



Covariation between leaf hydraulics and biomechanics is driven by leaf density in Mediterranean shrubs

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Abstract

Key message Leaf density links the resistance to mechanical and hydraulic stress in Mediterranean shrubs as it is associated with the water potential at turgor loss and the moduli of elasticity and strength.

Abstract Understanding the patterns of hydraulic and mechanical trait variation in vascular plants is critical to predicting species' stress tolerance. Although previous work has shown that hydraulic and mechanical traits are decoupled in stems, there is little information available for leaves, which are organs more diversified in structure, function, and possibly drought tolerance strategies across habitats. We tested for coordination between leaf hydraulic traits related to drought tolerance and the mechanical resistance of leaves, for 17 shrub species from the arid and semiarid vegetation of the California Floristic Province. Bayesian and phylogenetic correlations showed that across species, hydraulic and mechanical traits both had strong associations with the water potential at turgor loss, and with leaf tissue density. However, leaf maximum hydraulic conductance and the water potential at 50% and 80% loss of hydraulic conductance were statistically independent of two key mechanical traits, the leaf modulus of elasticity and leaf structural strength. Our results suggest that leaf biomechanical traits, which reflect construction costs and contribute to leaf longevity, are decoupled from hydraulic capacity and safety. The independence of hydraulic and mechanical protection in leaves enables a wide range of trait combinations in leaves, which would increase their adaptive potential across ecosystems.

Keywords Drought tolerance · Leaf hydraulic conductance · Leaf water potential at turgor loss point · Mechanical resistance

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Introduction

Drought is a critical and increasingly common abiotic stress that impacts plant structure and function across several levels of biological organization, from cells to organs to the assembly of plant communities (Engelbrecht et al. 2007; Kursar et al. 2009; Blackman et al. 2014; Bartlett et al. 2016). In response, plant species have been selected

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to either tolerate or avoid drought. Within drylands, plants have been selected to modulate leaf phenology, i.e., the annual cycles of leaf display and growth, ranging between nearly perennial and deciduous species (Cooper 1922; Parker et al. 2016). Perennial species can tolerate drought, through structures that are less susceptible to drought-induced collapse, such as xylem vessels of reduced size, at the cost of reduced rates of resource acquisition (“slow” species). In the opposite, extreme drought-deciduous species can achieve high rates of resource acquisition when resources are abundant, by rapidly displaying low-investment structures that are vulnerable to biotic and abiotic stresses (Grime 1979; Lambers and Poorter 1992; Grime et al. 1997; Reich 2014; Zhang et al. 2017). As biomechanical protection and drought tolerance are critical determinants of plant adaptation (Reich et al. 1997; Givnish et al. 2005; Wright et al. 2005; Scoffoni et al. 2011; Sterck et al. 2011; Mendez-Alonzo et al. 2012; Damian et al. 2018), the quantification of these two functions and its covariation across species may provide further understanding of the response of plants to catastrophic drought.

Previous research has found contradictory evidence of such coordination in stems. For example, at the tissue level, and particularly within the xylem, there is evidence of association between the hydraulic and biomechanical properties: to avoid the risks of conduit implosion; plants have adapted to increase xylem mechanical resistance at the cost of a reduction in maximum conductance (Mencuccini et al. 1997; Baas et al. 2004; Jacobsen et al. 2005; Pratt and Jacobsen 2017). Narrower conduits in turn, often reduce the sensitivity to the spread of embolism, assuming fewer pits vulnerable to air seeding (Savage et al. 2010; Brodribb et al. 2016). Simultaneously, increases in cell wall thickness relative to lumen diameters reduce the risk of mechanical deformation (McMahon 1973; Niklas 1992; Hacke et al. 2001). In stems, depending on the biome and traits studied, there are some studies that have shown strong correlations between the mechanical and hydraulic functions (Normand et al. 2008; Fan et al. 2017), and other studies that have found a lack of association between these two functions (Lachenbruch and McCulloh 2014; Gleason et al. 2016). However, few studies have evaluated the patterns of coordination between the hydraulic and mechanical function in leaves. For example, across ten diverse species, and six species of *Acer* and *Quercus*, leaf hydraulic vulnerability (quantified as the leaf water potential corresponding to 50% or 80% decline in leaf hydraulic conductance; $P50_{\text{leaf}}$ and $P80_{\text{leaf}}$, respectively) were inversely related to leaf mass per area (LMA; Scoffoni et al. 2011; Nardini et al. 2012), which is often associated with mechanical strength (Onoda et al. 2011). However, other studies have not found direct associations between $P50_{\text{leaf}}$ and LMA (Blackman et al. 2010).

In leaves, there seems a less direct necessity for coordination of hydraulic and mechanical functions based on tissue structure. The leaf hydraulic conductance (K_{leaf}) and its sensitivity to decline during dehydration depend on properties of both the vein xylem and the extra-xylary tissues, i.e., bundle sheath and mesophyll cells (Buckley et al. 2015; Trifiló et al. 2016; Scoffoni et al. 2014, 2016). The vein xylem may contribute to high K_{leaf} through larger and more numerous conduits, and gain resistance to hydraulic decline through greater major vein density, narrow vessels and adaptations of pit membranes (Blackman et al. 2010; Sack and Scoffoni 2013), while the conductivity and vulnerability of extra-xylem pathways would depend on cell membrane permeability and airspace porosity to vapor transport (Buckley et al. 2015). Both vein and mesophyll properties also contribute to biomechanical resistance (Mendez-Alonzo et al. 2013; Onoda et al. 2015). Leaves with higher major vein volume gain in flexural stiffness which acts to sustain a horizontal-cantilever form to intercept light, but these leaves tend to have reduced mechanical resistance of the mesophyll tissues (Niinemets and Fleck 2002). Further, the lamina mechanical resistance is highly variable across species and plant communities (Méndez-Alonzo et al. 2013) and has only a modest correlation with tissue density (Onoda et al. 2011, 2015). Furthermore, first- and second-order leaf veins are more important to determine the mechanical resistance of leaves than the subsequent order veins, which might be involved in maximizing the flow of water through the non-xylary compartments of leaves (Kawai and Okada 2016), suggesting that structural, mechanical and hydraulic traits within leaves may be decoupled.

