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RESEARCH ARTICLE

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Climate-induced plasticity in leaf traits of riparian plants

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Abstract

Aim: Leaf litter inputs from riparian vegetation and its decomposition play a key role in energy and nutrient transfer in many stream ecosystems. Instream leaf litter decomposition is driven by both leaf traits and environmental conditions. Therefore, understanding and predicting leaf trait variation under current environmental changes and their putative interactive effects on stream food webs is a critical challenge. Most studies have focussed on the assumed higher interspecific leaf trait variability, with little research addressing an intraspecific perspective.

Location: Andalusia, Spain.

Methods: We assessed the relative effects of climate and soil conditions on the plasticity of leaf traits of four common woody riparian species in permanent low-order Mediterranean streams across a wide aridity gradient. We used a space-for-time substitution approach to predict leaf trait changes and consequences for stream food webs in a future climate change scenario.

Results: Overall, we found that aridity had a major influence on leaf trait plasticity but with opposite patterns depending on plant functional type, although soil was the strongest predictor in some cases. Results indicated that leaf quality—linked to palatability and decomposability—of *Alnus glutinosa*, *Salix atrocinerea* and *Rubus ulmifolius* (deciduous/semi-deciduous) will decrease with forecasted aridification, whereas the palatability of the evergreen *Nerium oleander* will increase. We observed higher trait plasticity than interspecific variation for leaf P, Ca and Mg concentrations and C:P ratio.

Main conclusions: Our findings suggest a decrease of intraspecific leaf quality in riparian deciduous species with global warming in a relatively short term. In a longer term, this may merge with the forecasted dieback of deciduous species in riparian corridors of temperate climate zones. These changes have the potential to significantly impair ecosystem functioning of Mediterranean mountain streams currently under deciduous gallery forests.

KEYWORDS
Aridification, deciduous, evergreen, instream decomposition, litter quality, soil, space-for-time substitution

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1 | INTRODUCTION

The warming of the Earth system is unequivocal (IPCC, 2021). Globally, precipitation is also predicted to increase in the long term (Hewitson et al., 2015). However, forecasts in the Mediterranean basin point to a precipitation decrease of around 34%, along with a temperature increase of *ca*. 5°C for the period 2000–2099 (Harris et al., 2013). As a result, this region will face a climate much drier and hotter than at present, especially during warm seasons (Giorgi & Lionello, 2008), with direct effects on hydrologic regimes (Nohara et al., 2006; Vicente-Serrano et al., 2014) and soil moisture (Manabe et al., 2004). These changes may alter the functioning and structure of plant communities (e.g. Carnicer et al., 2011; Trivedi et al., 2008; Vicente-Serrano et al., 2012).

Small streams flowing through forested areas can be especially susceptible to climate change-induced alterations in plant communities, owing to their high dependence on organic matter inputs from the riparian vegetation, i.e. leaf litter (Wallace et al., 2015). Instream decomposition of leaf litter is a crucial ecosystem process, involving the cycling of nutrients and fuelling stream secondary production (Marks, 2019). The rate at which leaf litter decomposes and is incorporated into food webs highly depends on its quality, which fundamentally depends on after-life persistent traits (Graça & Cressa, 2010; Graça et al., 2001; Zhang et al., 2019). Thus, ecosystem functioning can be significantly altered if leaf litter inputs to streams experience physical and chemical changes (e.g. Casas et al., 2013; del Campo et al., 2021; López-Rojo et al., 2019). These changes can be interspecific, e.g. resulting from the forecasted substitution of deciduous by evergreen species (Kominoski et al., 2013; Salinas et al., 2018) and/or the decline of key plant species populations (e.g. alder; Alonso et al., 2021; Rubio-Ríos et al., 2021). Moreover, given that leaf traits are highly responsive to environmental changes (Heilmeier, 2019; Soudzilovskaia et al., 2013), intraspecific changes may also occur, e.g. due to genetic variability (Crutsinger et al., 2014; LeRoy et al., 2012) or phenotypic plasticity (Graça & Poquet, 2014; Henn et al., 2018; Jung et al., 2014).

Such relationship between leaf traits and the environment has been a recurrent theme of the study (e.g. Ordoñez et al., 2009; Read et al., 2014; Reich & Oleksyn, 2004). However, although recent results indicate that intraspecific variation may represent up to *ca*. 30% of total functional trait variability in plant communities (Albert et al., 2010; Siefert et al., 2015), most studies have focussed on the often assumed higher interspecific variability of many leaf traits (e.g. Hulshof & Swenson, 2010; Wright et al., 2004).

High rates of plasticity in leaf traits are expected in species distributed across ample environmental gradients (Cordell et al., 1998; Fajardo & Piper, 2011; Umaña & Swenson, 2019), as increases in niche breadth allow plants to respond to variation in climatic and other environmental conditions (Henn et al., 2018), whereas nearby individuals may share biotic and abiotic pressures and have close genetic relationships. Warming and reduced rainfall, i.e. increasing aridity, are usually reported to promote the production of thicker and smaller leaves (Wright et al., 2004)—in order to improve their water use efficiency and to increase their leaf life span—with low nutrient concentrations (Reich & Oleksyn, 2004). Such plasticity in important traits can, in turn, affect the palatability and decomposability of leaves, i.e. their acceptability and easiness to be consumed, along environmental gradients (Boyero et al., 2017; Graça & Poquet, 2014; Lecerf & Chauvet, 2008; LeRoy et al., 2007). Understanding how individual species traits, or their syndromes, are modulated by climatic or other environmental characteristics could allow us to refine predictions of potential effects on stream ecosystem functioning, both in green (based on primary production) and brown (based on detritus) food webs, in the face of climate change (Kominoski et al., 2021).

Here, using a 'space-for-time' (SFT) substitution approach (Blois et al., 2013; Pickett, 1989), we investigated how climate change might affect leaf quality, focusing on after-life traits affecting leaf decomposition. The SFT substitution approach is a useful tool to anticipate changes taking advantage of natural gradients (Fukami & Wardle, 2005); in the present study, a natural aridity gradient represents the forecasted aridification of the Mediterranean basin (Seager et al., 2014). We assessed plasticity in leaf traits of four common riparian species, with contrasting functional traits, in permanent low-order streams [*Alnus glutinosa* (L.) Gaertn., *Salix atrocinerea* Brot., *Rubus ulmifolius* Schott and *Nerium oleander* L.], extrapolating their possible variation in the forecasted climatic scenarios from that observed across a wide environmental gradient studied within a relatively small region. Using the same species along many areas differing in environmental conditions allowed us to control for species-specific traits, but not to assess the amount of trait variability due to genetic variability.

Given the high responsiveness of leaves to climate changes (Heilmeier, 2019; Soudzilovskaia et al., 2013) and the high water and nutrient availability in riparian soils of permanent streams (Naiman & Decamps, 1997), we hypothesize that (1) climate will exert a higher influence on leaf trait plasticity of the studied species compared to soil variables. We (2) expect a general trend of decreasing leaf quality—i.e. lower nutrient concentration, higher toughness—with the forecasted aridification (increasing temperature and decreasing precipitation) (Reich & Oleksyn, 2004). However, we also expect that the strength of the effects will vary among different species, as they belong to different functional groups (i.e. C allocation and/or N-fixing) and therefore have low similarity in their leaf traits (Salinas et al., 2018). Thus, we also hypothesize that (3) trait plasticity will be relatively low compared to interspecific variation.

2 | MATERIALS AND METHODS

2.1 | Area of study and selected plant species

Our study was conducted during summer 2013 in the riverbanks of 34 headwater streams with permanent flows distributed across nine natural protected areas (considered as pristine) located in Andalusia (south of the Iberian Peninsula), covering *ca*. 88,000 km^2. These

locations represent a wide climatic gradient within the context of a Mediterranean-type climate and possess a considerable lithological and topographical heterogeneity (Figure 1). The present (mean annual temperature range 10.8–17.4°C; mean annual precipitation range 261–845 mm; Table S1) and the projected climatic gradient studied (by the end of the 21st century) covers from arid to humid conditions according to the Emberger's bioclimatic coefficient (Table 1, Figure 2). This embraces the forecasted aridification, i.e. warming (mean temperature rise of 2–4°C) and reduction of precipitation (mean precipitation decrease of 10–40%), for the Mediterranean region (Seager et al., 2014), as a consequence of climate change towards the year 2100 (reviewed by Giorgi & Lionello, 2008).

We selected four abundant riparian plant species which represent different functional groups featuring different characteristics, including two deciduous riparian trees: black alder—*Alnus glutinosa* (an N-fixer), and grey willow, *Salix atrocinerea*; one semi-deciduous shrub: blackberry, *Rubus ulmifolius*; and one evergreen shrub: oleander, *Nerium oleander*, also known as laurel rose. Leaves of these species collected (June-July 2013) from each sampling sites were present (Table 1) from robust, well-grown and totally unshaded plants distanced from the stream by a maximum of 6 m. Those leaves directly exposed to sun light and without herbivory or pathogen symptoms were selected (Cornelissen et al., 2003). In each stream and for each species, we collected 102 leaves from six individuals (17 leaves per individual) randomly distributed on both stream sides along a 100 m stream reach. Leaves were air-dried at room temperature (20–23°C) for one week and stored in darkness in paper bags until processed. At each stream, the cover of each species was estimated using the Domin–Krajina scale of cover and abundance (Kent & Coker, 1992) in six plots (36 m^2 each) randomly distributed in both stream sides—three plots per side arranged from the edge of the wetted channel—along a 100 m stream reach (Salinas et al., 2018).

