with moist paper and rehydrated overnight in a dark saturated atmosphere before harvesting current-year grown, fully expanded leaves for all subsequent analyses. For compound-leaved species, whole leaves were used.

## 2.3 | Mechanistic trait measurements

Maximum tree height ( $H_{\text{max}}$ ) of all species was compiled from the Jepson Herbarium database (Jepson Flora Project, 2021). When not available, the  $H_{\text{max}}$  was recorded as the maximum value reported on the Jepson eFlora website (<https://ucjeps.berkeley.edu/eflora/>). The remaining functional traits were measured for three sun leaves per individual. Leaf saturated mass was measured using an analytical balance (XS205; Mettler-Toledo, OH, USA). Leaf area (LA) was measured using a flatbed scanner and analysed using software (ImageJ; <http://imagej.nih.gov/ij/>). After scanning, leaves were oven-dried at 70° for 72 h before measurement of dry mass. Leaf mass per





**FIGURE 2** Phylogenetic tree showing evolutionary relationships among 107 species from six California ecosystems. Symbols represent species of different ecosystems, with darker shades of blue representing greater water availability: mixed conifer-broadleaf forest (dark blue circles), mixed riparian woodland (triangles), montane wet forest (inverted triangles), chaparral (diamonds), coastal sage scrub (squares) and desert (light blue circles). Species were categorized according to the ecosystem they were sampled in (or, for species that occurred in multiple sites, that with climate closest to the mean aridity index, *AI*, of their climatic distribution).

area (*LMA*) was calculated as lamina dry mass divided by *LA* (Pérez-Harguindeguy et al., 2013).

The concentrations of leaf nitrogen and carbon per mass ( $N_{\text{mass}}$  and  $C_{\text{mass}}$ ) and the carbon isotope ratio ( $\delta^{13}\text{C}$ ) were determined from oven-dried leaves by continuous flow dual isotope analysis (Center for Stable Isotope Biogeochemistry, University of California, Berkeley; CHNOS Elemental Analyser interfaced to an IsoPrime100 mass spectrometer) (Kaklamanos et al., 2020).  $N_{\text{mass}}$  and  $C_{\text{mass}}$  were converted to a leaf area basis ( $N_{\text{area}}$  and  $C_{\text{area}}$ ) by multiplying by *LMA*. The carbon isotope discrimination ( $\Delta^{13}\text{C}$ ; in parts per thousand, ‰) was calculated following Farquhar and Richards (Farquhar &

Richards, 1984) as  $\Delta^{13}\text{C} = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{leaf}}}{1 + \frac{\delta^{13}\text{C}_{\text{leaf}}}{1000}}$ , assuming  $\delta^{13}\text{C}_{\text{air}}$  of -8‰ (NOAA Global Monitoring Laboratory, 2018). The  $\Delta^{13}\text{C}$  can be influenced by differences in atmospheric pressure across sites that vary in elevation (Hultine & Marshall, 2000; Seibt et al., 2008). Thus, we also calculated the difference in partial pressures of ambient ( $p_a$ ) and intercellular  $\text{CO}_2$  ( $p_i$ ),  $p_a - p_i$ , as a corrected measure of  $\Delta^{13}\text{C}$  (Hultine & Marshall, 2000; McDowell et al., 2010). We estimated the  $p_a$  by multiplying its mean atmospheric concentration ( $c_a$ ) for the years of sampling (Thoning et al., 2022) by the total barometric pressure (Hultine & Marshall, 2000). The  $p_i$  was estimated by multiplying the intercellular carbon concentration [ $c_i$ ; calculated as:  $c_i = \frac{(\Delta^{13}\text{C} - a) \times c_a}{b - a}$ ,

where  $a$  is the fractionation associated with diffusion in air (4.4‰) and  $b$  is the net fractionation associated with carboxylation by Rubisco (27‰–29‰) by the total barometric pressure (Farquhar et al., 1989; Hultine & Marshall, 2000).

We measured the wood density (WD) from 5-cm branch segments after bark removal using the water displacement method (Pérez-Harguindeguy et al., 2013). Branch segments were immersed in water and the mass of the displaced water was recorded; branch segments were then oven-dried at 70° for 120h and their dry mass was measured. WD was calculated as the segment dry mass divided by the mass of displaced water. Turgor loss point ( $\pi_{\text{tip}}$ ) was measured in two leaves from each of the 3–5 studied individuals. We used vapour-pressure osmometers (Vapro 5520 and 5600, Wescor, US) to obtain the osmotic concentration of the leaves and published calibration equations to estimate  $\pi_{\text{tip}}$  (Bartlett, Scoffoni, Ardy, et al., 2012).

## 2.4 | Environmental variables for species' native ranges

As in previous biogeographical trait–climate analyses, we modelled native climates on the basis of data for each species' natural occurrences from the Global Biodiversity Information Facility (GBIF; Baird et al., 2021; Fletcher et al., 2018; Sexton et al., 2009; Skelton et al., 2021) and using R software (version 3.4.4, R Core Team, 2018) to extract and calculate the mean, range and standard error of environmental variables. We focused on the relationships of traits with the mean climate of species distributions based on the assumption that given gene flow occurs among populations of a given species across its native range, species' mean phenotypic trait values would relate to their mean climate (Sexton et al., 2009).

Occurrence records were downloaded using the 'rgbif' package (Chamberlain et al., 2019) and filtered to keep herbarium records since 1950 and remove incomplete (latitude or longitude missing) and duplicated records, non-natural occurrences (e.g. records from botanical gardens or planted urban trees; Chamberlain et al., 2019; Riordan et al., 2015; see Extended data for download links and references for each species' occurrence records). We restricted the extent of observations to United States, Mexico and Canada unless the species had a known worldwide distribution. The resulting observations were manually screened for quality issues and outliers before the calculation of species-level descriptive statistics. We calculated species climatic envelopes using species occurrence points and not maps of distribution ranges because we were interested in the relationship between species' traits and climate variables, whereas range maps are based on ecological niche models (Harrison, 1997; Peterson, 1999) (ENMs) that are partially calculated from environmental variables and thus could potentially introduce bias in our climate analyses (Šimová et al., 2018).