In this study, we test for possible patterns of association between leaf hydraulics and biomechanics traits across 17 shrub species from the chaparral, coastal sage scrub, and Mojave Desert in southern California, USA; a region where water stress is a pervasive selective pressure (Davis et al. 2002; Paddock et al. 2013; Pratt et al. 2014). In particular, we explore the relation between the leaf elastic modulus and the tensile strength, two indicators of mechanical resistance of materials (Niklas and Spatz 2004; Gere and Goodno 2009) and four traits relevant to leaf hydraulic function of leaves, i.e., the maximum hydraulic conductance, the water potential at which 50 or 80% of leaf hydraulic conductance is lost (Sack et al. 2003; Brodribb and Jordan 2008; Blackman et al. 2010; Scoffoni et al. 2011), and the water potential at turgor loss (Bartlett et al. 2012a, b, 2014). The studied species include drought-deciduous to nearly evergreen species, and thus our first hypothesis is that evergreen species would achieve higher values of mechanical resistance and hydraulic resistance to dysfunction than drought-deciduous species. Our second hypothesis was that greater tissue toughness would reduce the decline of extra-xylem conductance, by reducing volume shrinkage during dehydration. We

tested this by associating K_{leaf} , $P50_{\text{leaf}}$, and $P80_{\text{leaf}}$ with the mechanical resistance of the whole leaf, the mechanical resistance of the leaf lamina (i.e., excluding the major veins), and the mechanical resistance of the leaf midrib. Our determination of K_{leaf} was performed using the evaporative flux method, which integrates the contribution of the xylary and extra-xylary conduits, which varies widely across species with the extra-xylary conduits contributing to most of the whole-leaf resistance in many species resistance (Sack et al. 2003; Scoffoni et al. 2012; Scoffoni and Sack 2017). Therefore, we predict that whole-leaf mechanical resistance and leaf hydraulic traits would be decoupled, as the former would be a product of vein resistance and the latter of extra-xylary resistance to shrinkage. Similarly, we expect that K_{leaf} would be negatively associated with mechanical resistance of leaf lamina, but unrelated to the whole-leaf and midrib mechanical resistance. By quantifying the patterns of trait covariation between leaf biomechanics and hydraulics we expect to increase the understanding of the strategies of resource acquisition across drylands.

Materials and methods

Mechanical and hydraulic traits were studied in fully expanded, sun-exposed leaves of 17 shrub species common in the flora of the seasonally dry ecosystems of California, USA (Table 1). The selected species included some of the most common shrub species of the coastal sage scrub (a

vegetation type mostly composed by semi-deciduous species), Chaparral (mostly evergreen species) and the Mojave Desert vegetation (a mix of evergreen, semi- and fully deciduous species) (Table 2). Traits were measured for three adult plants of each species growing in common garden conditions at Rancho Santa Ana Botanical Garden (RSABG), Claremont, CA, USA (34°06'49"N, 117°42'55"W, average summer temperature is 25 °C, average winter temperature is 10 °C, and average annual precipitation is 467 mm), from January 2012 to September 2013. The common garden plants were periodically irrigated to avoid excessive water stress, allowing us to experimentally determine the physiological adaptations of species, and controlling the effects of acclimation to local environments that would have been observed in the species' native ranges.

Leaf hydraulic conductance (K_{leaf}) and its vulnerability to dehydration were measured using the evaporative flux method (Sack et al. 2002; Scoffoni et al. 2012; Sack and Scoffoni 2013). Briefly, detached branches were immediately re-cut under water and transported to the lab in buckets covered with plastic bags on the same day. After overnight rehydration, K_{leaf} was measured for excised leaves that were subjected to a range of dehydration employing bench drying (at least six leaves per 0.5 MPa interval of water potential). Shoots having a minimum of three leaves were bagged for equilibration for 15–20 min before measuring the leaf water potential, using a pressure chamber (Model 1505D, PMS Instrument Co., Corvallis, OR). Two leaves were employed to quantify the water potential, and the third leaf

Table 1 Symbols, units, and functional significance of leaf hydraulic and mechanical traits quantified for 17 species from three arid communities in Southern California, USA

Symbols	Traits	Units	Functional significance	References
LA	Leaf area	cm ²	Light interception and gas exchange in plants	Wright et al. (2004, 2017)
LMA	Leaf mass per unit area	g/m ²	A measure of investment in carbon and nutrients within leaves	Poorter et al. (2009) and John et al. (2017)
LD	Leaf density	g/cm ³	Similar to LMA	Poorter et al. (2009)
TME	Tensile modulus of elasticity	MPa	Resistance of leaf tissue to elastic deformations	Méndez-Alonzo et al. (2013)
TS	Tensile strength	MPa	Maximum force required to fracture the leaf tissue per unit sectional area	Méndez-Alonzo et al. (2013)
K_{max}	Maximum leaf hydraulic conductance	mmol/m ² × s × MPa	Maximum water transport efficiency for transpiration in leaves	Sack et al. (2003) and Scoffoni et al. (2011)
$P50_{\text{leaf}}$	Water potential at 50% loss of leaf hydraulic conductance	MPa	An index of the tolerance of leaf hydraulic conductance to dehydration	Sack et al. (2003), Scoffoni et al. (2011) and Choat et al. (2012)
$P80_{\text{leaf}}$	Water potential at 80% loss of leaf hydraulic conductance	MPa	Similar to $P50_{\text{leaf}}$	Scoffoni et al. (2011) and Choat et al. (2012)
π_{tip}	Water potential at turgor loss	MPa	An index of drought tolerance; the soil and leaf water potentials at which leaf wilting occurs	Bartlett et al. (2012a, b, 2016)