2.2 | Environmental variables

Thirty-two environmental variables (altitude, 20 climatic and 11 edaphic; Table 1 and S1) were selected as potential predictors of leaf trait plasticity. Altitude was obtained *in situ* using a portable GPS. Historical (monthly average for the years 1970–2000) values of bioclimatic variables (spatial resolution of 30 seconds, i.e. ~1 × 1 km) recorded along the last period with available climatic data were obtained from the WorldClim database (Table S1; version 2.1; www.worldclim.org, Fick & Hijmans, 2017) using site location information (latitude and longitude). Future monthly values were estimated from the NCAR Community Model version 3 (2 × CO_2 climate change

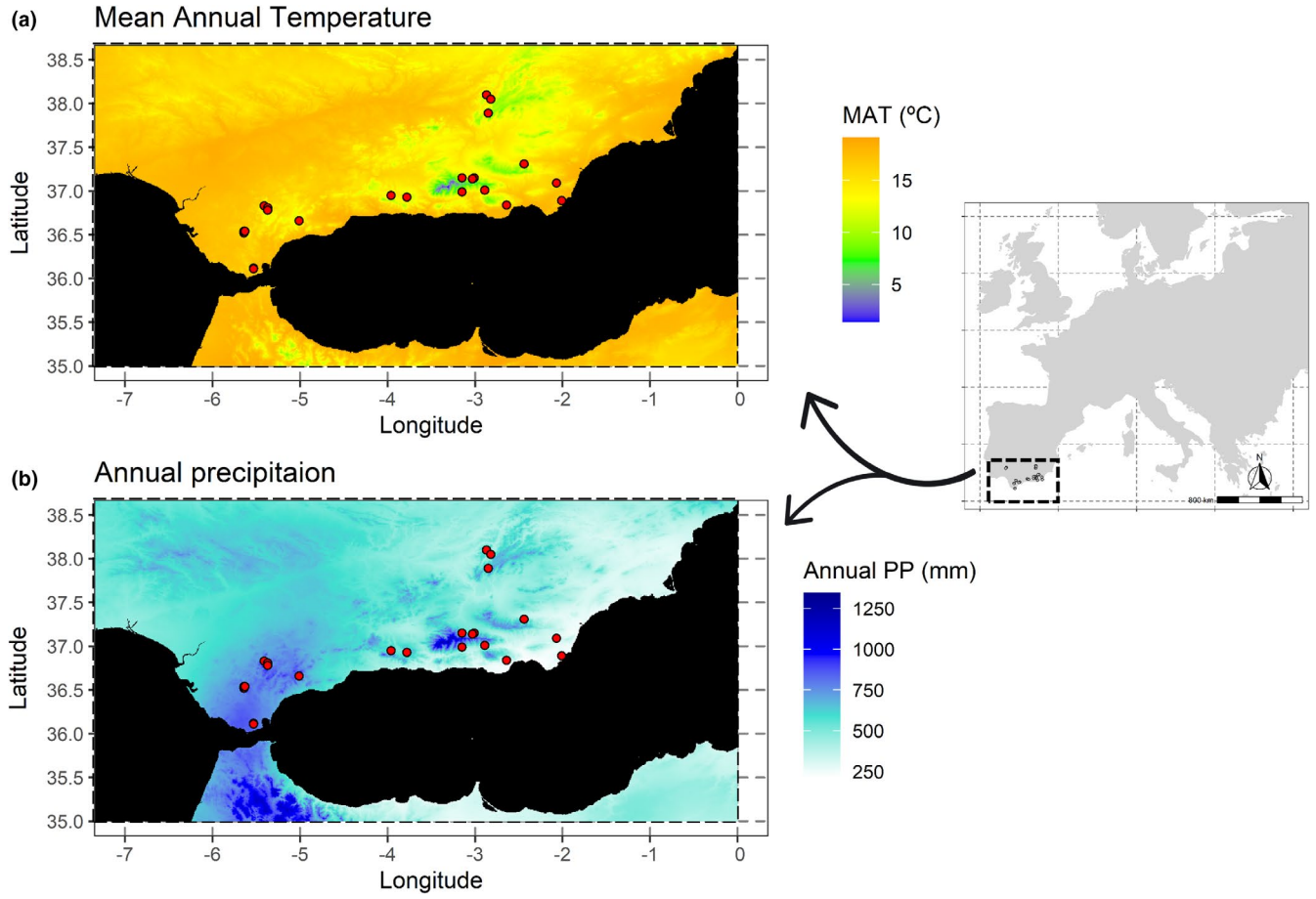


FIGURE 1 Map of the 34 sites of study located within Europe and over the mean annual temperature (a) and the annual precipitation (b) gradients

TABLE 1 Characteristics of sampling sites and cover (%) of each plant species studied

Basin name	Latitude	Longitude	Altitude (m a.s.l.)	Lithology	Land type	Emberger's coefficient (Q2)	Climate category according to Q2	*Alnus glutinosa*	*Salix atrocinerea*	*Nerium oleander*	*Rubus ulmifolius*
Rambla de las Negras	36.89	−2.01	47	Calcareous	Lowland	31.5	Semi-arid			13.8	
Río Aguas	37.09	−2.07	270	Calcareous	Lowland	33.8	Semi-arid			2.0	1.5
Barranco del Cura	36.84	−2.64	291	Calcareous	Lowland	40.4	Semi-arid			22.3	1.0
Arroyo de Aguamulas	38.05	−2.82	689	Calcareous	Midland	42.6	Semi-arid				8.8
Río Bacares	37.31	−2.44	943	Calcareous	Midland	51.9	Sub-humid		22.8		25.7
Río Vacal	36.92	−3.81	956	Calcareous	Midland	54.5	Sub-humid				6.8
Arroyo Los Marcos	37.30	−2.58	1019	Calcareous	Highland	55.1	Sub-humid		20.5		10.3
Río Mecina	36.99	−3.15	1136	Siliceous	Highland	56.5	Sub-humid	11.0	24.8		9.2
Río Turrillas	36.93	−3.78	991	Calcareous	Midland	59.0	Sub-humid				19.3
Río Andarax	37.01	−2.89	1013	Siliceous	Highland	60.4	Sub-humid	43.8	12.8		
Río Alhama	36.95	−3.96	959	Calcareous	Midland	61.2	Sub-humid				7.3
Ribera de Santa Ana	37.87	−6.70	546	Siliceous	Midland	62.5	Sub-humid	66.3			9.3
Arroyo Corterrangel	37.94	−6.60	462	Siliceous	Lowland	62.6	Sub-humid	15.8			12.7
Río Nacimiento	37.15	−2.91	1149	Siliceous	Highland	63.6	Sub-humid		17.9		2.4
Barranco del Dun Dun	37.94	−6.64	554	Siliceous	Midland	66.3	Sub-humid	52.5		1.5	3.0
Río Guadalentin	37.89	−2.85	1273	Calcareous	Highland	66.3	Sub-humid		22.9		5.5
Arroyo de Aguascebas	38.10	−2.87	1063	Calcareous	Highland	66.9	Sub-humid		3.0		4.0
Arroyo de la Garganta	37.90	−2.89	1356	Calcareous	Highland	67.1	Sub-humid				11.6
Río Chico Ohanes	37.05	−2.76	1038	Siliceous	Highland	72.1	Sub-humid		34.8	1.5	20.1
Barranco del Pueblo	37.15	−3.15	1394	Siliceous	Highland	74.8	Sub-humid	29.7	6.0		3.5
Arroyo Hondo	37.14	−3.03	1438	Siliceous	Highland	75.3	Sub-humid	51.4	3.5		15.0
Arroyo de los Castaños	37.15	−3.01	1321	Siliceous	Highland	75.3	Sub-humid	62.0	16.3		2.8
Arroyo de los Caballos	36.68	−4.91	350	Calcareous	Lowland	77.5	Sub-humid			17.7	7.1
Arroyo de los Molinos	36.81	−5.37	379	Calcareous	Lowland	85.0	Sub-humid			11.3	8.2
Arroyo de Bocaleones	36.83	−5.41	316	Calcareous	Lowland	88.6	Sub-humid			11.3	9.5
Arroyo Gaidovar	36.78	−5.37	695	Calcareous	Midland	92.3	Humid				36.8
Río Verde	36.66	−5.01	662	Calcareous	Midland	94.5	Humid			32.4	10.0
Arroyo de la Cruz	36.64	−5.03	897	Calcareous	Midland	94.5	Humid				1.2
Garganta del Caballo	36.54	−5.64	401	Siliceous	Lowland	102.2	Humid			11.9	35.9
Garganta del Aljibe	36.54	−5.63	432	Siliceous	Lowland	102.2	Humid	35.9			1.3
Garganta del Medio	36.54	−5.64	423	Siliceous	Lowland	102.2	Humid	17.3			2.3
Garganta de la Cierva	36.52	−5.64	550	Siliceous	Midland	102.2	Humid	42.9		6.7	8.5

TABLE 1 (Continued)

Basin name	Latitude	Longitude	Altitude (m a.s.l.)	Lithology	Land type	Emberger's coefficient (Q2)	Climate category according to Q2	*Alnus glutinosa*	*Salix atrocinerea*	*Nerium oleander*	*Rubus ulmifolius*
Garganta de la Garza	36.12	−5.53	429	Siliceous	Lowland	109.5	Humid	30.5			6.3
Garganta del Tesorillo	36.11	−5.53	532	Siliceous	Midland	109.5	Humid	28.0			6.3

Notes: Land type was defined by altitude (m a.s.l.): Low <500, Mid 500–1000, High >1000. Sites ranked in order of decreasing aridity according to the Emberger's bioclimatic coefficient Q2.

scenario, CCM3) for the year 2100 (Govindasamy et al., 2003) and subsequently downscaled and matched to the WorldClim estimates of current climate at a resolution of 2.5 minutes (i.e. ~4.5 × 4.5 km). From these variables, the Emberger's bioclimatic coefficient (Q2) for each site was calculated following Condés and García-Robredo (2012) as $100P/((M^2–m^2))$, where P is the annual rainfall in mm, M the average maximum of the warmest month, and m the average minimum of the coldest month. To measure soil variables, we collected a sample consisting of six core samples of the top 20 cm of the riverbank soil profile, obtained by a randomly stratified method from each stream side at a distance of approximately 3 m from the active channel. Samples from each site were mixed, air dried, sieved (2 mm) and stored in sealed polyethylene bags until analysed. Soil physical and chemical variables (Table S1) were measured as in Gil et al. (2004).

2.3 | Leaf traits

We measured nine leaf traits that often correlate with leaf litter decomposition rate (see Graça et al., 2015; Tonin et al., 2021) for each species: N, P, Ca, Mg, condensed tannins and lignin concentrations, C:N and C:P molar ratios and toughness. Before measurements, leaves were rehydrated by spraying with distilled water and stored for 12 h at 5°C. Leaf toughness, expressed in units of mass (g), was measured by performing distal and proximal punctures per individual leaf using a Texture Analyzer TA.XTPlus (Stable Micro Systems) equipped with a needle of 0.38 mm^2 tip surface. Thereafter, leaves were oven dried (60°C, 72 h) and ground to fine powder (Mixer Mill RETSCH MM 200). Concentrations of C and N (% dry mass, DM) of leaves were determined using a mass spectrometer (EA-Thermo DELTA V Advantage, Fisher Scientific®) following standard procedures (Flindt et al., 2020). The concentration of P (% DM) was measured spectrophotometrically after autoclave-assisted extraction (APHA 1998, Flindt et al., 2020). Concentrations of Ca and Mg (% DM) were determined by inductively coupled plasma mass spectrometry (ICP-MS, Perkin Elmer DRC II). Condensed tannins (mg Catechin Hydrate Equivalent per g of DM) were measured by the acid butanol assay (Gessner & Steiner, 2020). Concentration of lignin (% DM) was estimated gravimetrically using the acid detergent method of Goering and Van Soest (1970).