We extracted 30 environmental variables from open-access raster layers, relating to air temperature (WorldClim, CRU; Hijmans et al., 2005), precipitation (WorldClim; Hijmans et al., 2005), aridity (CGIAR-CSI, NCAR-UCAR; Zomer et al., 2008) and soil

characteristics (ISRIC Soilgrids; Hengl et al., 2017; see Table S3 for detailed description, download links and references for each variable). The raster layers with the same resolution were stacked using the *stack* function from the 'raster' package (Hijmans & van Etten, 2012) and the environmental variables for each occurrence record were extracted using the *extract* function from the 'dismo' package (Hijmans et al., 2011). Due to their coarse resolution, these environmental variables are effective in characterizing large scale patterns but do not reflect differences in microclimate, that is temperature, water and nutrient availability, irradiance and soil composition (Perez & Feeley, 2021). In the main text, we focus on the relationships between traits and the mean value of nine key environmental variables: mean annual temperature, MAT; maximum temperature of the warmest month,  $T_{\text{max}}$ ; minimum temperature of the coldest month,  $T_{\text{min}}$ ; growing degree-days above 5°C, GDD; mean annual precipitation, MAP; precipitation of the wettest month,  $P_{\text{wet}}$ ; precipitation of the driest month,  $P_{\text{dry}}$ ; aridity index, AI; and soil pH,  $\text{Soil}_{\text{pH}}$ . The relationships between traits and the mean and the range (max-min) of the remaining 21 environmental variables can be found in the supplemental tables. The complete dataset with species- and site-level environmental variables is available in the Extended data.

## 2.5 | Phylogenetic reconstruction

Sequences for all 107 species were automatically downloaded from GenBank and aligned with MAFFT (multiple alignment using fast Fourier transform; Matrix Maker; [github.com/wf8/matrixmaker](https://github.com/wf8/matrixmaker)) (Freyman & Thornhill, 2016). We focused on eight genes, ITS, matK, MatR, ndhF, rbcL, trnL-trnF, 18S and atpB. Each species was represented with at least one up to seven gene accessions, with an average of 3.3 genes. The genes were then concatenated for each species, and a maximum likelihood analysis of the phylogenetic relationships was conducted using a general time reversible (GTR) model of substitution (SeaView version 4; Gouy et al., 2010). To calibrate branch lengths, we used the *chronos* function in the R package 'ape' (Paradis & Schliep, 2019). The species relationships were assessed by comparing the angiosperm phylogeny group phylogeny with that reconstructed in this paper; all relationships were consistent between the two, with three exceptions in nodes with low support (Stevens, 2019). The output of species branch lengths was utilized to incorporate species relatedness into downstream analyses.

## 2.6 | Statistical analyses

All statistical analyses and plots were performed in R software (versions 3.4.4; R Core Team, 2018 and 4.0.2 R Core Team, 2020) and packages available from the CRAN platform. To test for differences among ecosystems in the mean climate of their constituent species' distributions, we performed one-way ANOVAs using the *aov* function from the 'stats' package followed by a Tukey test at 5% probability using *TukeyC* function and package (Sokal & Rohlf, 2012;

Tables S4 and S8). To test for differences in functional traits among ecosystems, we performed nested ANOVAs using the *aov* function, with species nested within ecosystems, followed by a Tukey test at 5% probability (Sokal & Rohlf, 2012). Trait and climate variables that did not fulfil the normality and homoscedasticity assumptions were log<sub>10</sub>-transformed prior to analyses. Variables that included both negative and positive numbers were incremented by a constant equal to the lowest species mean+1 before log-transformation, such that 1 was the lowest value for that variable (Tables S4 and S9). For  $\pi_{tip}$ , which is negative, we multiplied the values by -1 prior to log-transformation.

To summarize the variation in functional traits and the mean climate of the range of distribution of species, we performed principal component analyses (PCAs) on species means of eight nonredundant functional traits and climate variables using the *prcomp* function in the 'stats' package. We included eight of the 10 study traits to avoid strong collinearity; given that we included  $N_{mass}$ , we did not include  $N_{area}$  and C:N in any of the multivariate analyses. All variables were log-scaled prior to analyses. We extracted the species scores (scaled to range from -1 to 1) of PC axes 1 and 2, and used them to summarize trait and climate main axes of variation in subsequent analyses.

To test for relationships between single traits and environmental variables while accounting for species relatedness, we performed phylogenetic generalized least-squares analyses (PGLS; Felsenstein, 1985; Harmon, 2019) where the environmental parameters were the dependent variables and the 10 measured traits were the independent variables, using the *pgls* function from the 'caper' package (Orme et al., 2018) with lambda ( $\lambda$ ; metric of phylogenetic signal that quantifies the influence of shared history on trait distributions and ranges from 0 [phylogenetic independence] to 1 [species' traits covary proportionally to their shared evolutionary history]) optimized using maximum likelihood (Freckleton et al., 2002). Cross-species phylogenetic analyses required single values for each species, so for the 15 species collected at more than one site we calculated the mean trait values across the sites and assigned those species to the site most similar in aridity index (AI) to the mean of that species' range (Extended data).

Given the use of multiple significance tests of trait-climate correlations, we assessed the significance of the overall correlative pattern by applying a proportion test (after Baird et al., 2021). We thus calculated the number of significant correlations relative to the 132 correlations we hypothesized (Table 2 and citations therein) among, on one hand, the 10 functional traits plus the first two PCA axes for traits (Traits-PC1 and 2), and on the other hand, the nine climate variables included in the PCA analysis plus the first two PCA axes for climate variables (Climate-PC1 and 2). Then, we used the function *prop.test* in the 'stats' package to test if the proportion of significant correlations was greater than that expected from chance (0.05) (Table S10).

To highlight the trait variation that arose across the sampled ecosystems, in addition to cross species analyses, we also present trait-environment relationships averaged for species within ecosystems,

using the across-species mean trait values and the mean of the mean climate of their constituent species' distributions. We used Pearson's correlations on untransformed and log-transformed data, to test for either approximately linear or non-linear (i.e. approximate power-law) relationships respectively and report the higher correlation value in the text (Table S7).