Table 2 Study species, abbreviations and plant communities

Species	Family	Abbreviation	Community	Leaf phenology
<i>Arctostaphylos glandulosa</i> Eastw	Ericaceae	Ag	C	E
<i>Atriplex canescens</i> (Pursh) Nutt	Chenopodiaceae	Ac	D	SD
<i>Ceanothus cuneatus</i> (Hook.) Nutt	Rhamnaceae	Cc	C	E
<i>Ceanothus megacarpus</i> Nutt	Rhamnaceae	Cm	C	E
<i>Ceanothus oliganthus</i> Nutt	Rhamnaceae	Co	C	E
<i>Ceanothus spinosus</i> Nutt	Rhamnaceae	Cs	C	E
<i>Encelia californica</i> Nutt	Asteraceae	Ec	S	D
<i>Eriogonum cinereum</i> Benth	Polygonaceae	Erc	S	D
<i>Hazardia squarrosa</i> (Hook. & Arn.) E Greene	Asteraceae	Hs	S	D
<i>Peritoma arborea</i> Nutt	Capparaceae	Pa	D	SD
<i>Larrea tridentata</i> (DC.) Cov	Zygophyllaceae	Lt	D	E
<i>Malacothamnus fasciculatus</i> (Torrey & A. Gray) E Green	Malvaceae	Mf	S	D
<i>Malosma laurina</i> (Nutt.) Abrams	Anacardiaceae	MI	C	E
<i>Quercus berberidifolia</i> Liemb	Fagaceae	Qb	C	E
<i>Rhus ovata</i> S Watson	Anacardiaceae	Ro	C	E
<i>Salvia leucophylla</i> E. Greene	Lamiaceae	SI	S	D
<i>Salvia mellifera</i> E. Greene	Lamiaceae	Sm	S	D

C Chaparral, D Mojave Desert, S Coastal sage scrub, E Evergreen, D Deciduous, SD Semi-deciduous

was measured for K_{leaf} . To measure K_{leaf} , first we cut under-water the petiole (or a small shoots with multiple leaves for sessile or fasciculate species); second, we connected the petiole to water-filled tubing running to a container on a semi-microbalance (XS205, Mettler Toledo, Columbus, OH); and finally, the leaves were forced to transpire under high irradiance ($> 1000 \text{ mmol m}^{-2} \text{ s}^{-1}$ of photosynthetically active radiation at leaf surface) and on top of a box fan to reduce the thickness of the leaf boundary layer. K_{leaf} was calculated as the ratio of flow rate to final leaf water potential at steady state, normalized by leaf area and temperature (Scoffoni et al. 2012).

The bulk leaf turgor loss point (π_{tlp}) was determined using vapor pressure osmometry from six leaves for each of the three individuals per each species measured for K_{leaf} using a vapor pressure osmometer. This method directly quantifies the osmotic potential, and π_{tlp} is derived directly from this metric (VAPRO 5600, Wescor Inc. Logan, UT, USA; Bartlett et al. 2012a, b).

Tensile strength (TS) and tensile modulus of elasticity (TME) were compiled from previously published data for biomechanical properties and structural leaf traits measured on nine leaves for each of the same plants (Méndez-Alonzo et al. 2013). TS and TME were quantified in static tensile tests using screw side-action grips in an INSTRON 3345 mechanical testing machine with a 5 kN load cell (INSTRON Corporation, Canton, MA, USA). Structural leaf traits including leaf area (LA), LMA, and leaf density

(LD) were quantified for the same leaves used for mechanical tests. See Méndez-Alonzo et al. (2013) for further details.

Leaf hydraulic vulnerability indices were determined from K_{leaf} vulnerability curves (Fig. 1). For each species, a set of four functions was fitted to the K_{leaf} vs. water potential data: linear, sigmoidal, logistic and exponential (using the *optim* function in R 2.9.2). Maximum likelihood was employed to parameterize functions, and the function with the lowest Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002) was employed to estimate the maximum leaf hydraulic conductance for the fully hydrated leaf (K_{max}), and the leaf water potential at which 50 and 80% loss in K_{leaf} occurred ($P50_{\text{leaf}}$, $P80_{\text{leaf}}$) (Scoffoni et al. 2012).

Traits were compared among communities using Bayesian one-way ANOVAs applied to the species means, and the patterns of co-variation among traits were analyzed with Bayesian Pearson correlations, using Bayes Factors (BF) as significance metric, in JASP 0.7.5.6 (<https://jasp-stats.org/>). Bayesian analyses do not have *P* values, as these cannot be used to indicate the probability to accept or reject the null or alternative hypotheses (Wasserstein and Lazar 2016). In contrast, BF directly quantifies a ratio of the likelihood of occurrence for the alternative/null hypotheses, such that a BF ratio value > 3 indicates as strong evidence of support for the alternative hypothesis (Jarosz and Wiley 2014).

To determine evolutionary correlations, a phylogeny was assembled with Phylomatic (v.3; Webb et al. 2008),

