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RESEARCH ARTICLE

Simplification of woody plant trait networks among communities along a climatic aridity gradient

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Abstract

1. Plant ecological strategies are shaped by numerous functional traits and their trade-offs. Trait network analysis enables testing hypotheses for the shifting of trait correlation architecture across communities differing in climate and productivity.
2. We built plant trait networks (PTNs) for 118 species within six communities across an aridity gradient, from forest to semi-desert across the California Floristic Province, based on 34 leaf and wood functional traits, representing hydraulic and photosynthetic function, structure, economics and size. We developed hypotheses for the association of PTN parameters with climate and ecosystem properties, based on theory for the adaptation of species to low resource/stressful environments versus higher resource availability environments with greater potential niche differentiation. Thus, we hypothesized that across community PTNs, trait network connectivity (i.e., the degree that traits are intercorrelated) and network complexity (i.e., the number of trait modules, and the degree of trait integration among modules) would be lower for communities adapted to arid climates and higher for communities adapted to greater water availability, similarly to trends expected for phylogenetic diversity, functional richness and productivity. Further, within given PTNs, we hypothesized that traits would vary strongly in their network connectivity and that the traits most centrally connected within PTNs would be those with the least across-species variation.
3. Across communities from more arid to wetter climates, PTN architecture varied from less to more interconnected and complex, in association with functional richness, but PTN architecture was independent of phylogenetic diversity and ecosystem productivity. Within the community PTNs, traits with lower species variation were more interconnected.
4. *Synthesis*. The responsiveness of PTN architecture to climate highlights how a wide range of traits contributes to physiological and ecological strategies with an architecture that varies among plant communities. Communities in more arid environments show a lower degree of phenotypic integration, consistent with lesser

niche differentiation. Our study extends the usefulness of PTNs as an approach to quantify tradeoffs among multiple traits, providing connectivity and complexity parameters as tools that clarify plant environmental adaptation and patterns of trait associations that would influence species distributions, community assembly, and ecosystem resilience in response to climate change.

KEYWORDS

drought tolerance, ecophysiology, functional modules, functional traits, leaf economics, plant trait networks, trait multifunctionality

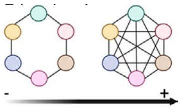
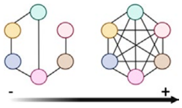
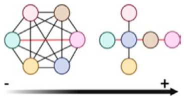
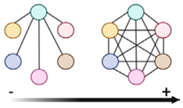
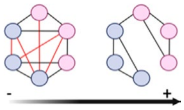
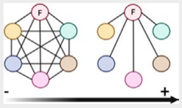
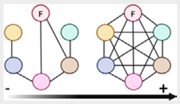
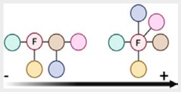
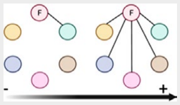
1 | INTRODUCTION

Functional traits are characteristics that influence organism vital rates and thereby fitness (Lavorel & Garnier, 2002; Medeiros et al., 2019; Poorter et al., 2008; Violle et al., 2007), and they have long been used to predict species distributions (Engelbrecht et al., 2007; Stahl et al., 2014; Thuiller et al., 2004), community composition (Cavender-Bares et al., 2004) and responses to changing climates (Tordoni et al., 2022; Trugman et al., 2019, 2020), with applications in species and ecosystem management (Carlucci et al., 2020; Foden et al., 2013; Loiseau et al., 2020). Much research has focused on using small sets of traits to estimate plant 'strategies', 'axes' or 'dimensions' of function (Díaz et al., 2004, 2016; Funk et al., 2017; Grime, 1979; Lavorel & Garnier, 2002; Maynard et al., 2022; Westoby, 1998; Wright et al., 2004). Yet, recent work highlights the enormous promise of considering extensive sets of traits and their associations across species (Belluau & Shipley, 2018; Fletcher et al., 2018; Grubb, 2016; He et al., 2020; Medeiros et al., 2019; Messier et al., 2017; Poorter et al., 2014; Sack et al., 2013; Sack & Buckley, 2020). New approaches have emerged to quantify 'phenotypic integration' within and among species, in terms of the network connectivity (i.e. the degree the traits that are correlated to each other) and network complexity (i.e. the number of structure–function modules) of the overall web formed by trait–trait relationships (He et al., 2020; Li et al., 2022; Messier et al., 2017).

The analysis of plant trait networks, henceforth PTNs, enables quantification of the overall architecture of the interconnected web of traits that underlie functional strategies of populations, species or communities, providing a means of integrating trait function at higher scales (Fontana et al., 2021; He et al., 2020; Li et al., 2022; Messier et al., 2017; Rao et al., 2023). Networks built with nodes and edges are based in graph theory with applications across fields of science (Brooks et al., 2020; Markett et al., 2018; Salt et al., 2008; Tompson et al., 2018), including, recently, trait ecology (Boisseaux et al., 2025; Flores-Moreno et al., 2019; He et al., 2020; Kleyer et al., 2019; Li et al., 2021, 2022; Messier et al., 2017; Rao et al., 2023). In these networks, traits are visualized as 'nodes' and statistical correlations between traits as connections ('edges'; Flores-Moreno et al., 2019; He et al., 2020). This approach enables the calculation of parameters that describe the connectivity and complexity of the network, including the designation of trait functional modules (Flores-Moreno et al., 2019; He et al., 2020; Li et al., 2021, 2022; Rao et al., 2023). These parameters are expected to encapsulate information on the functional strategies or syndromes that contribute to the success of species or communities under particular environmental conditions (Sanchez-Martinez et al., 2024). Further, besides parameters quantifying whole-network pattern, we can quantify within-network pattern, such as the contribution of each trait to the overall topology of the network, highlighting 'hub' and 'mediator' traits with, respectively, a disproportionally large number or centrality of connections with other traits, which may be of particular importance in the organization of the integrated phenotype (He et al., 2020).

Importantly, PTNs can be used to test hypotheses for how trait correlations may shift across communities that differ in climate, species, functional richness and/or productivity (He et al., 2020; Li et al., 2022; Medeiros et al., 2019; Sack & Buckley, 2020). According to the 'environmental filtering hypothesis' and the complementary 'physiological tolerance hypothesis', in communities of lower resource or stressful environments that fewer species can tolerate, individual traits would be more likely to specialize to a narrower number of niches; conversely, in communities of environments with higher resource availability and primary productivity more functionally diverse sets of species can be supported (Currie et al., 2004; Kraft et al., 2015; Le Bagousse-Pinguet et al., 2017). Notably, each trait can have several functions (Table 1), and traits may be associated across species due to developmental or structural coordination, contribution to a common functions and/or co-selection by environment (Ahrens et al., 2020; Li et al., 2022; Sack et al., 2003, 2012). According to theory, both trait variation and trait associations would tend to arise from trait divergence along a gradient of resource availability (e.g., low vs. high water supply or irradiance). Consequently, in communities accessing lower resources or experiencing greater environmental stress and thus providing fewer niches, traits would tend to optimize separately for stress adaptation, along fewer common spectra (He et al., 2020). Thus, given that plants can adapt to stress with alternative designs (Corrêa Dias et al., 2019; Marks & Lechowicz, 2006)—for example, plants can adapt to drought according to multiple strategies (e.g., 'avoidance' or 'resistance'; Fletcher et al., 2022; Laughlin, 2023)—adaptation to lower resources or stress would tend to result in a greater independence of traits, and fewer trait correlations (He et al., 2020). Thus, we expect that in environments with lower resources, or more stress, community

TABLE 1 Network parameters that characterize the architecture of plant trait networks (PTNs) and the centrality and connectivity of the included traits, applied for dominant and common species of sites across a climatic gradient in the California Floristic Province. Network connectivity increases with higher values of edge density, which reflect more interdependence of traits within the network, and lower values of density and average path length, which reflect less independence of traits within the network; PTN complexity increases with higher values of average clustering coefficient, which reflect a network that is less divided into subcomponents, and lower values of modularity, which reflect lower clustering of traits. Trait centrality increases with higher values of betweenness and connectedness, and trait connectivity increases with higher values of closeness and degree of connectedness. For each PTN parameter, we provide a visual guide of what networks with low versus high values for each parameter would look like (modified from He et al., 2020).