We tested the power of multiple traits to predict the mean environment of the distribution of each species using PGLS to predict Climate-PC1 from eight traits not redundant in their calculation (all but  $N_{area}$  and C:N, as explained above). To select the trait-based models that best predicted the climate variables, we tested the combination of all possible predictor variables and compared models using AICc (code available on GitHub). The comparison of models by AICc enables maximum likelihood selection of the model and its parameter values without bias by the number of parameters or models (penalizing models with more parameters; Burnham & Anderson, 2010). To determine the percentage contribution of each trait to the prediction of climate variables, we performed a hierarchical partitioning analysis using the 'hier.part' package (Chevan & Sutherland, 1991; Walsh & Mac Nally, 2013). In addition to testing models to predict Climate-PC1, we also tested models to predict individual widely used environmental variables from traits: maximum temperature of the warmest month ( $T_{max}$ ), mean annual precipitation (MAP), aridity index (AI) and soil pH ( $Soil_{pH}$ ; high  $Soil_{pH}$  is associated with low concentration of exchangeable soil phosphate and iron; Tyler, 1996; Table S11). Given that  $\Delta^{13}C$  may be influenced by site elevation, and also may include a potentially more direct influence of environmental factors in its determination than other traits, such as vapour pressure deficit (VPD) and temperature (Seibt et al., 2008), we also conducted this analysis with  $p_a-p_i$  (which corrects  $\Delta^{13}C$  for elevation), and also without including this trait (Table S11).

To discern the power of incorporating phylogeny in our analyses to predict species' mean climate, we performed multiple regression following the same workflow as in the evolutionary analysis but using ordinary least squares regression instead of PGLS. We compare the models using AIC,  $R^2$  and root mean squared error (RMSE; Table S2).

In addition to multiple regression analyses, we used principal component analyses to quantify the overarching power to predict species' mean climate variables from traits, and to estimate each species' "trait-climate mismatch". We regressed species' Traits-PC1 scores against their Climate-PC1 scores using PGLS and species' residuals from this regression were considered as their trait-climate mismatch (Gelman & Hill, 2007), that is the amount of trait variation not explained by mean climate (Table 3). Purposefully, the definition of trait-climate mismatch as residuals from the trait versus climate relationship renders trait-climate mismatch statistically independent of environmental variables and of the Climate-PC1. This approach enabled the subsequent testing of the relationship of trait-climate mismatch with climate variables, while avoiding the circularity that would have arisen if trait-climate mismatch had been defined as the residuals of climate versus traits. To simplify presentation, as Climate-PC1 values were negatively related to aridity and Traits-PC1

values positively related to adaptation to aridity, we multiplied Climate-PC1 scores by  $-1$  such that the relationship between the axes was positive (Table S6). Notably, in our definition of trait-climate mismatch, a higher value does not represent greater mis-adaptation to climate; rather, a higher trait-climate mismatch value represents greater adaptation of traits to aridity than would be expected from the all-species trait-climate relationship, and a lesser value represents a lesser adaptation of traits to aridity, though not necessarily to other environmental variables.

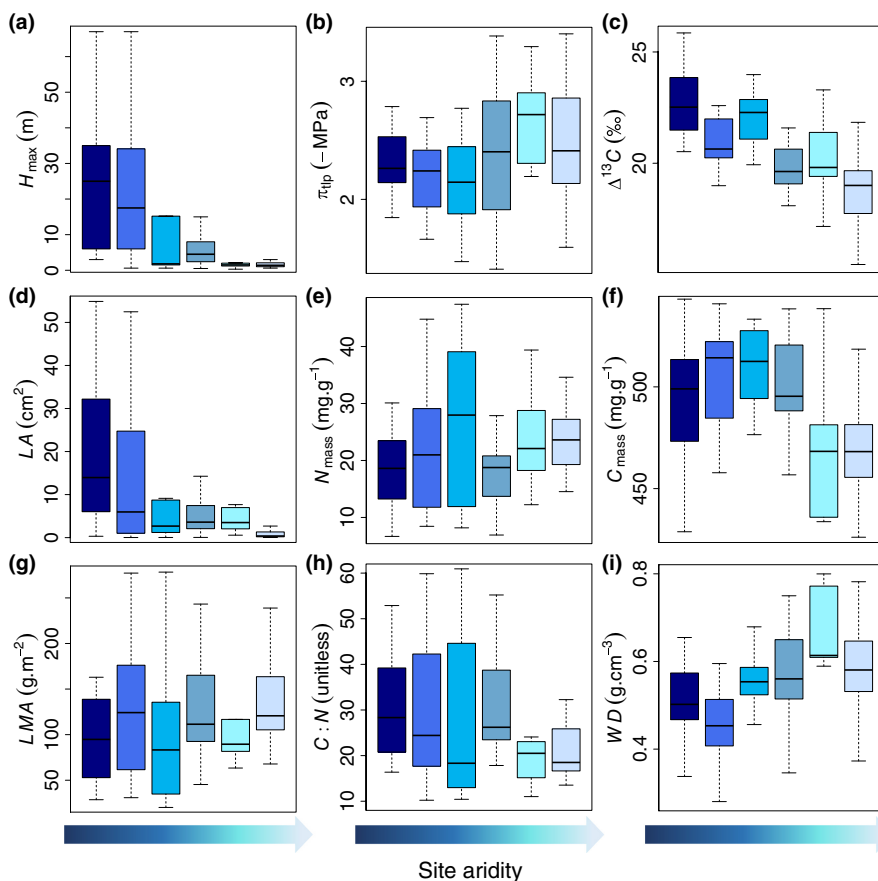
Given that species' traits may adjust plastically or genetically (ecotypically) in relation to climate, we conducted two analyses to test the potential importance of intraspecific trait variation across sites as an influence on trait-based climate prediction. First, for each of the 15 study species that occurred at more than one site, we applied a commonly used phenotypic plasticity index (Valladares et al., 2000; Table S12) to calculate indices of intraspecific trait variation (ITV) and intraspecific climate variation (ICV) for each trait and climate variable (Table 3) as  $\frac{(\max - \min)}{\max}$ , where  $\max$  and  $\min$  are the maximum and minimum values of a trait or climate variable measured from individuals of a given species across sites and tested relationships across species between intraspecific trait and climate variation indices using PGLS. Second, we tested whether species' trait-climate mismatch may depend on a climate sampling bias, calculated as the difference in a given climate variable between the sampling location and the mean of the species' distribution (after the "climate transfer distance" of Browne et al., 2019), such that a species sampled from

a more arid location than the mean of its distribution would have a higher climate sampling bias, whereas species sampled from a less arid location would have a lower climate sampling bias. We tested associations across species of the trait-climate mismatch with the climate transfer distance with respect to two climate variables, maximum temperature of the warmest month,  $T_{\max}$ , and mean annual precipitation, MAP, using PGLS.