2.4 | Data analysis

To elucidate the relationships between species cover and environmental variables, we ran a Canonical Correspondence Analysis (CCA; *cca* function of the 'vegan' package, Oksanen et al., 2019), after a forward selection (*ordistep* function of the 'vegan' package with 9999 permutations) of the most parsimonious subset of explanatory variables (PPSeasonality, PWettestM, MaxT, MinT and soil pH). Significance of all testable fractions was assessed using permutation tests. Environmental variables were transformed to improve the structure of the residuals using *log* or *arcsin* transformations for decimal and percentage values, respectively.

Differences in individual traits among species were assessed using one-way ANOVA and post hoc Tukey tests (*anova* and *TukeyHSD* functions of the 'stats' package). We performed Principal Component Analyses (PCAs; *prcomp* function in the 'stats' package) to examine patterns in leaf trait variability: one pooling the four species to examine interspecific variation *vs*. trait plasticity, and one for each species to extract the main gradients (2 first PCs) of trait plasticity (i.e. leaf quality). Previously, using Spearman rank correlations, leaf traits with high (>0.85) collinearity were removed (Figure S1). Seven traits were finally included in the PCA: N, P, Ca, Mg, condensed tannins, lignin and toughness. *Log* or *arcsin* transformations of variables were used when required in ANOVA and PCA analyses. The relative magnitude of interspecific variation *vs*. species plasticity for the overall pool of traits for each species was estimated as the proportion that each species covered in each of the dimensions of the general PCA. Besides, to quantify the relative magnitude of interspecific variation *vs*. species plasticity for each leaf trait, we performed variance partitioning analyses (*varcomp* function of the 'ape' package, Paradis & Schliep, 2019).

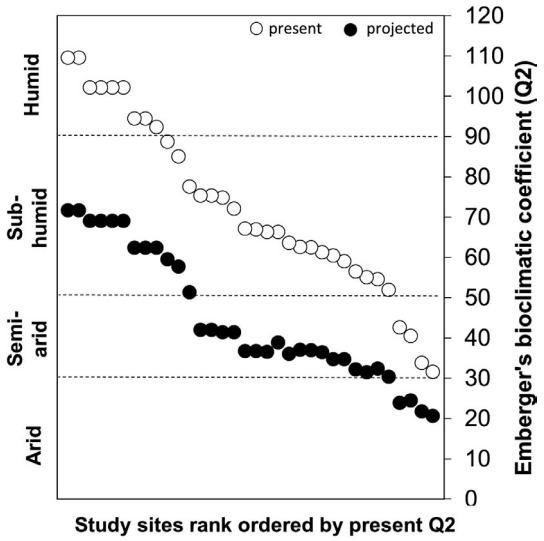


FIGURE 2 Present (open, 2000) and projected (closed, 2100) Emberger's bioclimatic coefficient values (Q2), estimated from the NCAR Community Model version 3 (CCM3) for the year 2100 (Govindasamy et al., 2003), for each of the 34 streams studied. Note that higher Q2 values denote lower aridity

We carried out partial least squares regressions (PLS; *plsr* function in the 'pls' package, Mevik et al., 2020) to evaluate the relative importance of climate and soil as predictors of leaf trait plasticity (first two PCA axes). Preliminary PLS regressions for each environmental matrix and plant species (Table S2) were used to reduce the number of variables by selecting those with the highest variable importance in projection (VIP; *VIP* function in the 'plsVarSel' package, Mehmood et al., 2012). Those variables with VIP ≥1 were considered relevant (Andersen & Bro, 2010). Spearman rank correlation analyses were used to equalize the size of the two matrices of environmental variables removing those variables with high collinearity within those with higher VIP values (Figure S2, Tables S3 and S4). A second PLS regression was performed for each species using the selected variables, and the influence of each group of environmental variables (climate and soil) and their combination (climate + soil) on leaf plasticity was assessed using the goodness of prediction (Q^2) and the goodness of fit (R^2(Y)) of models. A model was considered significant when $Q^2 > 0.097$ (Friden et al., 1994).

TABLE 2 Summary of univariate dependent variable PLS models fitted to the first two principal components of PCA (PC1 and PC2), summarizing leaf trait plasticity for each species, using three matrices (C, S and C+S) of selected (in preliminary PLS regressions) environmental variables as predictors

			Dependent variable					
			PC1			PC2		
Functional type	Plant species	Set of environmental predictors or combination	*N*	Q^2	R^2(Y)	*N*	Q^2	R^2(Y)
Deciduous N-fixer	*Alnus glutinosa*	Climate (C)	1	**0.63**	0.76	0	–	–
		Soil (S)	4	**0.26**	0.74	1	0.09	0.43
		C+S	1	**0.64**	0.78	1	−0.02	0.37
Deciduous	*Salix atrocinerea*	Climate (C)	2	**0.51**	0.74	1	**0.10**	0.42
		Soil (S)	1	**0.23**	0.47	2	**0.71**	0.91
		C+S	1	**0.36**	0.59	4	**0.58**	0.92
Evergreen	*Nerium oleander*	Climate (C)	3	**0.30**	0.71	1	−0.02	0.46
		Soil (S)	1	−0.01	0.42	**2**	**0.15**	0.60
		C+S	6	**0.70**	0.98	**1**	**0.13**	0.54
Semi-deciduous	*Rubus ulmifolius*	Climate (C)	1	**0.32**	0.41	1	−0.05	0.09
		Soil (S)	1	0.03	0.19	1	−0.02	0.11
		C+S	1	**0.26**	0.40	2	0.06	0.32

Notes: The number of PLS dimensions with lowest cross validation error (*N*), goodness of prediction (Q^2) and coefficient of determination of dependent variable (R^2) are shown for each model. Significant models ($Q^2 > 0.097$) are in bold.

In PLS regressions, all explanatory variables were scaled to unit variance (*scale* function) to give all variables the same relative importance. Regressions were carried out separately for each species and the number of extracted components (latent variables) and the robustness of the resulting models were determined by leave-one-out cross-validation (LOO). For each model, we determined the number of dimensions with the lowest cross-validation error. PLS regressions built with climatic variables, when statistically significant ($Q^2 > 0.097$; Table 2), were used to estimate the projected change of leaf quality under the forecasted climate change scenarios for 2100, using the *predict* function of the 'stats' package. Current and projected values of leaf quality (i.e. mean position over PC 1 or PC 2 of separate PCAs for each species) were compared using *t*-tests for paired samples. Hedge's *g* effect size was estimated using the *cohen.d* function of the 'effsize' package (Torchiano, 2020). See Supporting Methods in Supplementary Material for further details of data analyses.

3 | RESULTS

3.1 | Environmental variables and species distribution

Overall, the four species covered a large gradient of climatic conditions from semi-arid to humid bioclimatic types according to the Emberger's coefficient (Q2) (Table 1, Figure 2). The scenario for 2100 developed by the NCAR Community Model version 3 (CCM3) (Govindasamy et al., 2003) forecasts a significant aridification in the studied region, greater in presently humid sites (Figure 2).

Distribution of each species was rather clearly separated by the environmental gradients established by the first two dimensions of the CCA ($p < .001$; Figure 3a), which explained 91% of fitted constrained variation (53% of total variation). Soil pH was the most important variable explaining species distribution, given its significant and positive load (0.72) on CCA 1 (also loading - 0.60 on CCA 2). Moreover, minimum annual temperature was positively correlated (0.43) with CCA 1. The above variables essentially determined the separation of the acidophilic *A. glutinosa* (hereafter *Alnus*) from other species, particularly from *N. oleander* (hereafter *Nerium*), which can tolerate high pH soils and prefers lowland sites with mild winters (Figure 3a, b, d; Table S5). Precipitation seasonality and precipitation of the wettest month loaded significantly and positively (0.70 and 0.53, respectively) on CCA 2. This dimension basically segregated *S. atrocinerea* (hereafter *Salix*), abundant at low-precipitation and neutral to basic soil sites, from other species (Figure 3c; Table S5). *Rubus ulmifolius* (hereafter *Rubus*) showed its highest cover at sites with basic soils and/or mild winters, where deciduous tree species developing dense canopy cover (alder, willow or other) were absent or scarce (Figure 3e; Table S5). The studied species varied in the range of environmental conditions they occupied. *Rubus* was the most widely distributed species, occupying 100% and 92% of CCA1 and CCA2 gradients, respectively, followed by *Nerium* (80.1% of CCA1 and 84.2% of CCA2), *Alnus* (45.5% of CCA1 and 78.5% of CCA2) and *Salix* with the most constricted distribution (44.6% of CCA1 and 71.7% of CCA2) (Table 1, Tables S1 and S2; Figure 3).

3.2 | Interspecific variation and species plasticity of leaf traits

Species differed significantly in all leaf traits measured (one-way ANOVAs, all $p < .0001$) (Figure 4, Table S6). *Alnus* showed the lowest toughness and the highest N concentration, and consequently the lowest C:N ratio, being for these traits antithetical to *Nerium*, which in turn showed the highest Ca concentration and C:P ratio. *Salix* exhibited the highest P, tannins and lignin concentrations, and *Rubus* the highest Mg concentrations. The first two components of the PCA on leaf traits for the four pooled species explained 62.5% of the variation (Figure 5a): PC 1 represented a gradient of increasing nutrients (N and P) parallel to decreasing leaf toughness, segregating the deciduous (*Alnus* and *Salix*) and semi-deciduous (*Rubus*) species, from the evergreen *Nerium* with the highest toughness and lowest nutrient concentrations. Tannins and lignin heavily loaded (0.67 and 0.80, respectively) on positive PC 2, where *Salix* samples were clustered.

Overall, interspecific variation was higher than trait plasticity (Figure 5a). *Rubus*, the most widely distributed species, showed higher trait plasticity on PC 1, occupying 54% of this leaf quality gradient while other species ranged between 23% and 38%. However, the two species with more restricted distribution, *Alnus* and *Salix*, showed the highest trait plasticity on PC 2, occupying 66% and 51% of this leaf quality gradient, respectively, compared to the more widely distributed *Rubus* and *Nerium* (both 40%) (Figure 5a).

Regarding individual traits, variance partitioning analyses indicated, overall, higher interspecific variation than species plasticity in leaf traits (Figure S3). The highest interspecific variation (>80%) occurred in traits considered major determinants of litter decomposability-palatability—toughness, lignin, N and C:N—as expected dealing with species across different plant functional types. However, trait plasticity was higher than interspecific variation for P, Ca, Mg and C:P (ranging between 55% and 71%) and noticeably high for tannins (Figure S3).