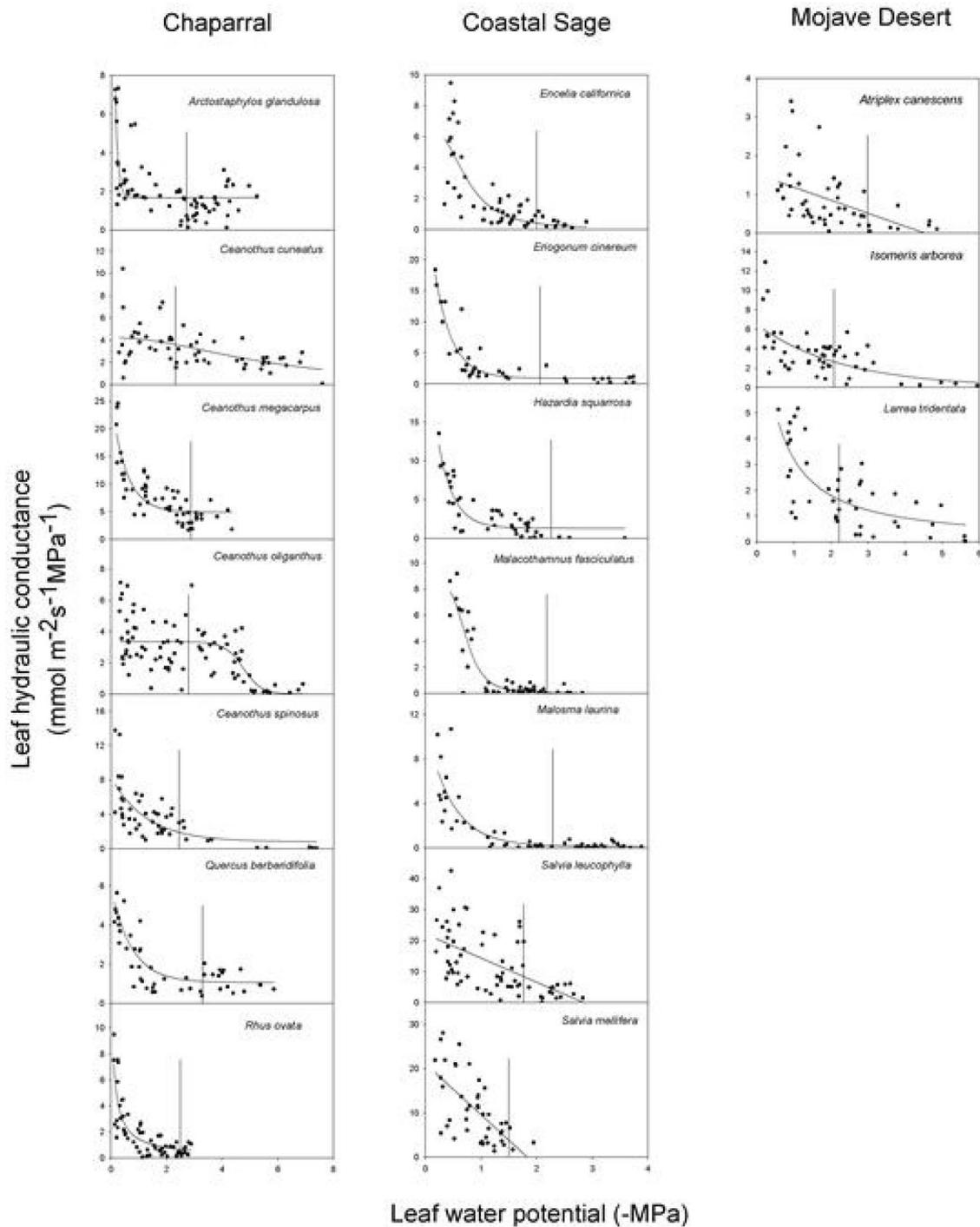


Fig. 1 Leaf hydraulic vulnerability curves for 17 species from three semi-arid environments in California, USA. Vertical lines represent the water potential at turgor loss. Maximum likelihood model selection was employed to determine the function of leaf water conductance decline (Scoffoni et al. 2012). For *Arctostaphylos glandulosa*, *Ceanothus megacarpus*, *Eriogonum cinereum*, *Malosma laurina*, and

Quercus berberidifolia exponential equations were fitted; for *Atriplex canescens*, *Salvia leucophylla* and *Salvia mellifera*, linear equations were fitted; for *Ceanothus oliganthus*, a sigmoidal equation was fitted. Logistic equations were fitted for the rest of species (model parameters in Table S1). Note that the x-axis scales are different for the three community types shown

following a reconstruction of the relationships among species using the Angiosperm Phylogeny Website (Stevens 2001) and a current phylogeny for the diverse and endemic genus *Ceanothus*, including species from the subgenera *Ceanothus* and *Cerastes* (Burge et al. 2011). Phylogenetic independent contrasts (PICs) were calculated, and the correlations were evaluated using PICs with the *ape* package in R v. 2.92.2 (R Core Team 2015).

The patterns of co-variation among traits were summarized using principal component analyses (PCA) on the correlations in JASP 0.7.5.6, for the traits that were available for all the species, i.e., excluding *Larrea tridentata*, for which leaf tensile moduli of elasticity (TME) and leaf tensile strength (TS) were unavailable.

Results

The species varied strongly in all measured hydraulic traits. Leaf maximum hydraulic conductance (K_{\max}) varied from 1.5 to 22.1 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ (average 11.4 ± 1.59 SE), the leaf water potential at 50% loss of hydraulic conductance ($P50_{\text{leaf}}$) ranged from -0.15 to -5.42 MPa (average -1.74 ± 0.38 SE), the leaf water potential at 80% loss of hydraulic conductance ($P80_{\text{leaf}}$) ranged from -0.29 to -10.6 MPa (average -3.17 ± 0.73 SE), and leaf water potential at turgor loss (π_{tlp}) ranged from -1.49 to -3.27 MPa (average -2.36 ± 0.11 SE) (Table 3).

The communities did not differ on average in K_{\max} , $P50_{\text{leaf}}$ or $P80_{\text{leaf}}$ (K_{\max} , BF = 0.71; $P50_{\text{leaf}}$, BF = 0.88; $P80_{\text{leaf}}$, BF = 0.92). However, chaparral species exhibited a more negative π_{tlp} alongside their higher mechanical resistance than desert or coastal sage scrub species (BF = 9.29; Table 3; Mendez-Alonzo et al. 2013). Evergreen species had a significantly higher LMA and LD than deciduous

species (LMA: 0.19 ± 0.02 vs. 0.08 ± 0.03 , BF = 31; LD: 0.43 ± 0.09 vs. 0.24 ± 0.08 , BF = 104), but there was no difference between evergreen and deciduous species in the other traits quantified in this study.

Across all species, K_{\max} , $P50_{\text{leaf}}$ and $P80_{\text{leaf}}$ were statistically independent of mechanical traits, either for whole leaves (Fig. 2; Table 4) or for the mechanical traits of the lamina and midrib (Table S2). In general, biomechanical traits were correlated across species with π_{tlp} in both ahistorical Bayesian tests and evolutionary correlation tests (Table 4). Among the nine measured traits, five were significantly associated with at least one other trait in our Bayesian correlation matrix, with leaf density showing the highest number of associations (Table 4; Fig. 3), closely followed by π_{tlp} (Table 4; Fig. 4).