### 3 | RESULTS

#### 3.1 | Functional trait variation in relation to climate

Species differed strongly within and across the six California ecosystems in the 10 functional traits (Figure 3; Table S4), with 15%–40% of variation in given traits explained by the ecosystem type, 42%–79% by species and 2%–18% intraspecifically (nested ANOVAs; Table S4). All 10 traits varied across ecosystems with climatic aridity as hypothesized (Figures 1b and 3; Table 2): species of more arid ecosystems had lower water potential at turgor loss point ( $\pi_{\text{tlp}}$ ), lower carbon isotope discrimination ( $\Delta^{13}\text{C}$ ), smaller individual leaf area (LA), and maximum height ( $H_{\max}$ ), and higher nitrogen concentration per leaf area ( $N_{\text{area}}$ ), leaf mass per area (LMA), carbon-to-nitrogen ratio (C:N) and wood density (WD), whereas species of wetter ecosystems had opposite tendencies for trait values, associated with competitive resource use and investment in anti-herbivory defence,



**FIGURE 3** Variation across ecosystems, from wettest to driest, in functional traits. Symbols represent species of different ecosystems, with darker shades of blue representing greater water availability: mixed conifer-broadleaf forest (dark blue circles), mixed riparian woodland (inverted triangles), montane wet forest (diamonds), chaparral (squares), coastal sage scrub (light blue circles), desert (light blue circles). (a) maximum plant height ( $H_{\max}$ ), (b) absolute turgor loss point ( $\pi_{\text{tlp}}$ ), (c) carbon isotope discrimination ( $\Delta^{13}\text{C}$ ), (d) leaf area (LA), (e) nitrogen per mass ( $N_{\text{mass}}$ ), (f) carbon per mass ( $C_{\text{mass}}$ ), (g) leaf mass per area (LMA), (h) carbon to nitrogen ratio (C:N) and (i) wood density (WD). All nine traits and  $N_{\text{area}}$  were significantly different across ecosystems (Nested ANOVAs; Table S4;  $p < 0.001$ ).

including higher nitrogen and carbon concentrations per leaf mass ( $N_{\text{mass}}$  and  $C_{\text{mass}}$ ) (Figure 3; Table S4).

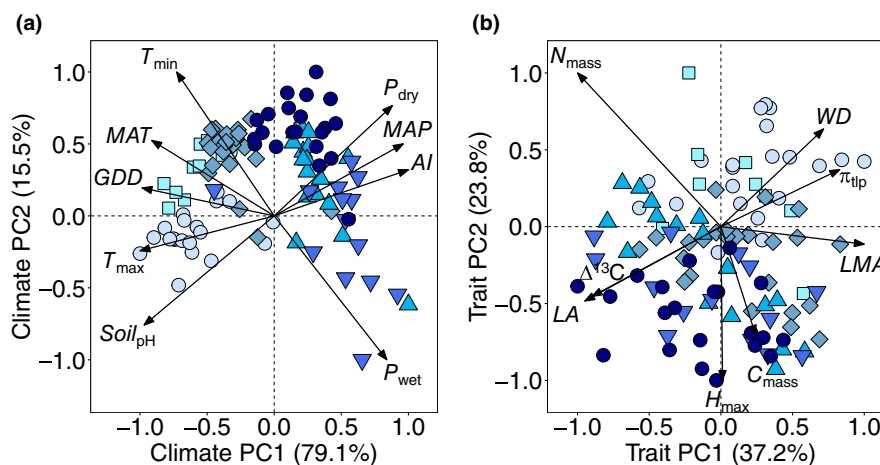
The strong importance of climatic aridity was also highlighted by principal component analyses of climate variables and trait values (Climate-PCA and Traits-PCA, for nine environmental variables and eight traits respectively). The first two Climate-PCA axes (Climate-PC1 and PC2; Figure 4a; Table S5) accounted for 79.1% and 15.5% of variation respectively. Climate-PC1 corresponded to climatic warmth and aridity, including higher mean annual temperature (MAT), maximum temperature of the warmest month ( $T_{\text{max}}$ ), lower annual precipitation (MAP) and aridity index (AI), and to more basic soil ( $\text{Soil}_{\text{pH}}$ ). Climate-PC2 corresponded to the minimum temperature of the coldest month ( $T_{\text{min}}$ ). The Traits-PCA also showed the strong correspondence of traits with adaptation to aridity across species. Traits-PC1 and PC2 accounted for 37.2% and 23.8% of variation, respectively: high Traits-PC1 values corresponded to low  $\pi_{\text{tjp}}$ , small LA, high LMA, high WD, and low  $N_{\text{mass}}$  and high Traits-PC2 values to lower  $H_{\text{max}}$  and  $C_{\text{mass}}$  (Figure 4b; Table S6).

Across species, Traits-PC1 was correlated with Climate-PC1 (PGLS;  $r=0.63$ ;  $p<0.001$ ; Table S9), and Traits-PC2 with both Climate-PC1 and 2 ( $r=0.45$  and  $-0.44$ , respectively;  $p<0.001$ ; Table S9). Species' Climate-PC1 scores were correlated with  $\pi_{\text{tjp}}$  (Figure 5a), LMA,  $N_{\text{area}}$ , C:N, WD,  $\Delta^{13}\text{C}$ , LA,  $N_{\text{mass}}$  and  $C_{\text{mass}}$  ( $|r|=0.22$ – $0.56$ ;  $p<0.05$ ; Figure S2; Table S9), and species' Climate-PC2 scores with Traits-PC2,  $\Delta^{13}\text{C}$ , C:N,  $H_{\text{max}}$ ,  $N_{\text{mass}}$  and  $N_{\text{area}}$  ( $|r|=0.28$ – $0.44$ ;  $p<0.05$ ; Table S9;  $|r|$  is presented to highlight relationship strengths, whether relationships are positive or negative, as indicated in the Figures and Tables). We found support for 103/132 (78%) of our