		Hypotheses for parameter shifts with				
Parameters	**Definition**	**Climatic aridity**	**Functional richness and/or phylogenetic diversity**	**Net primary productivity**	**Trait variation**	**Rationale**
Whole-network parameters						
Network connectivity						
	The proportion of connections out of all possible connections	Decrease	Increase	Increase	-	In more arid climates, with lower functional richness, multiple traits may independently optimize for stress adaptation, leading to greater independence of traits; this may correspond to a lower productivity (Ahrens et al., 2020; He et al., 2020; Li et al., 2022)
	The network-averaged shortest distance between traits	Increase	Decrease	Decrease	-	
Diameter 	The maximum shortest distances between traits in the network	Increase	Decrease	Decrease	-	
Network complexity						
Average clustering coefficient 	The network-averaged clustering coefficient of all traits	Decrease	Increase	Increase	-	Traits may be divided into more modules in the moister sites, consistent with the diversification of overall phenotype and function for the occupation of more niches (Currie et al., 2004; He et al., 2020)
Modularity 	Measures the degree of separation of trait clusters within the network	Increase	Decrease	Decrease	-	Traits within each module may be more independent of traits in separate modules in the more arid sites, consistent with adaptation to drought stress and lower resource availability (Currie et al., 2004; He et al., 2020)
Within-network parameters						
Trait centrality 	The number of shortest paths going through a focal trait	-	-	-	Decrease	Traits more central and connected within a PTN would be those involved in mediating and compromising among multiple functions (He et al., 2020), and thus would have a lower variation across species
Clustering coefficient 	The proportion of connections between a focal trait and its neighbouring traits out of all possible connections	-	-	-	Decrease	
Trait connectedness 	The mean shortest path between a focal trait and all other traits in the network	-	-	-	Decrease	
Degree of connectedness 	The number of connections of a focal trait	-	-	-	Decrease	

trait networks would show lower connectivity parameters (such as lower edge density and larger average path length and diameter; Table 1). By contrast, for communities accessing higher resources, with less stress, trait network connectivity may be higher, indicating the greater potential for multiple traits within the network to adapt collectively for optimization in specific niches, thus increasing 'phenotypic integration' (Vasseur et al., 2022). Beyond connectivity, measures of greater network complexity (such as a larger average clustering coefficient and lower modularity; Table 1) indicate a greater diversity of types of trait inter-correlations. Network complexity would also be expected to be lower in lower resource, stressful environments in which traits would adapt to stresses according to alternative designs, whereas network complexity would be greater in high resource environments with greater niche differentiation, as more semi-independent trait modules would be associated with the adaptation of different processes to a greater number of different niche axes within the ecosystem (He et al., 2020; Li et al., 2021). Thus, we hypothesized that PTNs will be less connected and complex in communities in more arid environments, which also tend to have lower phylogenetic diversity and functional richness and productivity, and, by contrast, PTNs will be more connected and complex in cooler, moister environments, which tend to be associated with higher phylogenetic diversity, functional richness and productivity (Table 1; Currie et al., 2004; Li et al., 2022).

Previous studies have provided partial support for these hypotheses across continental or global latitudinal gradients. One previous study tested variation in PTNs based on 35 leaf structure and composition traits across communities, considering forests across latitudes in China from cold boreal sites to warm, moist tropical sites. That study found that PTN connectivity and complexity increased from colder climate forests to wetter and warmer tropical forests with greater species richness (Li et al., 2021, 2022). Another previous study utilized a compiled global database for 10 traits to consider shifts in parameters across biomes from boreal to tropical regions and found that for woody plants, trait network connectivity and network complexity were lower in polar than in other global regions (Flores-Moreno et al., 2019).

Notably, both those previous studies investigated the relationship of PTN connectivity and complexity with the greater warmth and moisture at lower latitudes, and thus neither focused on climatic aridity, that is, whether soil or atmospheric drought (as opposed to cold climates) could be a driver of PTN shifts. In this study, we focused on communities across an aridity gradient in the California bioregion, from forests in cool, moist climates to semi-desert in hot, dry climates. Here, we provide a first test of trait network shifts for communities across a marked aridity gradient, from cool, moist to hot, dry sites, providing insights into drought adaptation of species and communities, a topic of increasing urgency given global change increases the frequency and intensity of high-temperature drought conditions in many regions. We also introduce tests of the relationship of network complexity to primary productivity (gross and net primary productivity [GPP and NPP]), and functional richness, which tend to be associated with environments with higher resource availability and lower stress (Currie et al., 2004; Kraft et al., 2015; Le Bagousse-Pinguet et al., 2017; Li et al., 2022).

In addition to our novel focus on the shifts in plant community trait networks across an aridity gradient, we also tested a new hypothesis for the patterning of variation among traits within a network, that is, that traits that are more connected and 'hub-like' in PTNs tend to be those with low variation across species means (i.e., with a low coefficient of variation). We thus tested how the connectedness and centrality of the traits within the networks relate to trait variability (Table 1). Certain traits, such as, by hypothesis, the leaf mass per area, may be involved in multiple axes of function (including, e.g., resource retentiveness and drought tolerance, John et al., 2017; Wright et al., 2004). A previous study of forests across a continental latitudinal gradient found that trait connectivity within networks was conserved, with certain traits playing a stronger integrating role in the phenotype regardless of the species set (He et al., 2020), implying potential involvement in multiple functions (cf. Marks, 2007). We hypothesized that traits with greatest connectivity within the PTN, being involved in mediating multiple functions, would tend to show lower variation across species relative to other traits less connected in the PTN (Table 1).

To test these hypotheses, we built a novel database of high resolution, standard mechanistic functional traits, including hydraulic, anatomical, composition, economic and structural, for diverse communities across a bioregion in the California Floristic Province (CAFP), an endemism-rich biodiversity hotspot (Baldwin, 2014). We quantified 34 functional traits (listed with functions, symbols and units in Table 2) in 118 unique species (Table S1) sampled from six key plant communities that represent approximately 70% of the CAFP land area (Thorne et al., 2017), including desert, coastal sage scrub, chaparral, montane wet forest, mixed riparian woodland and mixed conifer-broad-leaf-forest sites (Table 3). A previous study focused on 10 key traits that were strongly associated with aridity in species' native ranges along this gradient (Medeiros et al., 2023). In this study, we consider an expanded, three times larger trait dataset representing multiple levels of plant function, including hydraulics, nutrient composition, plant size, and leaf and wood economics and structure (Table 2). We built PTNs for each plant community and tested the hypothesized relationships of trait connectivity (through the PTN parameters edge density, average path length and diameter) and network complexity (through the PTN parameters average clustering coefficient and modularity) with site aridity, functional richness and primary productivity.