Trait plasticity was described by the first two principal components of the PCA performed for each species (Figure 5b–e), which explained a considerable proportion of trait plasticity: ranging between 54% in *Nerium* and 73% in *Alnus*. The first principal component (PC 1) represented for all species a gradient of increasing leaf quality (Figure 5b–e; Table S7) positively related with decomposability and digestibility, owing to its high positive correlation with leaf N (0.57–0.87) or P (0.56–0.93) concentrations, but negative with tannins (−0.90–0.29), lignin (−0.73–0.08) or toughness (−0.82 to −0.32). However, dimension PC 2 did not exhibit a common trend across species (Figure 5b–e; Table S7). For *Alnus* and *Salix*, PC 2 was positively correlated with N, but negatively with tannins and Mg, respectively; this component covaried positively with Ca but

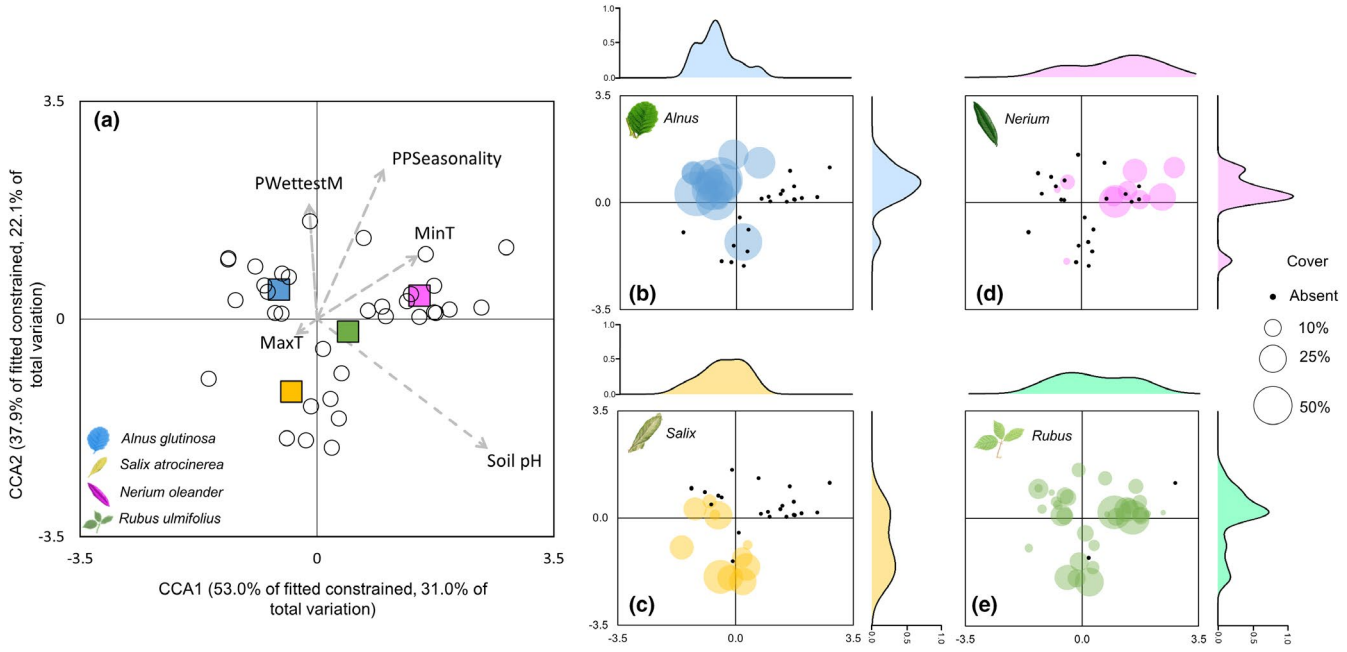


FIGURE 3 Ordination of sampling sites for the first two CCA axes (90.87% of fitted constrained variance explained) based on the environmental variables. In a, vectors represent the weight of each environmental variable; open circles denote sampling sites; and squares show the mean weighted position of each plant species over the environmental gradient. In b–e, coloured circles and their sizes represent the sampling site where each plant species was present and the percentage of canopy cover in each site, respectively; black circles represent sampling sites where each corresponding species did not appear. Marginal density plots show distribution of data for parsimonious CCA values of each plant species

negatively with tannins in *Nerium*, and negatively with Ca, Mg, lignin and toughness in *Rubus*.

3.3 | Relative importance of climate and soil factors, and best climatic predictors of leaf trait plasticity

Univariate dependent variable PLS models indicated that leaf trait plasticity (PC 1) of the four species responded significantly and predominantly to climatic variables (Table 2). Adding soil factors to climate increased noticeably the goodness of prediction in *Nerium*, but produced a highly complex model with six latent variables. Models predicting leaf trait plasticity associated to PC 2 were only significant for *Nerium* and *Salix*, but especially for the latter, in which the set of soil variables significantly predicted a high proportion of variance of leaf trait plasticity, but the model including just the set of climate variables was still significant (Table 2).

Overall, climatic predictors with the highest influence (VIP close or >1) on leaf trait plasticity associated to PC 1 (Table 3) varied among species, although most notable differences arose between broad functional groups. Mean temperature of the wettest quarter (late winter-early spring) was an important predictor with negative effects on leaf quality for deciduous/semi-deciduous species. Conversely, maximum annual temperature was the main predictor with high positive effect on leaf quality for the evergreen *Nerium*. Temperature annual range was an important predictor of leaf quality (PC 1) for *Nerium* and *Alnus*, although with contrasting sign (negative and positive, respectively), highlighting the opposite response that species belonging to different plant functional types may have the same climatic variable. Moreover, precipitation variables (Table 3) did not have substantial effects on the evergreen *Nerium*, but were important predictors of leaf quality (PC 1) for deciduous/semi-deciduous species, with notable positive effects on *Salix* and *Rubus*, but slightly negative on *Alnus*. Leaf quality of *Salix* associated to PC 2 was primarily predicted by temperature annual range (positive effect) and winter temperature (negative effect), with precipitation variables (Table 3) being other important predictors with positive effects on leaf quality. Over this dimension, soil EC and P (with negative effects) and soil $CaCO_3$ (with positive effects) were important predictors on leaf quality of *Salix*.

3.4 | Forecasted intraspecific changes in leaf quality induced by climate change

Our modelling projections showed that the four plant species would respond differently to the forecasted scenario of aridification by the year 2100 ($2 \times CO_2$ climate change scenario) in the studied region, although with remarkable congruence within broad functional groups in terms of response direction (Figure 6; Figure S4). For *Alnus* and *Salix* (PC 1), we observed weak evidence of overall variation in leaf quality ($t = 1.523$, $p = .154$; $t = -2.071$, $p = .065$, respectively; *Hedge's g* = 0.232 and −0.295, respectively; Figure 6). *Salix* (PC 2;

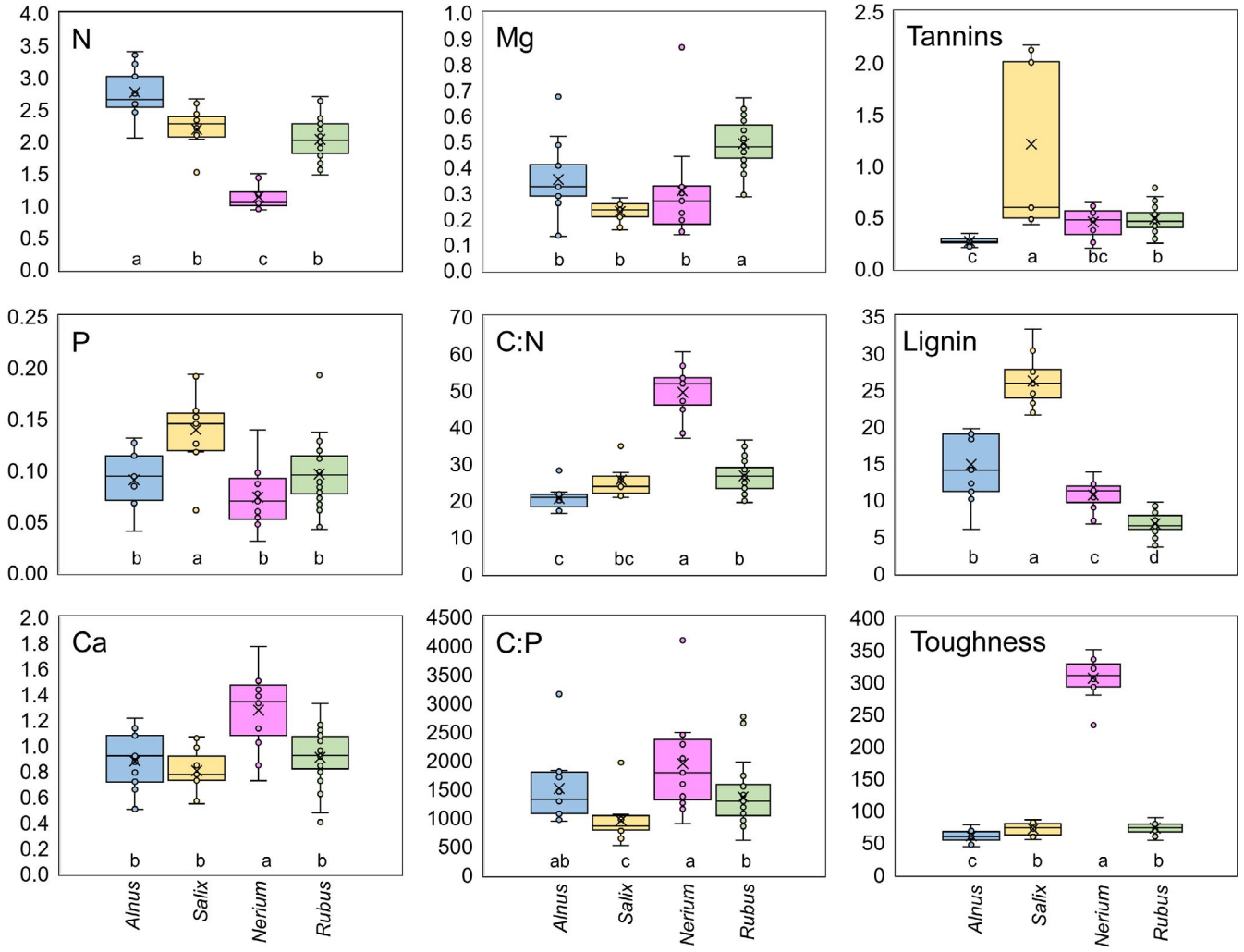


FIGURE 4 Box-and-whisker plots for selected leaf trait variables of the four plant species studied: nitrogen (N), phosphorus (P), calcium (Ca) and magnesium (Mg) concentrations (% DM), molar elemental ratios (C:N and C:P), lignin concentrations (% DM), condensed tannins concentrations (mg Catechin Hydrate Equivalent g DM^{-1}) and toughness (g) of each plant species. Box represents median and 25th and 75th percentile levels, crosses are the mean, whiskers are the range, and dots are replicates. Different letters indicate significant differences ($p < .05$) among plant species, on the basis of linear models followed by pairwise multiple comparisons (Tukey test)

Figure S4) and *Rubus* (PC 1; Figure 6) showed large (62% and 57% decrease in mean position, respectively) and significant depletion of their leaf quality ($t = 2.423$, $p = .036$; $t = -8.277$, $p < .0001$; respectively), with large effect size (*Hedge's g* = 1.242 and 1.064, respectively). Conversely, leaf quality of *Nerium* is projected to increase consistently and significantly (87% increase in PC 1; $t = -8.277$, $p < .0001$, *Hedge's g* = −1.437) in the scenario of rising aridity used for our predictions.