We summarized the patterns of co-variation for the nine hydraulic, mechanical and structural traits using principal components analysis. Overall, 73.9% of trait variation was explained by two axes. The first axis, accounting for 48.7% of the variation, included five hydraulic, structural and biomechanics traits, and was negatively related to π_{tlp} , and positively related to the tensile modulus of elasticity (TME), the tensile strength (TS), the leaf mass per unit area (LMA) and leaf density (LD). The second axis, accounting for 25.2% of the variation, was negatively related to leaf area (LA) and positively related to $P50_{\text{leaf}}$ and $P80_{\text{leaf}}$ (Fig. 5a). Species were clearly separated according to leaf economics, phenology, and hydraulic and biomechanical resistance, ranging from “slow” species, with high resistance to biomechanical failure and hydraulic dysfunction (chaparral species in Fig. 5b), to “fast” species (coastal sage species in Fig. 5b), including most deciduous species, and two evergreen species with relatively large leaves and high vulnerability to hydraulic dysfunction (Anacardiaceae in Fig. 5b).

Table 3 Mean trait variation across species and communities from three semiarid communities in California

Trait	Max	Mean \pm SE	Min	C mean \pm SE	S mean \pm SE	D mean \pm SE	BF
LA	27.53	6.47 \pm 1.98	0.69	7.1 \pm 3.1	8 \pm 3.1	1.4 \pm 4.8	0.43
LMA	0.33	0.15 \pm 0.02	0.04	0.2 \pm 0.02	0.1 \pm 0.02	0.09 \pm 0.03	18.7
LD	0.58	0.36 \pm 0.03	0.11	0.49 \pm 0.03	0.25 \pm 0.03	0.31 \pm 0.04	445
TME	69.96	16.1 \pm 4.3	2.08	28 \pm 5	4 \pm 5	16 \pm 9	5.94
TS	2.97	1.15 \pm 0.17	0.44	1.6 \pm 0.2	0.64 \pm 0.2	1.31 \pm 0.4	6.78
K_{\max}	22.10	11.4 \pm 1.6	1.52	10.4 \pm 2.4	14.4 \pm 2.4	6.8 \pm 3.6	0.71
$P_{50\text{leaf}}$	-0.15	-1.74 \pm 0.38	-5.42	-2.5 \pm 0.6	-0.9 \pm 0.6	-2 \pm 0.9	0.88
$P_{80\text{leaf}}$	-0.29	-3.17 \pm 0.73	-10.61	-4.6 \pm 1.1	-1.7 \pm 1.1	-3.3 \pm 1.6	0.92
π_{tlp}	-1.49	-2.36 \pm 0.11	-3.27	-2.7 \pm 0.1	-2 \pm 0.1	-2.4 \pm 0.2	9.22

Trait and abbreviations as in Table 1. The significance of community comparisons was obtained using the Bayes factor (BF) inverse values obtained from Bayesian one-way ANOVAs on species means. BF is considered significant when larger than 3.0 (in bold)

C chaparral, S coastal sage scrub, D Mojave Desert

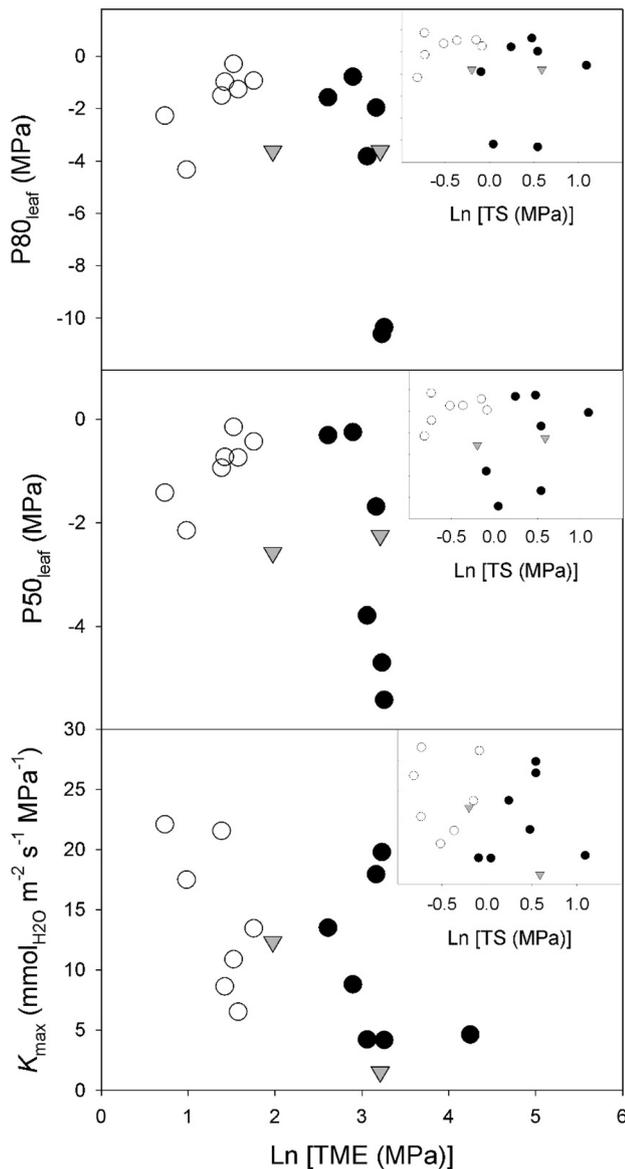


Fig. 2 The independence of leaf hydraulic and biomechanical traits for 17 species from three arid communities in Southern California, USA., including leaf maximum hydraulic conductance (K_{\max}), and leaf vulnerability to hydraulic dysfunction, as quantified by the leaf water potential at 50 and 80% decline in leaf hydraulic conductance ($P50_{\text{leaf}}$ and $P80_{\text{leaf}}$), tensile modulus of elasticity (TME, Ln-transformed data) and tensile strength (TS, Ln-transformed data). Closed circles: chaparral species, open circles: coastal sage species, and shaded circles: desert species

Discussion

This study found evidence of decoupling of function between leaf mechanical traits and water transport traits, including maximum leaf hydraulic conductance (K_{\max}) and vulnerability to hydraulic dysfunction ($P50_{\text{leaf}}$ or $P80_{\text{leaf}}$) for species of southern California Mediterranean ecosystems.

The notion that leaf hydraulic and structural function may be independent is in agreement with some previous reports that have found that leaf function is unrelated to leaf economic traits, both at the intraspecific and interspecific scales (Li et al. 2015; Blackman et al. 2016). The independence of function may arise from the intrinsic variability of structures within leaves, where the mechanical traits may be associated with xylem veins, but the hydraulic function may find its structural basis in the interface between minor veins and extra-xylary tissues. This diversity of structures within leaves may have provided a way to diversify leaf form and function across the Californian flora.