2 | MATERIALS AND METHODS

2.1 | Study sites

We sampled 3–5 individuals per species, resulting in a total of 683 individuals from 118 unique species in six plant communities (Figure 1; Figure S1) distributed across a gradient of climatic aridity in the CAFP, from northern California to northern Mexico, differing

TABLE 2 List of traits, their functions and completeness (the percent of species with observations). We present symbols and units for the 34 traits quantified for 118 species from six plant communities across a climatic gradient in the California Floristic Province. The traits relate to six measurement categories: Epidermal morphology, leaf economics and structure, wood economics and structure, leaf composition, hydraulics and plant size. Functions: 1. Gas exchange (photosynthesis and transpiration); 2. Light relations; 3. Herbivory defence; 4. Metabolism; 5. Organ structure; 6. Water transport; 7. Seed dispersal.

Trait	Symbol	Unit	Function(s)	Trait completeness (%)
Epidermal morphology				
Stomatal density	*d*	n μm^{-2}	1	82
Stomatal area	*s*	μm^{2}	1	88
Epidermal pavement cell area	*e*	μm^{2}	4, 5	94
Trichome density	*t*	n μm^{-2}	1, 2, 3	90
Leaf economics and structure				
Leaf area	*LA*	cm^{2}	1, 2, 5, 6	98
Leaf mass per area	*LMA*	$g\,m^{-2}$	1, 2, 3, 4, 5	98
Leaf thickness	*LT*	mm	1, 2, 3, 4, 5	98
Leaf dry matter content	*LDMC*	$g\,g^{-1}$	1, 3, 4, 5	98
Percentage loss area (dry)	PLA_{dry}	%	5, 6	91
Wood economics and structure				
Wood density	*WD*	$g\,cm^{-3}$	3, 5, 6	100
Leaf composition				
Carbon per leaf mass	C	$mg\,g^{-1}$	1, 3, 4, 5	94
Nitrogen per leaf mass	N	$mg\,g^{-1}$	1, 2, 3, 4	94
Phosphorus per leaf mass	P	$mg\,g^{-1}$	1, 2, 4	88
Potassium per leaf mass	K	$mg\,g^{-1}$	1, 4, 6	88
Calcium per leaf mass	Ca	$mg\,g^{-1}$	1, 4, 5, 6	88
Magnesium per leaf mass	Mg	$mg\,g^{-1}$	1, 2, 4	88
Iron per leaf mass	Fe	ppm	1, 2, 4	88
Boron per leaf mass	B	ppm	4, 5	88
Manganese per leaf mass	Mn	$mg\,g^{-1}$	1, 2, 4	88
Sodium per leaf mass	Na	$mg\,g^{-1}$	4, 6	88
Zinc per leaf mass	Zn	$mg\,g^{-1}$	1, 2, 4	88
Copper per leaf mass	Cu	$mg\,g^{-1}$	1, 2, 4, 5	88
Molybdenum per leaf mass	Mo	$mg\,g^{-1}$	1, 2, 4	88
Cobalt per leaf mass	Co	$mg\,g^{-1}$	4	88
Aluminium per leaf mass	Al	$mg\,g^{-1}$	4	88
Arsenic per leaf mass	As	$mg\,g^{-1}$	4	88
Cadmium per leaf mass	Cd	$mg\,g^{-1}$	4	88
Rubidium per leaf mass	Rb	$mg\,g^{-1}$	4	88
Strontium per leaf mass	Sr	$mg\,g^{-1}$	4	88
Chlorophyll per mass	*Chl*	SPAD $g^{-1}m^{2}$	1, 2, 4	86
Carbon isotope discrimination	$\Delta^{13}C$	‰	1	94
Hydraulics				
Water potential at turgor loss point	π_{tlp}	MPa	1, 6	98
Plant size				
Maximum height	H_{max}	m	1, 2, 5, 6	100
Seed mass	*SM*	mg	7	78

by 10°C in mean annual temperature (MAT) and sixfold in mean annual precipitation (MAP). The sites also varied strongly in plant community composition (Figure S1; Table 3). Permits were obtained for work in the University of California Natural Reserve System (UCNRS) sites (desert, chaparral, mixed riparian woodland and mixed conifer-broadleaf forest) and the Centro de Investigación Científica y de

TABLE 3 Plant communities sampled across California (United States) and Baja California (Mexico), including site abbreviations and names, dominant vegetation type, latitude and longitude of the site centroid, number of species and families sampled, the aridity index, AI (lower AI values signify higher climatic aridity), mean annual precipitation, MAP and temperature, MAT. Site climate was modelled from a 100-ha buffer zone around each site's centroid. From left to right, sites are ordered from low to high climatic aridity.

	Mixed conifer-broadleaf forest	Mixed riparian woodland	Montane wet forest	Chaparral	Coastal sage scrub	Desert
Site	Angelo Coast Range Reserve	Onion Creek	Yosemite Forest Dynamics Plot	Stunt Ranch Santa Monica Mountains Reserve	Centro de Investigación Científica y de Educación Superior de Ensenada	Sweeney Granite Mountains Desert Research Center
Vegetation type	Mixed conifer-broadleaf-forest	Mixed riparian woodland	Montane wet forest	Chaparral	Coastal sage scrub	Desert
Latitude	39.7185431	39.274627	37.8529772	34.0955321	31.869475	34.7813355
Longitude	−123.65505	−120.36545	−119.83129	−118.66148	−116.66689	−115.65598
N species sampled	21	19	20	26	22	28
Dominant functional types	Mixed deciduous and evergreen shrubs and trees	Mixed deciduous and evergreen shrubs and trees	Deciduous shrubs and evergreen needleleaf trees	Evergreen shrubs	Evergreen shrubs	Deciduous/semi-deciduous shrubs
AI	1.18	0.755	0.539	0.215	0.121	0.0959
MAP (mm)	1613	1122	977	412	256	263
MAT (°C)	11.4	6.46	10.7	16.4	16.4	16.6

Educación Superior de Ensenada (CICESE) site 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 the drivers of connectivity in PTNs across forests along a gradient of aridity, we followed previous studies of PTNs that focused on one ecosystem per type; sampling one location per ecosystem type provides limited information about the drivers of connectivity in traits across ecosystem categories, but is robust for relating PTN parameters to climate variables (Li et al., 2021, 2022; Messier et al., 2017; Rao et al., 2023).

2.2 | Sampling for leaf trait measurements

Given the infeasibility of sampling all species in each site for functional traits due to the large number of species, we targeted the most abundant tree and shrub species at each site, including those most biomass-dominant and most representative of overall ecosystem structure and functioning and the largest contributors to ecosystem productivity, based on information from reserve managers and forest inventories. The sampling spanned 37 families, with the greatest species representation in Asteraceae (17), Rosaceae (12), Rhamnaceae (9), Ericaceae (8) and Pinaceae (8). At each site, we sampled 3–5 individuals from 19 to 28 species, collecting a mature, sun-exposed and non-epicormic branch, with minimal signs of damage or herbivory using pole pruners or a slingshot. Branches were transported to the laboratory in dark plastic bags with moist paper and rehydrated overnight in a dark saturated atmosphere before harvesting current-year grown, fully expanded leaves for subsequent analyses. For compound-leafed species, whole leaves, not leaflets, were used.

In selecting traits for the PTNs, we excluded traits that would be mathematically determined from other traits. Thus, for example, as we included leaf mass per area (LMA) and leaf thickness (LT), we did not include leaf density (which would typically be calculated as LMA/LT), and we did not include foliar nutrient concentrations per unit leaf area (LA), as these would be calculated as the concentrations per unit leaf dry mass multiplied by LMA.