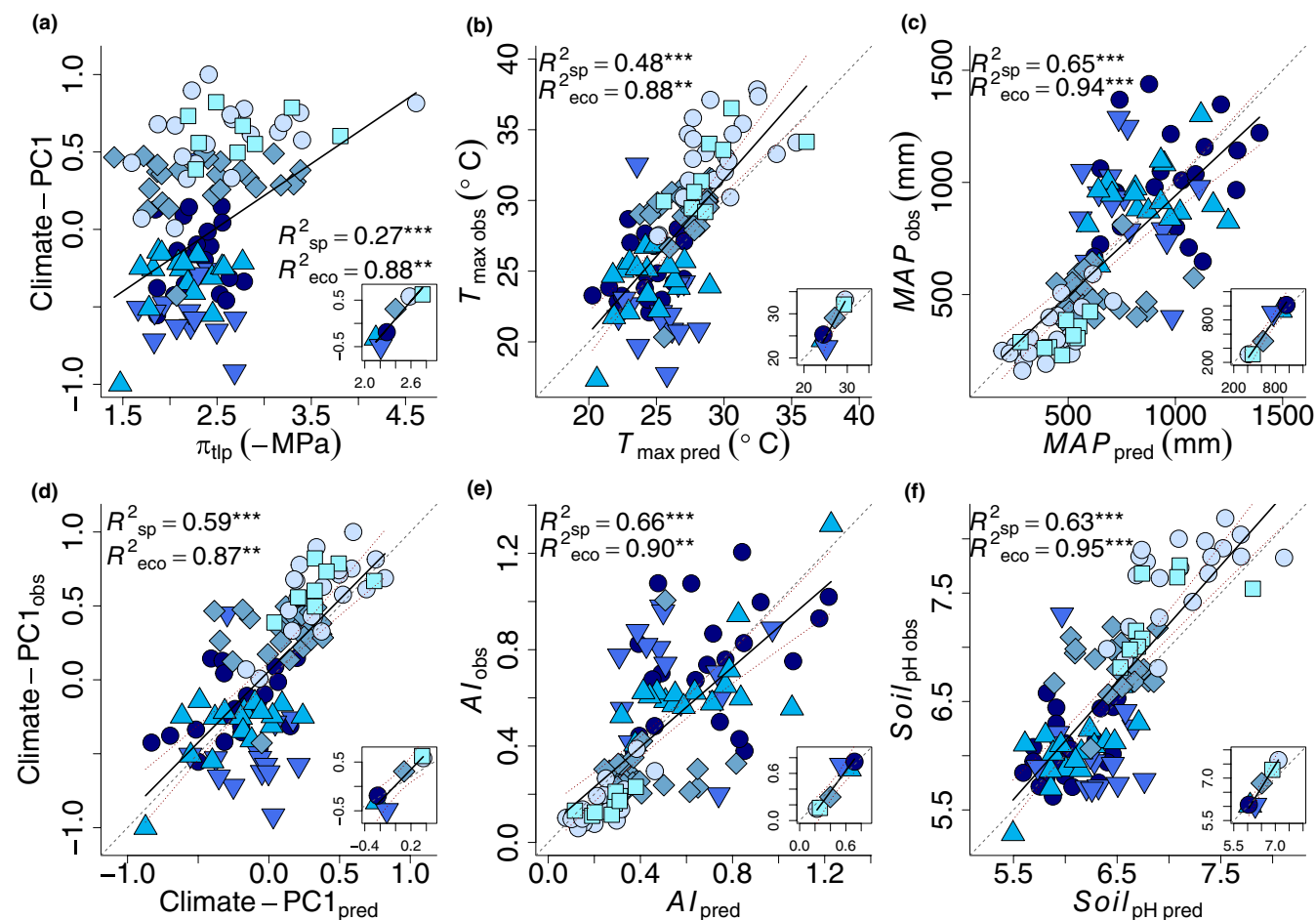
hypothesized trait-environmental variable relationships (Table S10) a proportion far higher than our null hypothesis of chance (0.05;  $p=1.05\text{E}-10$ ; proportion test). Indeed, all nine of the climate variables representing the mean of species ranges were correlated with species' values for one or more individual traits ( $|r|=0.20$ – $0.70$ ;  $p<0.05$ ; Tables S9 and S10). Across the six ecosystems, means for four traits were correlated with Climate-PC1, that is,  $\pi_{\text{tjp}}$  (Figure 5a-inset),  $H_{\text{max}}$ , WD and  $C_{\text{mass}}$  ( $|r|=0.83$ – $0.94$ ;  $p<0.05$ ; Figure S2-insets; Table S7).

### 3.2 | Functional trait-based prediction of species' native climate

Our analyses demonstrated the power of mechanistic traits to predict variables representing the mean climate of species' ranges. Regression models predicted Climate-PC1 from traits; six of the eight nonredundant traits included in the analysis were selected as best predictors, in order of importance according to hierarchical partitioning:  $\Delta^{13}\text{C}$ , LMA,  $\pi_{\text{tjp}}$ ,  $C_{\text{mass}}$ , WD and  $N_{\text{mass}}$  (adjusted  $R^2=0.59$ ;  $p<0.001$ ; Figure 5d; Table S11). For the six ecosystems, the across-species average values of observed Climate-PC1 scores were strongly predicted by the mean of Climate-PC1 scores estimated for each species from multivariate regression ( $R^2=0.87$ ;  $p<0.01$ ; Figure 5d-inset; Table S7). Multivariate regression models also predicted individual environmental variables from functional traits, with  $\Delta^{13}\text{C}$ , LMA and  $C_{\text{mass}}$  selected in the best-fit models for  $T_{\text{max}}$ , MAP, AI and  $\text{Soil}_{\text{pH}}$  ( $R^2=0.48$ – $0.66$ ;  $p<0.001$ ; Figure 5b,c,e-f;



**FIGURE 4** Principal component analyses (PCA) of (a) mean climate variables for species' ranges of distribution (Table S5) and (b) a set of non-redundant species traits for 107 species from six California ecosystems (Table S6). The climate variables included were mean annual temperature, MAT, maximum temperature of the warmest month,  $T_{\text{max}}$ , minimum temperature of the coldest month,  $T_{\text{min}}$ , mean annual precipitation, MAP, precipitation of the wettest month,  $P_{\text{wet}}$ , precipitation of the driest month,  $P_{\text{dry}}$ , aridity index, AI, growing degree-days, GDD, and soil pH,  $\text{Soil}_{\text{pH}}$ . For all tests of relationships with "Climate-PC1" we multiplied by "–1" so the relationship between Climate-PC1 and Traits-PC1 is positive, for clarity, as these reflected climatic aridity and adaptation to aridity respectively. The traits included were maximum adult height,  $H_{\text{max}}$ , turgor loss point,  $\pi_{\text{tjp}}$  (multiplied by "–1" prior to PCA), carbon isotope discrimination,  $\Delta^{13}\text{C}$ , leaf area, LA, leaf mass per area, LMA, foliar nitrogen and carbon concentrations,  $N_{\text{mass}}$  and  $C_{\text{mass}}$ , and wood density (WD). Symbols represent species of different ecosystems, with darker shades of blue representing greater water availability: mixed conifer-broadleaf forest (dark blue circles), mixed riparian woodland (triangles), montane wet forest (inverted triangles), chaparral (diamonds), coastal sage scrub (squares), desert (light blue circles).