4 | DISCUSSION

Functional trait-based approaches are potentially useful to understand how species respond to environmental changes (Soudzilovskaia et al., 2013; Zhang et al., 2020) and, therefore, are important for an ecologically sensitive management of ecosystems. Here, we assessed how climate change might affect leaf quality of different riparian woody species from an intraspecific perspective, which has been much disregarded based on the general assumption that intraspecific variation accounts only for an irrelevant portion of total trait variability (Garnier et al., 2001). Overall, in support of our first hypothesis, but contrary to previous studies (Graça & Poquet, 2014; Ordoñez et al., 2009), climate showed larger influence than soil explaining most leaf trait plasticity. Our second hypothesis of decreasing intraspecific leaf quality—linked to determinant traits of palatability and decomposability—with increasing aridity was partially supported, given that increasing temperature had negative effects on leaf quality of deciduous and semi-deciduous species, but not on the evergreen *Nerium*, which displayed the opposite response. These results suggest potential effects on stream ecosystem functioning (Fenoy et al., 2021; Martínez et al., 2013), but with inverse sign depending on the identity of dominant species in the riparian vegetation. Moreover, in support of our third hypothesis, we generally observed higher variation among species than plasticity within

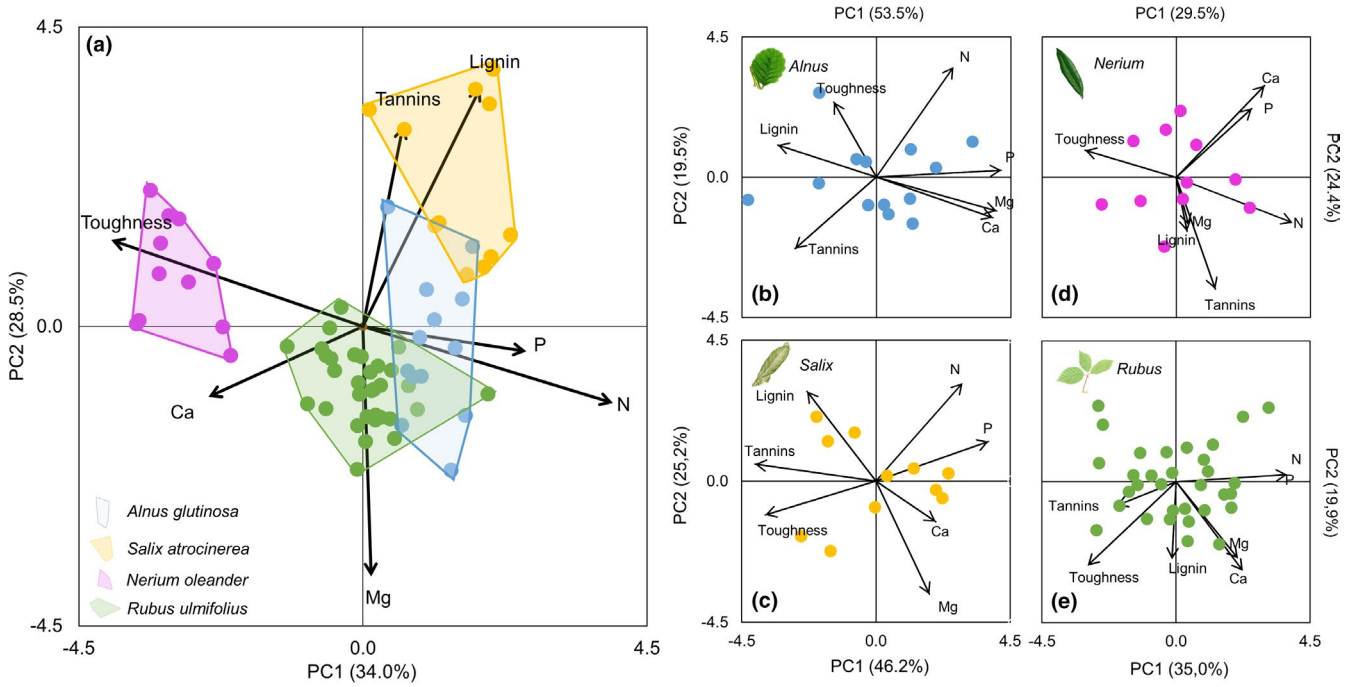


FIGURE 5 Projection of the first two principal components of PCAs showing ordination of leaf samples of four species (circles) as a function of selected leaf traits (vectors). (a) interspecific variation (polygons of different colours) *versus* trait plasticity (circles in each polygon); (b–e) trait plasticity of each plant species separately: (b) *Alnus glutinosa*, (c) *Salix atrocinerea*, (d) *Nerium oleander*, (e) *Rubus ulmifolius*

species, except for a few traits (e.g. P, Ca and Mg concentrations and C:P ratio) that exhibited remarkable leaf trait plasticity (Albert et al., 2010; Fajardo & Piper, 2011). Nonetheless, ranges of trait plasticity found here for some traits (e.g. %N, %P and %lignin) are similar, or higher, than those reported before for other species (e.g. Lecerf & Chauvet, 2008; LeRoy et al., 2007; Oliveira et al., 2021).

4.1 | Relative influence of climate and soil factors

Over the environmental gradient studied, climate exhibited an overall higher influence than soil on most species' leaf trait plasticity, although soil was the strongest predictor in some cases (e.g. *Salix* and *Nerium* PC 2). We presumed higher responsiveness of leaf traits to climate than soil in species with distributions highly constrained by soil conditions. This appears to be the case for the acidophilic *Alnus* (Miles, 1985), the species with the highest control of climate on its leaf trait plasticity. The fact that *Alnus* is an N-fixer may have further contributed to make this species less sensitive to soil nutrients. However, other species with less restricted soil-related distributions, such as *Rubus*—spread out across almost the entire study area—or *Nerium*, also showed a prominent role of climate influence on leaf trait plasticity. Similar patterns have been observed when assessing the abundance of plant functional types in the same region and across environmental gradients (Salinas et al., 2018). This lower predictive role of soil variables may stem from the high dynamics of alluvial soils and their permanent water availability, which would tend to homogenize conditions—i.e. nutrient availability—among sites (Naiman & Decamps, 1997). Yet our results are counter to other findings recorded at much larger spatial scales that observed substantial importance of soil predictors explaining intraspecific changes in leaf traits (Graça & Poquet, 2014; Ordoñez et al., 2009). This suggests that other factors not considered here, such as the great topographic variability present in our spatial gradient, or genotype differences, might be overriding soil effects.

4.2 | Main climatic predictors of leaf trait plasticity

Among climatic the factors, temperature exhibited much clearer patterns than precipitation on the main dimension of leaf trait plasticity (PC 1). This is to be expected in riparian belts of permanent streams where soil moisture tends to be relatively high and constant in the absence of extreme drought events (Moore et al., 2016), preventing major water stress in plants and its consequences on leaf characteristics (e.g. García-Palacios et al., 2016; LeRoy et al., 2014). However, climate-driven changes in streamflow may worsen the effects of aridification on such ecosystems (Perry et al., 2012).

Despite clear differentiation in distribution extent among species, we detected a common negative relationship between temperature and leaf quality in the deciduous and semi-deciduous species. On the contrary, this relationship was positive for the evergreen *Nerium*. Overall, nutrient concentrations (N, P, Ca and Mg) decreased, but tannin and/or lignin concentrations, and/or toughness increased with increasing temperature for deciduous/semi-deciduous species, whereas *Nerium* roughly exhibited the opposite pattern. Thus, within the frame of the leaf economic spectrum (Reich et al., 1997; Wright et al., 2004), the above seems to reveal antithetical syndromes of

TABLE 3 Variable importance in the projection (VIP) and standardized coefficients of the environmental variables used in the PLS models developed for the first dimension of the PCA (PC1) of each species and also for the second dimension of the PCA (PC 2) of *Salix* and *Nerium* as response variables

	Alnus glutinosa		*Salix atrocinerea*				*Nerium oleander*				*Rubus ulmifolius*	
	PC1		PC1		PC2		PC1		PC2		PC1	
Climatic predictor	VIP	Standardized coefficient	VIP	Standardized coefficient	VIP	Standardized coefficient	VIP	Standardized coefficient	VIP	Standardized coefficient	VIP	Standardized coefficient
Isothermality			0.83	0.03								
TSeasonility	**1.05**	**0.06**										
MaxT							**1.13**	**0.54**				
TAnnualRange	**1.03**	**0.06**			**1.11**	**0.05**	**1.04**	**−0.36**				
TColdestQ					**1.03**	**−0.04**						
TWettestQ	0.95	−0.05	**1.33**	**−0.21**							**1.00**	**−0.10**
TDriestQ							0.79	−0.53				
PDriestM					0.99	0.04						
PPSeasonality			**1.14**	**0.14**								
PWettestQ	0.97	−0.06			0.92	0.04						
PDriestQ			0.47	0.04							**1.00**	**0.10**
PWarmestQ					0.95	0.04						
Soil predictor												
EC					**1.25**	**−0.21**						
pH			**1.15**	**−0.08**					0.60	0.03		
$CaCO_3$			0.93	−0.07	**1.16**	**0.12**						
Organic C									0.71	−0.01		
CEC	**1.00**	**−0.15**							**1.28**	**−0.15**		
BasSat	0.80	−0.05	0.99	−0.07	0.7	−0.09						
ESP	0.64	−0.02			0.59	−0.1						
P	**1.40**	**0.27**	0.90	0.06	**1.11**	**−0.1**			**1.23**	**0.16**		

Notes: Isothermality (%); TSeasonility, Temperature Seasonality (%); MaxT, Maximum Temperature of Warmest Month (°C), TAnnualRange, Temperature Annual Range (°C); TColdestQ, Mean Temperature of Coldest Quarter (°C); TWettestQ, Mean Temperature of Wettest Quarter (°C); TDriestQ, Mean Temperature of Driest Quarter (°C); PDriestM, Precipitation of Driest Month (mm); PPSeasonality, Precipitation Seasonality (%); PWettestQ, Precipitation of Wettest Quarter (mm); PDriestQ, Precipitation of Driest Quarter (mm); PWarmestQ, Precipitation of Warmest Quarter (mm); EC, Soil Electric conductivity ($\mu S\ cm^{-1}$); pH, Soil pH; $CaCO_3$, Soil $CaCO_3$ (%); Organic C, Soil Organic Carbon (%); CEC, Soil Cation exchange capacity ($cmol^+\ kg^{-1}$); BasSat, Soil Base saturation (%), ESP, Soil Exchangeable Sodium Percentage (%); P, Soils Phosphorus (%).