2.3 | Epidermal morphology

We measured epidermal traits on one leaf from each of 3–5 individuals per species. After rehydration, we fixed the leaves in FAA (48% ethanol: 10% formalin: 5% glacial acetic acid: 37% water). Epidermal measurements were obtained from microscopy images taken from nail varnish impressions of both leaf surfaces, from which we measured stomatal density (*d*), stomatal area (*s*), epidermal pavement cell area (*e*) and trichome density (*t*). To determine leaf-level epidermal trait values for cell dimensions, we calculated an average value as the arithmetic mean of the abaxial and adaxial surfaces. For leaf-level cell densities, we calculated a total trait value as the sum of abaxial and adaxial values. All images were analysed, and anatomical traits were measured using the software ImageJ (http://imagej.nih.gov/ij/; Schneider et al., 2012).

2.4 | Leaf economics and structure

Leaf saturated mass was measured using an analytical balance (0.01 mg; XS205; Mettler-Toledo, OH, USA) and LT using digital callipers (0.01 mm; Fowler, Chicago, IL, USA). The LA was measured using a flatbed scanner and analysed using the software ImageJ (http://imagej.nih.gov/ij/). After scanning, leaves were oven-dried at 70° for 72 h, and their dry mass and area were measured again. LMA was calculated as lamina dry mass divided by saturated area; leaf dry matter content (LDMC) as dry mass divided by saturated mass; percentage loss in area after drying ($\mathrm{PLA}_{\mathrm{dry}}$) as the per cent decline in area from saturated to dry leaves (Ogburn & Edwards, 2012; Pérez-Harguindeguy et al., 2013; Witkowski & Lamont, 1991).

2.5 | Wood economics and structure

We measured wood density (WD) as fresh volume over dry mass from one 5 cm branch segment of each of the studied individuals after bark removal by water displacement (Pérez-Harguindeguy et al., 2013; Swenson & Enquist, 2008). We measured the density of the branch stem, and not a core of the main stem, to minimize the disturbance of our sampling methods on the tree function and survival (Tsen et al., 2015).

2.6 | Leaf nutrient and isotope composition and wilting point

The concentrations of four macronutrients (potassium, calcium, phosphorus and magnesium) and 13 micronutrients (iron, boron, manganese, sodium, zinc, copper, molybdenum, cobalt, aluminium, arsenic, cadmium, rubidium and strontium) were determined from ground oven-dried leaves using high-throughput elemental profiling (ionomics; Salt et al., 2008) by the USDA-ARS/Danforth Center Ionomics facility at the Donald Danforth Plant Science Center. Additionally, elemental carbon and nitrogen concentrations and their isotope ratios were measured by the University of California, Berkeley, Center for Stable Isotope Biogeochemistry, by continuous flow dual isotope analysis using a CHNOS Elemental Analyzer interfaced to an IsoPrime100 mass spectrometer (Fry et al., 1996; Pérez-Harguindeguy et al., 2013). The carbon isotope discrimination (Δ^{13}C; in parts per thousand, ‰) was calculated following Farquhar et al., 1989. The chlorophyll concentration was measured using a SPAD meter, which provides a correlate of total chlorophyll $a+b$ concentration per area in SPAD units (Brown et al., 2022; Monje & Bugbee, 1992; SPAD-502, Konica Minolta, Japan) and the chlorophyll concentration per mass (Chl) was determined by dividing by LMA.

We measured the turgor loss (i.e. wilting) point (π_{tlp}) in two leaves for each studied individual, for the five individuals per species. We used a vapour-pressure osmometer (Vapro 5520 and 5600, Wescor, United States) to obtain the osmotic concentration of the leaves at full turgor and used calibration equations to estimate π_{tlp} (Bartlett et al., 2012).

2.7 | Plant size

Species maximum height (H_{max}) and seed dry mass values (SM) were compiled from the Ecological Flora of California database (Jepson Flora Project, 2021). Whenever H_{max} was not available for a species in the database, it was recorded as the maximum value reported on the Jepson eFlora website (https://ucjeps.berkeley.edu/efc/).

2.8 | Ecosystem climate and structure

We extracted the historical aridity index, calculated as the ratio of precipitation and potential evapotranspiration (CGIAR-CSI, NCAR-UCAR; Zomer et al., 2008), and the MAT and MAP (WorldClim; Hijmans et al., 2005) from a 100-ha area around the centroid of each sampling location (Table 3; Table S3). The site productivity was quantified using the GPP and NPP derived from MODIS/Terra (Running & Zhao, 2019, 2023). The data were downloaded using the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS, 2023) for the centroid of the sites and calculated as the annual mean during the sampling period, 2016–2018 (Table S3).

2.9 | Plant trait networks

Across all traits, we had observations for 91% of the species on average (Table 2). The trait with the least observations was seed mass due to the sparseness of measurements for CAFP species in the literature (78%; Table 2). To build weighted PTNs, we calculated trait–trait correlation matrices using ordinary least squares regressions from species mean values for each plant community and for all communities together. Trait–trait relationships were considered as edges if the Pearson correlation was significant at $p < 0.05$, corresponding to absolute Pearson coefficient thresholds of $|r| > 0.39$–0.46 for the individual sites, corresponding to species n values of 19–28, and $|r| > 0.18$ for the all-species network (species $n = 136$). The matrices were then converted into adjacency matrices $A = [a_{i,j}]$, where we assigned the correlation coefficient to relationships that were above the significance threshold and 0 to those below the threshold. Additionally, we built PTNs considering as edges relationships where the Pearson and Spearman correlation coefficients of log-transformed and ranked data, respectively, had $p < 0.05$ (Table S2). The PTNs showed similar trends of variation with climate, so we show PTNs built from raw data in the main text. These networks were visualized using the '*qgraph*' package (version 1.9.8)