Putative mechanisms for the independence of leaf hydraulics and biomechanics

The K_{\max} , $P50_{\text{leaf}}$ and $P80_{\text{leaf}}$ were independent of the tensile strength (TS), the tensile modulus of elasticity (TMA), and the leaf mass per unit area (LMA) across species. Unlike in stems, where the xylem conduits and tracheids contribute both to hydraulic efficiency and mechanical support, in leaves, the hydraulic and mechanical systems are structurally decoupled. In leaves, the hydraulic system is comprised of the xylem conduits within leaf major and minor veins. The venation architecture, i.e., vein density, and also the outside-xylem pathways, depend on mesophyll properties such as membrane permeability and cell wall thickness (Buckley et al. 2015).

In contrast, the leaf mechanical properties are mainly based on the overall mechanical properties of the first- and second-order veins (Kawai and Okoda 2016; Blonder et al. 2018), with minor veins being relevant for hydraulic distribution (Sack et al. 2012; Kawai and Okoda 2016). Also, hydraulic capacity is influenced by the abundance of non-xylem cell types in the vascular bundle (parenchyma, collenchyma, sclerenchyma, and bundle sheath cells) and mesophyll cell wall toughness (Balsamo et al. 2006). For example, it is entirely feasible to have a tough leaf with high TME and TS with very negative $P50_{\text{leaf}}$ (e.g., *Ceanothus cuneatus*, with a TME = 25.9 MPa, and $P50_{\text{leaf}} = -5.4$ MPa), or a leaf with high TME and TS with a sensitive $P50_{\text{leaf}}$ (e.g., *Arctostaphylos glandulosa*, with a TME = 23.4 MPa, and $P50_{\text{leaf}} = -1.9$ MPa), given that the $P50_{\text{leaf}}$ was quantified using EFM. This technique determines the hydraulic dysfunction due to leaf shrinkage, particularly in the outer xylem compartments, and thus acts independently of the hydraulic or mechanical resistance within the primary and secondary veins of the leaves (Scoffoni and Sack 2017). One limitation of our study is that we were unable to quantify the hydraulic decline within the vascular system of leaves, which would have the same structural basis as leaf mechanics. Further experiments may use the newly developed optical methods to study the resistance to dysfunction of the

Table 4 Bayesian associations and evolutionary correlation tests for nine hydraulics and biomechanics traits in leaves of 17 species across three arid and semiarid plant communities in Southern California, USA

	LA	LMA	LD	TME	TS	K_{\max}	P_{50l}	P_{80l}	π_{tlp}
LA		0.28	0.16	-0.11	-0.05	-0.03	0.47	0.44	0.00
LMA	0.22		0.75*	0.42	0.46	0.20	-0.38	-0.41	-0.44
LD	0	0.71*		0.76*	0.71	-0.29	-0.33	-0.36	-0.72*
TME	-0.1	0.32	0.57		0.92*	-0.43	-0.24	-0.32	-0.81*
TS	0.01	0.28	0.53	0.85*		-0.29	-0.08	-0.20	-0.81*
K_{\max}	0.35	0.26	-0.09	-0.46	-0.08		0.09	0.30	0.49
P_{50l}	-0.45	0.24	0.04	0.22	-0.08	-0.29		0.93*	0.25
P_{80l}	-0.54	0.28	0.03	0.28	0.11	-0.11	0.88*		0.28
π_{tlp}	0.11	0.25	0.38	0.67	0.57	-0.23	0.09	0.07	

Bayesian–Pearson correlations, upper panel; correlations based on phylogenetic independent contrasts calculated from raw data, lower panel. The significance of Bayesian trait correlations was obtained using the Bayes factor (BF) inverse values, which are considered significant when larger than 3.0. Bold upper panel = Bayes factors > 3, *Bayes factors > 10; Bold lower panel = $P < 0.05$, * $P < 0.01$. For abbreviations, see Table 1

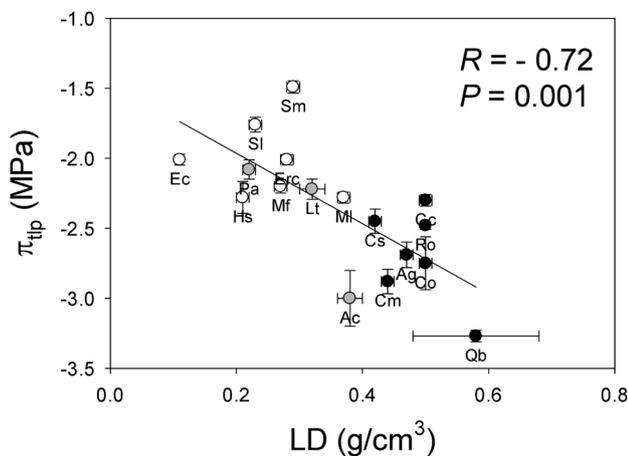


Fig. 3 Correlations between leaf density (LD) and the water potential at turgor loss (π_{tlp}), for 17 species of three arid environments of California, USA. Closed circles: chaparral species, open circles: coastal sage species, and shaded circles: desert species

vascular and non-vascular leaf hydraulic pathways and the mechanical resistance of leaf laminas and veins (Brodrribb et al. 2017; Skelton et al. 2018), providing a more complete view of the processes involved in leaf resistance to drought and mechanical stress.