Relevant variables (VIP > 1) are in bold.

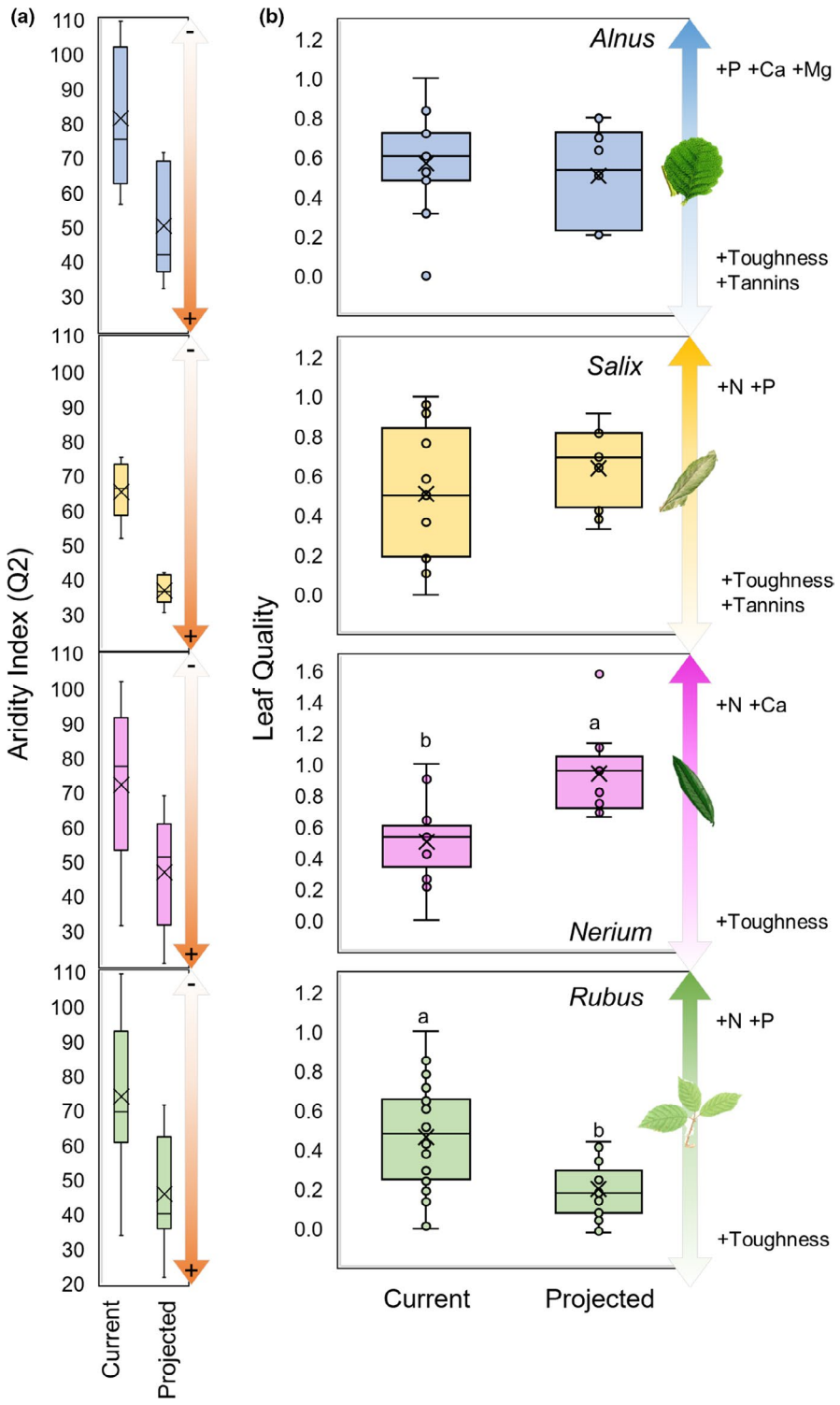


FIGURE 6 Boxplots showing (a) the aridity range covered by the distribution of each species according to the Emberger's bioclimatic coefficient (Q2); and (b) the leaf quality (PC1) of each plant species at present (Current) and in future climate change scenarios according to the NCAR Community Model version 3 (CCM3) for the year 2100 (Projected). Note that leaf quality ranges (PCA dimensions) are scaled to unit for simplicity. Different letters indicate significant different based on *t*-test analyses

leaf traits between functional groups in response to temperature, in which the intraspecific intercorrelated leaf traits along our quality gradient represent physiological and structural trade-offs (Boyero et al., 2017; Onoda et al., 2017).

Decreasing leaf N and/or P concentrations with increasing temperature has been reported before in woody deciduous species (Chen et al., 2011; Kudo et al., 2001; Sun et al., 2015). This may be explained by an increase of the catalytic capacity of photosynthetic enzymes at higher temperatures, requiring lower enzyme amounts (e.g. lower N concentration) to maintain photosynthetic rates (i.e. the photosynthetic rate is achieved with lower amounts of such enzyme; Scafaro et al., 2017). Alternatively, or additionally, higher temperature is often associated with increasing length of the growing season in deciduous species, which in turn promotes long leaf life span. Long-lived leaves often invest more in structure/protection at the expense of reducing photosynthetic efficiency (Kudo et al., 2001; Onoda et al., 2017). Similarly, other authors have reported that deciduous plants growing under relatively elevated temperatures develop

tougher leaves (Wright et al., 2017) or leaves with higher tannin (Top et al., 2017) and lignin (Graça & Poquet, 2014) concentrations.

Reduction of nutrients and strengthening of leaf traits to confer resistance (e.g. increasing toughness) have been reported in evergreen *Quercus* species in response to decreasing winter temperatures. This is interpreted as a higher cost for evergreens at cooler sites compared with deciduous trees (González-Zurdo et al., 2016). However, this finding is not totally consistent with our results for *Nerium* as winter temperatures did not exhibit any effect on its leaf quality. We observed the strongest positive effect on leaf quality of *Nerium* from maximum temperature, but a more negative effect from annual temperature range. This suggests that *Nerium* develops more nutrient-rich and softer leaves in its optimum distributional range (areas with mild winters and maritime influence), with negligible effects from harsh low-winter temperatures, which are infrequent in its area of distribution. Nevertheless, we cannot rule out the possibility that our results are species-specific, and projection of such results to the entire functional group needs to be confirmed with the study of further evergreen species.

A substantial amount of leaf trait plasticity (25%) in *Salix* (PC 2)—positively related to leaf N and lignin, and negatively to Mg concentrations—was significantly explained by climatic conditions, but much more by soil variables. The strong positive association of N and lignin on PC 2 suggest that this N fraction is structural, possibly lignin-bound N, therefore not readily available to decomposers and detritivores (Berendse et al., 1987). Thus, PC 2 represents a structural reinforcement of *Salix* leaves positively related with temperature annual range and negatively with winter temperature, but also, and mostly, negatively with soil P. A structural reinforcement of leaves (increasing leaf mass per area and lignin concentration) with decreasing soil fertility has been documented elsewhere (e.g. Diehl et al., 2008).

The trait plasticity observed in this study can arise from responses to environmental conditions, but also from genetic variability. Genotypes, although largely influenced and selected by local environments, represent an important source of trait variability unaccounted for here. Genetic variability has been exhibited to strongly influence litter quality and, consequently, associated ecosystem processes (e.g. litter decomposition) and communities (Crutsinger et al., 2014; LeRoy et al., 2006, 2007, 2012). Given that leaf traits differ in their heritability, for example, tannins appear to be highly heritable whereas C:N ratios are environmentally controlled (Crutsinger et al., 2014), further research assessing how environment × genotype interaction affects leaf traits is important for improving predictions of potential effects on ecosystem functioning, particularly, in the face of climate change.

4.3 | Projecting climate change-driven variation of species leaf quality: implications for stream ecosystems

Litter trait variation across species constitutes the main driver of instream litter decomposition worldwide (Boyero et al., 2017; García-Palacios et al., 2016; Zhang et al., 2019), indicating an essential role of plant phylogenetic history on controlling such process (LeRoy et al., 2019). Although less studied, some evidence indicates that the control exerted by trait plasticity on litter decomposition, nutrient cycling and trophic dynamics could be almost as important as interspecific changes (Jackrel & Morton, 2018; Jackrel et al., 2016; Lecerf & Chauvet, 2008; LeRoy et al., 2007; Oliveira et al., 2021). Here, we assessed the plasticity of selected traits of green leaves of riparian plants aimed at forecasting potential consequences of climate change on stream ecosystems highly dependent on these resources (i.e. forest streams; Wallace et al., 2015). Although inputs of leaves to streams are mainly in the form of leaf litter, it has been reported that some traits of green leaves tend to persist after senescence and control rates of litter decomposition (Cornelissen et al., 1999; Cornwell et al., 2008). Therefore, if nutrient resorption efficiency remains fundamentally invariable across climatic conditions (Norby et al., 2000, Aerts et al., 2007, but see Yuan & Chen, 2009b), understanding how green leaves respond to climate change may allow us to anticipate effects of leaf quality changes on stream ecosystem functioning. In support of this idea, a recent study suggests that traits of green leaves can be used to accurately predict decomposition rates (Rosenfield et al., 2020). However, as others have pointed out that traits of litter can differ from those of fresh leaves (Hättenschwiler et al., 2008; Hättenschwiler & Vitousek, 2000; Horner et al., 1987; Yuan & Chen, 2009a), the potential effects on headwater stream functioning exposed here should be interpreted with caution.

Litter decomposition is often reported to be enhanced by its high N and P concentrations (García-Palacios, McKie, et al., 2016; MacKenzie et al., 2013). Elevated litter concentrations of Ca and Mg—reported to be important for fungal decomposers (Jenkins & Suberkropp, 1995) and macroinvertebrates (Makkonen et al., 2012; National Research Council, 2005)—can also accelerate decomposition (Santonja et al., 2019). Moreover, tannins (Coq et al., 2010; Irons et al., 1988), lignin (Ferreira et al., 2016; Ramos et al., 2021; Schindler & Gessner, 2009) and toughness (Fenoy et al., 2021; Li et al., 2009) primarily tend to reduce litter consumption by detritivores. Our results point to a general decrease in leaf quality as a response to aridification in the three deciduous/semi-deciduous species. This decrease was generally related to a reduction in leaf N and P, but also Ca and Mg, versus an increase in tannins or lignin, and leaf toughness.