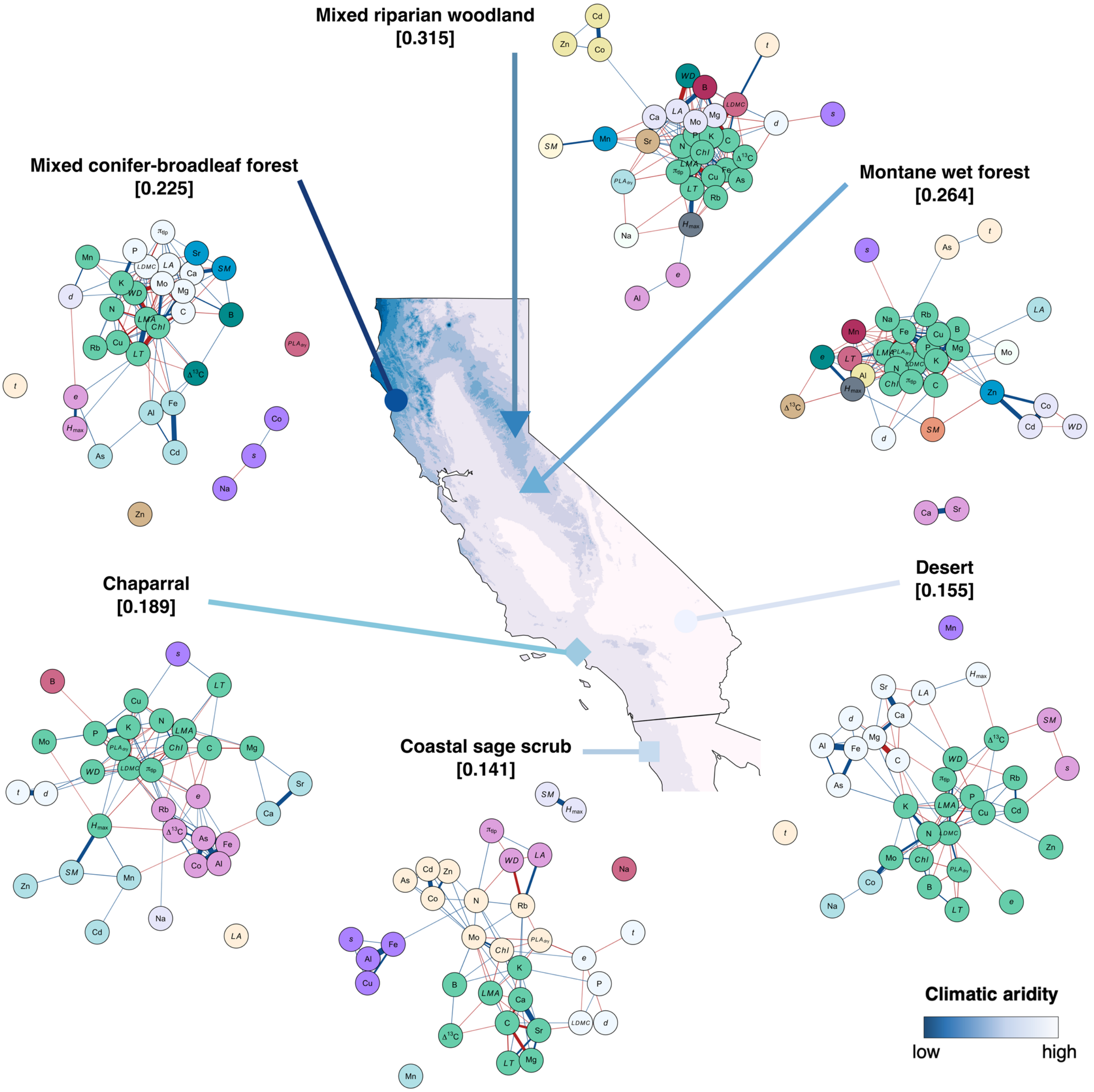


FIGURE 1 Shifts in the architecture of plant trait networks (PTNs) of six plant communities across the California Floristic Province. The map shows the centroid of the sampling location of each of the six plant communities in a landscape of aridity. Symbols represent different plant communities, with 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). In brackets, we provide the proportion of connections out of all possible connections among traits, the edge density, of each PTN. PTNs built from species sampled in each of the six sites. Blue edges represent positive and red edges represent negative relationships between traits; edge thickness and distance represent the correlation strength ($p < 0.05$). Nodes with the same colours are grouped into the same modules by the clustering algorithm (Table S7).

and all network parameters were calculated using functions available in the '*igraph*' package (version 1.3.4) in the R Software (R Core Team, 2022).

We calculated five parameters to describe PTN topology, three that quantify the 'connectivity' of the PTN: the edge density, the average path length, and the diameter; and two parameters to quantify the 'network complexity' of the PTN: the average clustering coefficient and the modularity (Table 1; He et al., 2020). Networks with higher values of edge density and lower values of average path length and diameter have higher connectivity; networks with higher values of average clustering coefficient and lower values of modularity have higher network complexity (Table 1; He et al., 2020).

We also calculated four parameters to describe the importance of traits within PTNs (Table 1). To quantify the 'centrality' of each trait, we determined the betweenness and the clustering coefficient. The betweenness is defined as the number of shortest paths going through a focal trait, with high values reflecting a central 'mediator' trait within the network. The clustering coefficient is the proportion of connections between a focal trait and its neighbouring traits out of all possible connections, and traits with high values are those at the centre of different trait clusters. To quantify the 'connectedness' of each trait, we determined the degrees of connectedness and the closeness. The degree of connectedness is a measure of the number of connections for a given trait, and traits with high values are considered 'hubs' within the network. The closeness represents the mean shortest path between a focal trait and all other traits in the network, and traits with high values are traits closely connected to many other traits.

2.10 | Statistical analyses

All statistical analyses were performed and plots created using R software (version 4.2.1; R Core Team, 2022) and packages available from the CRAN platform. Prior to testing correlations among traits and constructing PTNs, we tested for the overall variation in traits across species and sites. We performed nested ANOVAs to test for differences in functional traits among plant communities and species, with functional traits coded as the dependent variable, communities as the independent variable and species nested within communities (Sokal & Rohlf, 2012).

We calculated the phylogenetic diversity index for each site (PDI; Faith, 1992), as the sum of the lengths of all the branches in a phylogenetic tree weighted by species richness to test if the PTN parameter differences across sites were driven by differences in phylogenetic diversity. PDI was calculated using the '*PhyloMeasures*' package (Tsirogiannis & Sandel, 2015).

We calculated the functional richness index, FRic, for species in each community (Cornwell et al., 2006), using the '*fundiversity*' package (Grenié & Gruson, 2023). This functional richness index does not require abundances (which are not available for most of our sampled sites) and performs better than the other equivalent indices (Mouchet et al., 2010). For the calculation of FRic, we selected five of the functional traits from different measurement categories with the most complete observations and that were involved in many functions (Table 2), leaf mass per area, wood density, water potential at turgor loss point, leaf nitrogen concentration and maximum plant height.

We calculated the coefficient of variation, CV (%), of each trait in each site ($\mathrm{CV} = \frac{\sigma}{\mu} \times 100$, where σ is the standard deviation and μ is the mean of a given trait across the species sampled in a given site), and then calculated the mean CV of each trait across all sites.

To test the relationships between the PTN parameters and site climate variables, primary productivity, PDI and FRic, we performed ordinary least squares regression analyses (OLS) using the '*stats*' package. Analyses were performed for untransformed and log-transformed data, to test for either approximately linear or non-linear relationships, respectively, and the higher correlation value is reported in the text; we present the results of both untransformed and log-transformed data in supplemental Table S6. Given the use of multiple significance tests applied when testing relationships between PTN parameters and environmental variables, we assessed the significance of the overall correlative pattern by applying proportion tests (Baird et al., 2021; Medeiros et al., 2023). We calculated the proportion of significant correlations for the correlations we hypothesized among, on one hand, the site climate variables (aridity index, MAP and MAT), primary productivity, PDI, and FRic, and on the other hand, the five PTN parameters (edge density, average path length, diameter, average clustering coefficient and modularity) for each of the six sites. We used the '*stats*' package to test if the proportion of significant correlations was greater than that expected from chance (0.05).

We also performed OLS regression analyses and calculated the Pearson's correlation coefficient to test the relationships between the CV of individual traits and trait-level PTN parameters following the same procedures described above for the relationships between the PTN parameters and environmental variables. Further, we calculated the proportion of significant correlations for the 24 correlations we hypothesized across traits ($n = 34$ traits) among, on one hand, the trait CVs and on the other hand, the four trait-level PTN parameters (betweenness, closeness, clustering coefficient and degree of connectivity) for each of the six sites.

The PTNs were built using traits that are intrinsically related within measurement categories, which differed in the numbers of traits included (Table 2). Thus, we tested for a relationship between trait-level parameters of connectedness and centrality, averaged per measurement category with the number of traits within each category using OLS. For example, the 'Wood economics and structure' measurement category included one trait, while the 'Leaf composition' measurement category included 21 traits.