**FIGURE 5** The prediction of plant climate distribution means from functional traits for 107 species from six California ecosystems demonstrated using a phylogenetic multivariate approach. (a) Illustration of an across species climate-trait relationship: the first axis of a principal components analysis of species' climate variables (Climate-PC1) plotted against turgor loss point,  $\pi_{\text{tlp}}$  (main panel; phylogenetic generalized least squares;  $\lambda=0.83$ ; Table S9) and ecosystems (inset; ordinary least squares; Table S7). (b–f) Relationships between observed climate variables and the values predicted by multiple functional traits (PGLS;  $\lambda$  ranged from 0.70 to 0.80; Table S11); (b) maximum temperature of the warmest month,  $T_{\text{max}}$ , (c) mean annual precipitation, MAP, (d) scores of Climate-PC1, (e) aridity index, AI, and (f) soil pH,  $\text{Soil}_{\text{pH}}$ . Main plots show relationships for species (phylogenetic generalized least squares,  $R^2_{\text{sp}}$ ), and inset plots show the relationships among ecosystem mean values (ordinary least squares,  $R^2_{\text{eco}}$ ), with the dashed lines representing the 1:1 relationship and dotted red lines the confidence intervals. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

Table S11). As  $\Delta^{13}\text{C}$  may be influenced by site elevation, and also may include a potentially more direct influence of environmental factors in its determination than other traits, such as vapour pressure deficit (VPD) and temperature (Seibt et al., 2008), we also conducted this analysis with  $p_a - p_i$  (which corrects  $\Delta^{13}\text{C}$  for elevation and temperature), and also without including this trait. Notably,  $p_a - p_i$  was highly correlated with  $\Delta^{13}\text{C}$  across species ( $r=0.96$ ;  $p < 0.001$ ), and  $\Delta^{13}\text{C}$  was not correlated with VPD or temperature across species or sites (Figure S1). Further, conducting this analysis substituting  $p_a - p_i$  for  $\Delta^{13}\text{C}$ , or removing  $\Delta^{13}\text{C}$  altogether yielded similar results in the predictive models (Table S11), so we focus on  $\Delta^{13}\text{C}$  in the main text.

Our test of the value of an explicit evolutionary analysis incorporating phylogeny relative to a historic analysis for the multiple regression prediction of Climate-PC1 (i.e. comparing PGLS with OLS) showed that the evolutionary analysis was selected with higher

likelihood (AIC lower by  $>2$ ), though with similar predictive power with respect to  $R^2$  and RMSE as the PGLS approach (Table S2).

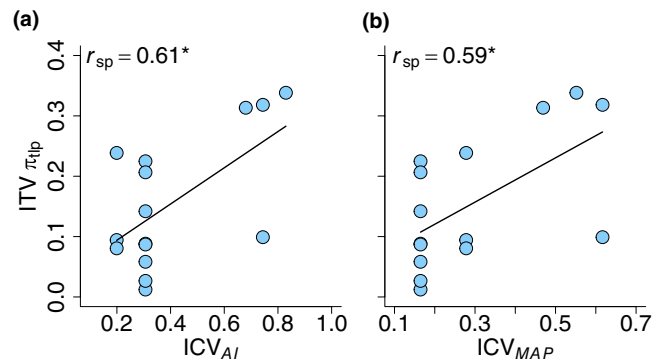
### 3.3 | Quantifying species trait-climate mismatch and its relationship to intra-specific trait variation

We estimated species' trait-climate mismatch as residuals from the relationship of Trait-PC1 to Climate-PC1 (Figure 7a). The species with highest trait-climate mismatch (indicating traits more xeromorphic than expected based on its mean climate) included especially those with high LMA and low  $\pi_{\text{tlp}}$ , such as conifers (*Abies concolor*, *A. magnifica*, *Calocedrus decurrens*, *Juniperus occidentalis*, *Pinus albicaulis*, *P. contorta*, *P. lambertiana*) and some of the most drought-tolerant species across ecosystems (*Adenostoma fasciculatum*, *Arctostaphylos*

*nevadensis*, *Arctostaphylos patula*, *Larrea tridentata* and *Quercus vaciniifolia*; Extended data).

Our analyses indicated that on average, species were sampled in ecosystems in locations representative of their climate distribution. Thus, the climate variables for the ecosystem location were correlated with the mean climate variables of their component species for  $T_{max}$ , MAP, AI,  $Soil_{pH}$  and Climate-PC1 scores ( $|r|=0.85-0.96$ ;  $p<0.05$ ; Figure S3; Table S7). Yet, our data supported the hypothesis that the difference between the climate of the sampling location and that of the species' mean distribution influenced trait-climate

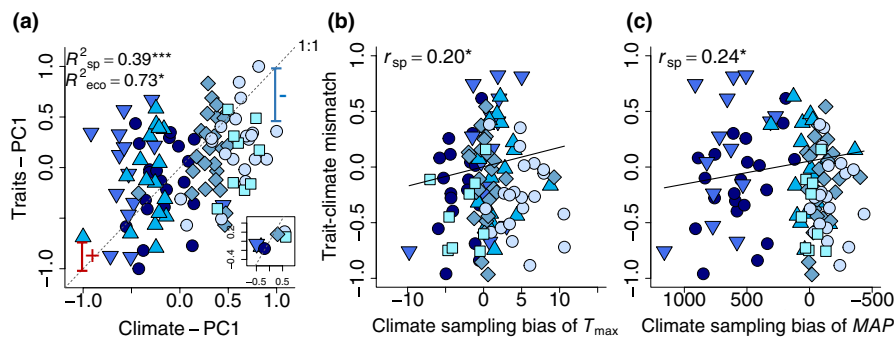
mismatch, due to plastic or ecotypic trait adjustment to climate in the sampled ecosystem (Table 3). First, for the 15 species that occurred in more than one ecosystem across species, intraspecific trait variation (ITV) was associated with the intraspecific climate variation index (ICV) for multiple traits; ITV in  $\pi_{tjp}$  was positively correlated with ICV in AI, MAP and  $P_{wet}$ ; ITV in  $N_{mass}$  and N:C were positively correlated with ICV in GDD and/or  $T_{min}$ ; and ITV in  $C_{mass}$  was positively correlated with ICV in with  $Soil_{pH}$  ( $|r|=0.59-0.62$ ;  $p<0.05$ ; Figure 6; Tables S12 and 13). Second, across all 107 species, trait-climate mismatch was positively correlated with the climate sampling bias, that is, the difference in climate between the species' sampling site and the mean climate of its native range ( $|r|=0.21-0.24$  for  $T_{max}$  and MAP;  $p<0.05$ ; Figure 7b,c; Table S9). Thus, species sampled at sites more arid than the mean of their range had traits more xeromorphic than expected from the mean climate of their distribution (Figure 7b,c).