Our results show that K_{\max} and leaf hydraulic vulnerability were independent of LMA, which is in agreement with other studies reporting K_{\max} per leaf area (Sack et al. 2003; Blackman et al. 2010). However, if K_{\max} is divided by LMA to produce a mass-based K_{\max} , then this variable is typically negatively related to LMA, indicating diminishing returns of enhancing K_{\max} per investment in leaf mass (Simonin et al. 2012). Across diverse species sets, there have been contrasting findings for the association between leaf structural and hydraulic traits, ranging from positive associations between LMA and P_{50leaf} or P_{80leaf}

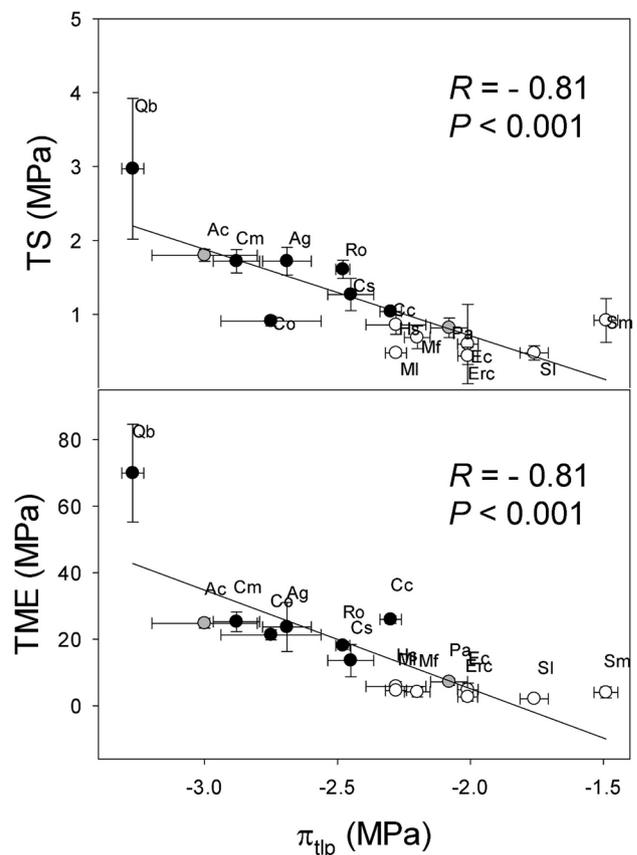


Fig. 4 Correlations between the water potential at turgor loss (π_{tlp}) and the maximal tensile strength (TS) and the leaf modulus of elasticity (TME) for 17 species of three arid environments of California, USA. Closed circles: chaparral species, open circles: coastal sage species, and shaded circles: desert species

(Scoffoni et al. 2011; Nardini et al. 2012) to a case where P_{50leaf} and P_{80leaf} were independent of LMA (e.g., Blackman et al. 2010). Partial correlation analysis has indicated

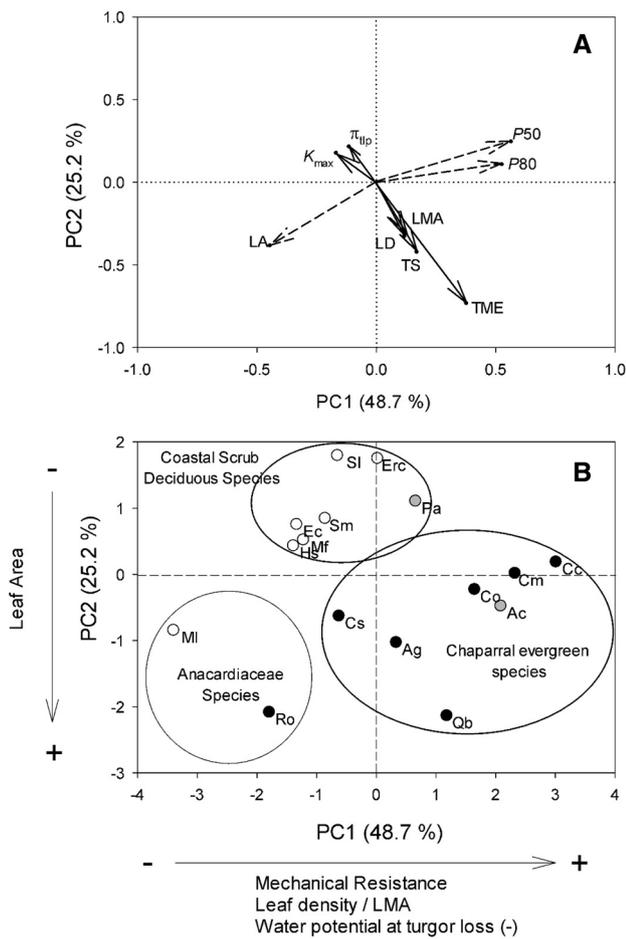


Fig. 5 Study species arranged by their leaf traits. Loading plot (a) and score plot (b) of a principal component analysis summarizing 9 hydraulic, mechanical and morphological leaf traits for 16 species of 3 arid environments of California, USA. Due to incomplete information, *Larrea tridentata* was omitted. **a** Traits that influenced PC1 (explaining 48.7% of variance) are shown with solid lines, and traits influencing PC2 (explaining 25.1% of variance) are shown with dashed lines. Species abbreviations are in Table 1, and trait abbreviations in Table 2. The λ values were 2.09 and 1.51 for the first and second components, respectively. **b** Species arrangement according to the first and second values of PCA scores. Closed circles: chaparral species, open circles: coastal sage species, and shaded circles: desert species

that these are mechanistically independent traits, but both can be co-selected for greater drought tolerance (Scoffoni et al. 2011). The lack of correlation between structural and hydraulic traits in our dataset is consistent with the wide variability in hydraulic designs that has occurred in Mediterranean environments, and the different ways to develop higher drought tolerance via different hydraulic pathways in the leaf tissues, as previously proposed for stem hydraulics and gas exchange responses to drought (Pivovarov et al. 2014).