3 | RESULTS

3.1 | Variation in traits across plant communities

Prior to constructing PTNs, we tested for variation in functional traits across species and communities. Of the 34 traits, 32 differed across species and 29 across communities (nested ANOVAs; $p < 0.05$; Table S4). Most of the total trait variance (65%) was explained by species differences, whereas community and intraspecific variation explained 17% each (Table S4). Many individual traits varied across communities in association with their climate. For example, on average, species in the more arid sites had smaller and thicker leaves with higher trichome density, a smaller reduction in leaf area when dry, denser wood and more negative turgor loss points than species from the more mesic sites ($p < 0.05$; Table S4). Species from more arid sites also had lower concentrations of mass-based nutrients, including carbon, nitrogen, potassium, and phosphorus and low carbon isotope discrimination (nested ANOVAs; $p < 0.05$; Table S4).

3.2 | Variation in PTNs across plant communities and relationships with ecosystem climate and structure

The architecture and properties of the PTNs varied significantly across the six sites (Figure 1). The PTNs of the drier sites were 'looser', that is, less connected (with lower edge density and higher average path lengths) and less complex (with lower average clustering coefficient and higher modularity) than those for the more mesic sites (Figure 1; Table S6). Thus, the PTNs of the higher aridity sites had traits that were overall less interconnected and grouped into a smaller number of clusters. That is, these networks had lower values of edge density and average clustering coefficient and higher values of average path length and modularity than the networks of the more mesic sites (Figure 1; Table S6). The network diameter did not differ across sites (Table S6).

Thus, the connectedness and complexity of the community PTNs tended to decrease across sites with increasing climatic aridity (lower values of aridity index, AI, and MAP and higher values of MAT) and yalso with lower functional richness, FRic (Figure 2; Figure S5; Table S6). Both network edge density and average clustering coefficient decreased for communities at lower AI and MAP and higher MAT ($|r|$ ranged from 0.85 to 0.97; $p < 0.05$; Figure 2a,d; Figure S5; Table S6). The network average path length increased for communities at lower AI and MAP ($r = 0.84$ and 0.85, respectively; $p < 0.05$; Figure 2c; Table S6) and was independent of MAT (Figure S5; Table S6). The network modularity increased for communities at higher MAT ($r = 0.94$; $p = 0.005$; Figure S5; Table S6) and was independent of AI and MAP, and the network diameter was independent of AI, MAP and MAT ($p > 0.05$; Figure 2d; Figure S5; Table S6). Both edge density and average clustering coefficient increased, and modularity decreased for communities with greater values of FRic ($|r| = 0.91$–0.96; $p < 0.05$; Figure 2b,e,k; Table S6), while average path length was not correlated with FRic ($p = 0.32$; Figure 3h; Table S6).

3.3 | Trait connectedness and centrality within trait networks and relationship with trait variation

From the PTNs, we identified traits central to the networks; that is, traits with high betweenness and closeness (mediator traits) and traits with high clustering coefficient and degree of connectedness (hub traits). Across the PTNs for the six plant communities, K concentration, N concentration, leaf dry matter content, Fe concentration and the leaf mass per area were resolved as mediator traits with highest betweenness values averaged across communities, 32–49 (Figure S3; Table S7), and Ca concentration, Sr concentration, maximum tree height, seed mass, and stomatal area with highest closeness values, 0.02–0.21 (Figure S3; Table S7). The leaf mass per area, K concentration, leaf dry matter content, chlorophyll concentration, and N concentration were resolved as hub traits with the highest clustering coefficient and degree of connectedness values, with averages across communities of 0.72–0.85 and 11–14, respectively (Figure S3; Table S7). Notably, the traits with highest betweenness, closeness, clustering coefficient and degree of connectedness values varied across sites (Figure S4; Table S7).

We found no relationship between the number of traits considered in each of the eight trait categories (i.e. 'Leaf composition' (21), 'Leaf economics and structure' (5), 'Epidermal morphology' (4), 'Plant size' (2), 'Wood economics and structure' (1) and 'Hydraulics' (1)) and the trait-level PTN parameters (Figure S6). Further, all PTN parameters were independent of the phylogenetic diversity index, PDI ($p > 0.05$; Table S6).

Across the traits, trait centrality and connectedness in the plant trait networks were strongly related to trait variation within and across sites. Thus, across species within each site and across all species, we found strong negative relationships of the trait CVs with parameters describing PTN connectedness and centrality, i.e., with betweenness, closeness, clustering coefficient and degree of connectedness (r ranging from −0.53 to −0.34; $p < 0.05$; Figure 3; Figure S7; Table S8). Indeed, across the tested relationships of trait CVs with the four PTN trait-level parameters, 12 of the 24 tested relationships (50%) were statistically significant ($p < 0.05$; Figure 3; Table S8), a proportion significantly higher than our null hypothesis of chance (0.05; $\chi^2 = 93.06$; $p < 2.2 \times 10^{-16}$; proportion test).

4 | DISCUSSION

In our study of communities across a bioregional aridity gradient, from forests to semi-desert, the PTN approach resolved shifts in the integrated relationships among multiple traits with ecosystem climate and structure, enabled the identification of trait clusters, and indicated the relative importance of traits within the network. Across plant communities, the PTNs were less connected (i.e. the traits that make up the network were less interconnected) and complex (i.e. divided into fewer subcomponents or clusters) with increasing climatic aridity and decreasing functional richness across communities (Figures 1 and 2; Table S6). This pattern is consistent with the hypothesis that under lower resource or stressful environments which fewer species can tolerate, individual traits would be more likely to specialize similarly, to a narrower number of niches. The fewer correlations among traits overall, in combination with a lower modularity, would signify less diversification of trait complexes, and thus of functions, across the species of the community (see elaboration in Introduction). By contrast, the moister sites would support a higher species and functional richness, with divergence in specializations for the optimal use of specific resources (Harrison et al., 2020; Spasojevic et al., 2014). We did not find support for the hypotheses that PTN connectivity and complexity would be associated with phylogenetic diversity or NPP.

Our study provides new insights important to expand theories about species community assembly, adaptation to aridity, and the