**FIGURE 6** The influence of plasticity on functional traits for 15 species that were sampled from more than one California ecosystem. For the 15 species (Table S12), the relationship of the intraspecific variation in the osmotic potential at turgor loss,  $ITV_{\pi_{tjp}}$ , with (a) the intraspecific variation in aridity,  $ICV_{AI}$ , and (b) mean annual precipitation,  $ICV_{MAP}$  (phylogenetic generalized least squares; Table S13). Similar relationships were found for other traits and climate variables (Table S13). \* $p<0.05$ .

## 4 | DISCUSSION

Our findings demonstrate the strong power of traits for estimation of species and ecosystem climate distributions and support theory for the optimization of traits versus climate (Parkhurst & Loucks, 1972; Sack & Buckley, 2020; Xu et al., 2021). Thus, the striking quantitative association of mechanistic traits with climate variables evidently arose from millennia of evolution and community assembly that matched plant physiology to climate across California (Cornwell & Ackerly, 2009; Cornwell et al., 2006; Mitchell et al., 2018), with species tracking climate as it changed (Wang et al., 2023), and with a potential further reinforcement arising over long time scales



**FIGURE 7** The association of traits with climate across species and ecosystems, the derivation of trait-climate mismatch, and two potential influences arising from intra-specific trait variation. Symbols represent species of different ecosystems, with darker shades of blue representing greater water availability: mixed conifer-broadleaf forest (dark blue circles), mixed riparian woodland (triangles), montane wet forest (inverted triangles), chaparral (diamonds), coastal sage scrub (squares) and desert (light blue circles). (a) A principal components analysis of species' climate variables and trait variables yielded first axes (Traits-PC1 and Climate-PC1, respectively) that represented climatic aridity and trait values associated with adaptation to aridity, and the two are strongly related across species (main plot; phylogenetic generalized least squares,  $R^2_{sp}$ ; Table S9) and ecosystems (inset; ordinary least squares,  $R^2_{eco}$ ; Table S7). Thus, the residuals from this relationship represent the trait-climate mismatch where a species with higher values possesses traits more xeromorphic than expected from the all-species relationship. Trait-climate mismatch represents a species' trait divergence from the mean association with climate across species and may entail either a stronger or lesser adaptation to climate extremes, and therefore may pre-adapt a species, or render it more vulnerable to climate change. (b, c) Testing hypotheses for influences on trait-climate mismatch arising from intra-specific trait variation. Relationship between the trait-climate mismatch and species' climate sampling bias in terms of (b) maximum temperature of the warmest month,  $T_{max}$ , and (c) mean annual precipitation, MAP (PGLS;  $\lambda=0.86$  and  $0.89$ , respectively; Table S9). \* $p<0.05$ ; \*\* $p<0.01$ ; \*\*\* $p<0.001$ .

when ecosystems can influence their local and regional climate via the water cycle, soil accumulation and other processes (Bounoua et al., 2010; Boyce et al., 2009; Boyce & Lee, 2010; Crous, 2019; Wang et al., 2009).

The successful prediction of species' mean climate from mechanistic traits provides an optimistic counterpoint to the generally weak trends shown by previous studies of trait-climate relationships for diverse species at large geographical scales, especially when based on single traits compiled from large databases (e.g. Moles et al., 2014; Šímová et al., 2018; Taugourdeau et al., 2014; van der Plas et al., 2020; Veski et al., 2020). Across this gradient of aridity,  $\Delta^{13}\text{C}$ ,  $LMA$  and  $\pi_{\text{tip}}$  were the traits that individually best predicted Climate-PC1 but with limited power individually ( $R^2 = 0.25\text{--}0.31$ ;  $p < 0.001$ ; Table S9). Using multivariate models, the variation in Climate-PC1 explained by traits doubled (Figure 5; Table S11). Across California, species with high Climate-PC1 scores, which are adapted to drier warmer climates and more alkaline soils, have thicker and denser leaves, more negative turgor loss point and lower carbon discrimination rates, which confer higher tolerance to aridity by allowing the plants to continue photosynthesis when water availability is low and/or contributing to fast growth when water is available (Bartlett, Scoffoni, & Sack, 2012; Fletcher et al., 2018; Kramp et al., 2022).

The power of our approach to resolve relationships despite the many potential sources for mismatch of species' traits from their current climate distributions (Table 1) can be attributed to the methodology described here, including the quantification of relationships along a strong regional biogeographic gradient, and the measurement in standard ways of traits with mechanistic significance across sites relatively close to the mean of their climate distribution. The particular importance of sampling species for traits near the mean of their climate distribution was highlighted by our analyses showing that intra-specific variation arising from plastic and ecotypic adjustment led to an association across species of trait-climate mismatch with climate sampling bias (Tables S9 and S13). Our ITV and climate mismatch analysis helped to reveal the role that within-species variation plays in complicating trait-climate relationships. Unsurprisingly, larger ITV arose for species sampled across larger climate gradients (Figure 6) and a significant fraction of the residual variation in trait-climate space is explained by how far outside the niche center traits were measured. These findings point to the important influence of ITV on trait-climate relationships.