Associations between leaf hydraulics and biomechanics and leaf turgor loss point

Across species, both structural and mechanical traits were associated with the π_{tlp} . The enhancement of drought tolerance via π_{tlp} enables sustained transpiration at low water supply (Bartlett et al. 2012a, b, 2016). We did not find a relationship of leaf hydraulic vulnerability with π_{tlp} across southern California species, though these traits were associated in previous studies of diverse species (Scoffoni et al. 2012; Li et al. 2018) and compiled data (Bartlett et al. 2016). Recent work has suggested that these traits would be mechanistically independent, as $P50_{leaf}$ and $P80_{leaf}$ would be determined by xylem and mesophyll traits other than cell osmotic concentration, and even in studies that found them to be correlated, the coordination of π_{tlp} and leaf hydraulic vulnerability can be highly variable (Scoffoni and Sack 2017). Thus, there may be advantages for some species to maintain open stomata even as the hydraulic conductance declines, i.e., enabling sustained gas exchange, and in other species, advantages for shutting stomata before leaf hydraulic decline, i.e., in preserving the hydraulic system especially for species that show limited or delayed hydraulic recovery (Jones and Sutherland 1991; Scoffoni and Sack 2017). Notably, in our study *Quercus berberidifolia* is an example of the former, maintaining turgor even below P80, while three of the *Ceanothus* species are examples of the latter, with very strongly negative $P50_{leaf}$ and $P80_{leaf}$ values, well below the π_{tlp} . These results are divergent with those of Skelton et al. (2018), who found that *Q. berberidifolia* is the oak species of California with the highest resistance to cavitation, both in the stem and leaf. The divergence between our results and those from Skelton et al. (2018) arises from our use of EFM to quantify leaf dysfunction, as the optical method employed by Skelton determines the degree of dysfunction in the vascular system, and EFM mostly determines the dysfunction in the extra-xylary hydraulic pathways.

A novel finding of our study was the strong coordination of leaf biomechanical protection with π_{tlp} such that species that achieve very negative π_{tlp} have higher TME and higher TS. For example, *Salvia mellifera* had leaves very sensitive to drought and biomechanical damage, with π_{tlp} of -1.49 MPa and TME of 3.99 MPa, whereas *Quercus berberidifolia* was highly resistant to turgor loss and also highly protected mechanically, with π_{tlp} of -3.27 MPa and TME of 69.9 MPa. Evergreen chaparral species would benefit by enhancing leaf mechanical resistance enough to maintain their relative water content at turgor loss point above the threshold for damage, and additionally reducing susceptibility to herbivory and physical damage (Bartlett et al. 2012a, b; Méndez-Alonzo et al. 2013). In contrast, coastal scrub and Mojave desert species may benefit from low cost and short-lifespan leaves, due to the unpredictability of water

availability (Jacobsen et al. 2008; Parker et al. 2016). The short-lifespan leaves may achieve high rates of gas exchange when water is available, and close stomata and ultimately lose leaves during dry periods (Parker et al. 2016). During drought, such leaves could additionally fine-tune their investment in compatible solutes to regulate turgor via osmotic adjustment (Polle and Chen 2015, Mendez-Alonzo et al. 2016), thus sustaining turgor while acquiring water from dehydrating soils, without investing in extreme drought tolerance structures.

The role of independent variation in leaf hydraulic and biomechanical traits in determining community and niche differences within communities

The mediterranean environment enables a wide range of morphological and functional variability, allowing adaptation across a variety of abiotic and biotic selective pressures (Nardini et al. 2014). Deciduous species, including most coastal sage shrubs, tended to display lower turgor loss points and mechanical resistance with lower LMA and LD, versus chaparral shrub evergreen species, tending to display highly negative turgor loss points, and high mechanical protection, with larger LMA and LD. Given the seasonality of Mediterranean climates, with rains falling in winter, but fog water incomes potentially occurring throughout the year, species with evergreen habit may require multiple means to tolerate drought focusing on stem and leaf hydraulics and stomatal closure (Pivovarov et al. 2014; Skelton et al. 2015). Evergreen species thus may require high mechanic resistance to persist through several years, regardless of the precipitation in those years. In contrast, deciduous species would only display foliage during the brief rainy season, lasting in California less than 3 months, and providing a window of opportunity to enhance plant productivity and posteriorly entering in a dormant state. The seasonality in water availability has selected for low-investment leaves (with low LMA and LD) of low mechanical resistance and high hydraulic vulnerability in deciduous species.

Further, we found exceptions to the fast–slow continuum in the two broad-leaved, evergreen species of the Anacardiaceae that have evergreen leaf habit, but leaf traits that are consistent with the “fast” economic spectrum, such as low LMA, low leaf mechanical resistance and low hydraulic resistance to drought. In this study, *M. laurina* was the species with the highest values of $P50_{leaf}$, at ca. -0.15 MPa, closely followed by the other member of Anacardiaceae, *R. ovata*, at -0.25 MPa. Coincidentally, these species also differed from other common semiarid and arid species in their stem traits, particularly in their xylem vulnerability to embolism: for *M. laurina* the reported values of P50 in stems range from -0.52 to -0.68 MPa, and for *R. ovata* the P50 is ca. -0.56

(Jacobsen et al. 2007). Such departure from the trend shown by other species may be associated with facultative phreatophytic behavior, with a constant input of water throughout the year allowing for large leaf areas, evergreen phenology and low resistance to hydraulic dysfunction, perhaps involving daily embolism and repair. Phreatophytes have been considered as a distinct functional group, departing from attempts to categorize Mediterranean chaparral and coastal scrub by their functional traits (Méndez-Alonzo et al. 2013; Thomas 2014; Parker et al. 2016).

The species of this study represent part of the wide variability in ecological and physiological strategies of the semiarid flora of the California Floristic Province. Previous compilations for distinct Mediterranean environments also show a wide range of trait variation, from low to high resistance to mechanical and hydraulic dysfunction (Nardini et al. 2014). Functional traits associated with phenology, hydraulic adaptation, and resistance to foliar damage can influence species' vital rates, abundance and persistence within local environments (Brodribb et al. 2003; Markesteijn et al. 2011; Onoda et al. 2011; Mencuccini et al. 2015; Anderegg et al. 2016; Bartlett et al. 2016). Thus, the wide variability and lack of constrained association among leaf mechanical and hydraulic traits would contribute to the ability of species to occupy a wide range of ecological niches. As recent studies have shown that individual functional traits can predict species niches (Shipley et al. 2017); further studies are needed to disentangle how physiological trait combinations across organs scale up to influencing adaptation and performance across environments. Thereby, it is feasible to expect that the decoupling of traits, such as leaf hydraulic and biomechanical resistances, scale up to providing both different means to tolerate stresses, and the ability to perform effectively across a wide range of environments among contrasting communities.

Author contribution statement RMA, FWE and LS designed the experiments; RMA performed the experiments with assistance of CS and MKB. All authors contributed to writing the paper.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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