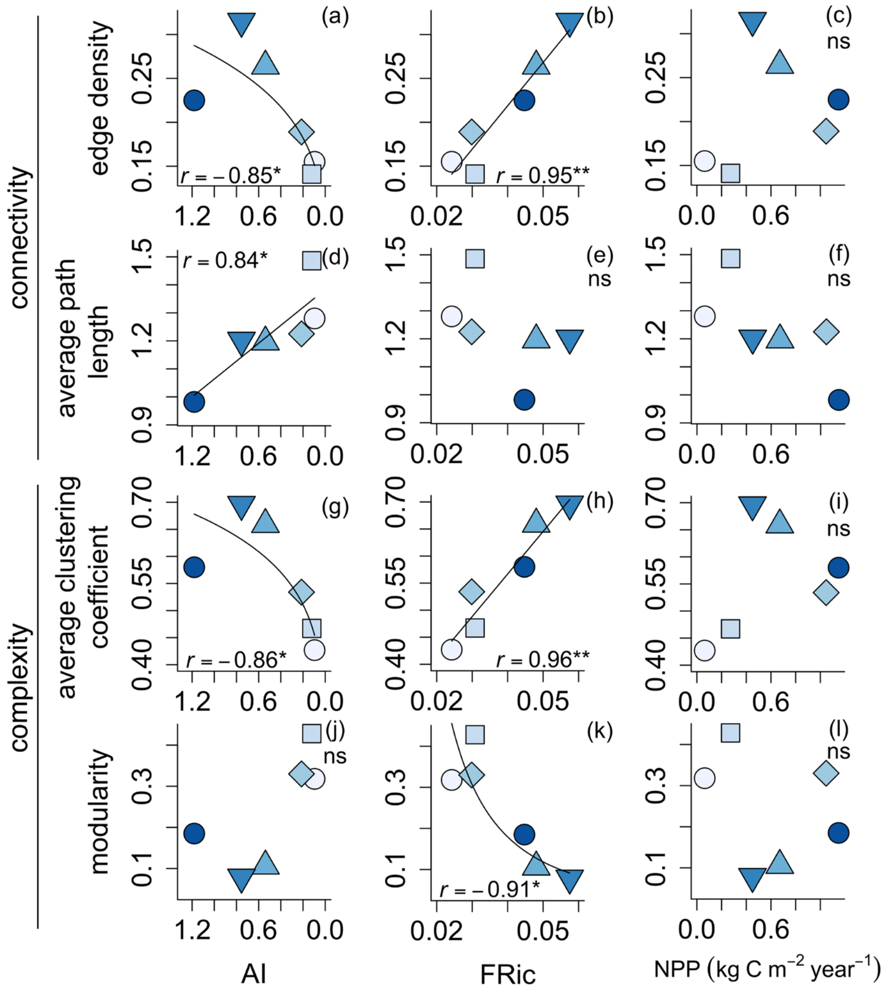


FIGURE 2 Relationships of plant trait network (PTN) parameters with increasing climatic aridity and ecosystem structure and independence from primary productivity across an aridity gradient. Relationships across plant communities (each shape point is a community, with darkness of blue representing site moisture) of the aridity index, AI, of the site's climate (left column), with the site's functional richness, FRic (middle column) and the site net primary productivity, NPP (right column), plant network parameters edge density (a–c), average clustering coefficient (d–f), average path length (g–i) and modularity *Q* (j–l). The network diameter did not vary across sites and none of the PTN parameters varied with site phylogenetic diversity (Table S6). Symbols represent different plant communities, 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). Solid lines describe the fit of ordinary least squares regression analyses (Table S6). $^*p<0.05$; $^{**}p<0.01$.

organization of traits in the integrated phenotype within and across communities. We found that warmer/drier communities had simpler networks than cooler/moister communities, from semi-desert to forests across a bioregional aridity gradient. This pattern is distinct, yet aligned with those shown in two previous studies across a latitudinal continental gradient in which the cold boreal sites, which have more stressful conditions, had simpler networks than warm moist tropical forests (Flores-Moreno et al., 2019; He et al., 2020; Li et al., 2022). Our results overall supported the association of PTN interconnectedness and complexity with resource availability and species richness across plant assemblages, as indicated by the studies across biomes globally and across the latitudinal gradient in China and extend this finding across a strong aridity gradient within a key bioregion, and including traits relating to multiple functional axes, from cells to the whole plant (Table 2), with important novel insights for specific network-level architecture parameters in community ecology (Table 1). Thus, our paper indicates the centrality of abiotic stress in driving the simplification of trait networks, an explanation that would be applicable in the context of both the bioregional and continental latitudinal gradients. Further, our study showed that among traits within a PTN the trait connectedness within the network is higher for traits with relatively low variation across species, providing a new hypothesis for the reason some traits are more 'hub-like', across diverse species assembled in communities across an aridity gradient.

Beyond cold climate, our study showed that meteorological drought would be a driver of PTN shifts. The climate variables were strongly associated with the topology of PTNs, and functional

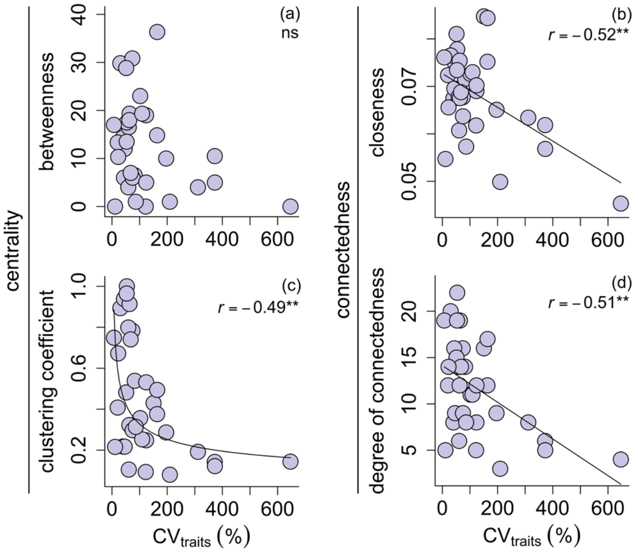


FIGURE 3 Relationships of trait-level parameters of the all-species plant trait network with the trait variability, assessed as the trait coefficient of variation across all species. Relationships of the trait coefficient of variation, CV, with the trait betweenness (a), closeness (b), clustering coefficient (c) and the degree of connectedness (d). Each point represents the mean CV of one trait across all 118 unique species sampled across six plant communities in a gradient of aridity. Solid lines describe the fit of ordinary least squares regression analyses (Table S9). $^{**}p < 0.01$. Relationships for individual plant communities are shown in Figures S8–S11.

richness was a strong community structure driver of PTN topology. In communities of the more arid sites, with warmer temperatures, the PTNs were looser, with lower edge density and average clustering coefficient, and higher average path lengths and modularity (Figure S5). Since the species were sampled from natural ecosystems, the sites differed not only in climate, NPP and soil composition but also in many other factors, including disturbance history (such as fire and logging) that may also have a role in driving differences in PTN architecture. On one hand, the variation in PTNs across communities may therefore be driven to an unknown degree by other factors correlated with climate; on the other hand, the resolution of strong relationships of PTN parameters with climate despite confounding variables suggests their robustness (Medeiros et al., 2023). Further studies are needed to fully disentangle the influences of individual environmental factors on community PTNs.

Our study did not support the hypotheses that PTN connectivity and complexity would be associated with phylogenetic diversity or NPP. We propose that the lack of a relationship of PTN architecture with phylogenetic structure and NPP would have been due to our consideration of diverse ecosystems (from desert to forests), for which numbers of niches may not correspond strongly to phylogenetic diversity or productivity. Future studies testing PTN parameter shifts across communities of a given type (e.g. forests, deserts or grasslands) may thus highlight relationships of PTN structure to productivity and phylogenetic diversity that were not resolved here. Additionally, this study focused on the woody species, as these were biomass-dominant and most representative of overall ecosystem structure and functioning and the largest contributors to ecosystem productivity. However, our findings for the shifts in PTNs with climate and with diversity may differ for nonwoody species, or when considering the entire species pool, combining woody and nonwoody species, as this would expand the diversity of niches within ecosystems. The higher stratification of the forests may also result in a greater diversity of light niches relative to desert. Our study points to a number of important avenues for future research. First, our study suggests the need for comparison of PTNs for different life forms within and across communities, beyond only woody species. Second, the association of PTN parameters with functional diversity in our study may be further disentangled given studies designed to separate the role of variation in species richness from that of functional diversity independently of species richness, especially given our finding that PTN parameters were not associated with our phylogenetic diversity index across communities. Notably, both FRic and the phylogenetic diversity index used in this study would be related to species richness (Mouchet et al., 2010; Sandel, 2018). Thus, the relationships of additional metrics of diversity beyond the FRic index used here could potentially provide additional resolution of these associations, especially if applied in studies of communities with species presence/absence and biomass census data beyond those available for our sites. Notably, the linkage of PTN parameters with functional diversity may be indirect, for example, via climate, or potentially may involve bidirectional causality. For example, the trait relationships represented in PTNs include trade-offs that may constrain phylogenetic and functional diversification during evolution, or, alternatively or additionally, these trait relationships might themselves arise from constraints on phylogenetic and functional diversification driven by other factors (Mouchet et al., 2010; Sandel, 2018). Indeed, the disentangling of the causal basis for trait diversity and trait–trait relationships in terms of phylogeny and independently of phylogeny is a topic of strong current interest, with new approaches in development (cf. De Bello et al., 2021, pp. 170–173), (Sanchez-Martinez et al., 2024).