In particular, changes in leaf quality of the deciduous N-fixer *Alnus* could have major consequences given the key role of this species on stream ecosystem processes (Alonso et al., 2021; Pérez, Basaguren, et al., 2021; Rubio-Ríos et al., 2021). We reported here for *Alnus* ranges of %N, %P and %lignin variation similar to those reported at the European continental scale (Lecerf & Chauvet, 2008), and 53% of its species leaf trait plasticity was remarkably explained by climatic variables, yet our forecasted decrease in leaf quality was relatively low (11%) and not statistically significant, compared to other species. Nonetheless, apparent subtle changes in litter traits

might result in major effects in consumer fitness (Pérez et al., 2021). Furthermore, this projected minor decrease in leaf quality adds to the decline of populations of this key species through Europe due to a disease caused by the pathogen *Phytophthora alni* (Bjelke et al., 2016), which also has been recently reported to alter the nutritional quality of leaf litter (Ferreira et al., 2021). Both factors are likely to trigger significant alterations to the functioning of forested streams (Alonso et al., 2021). Moreover, if a general decrease in leaf quality occurs in other deciduous species, as those forecasted here for *Salix* and *Rubus*, the negative influences on stream food webs will increase.

Thus, our results indicated that decreases of leaf quality of individual deciduous species may occur in a relatively short term (via phenotypic plasticity; Nicotra et al., 2010; but see Valladares et al., 2007), which in the long term will add to the forecasted dieback of deciduous woody species in riparian corridors of temperate climate zones (Kominoski et al., 2013; Salinas et al., 2018). Both riparian changes have the potential to significantly impair instream ecosystem processes, particularly in mountain streams presently dominated by deciduous vegetation (Fenoy et al., 2021), more than in lowland streams where deciduous species actually represent a minor component of the riparian belt.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data openly available in a public repository https://doi.org/10.5061/dryad.bzkh1899h.

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REFERENCES

Aerts, R., Cornelissen, J. H. C., Van Logtestijn, R. S. P., & Callaghan, T. V. (2007). Climate change has only a minor impact on nutrient resorption parameters in a high-latitude peatland. *Oecologia*, *151*, 132–139. https://doi.org/10.1007/s00442-006-0575-0

Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S., & Lavorel, S. (2010). A multi-trait approach reveals the structure and the relative importance of intra-vs. interspecific variability in plant traits. *Functional Ecology*, *24*, 1192–1201.

Alonso, A., Pérez, J., Monroy, S., López-Rojo, N., Basaguren, A., Bosch, J., & Boyero, L. (2021). Loss of key riparian plant species impacts stream ecosystem functioning. *Ecosystems*, *24*, 1436–1449. https://doi.org/10.1007/s10021-020-00592-7

Andersen, C. M., & Bro, R. (2010). Variable selection in regression—a tutorial. *Journal of Chemometrics*, *24*, 728–737. https://doi.org/10.1002/cem.1360

APHA (1998). Phosphorus: Automated ascorbic acid reduction method, 4500-P, F. In M. A. H. Franson (Ed.), *Standard methods for the examination of water and wastewater*, 20th ed. (pp. 148–149). American Public Health Association.

Berendse, F., Berg, B., & Bosatta, E. (1987). The effect of lignin and nitrogen on the decomposition of litter in nutrient-poor ecosystems: A theoretical approach. *Canadian Journal of Botany*, *65*, 1116–1120. https://doi.org/10.1139/b87-155

Bjelke, U., Boberg, J., Oliva, J., Tattersdill, K., & McKie, B. G. (2016). Dieback of riparian alder caused by the Phytophthora alnicomplex: Projected consequences for stream ecosystems. *Freshwater Biology*, *61*, 565–579.

Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 9374–9379. https://doi.org/10.1073/pnas.1220228110

Boyero, L., Graça, M. A. S., Tonin, A. M., Pérez, J., J. Swafford, A., Ferreira, V., Landeira-Dabarca, A., A. Alexandrou, M., Gessner, M. O., McKie, B. G., Albariño, R. J., Barmuta, L. A., Callisto, M., Chará, J., Chauvet, E., Colón-Gaud, C., Dudgeon, D., Encalada, A. C., Figueroa, R., … Pearson, R. G. (2017). Riparian plant litter quality increases with latitude. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/s41598-017-10640-3

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., & Penuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 1474–1478. https://doi.org/10.1073/pnas.1010070108

Casas, J. J., Larrañaga, A., Menéndez, M., Pozo, J., Basaguren, A., Martínez, A., Pérez, J., González, J. M., Mollá, S., Casado, C., Descals, E., Roblas, N., López-González, J. A., & Valenzuela, J. L. (2013). Leaf litter decomposition of native and introduced tree species of contrasting quality in headwater streams: How does the regional setting matter? *Science of the Total Environment*, *458*, 197–208. https://doi.org/10.1016/j.scitotenv.2013.04.004

Chen, Y., Han, W., Tang, L., Tang, Z., & Fang, J. (2011). Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form. *Ecography*, *36*, 178–184. https://doi.org/10.1111/j.1600-0587.2011.06833.x

Condés, S., & García-Robredo, F. (2012). An empirical mixed model to quantify climate influence on the growth of *Pinus halepensis* Mill. stands in South-Eastern Spain. *Forest Ecology and Management*, *284*, 59–68.

Coq, S., Souquet, J.-M., Meudec, E., Cheynier, V., & Hättenschwiler, S. (2010). Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of French Guiana. *Ecology*, *91*, 2080–2091. https://doi.org/10.1890/09-1076.1

Cordell, S., Goldstein, G., Mueller-Dombois, D., Webb, D., & Vitousek, P. (1998). Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: The role of phenotypic plasticity. *Oecologia*, *113*, 188–196. https://doi.org/10.1007/s004420050367

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Steege, H. T., Morgan, H. D., Heijden, M.

G. A. V. D., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*, 335–380. https://doi.org/10.1071/BT02124

Cornelissen, J. H. C., Pérez-Harguindeguy, N., Díaz, S., Grime, J. P., Marzano, B., Cabido, M., Vendramini, F., & Cerabolini, B. (1999). Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist*, *143*, 191–200. https://doi.org/10.1046/j.1469-8137.1999.00430.x

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., … Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, *11*, 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Crutsinger, G. M., Rudman, S. M., Rodriguez-Cabal, M. A., McKown, A. D., Sato, T., MacDonald, A. M., Heavyside, J., Geraldes, A., Hart, E. M., LeRoy, C. J., & El-Sabaawi, R. W. (2014). Testing a 'genes-to-ecosystems' approach to understanding aquatic–terrestrial linkages. *Molecular Ecology*, *23*, 5888–5903. https://doi.org/10.1111/mec.12931

del Campo, R., Corti, R., & Singer, G. (2021). Flow intermittence alters carbon processing in rivers through chemical diversification of leaf litter. *Limnology and Oceanography Letters*, *6*(5), 232–242.

Diehl, P., Mazzarino, M. J., & Fontenla, S. (2008). Plant limiting nutrients in Andean-Patagonian woody species: Effects of interannual rainfall variation, soil fertility and mycorrhizal infection. *Forest Ecology and Management*, *255*, 2973–2980. https://doi.org/10.1016/j.foreco.2008.02.003

Fajardo, A., & Piper, F. I. (2011). Intraspecific trait variation and covariation in a widespread tree species (*Nothofagus pumilio*) in southern Chile. *New Phytologist*, *189*, 259–271.

Fenoy, E., Rubio-Ríos, J., González, J. M., Salinas, M. J., Moyano, F. J., & Casas, J. J. (2021). Strategies of shredders when feeding on low-quality leaf-litter: Local population adaptations or fixed species traits? *Limnology and Oceanography*, *66*, 2063–2077. https://doi.org/10.1002/lno.11745

Ferreira, V., Pazianoto, L. H., & Solla, A. (2021). Invasive forest pathogens affect the characteristics, microbial colonisation, and decomposition of leaf litter in streams. *Freshwater Biology*, *67*(2), 416–429. https://doi.org/10.1111/fwb.13851

Ferreira, V., Raposeiro, P. M., Pereira, A., Cruz, A. M., Costa, A. C., Graça, M. A. S., & Gonçalves, V. (2016). Leaf litter decomposition in remote oceanic island streams is driven by microbes and depends on litter quality and environmental conditions. *Freshwater Biology*, *61*, 783–799. https://doi.org/10.1111/fwb.12749

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Flindt, M. R., Lillebø, A. I., Pérez, J., & Ferreira, V. (2020). Total phosphorus, nitrogen and carbon in leaf litter. In F. Barlochër, M. O. Gessner, & M. A. S. Graça (Eds), *Methods to study litter decomposition* (pp. 91–105). Springer.

Friden, H., Koivula, K., & Wold, S. (1994). *Simca for windows*. UMETRI AB.

Fukami, T., & Wardle, D. A. (2005). Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2105–2115. https://doi.org/10.1098/rspb.2005.3277

García-Palacios, P., McKie, B. G., Handa, I. T., Frainer, A., & Hättenschwiler, S. (2016). The importance of litter traits and decomposers for litter decomposition: A comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology*, *30*, 819–829. https://doi.org/10.1111/1365-2435.12589

García-Palacios, P., Prieto, I., Ourcival, J.-M., & Hättenschwiler, S. (2016). Disentangling the litter quality and soil microbial contribution to leaf and fine root litter decomposition responses to reduced rainfall. *Ecosystems*, *19*, 490–503. https://doi.org/10.1007/s10021-015-9946-x

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., Roumet, C., & Navas, M. L. (2001). Consistency of species ranking based on functional leaf traits. *New Phytologist*, *152*, 69–83. https://doi.org/10.1046/j.0028-646x.2001.00239.x

Gessner, M. O., & Steiner, D. (2020). Acid butanol assay to determine bulk concentrations of condensed tannins. In F. Barlochër, M. O. Gessner, & M. A. S. Graça (Eds). *Methods to study litter decomposition* (pp. 169–177). Springer.

Gil, C., Boluda, R., & Ramos, J. (2004). Determination and evaluation of cadmium, lead and nickel in greenhouse soils of Almería (Spain). *Chemosphere*, *55*, 1027–1034. https://doi.org/10.1016/j.chemosphere.2004.01.013

Giorgi, F., & Lionello, P. (2008). Climate change projections for the Mediterranean region. *Global and Planetary Change*, *63*, 90–104. https://doi.org/10.1016/j.gloplacha.2007.09.005

Goering, H. K., & Van Soest, P. J. (1970). *Forage fiber analyses: Apparatus, reagents, procedures, and some applications*. Agricultural Research Service, US Department of Agriculture.