Notably, we focused on 10 traits with mechanistic importance in the climate-dependency of vital rates and community assembly (Adler et al., 2014; Anderegg, 2023; Kraft et al., 2008, 2015; McGill et al., 2006; Medeiros et al., 2019; Poorter et al., 2008; Sobral, 2021; Uriarte et al., 2016; Violle et al., 2007, 2011; Voltaire et al., 2020). These traits include so-called 'hard' physiological traits (e.g.  $\pi_{\text{tip}}$  and  $\Delta^{13}\text{C}$ ) which may be more directly mechanistically linked with plant adaptation to withstand aridity, as well as 'soft' morphological traits that may contribute indirectly, or as part of a correlated complex of traits (e.g.  $H_{\text{max}}$ , leaf size and  $LMA$ ). The inclusion of additional traits would likely improve predictive power, including

hydraulic vulnerability, stomatal and vein traits, additional nutrient concentrations, photosynthetic responses, and, in addition, life history traits such as seed size, especially if other life forms including non-woody species are considered. We found that the inclusion of phylogeny strongly increased the likelihood (and reduced the AICc) of the model, but did not add additional predictive power relative to an ahistorical model based on our analysis of the  $R^2$  and RMSE of multiple regression models (Table S2). We expect that including more species that would be closely-related within given lineages with well-resolved phylogenies (Dunbar-Co et al., 2009; Fletcher et al., 2018; Scoffoni et al., 2016) may increase the predictive value of phylogeny in trait-based climate prediction relative to in our study design, which focused on diverse species and a broad phylogeny (Edwards, 2006; Schmerler et al., 2012). Predictive power may also be gained by considering trait variation within and among populations of given species, and finer scale climate data, including microclimate, reflecting topography and vegetation cover, and, potentially data on biotic stressors, such as the presence of specific herbivores (Opedal et al., 2015; Perez & Feeley, 2021). Addressing all the other potential factors contributing to trait climate mismatch (Table 1) is an important avenue for future studies.

The power of traits to predict species' mean climate was substantial relative to using sampling site as a predictor; the  $R^2$  of the multiple regression incorporating phylogeny was 0.58, and the variation in Climate-PC1 explained by site in a one-way ANOVA was 78% (Tables S2 and S4). Given that site climate was highly correlated with the mean climate of species' distributions averaged for sites (Figure S3), the finding that trait-based prediction can achieve  $0.58/0.78 = 75\%$  of the power to explain variation relative to site is another confirmation of the promise of the trait-based approach to predict species' climate niches.

The feasibility of predicting climate preference from traits points to avenues not only for improved understanding of the physiological basis for climate niches, but also multiple critical applications in improving and validating models for species persistence and performance with respect to climate, and for the management of threatened species. First, this study demonstrates that traits can provide an important stream of quantitative information useful for predicting species' climate niches. Many recent analyses, including ours, estimated species' climate distributions based on collection databases and modelled climate, resulting in uncertainty in the estimated climate mean, as collections are not proportional to abundance with respect to climate, and rare species may not exist in their most preferred climates. By providing another line of evidence for climate adaptation, trait-based approaches can provide a critical cross-validation. Important avenues for future study include the analysis of whether traits can powerfully predict not only climate means, as shown here, but also species' climate niche breadths (ranges) and climate limits; studies of some traits indicate a stronger relationship with climate limits, representing thresholds for persistence (Brodribb et al., 2014; Skelton et al., 2021; Stahl et al., 2014). Further, future studies are needed to determine whether species' abundances in a given climate can be predicted from traits, beyond



our analysis of the mean climate of species' occurrences. Second, managers may improve their prioritization of threatened species for conservation based on consideration of traits (Schönbeck et al., [in review](#); Foden et al., 2013; Loiseau et al., 2020), that is, if the traits of the threatened species indicate that its mismatch from its optimal climate is escalating. Third, trait-based climate niches can be used to improve the designation of ex-situ conservation sites, matching the most vulnerable species to their climate niches and facilitating "assisted migration", extending recent taxonomic, phylogenetic and genomic approaches to mitigate impacts of climate change (Browne et al., 2019; Brum et al., 2017; Chen et al., 2022; Csilléry et al., 2020; Merchant et al., 2023). Fourth, the repeated quantification of trait-climate mismatch may improve assessments of climate vulnerability, with increasing trait-climate mismatch suggesting a too slow shift in a species' distribution due to migration and evolution relative to the rapidity of climate change (Aitken et al., 2008; Keenan, 2015). Tests of this idea may be developed using species' abundances based on herbaria or botanical surveys. Fifth, trait-based estimation of species' climatic ranges can improve process-based modelling of plant growth in given resource conditions (Buckley & Roberts, 2006; Marks & Lechowicz, 2006a, 2006b; Trugman et al., 2019). Finally, trait-based climate niches can improve the representation of species' distributions in dynamic global vegetation models (DGVMs) used to predict climate change impacts on species and biomes, and their feedbacks on the climate system, an urgent priority in global change research (Konings et al., 2021; van Bodegom et al., 2014; Yang et al., 2019; Yang, Zhu, et al., 2015). Overall, our findings indicate that this approach is worthy of testing in other ecosystems and with a larger set of traits, to determine the generality and context-dependence of trait-based estimation of species' climate niches.

## AUTHOR CONTRIBUTIONS

Camila D. Medeiros and Lawren Sack conceived the ideas and experimental design, Camila D. Medeiros, Christian Henry, Santiago Trueba, Samantha Dannet Diaz de Leon Guerrero, Alexandria Pivovarovoff, Leila R. Fletcher, Grace P. John, James A. Lutz, Rodrigo Méndez Alonzo and Lawren Sack sampled species in the field, Camila D. Medeiros, Santiago Trueba, Alexandria Pivovarovoff and Grace P. John collected trait data, Ioana Anghel built the phylogenetic tree, Camila D. Medeiros and Lawren Sack analysed the data and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

All trait and climate data collected for this paper are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cnp5hqcb2> (Medeiros et al., 2023). Relevant code is available on Zenodo: <https://doi.org/10.5281/zenodo.8264651>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1.** Description of sampling sites.

**Table S2.** Models predicting Climate PC1 from functional traits.

**Figure S1.** Relationships between the carbon isotope discrimination,  $\Delta^{13}\text{C}$ , with site climate and the values corrected for differences in elevation and temperature across sites.

**Figure S2.** Relationships between the Climate PC1 and individual traits.

**Figure S3.** Relationships between the site climate and the average climate of species' natural climatic distributions averaged for each site.

**Table S3.** List of environmental variables, their calculations and sources.

**Table S4.** ANOVA results for differences in functional trait and PCA axes across sites and species.

**Table S5.** Results of PCA of climate variables.

**Table S6.** Results of PCA of functional traits.

**Table S7.** Associations of the mean site values of traits and environmental variables.

**Table S8.** ANOVA results for differences in climate variables across sites.

**Table S9.** Associations of traits and climate variables representing the climate of species' native distributions.

**Table S10.** Hypotheses and results for relationships between functional traits and climate variables.

**Table S11.** Regression models predicting climate variables from functional traits.

**Table S12.** Trait plasticity and environmental variation between sites.

**Table S13.** Associations between trait plasticity and environmental variation between sites.

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