Beyond comparisons across ecosystems, the PTNs allowed us to identify the traits within each PTN with larger betweenness, closeness, clustering coefficient and degree of connectiveness in each of the six sites, indicating special importance for the functional stability of the phenotype due to the dependence of other traits on these traits (Figure 1) (Flores-Moreno et al., 2019; He et al., 2020; Li et al., 2022). We found that despite the relative consistency of trait-level PTN parameters across sites (Figures S8–S11; Table S8), the importance of individual traits within the PTNs changes according to the sampling location (Figure S4). The traits that emerged as hub and mediator traits included those typically associated with leaf structural support, photosynthesis and fluxes (Figures S3 and S4). Overall, the traits that are involved in multiple key functions or mediating the specific functions of multiple traits, such as LDMC, leaf carbon concentrations and leaf mass per area, were more conserved and serve as hubs and mediators of the PTNs. For example, the leaf concentration of carbon, which is widely recognized as one of the most stable and conserved traits across plants and involved in the protection of leaves against herbivory (Ma et al., 2018), had one of the lowest CVs in all six communities and emerged as one of the traits with the highest degree of connectiveness and betweenness (Figures S3 and S4). The LDMC and leaf mass per area, also among the least variable traits within the community, are mechanistically involved in many aspects of physiology, such as photosynthesis and tolerance of low resources (de la Riva et al., 2016; John et al., 2017; Sack et al., 2013; Sack & Buckley, 2020). Additionally, the leaf mass per area is also a component of many other traits since it mediates the conversion of trait values from mass to area-based (Wright et al., 2004). Notably, we did not find support for an effect of the number of traits within a measurement category and their betweenness, closeness, clustering coefficient and degree of connectiveness values (Figure S6), consistent with hub traits being key connectors of traits across measurement categories. The predominance of traits related to plant economics, including whole plant and wood traits, such as maximum height and WD, and of traits related to drought tolerance, among the most central and interconnected in the PTNs of all sites point to an optimization of drought adaptation across the CAFP (Bohnert et al., 1995; Harrison et al., 2020).

Whereas single trait-climate relationship analyses provide an atomistic view of the adaptation of whole phenotypes, PTNs enable a broader view of the trait–trait correlations in ensemble, leading to a clearer resolution of trait organization within the integrated phenotype. Our study points to new conclusions about community assembly and adaptation to aridity and the organization of traits in the integrated phenotype for species within and across communities. While a previous study found that cool/dry sites had simpler networks across a latitudinal continental gradient, we found that warmer/drier sites had simpler networks across a bioregional aridity gradient (Li et al., 2022). Thus, our paper supports a role for stress and especially drought in simplifying trait networks, an explanation that would be applicable in both the bioregional and continental contexts. Our study also introduced new tests of the relationship of network complexity to phylogenetic diversity, functional richness and productivity. Further, our study tested the association between the relative connectedness of traits within a PTN and their variation (using the coefficient of variation) across species. We found a new pattern of variation among traits within the network, testing for why some traits are more 'hub-like', and finding that those traits that vary less across species tend to be highly connected centrally in trait networks and provide a new hypothesis to explain this.

5 | CONCLUSION

Our results, indicating the responsiveness of PTN architecture to climate and its reflection of functional richness, reinforce the idea that a wide range of traits is organized into multiple modules representing physiological and ecological strategies that vary among plant communities. Our study extends the usefulness of PTN approaches for quantifying functional trait patterns at ecosystem and bioregional scales. We show that PTN parameters representing connectivity and modularity, like key single or sets of multiple functional traits, or axes of trait variation representing 'trait spectra' or 'trait strategies' or 'syndromes' (Díaz et al., 2004, 2016; Funk et al., 2017; Grime, 1979; Lavorel & Garnier, 2002; Maynard et al., 2022; Westoby, 1998; Wright et al., 2004), relate to functional richness and productivity. Indeed, PTN parameters such as edge density and modularity have potential applications as alternative or complementary indices of functional diversity to hypervolumes (cf. Cornwell et al., 2006; Lamanna et al., 2014), where PTN parameters would encapsulate information about the inter-correlative pattern of trait variation, complementing the range indicated by hypervolumes. PTNs thus provide various avenues to clarify plant environmental adaptation and trait associations that would influence current and future species distributions and ecosystem resilience in response to climate change.

AUTHOR CONTRIBUTIONS

Camila D. Medeiros and Lawren Sack conceived the ideas and experimental design; Camila D. Medeiros, Santiago Trueba, Christian Henry, Leila R. Fletcher, James A. Lutz, Rodrigo Méndez Alonzo and Lawren Sack sampled species in the field; Camila D. Medeiros and Santiago Trueba collected trait data; Camila D. Medeiros analysed the data with contributions from Lawren Sack and Nathan J. B. Kraft; and Camila D. Medeiros and Lawren Sack wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70010.

DATA AVAILABILITY STATEMENT

All trait and climate data collected for this paper are available from the Dryad Digital Repository: http://datadryad.org/stash/share/1Tbci25p7P7TnTdy4ZwXzF-zliNMfY8eXPuvmxVWtC0 (Medeiros et al., 2025). Relevant code is available on Zenodo: https://doi.org/10.5281/zenodo.13922148 (Medeiros, 2024).

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SUPPORTING INFORMATION

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

Figure S1. Diversity in traits across species.

Figure S2. Weighted plant trait networks.

Figure S3. Variation in trait-level parameters of the plant trait networks.

Figure S4. Variation in trait-level parameters describing the centrality and the connectedness of traits within networks.

Figure S5. Association of plant trait network parameters with site climate.

Figure S6. (a) Association among trait-level plant trait network (PTN) parameters and the number of traits in each measurement category. (b) Relationships among the number of traits per category and the network-level PTN parameters.

Figure S7. Relationships across traits of the coefficient of variation with trait parameters within plant trait networks.

Figure S8. Relationships among the betweenness of traits across the PTNs of each of the sampled communities.

Figure S9. Relationships among the closeness of traits across the PTNs of each of the sampled communities.

Figure S10. Relationships among the clustering coefficient of traits across the PTNs of each of the sampled communities.

Figure S11. Relationships among the degree of connectedness of traits across the PTNs of each of the sampled communities.

Table S1. List of species.

Table S2. Network parameters and attributes.

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

Table S4. Differences in functional traits among species and plant communities.

Table S5. Associations of traits for the complete set of 136 species and for species sampled in each of the sampled communities.

Table S6. Associations of plant trait network parameters from the PTNs and environmental variables of the sampling locations.

Table S7. The coefficient of variation of each trait and trait-level plant network parameters for all species together and for species sampled in each community.

Table S8. Associations of the trait coefficient of variation with trait-level plant network parameters for all species together and for species sampled in each community.

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