González-Zurdo, P., Escudero, A., Babiano, J., García-Ciudad, A., & Mediavilla, S. (2016). Costs of leaf reinforcement in response to winter cold in evergreen species. *Tree Physiology*, *36*, 273–286. https://doi.org/10.1093/treephys/tpv134

Govindasamy, B., Duffy, P. B., & Coquard, J. (2003). High-resolution simulations of global climate, part 2: Effects of increased greenhouse cases. *Climate Dynamics*, *21*, 391–404. https://doi.org/10.1007/s00382-003-0340-6

Graça, M. A. S., & Cressa, C. (2010). Leaf quality of some tropical and temperate tree species as food resource for stream shredders. *International Review of Hydrobiology*, *95*, 27–41. https://doi.org/10.1002/iroh.200911173

Graça, M. A. S., Cressa, C., Gessner, M. O., Feio, M. J., Callies, K. A., & Barrios, C. (2001). Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. *Freshwater Biology*, *46*, 947–957. https://doi.org/10.1046/j.1365-2427.2001.00729.x

Graça, M. A. S., Ferreira, V., Canhoto, C., Encalada, A. C., Guerrero-Bolaño, F., Wantzen, K. M., & Boyero, L. (2015). A conceptual model of litter breakdown in low order streams. *International Review of Hydrobiology*, *100*, 1–12. https://doi.org/10.1002/iroh.201401757

Graça, M. A. S., & Poquet, J. M. (2014). Do climate and soil influence phenotypic variability in leaf litter, microbial decomposition and shredder consumption? *Oecologia*, *174*, 1021–1032.

Harris, G. R., Sexton, D. M., Booth, B. B., Collins, M., & Murphy, J. M. (2013). Probabilistic projections of transient climate change. *Climate Dynamics*, *40*, 2937–2972. https://doi.org/10.1007/s00382-012-1647-y

Hättenschwiler, S., Aeschlimann, B., Coûteaux, M. M., Roy, J., & Bonal, D. (2008). High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. *New Phytologist*, *179*, 165–175. https://doi.org/10.1111/j.1469-8137.2008.02438.x

Hättenschwiler, S., & Vitousek, P. M. (2000). The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology & Evolution*, *15*, 238–243. https://doi.org/10.1016/S0169-5347(00)01861-9

Heilmeier, H. (2019). Functional traits explaining plant responses to past and future climate changes. *Flora*, *254*, 1–11. https://doi.org/10.1016/j.flora.2019.04.004

Henn, J. J., Buzzard, V., Enquist, B. J., Halbritter, A. H., Klanderud, K., Maitner, B. S., Michaletz, S. T., Pötsch, C., Seltzer, L., Telford, R. J., Yang, Y., Zhang, L. I., & Vandvik, V. (2018). Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. *Frontiers in Plant Science*, *9*, 1548. https://doi.org/10.3389/fpls.2018.01548

Hewitson, B., Janetos, A. C., Carter, T. R., Giorgi, F., Jones, R. G., Kwon, W. T., Mearns, L. O., Schipper, E. L. F., & Van Aalst, M. K. (2015).

Regional context. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea & L. L. White (Eds.), *Climate Change 2014: Impacts, Adaptation and Vulnerability: Part B: Regional Aspects: Working Group II Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1133–1197). United Kingdom and New York, NY, USA: Cambridge University Press.

Horner, J., Cates, R., & Gosz, J. (1987). Tannin, nitrogen, and cell wall composition of green vs. senescent Douglas-fir foliage. *Oecologia*, *72*, 515–519. https://doi.org/10.1007/BF00378976

Hulshof, C. M., & Swenson, N. G. (2010). Variation in leaf functional trait values within and across individuals and species: An example from a Costa Rican dry forest. *Functional Ecology*, *24*, 217–223. https://doi.org/10.1111/j.1365-2435.2009.01614.x

IPCC (2021). V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu & B. Zhou (Eds.), Climate change 2021: The physical science basis. contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change Cambridge University Press.

Irons, J. G., Oswood, M. W., & Bryant, J. P. (1988). Consumption of leaf detritus by a stream shredder: Influence of tree species and nutrient status. *Hydrobiologia*, *160*, 53–61. https://doi.org/10.1007/BF00014278

Jackrel, S. L., & Morton, T. C. (2018). Inducible phenotypic plasticity in plants regulates aquatic ecosystem functioning. *Oecologia*, *186*, 895–906. https://doi.org/10.1007/s00442-018-4094-6

Jackrel, S. L., Morton, T. C., & Wootton, J. T. (2016). Intraspecific leaf chemistry drives locally accelerated ecosystem function in aquatic and terrestrial communities. *Ecology*, *97*, 2125–2135. https://doi.org/10.1890/15-1763.1

Jenkins, C. C., & Suberkropp, K. (1995). The influence of water chemistry on the enzymatic degradation of leaves in streams. *Freshwater Biology*, *33*, 245–253. https://doi.org/10.1111/j.1365-2427.1995.tb01165.x

Jung, V., Albert, C. H., Violle, C., Kunstler, G., Loucougaray, G., & Spiegelberger, T. (2014). Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology*, *102*, 45–53. https://doi.org/10.1111/1365-2745.12177

Kent, M. & Coker, P. (1992). Vegetation description and analysis - a practical approach. John Wiley & Sons.

Kominoski, J. S., Chapman, S. K., Dodds, W. K., Shah, J. J. F., & Richardson, J. S. (2021). Causes and consequences of changes in riparian vegetation for plant litter decomposition throughout river networks. In C. M. Swan, L. Boyero, & C. Canhoto (Eds.), *The ecology of plant litter decomposition in stream ecosystems* (pp. 273–296). Springer.

Kominoski, J. S., Shah, J. J. F., Canhoto, C., Fischer, D. G., Giling, D. P., González, E., Griffiths, N. A., Larrañaga, A., LeRoy, C. J., Mineau, M. M., McElarney, Y. R., Shirley, S. M., Swan, C. M., & Tiegs, S. D. (2013). Forecasting functional implications of global changes in riparian plant communities. *Frontiers in Ecology and the Environment*, *11*, 423–432. https://doi.org/10.1890/120056

Kudo, G., Molau, U., & Wada, N. (2001). Leaf-trait variation of tundra plants along a climatic gradient: An integration of responses in evergreen and deciduous species. *Arctic, Antarctic, and Alpine Research*, *33*, 181–190. https://doi.org/10.1080/15230430.2001.12003421

Lecerf, A., & Chauvet, E. (2008). Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology*, *9*, 598–605. https://doi.org/10.1016/j.baae.2007.11.003

LeRoy, C. J., Hipp, A. L., Lueders, K., Follstad Shah, J. J., Kominoski, J. S., Ardón, M., Dodds, W. K., Gessner, M. O., Griffiths, N. A., Lecerf, A., Manning, D. W. P., Sinsabaugh, R. L., & Webster, J. R. (2019). Plant phylogenetic history explains in-stream decomposition at a global scale. *Journal of Ecology*, *108*, 17–35. https://doi.org/10.1111/1365-2745.13262

LeRoy, C. J., Whitham, T. G., Keim, P., & Marks, J. C. (2006). Plant genes link forests and streams. *Ecology*, *87*, 255–261. https://doi.org/10.1890/05-0159

LeRoy, C. J., Whitham, T. G., Wooley, S. C., & Marks, J. C. (2007). Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. *Journal of the North American Benthological Society*, *26*, 426–438. https://doi.org/10.1899/06-113.1

LeRoy, C. J., Wooley, S. C., & Lindroth, R. L. (2012). Genotype and soil nutrient environment influence aspen litter chemistry and in-stream decomposition. *Freshwater Science*, *31*, 1244–1253. https://doi.org/10.1899/12-029.1

LeRoy, C. J., Wymore, A. S., Davis, R., & Marks, J. C. (2014). Indirect influences of a major drought on leaf litter quality and decomposition in a southwestern stream. *Fundamental and Applied Limnology*, *184*, 1–10. https://doi.org/10.1127/1863-9135/2014/0505

Li, A. O., Ng, L. C., & Dudgeon, D. (2009). Effects of leaf toughness and nitrogen content on litter breakdown and macroinvertebrates in a tropical stream. *Aquatic Sciences*, *71*, 80–93. https://doi.org/10.1007/s00027-008-8117-y

López-Rojo, N., Pozo, J., Pérez, J., Basaguren, A., Martínez, A., Tonin, A. M., Correa-Araneda, F., & Boyero, L. (2019). Plant diversity loss affects stream ecosystem multifunctionality. *Ecology*, *100*, e02847. https://doi.org/10.1002/ecy.2847

MacKenzie, R. A., Wiegner, T. N., Kinslow, F., Cormier, N., & Strauch, A. M. (2013). Leaf-litter inputs from an invasive nitrogen-fixing tree influence organic-matter dynamics and nitrogen inputs in a Hawaiian river. *Freshwater Science*, *32*, 1036–1052. https://doi.org/10.1899/12-152.1

Makkonen, M., Berg, M. P., Handa, I. T., Hattenschwiler, S., van Ruijven, J., van Bodegom, P. M., Aerts, R., & Klironomos, J. (2012). Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology Letters*, *15*, 1033–1041. https://doi.org/10.1111/j.1461-0248.2012.01826.x

Manabe, S., Milly, P., & Wetherald, R. (2004). Simulated long-term changes in river discharge and soil moisture due to global warming/Simulations à long terme de changements d'écoulement fluvial et d'humidité du sol causés par le réchauffement global. *Hydrological Sciences Journal*, *49*, 625–642. https://doi.org/10.1623/hysj.49.4.625.54429

Marks, J. C. (2019). Revisiting the fates of dead leaves that fall into streams. *Annual Review of Ecology, Evolution, and Systematics*, *50*, 547–568. https://doi.org/10.1146/annurev-ecolsys-110218-024755

Martínez, A., Larrañaga, A., Pérez, J., Basaguren, A., & Pozo, J. (2013). Leaf-litter quality effects on stream ecosystem functioning: A comparison among five species. *Fundamental and Applied Limnology/Archiv Für Hydrobiologie*, *183*, 239–248. https://doi.org/10.1127/1863-9135/2013/0514

Mehmood, T., Liland, K. H., Snipen, L., & Sæbø, S. (2012). A review of variable selection methods in partial least squares regression. *Chemometrics and Intelligent Laboratory Systems*, *118*, 62–69. https://doi.org/10.1016/j.chemolab.2012.07.010

Mevik, B.-H., Wehrens, R. & Liland, K. H. (2020). pls: Partial least squares and principal component regression. R package version 2.7. Retrieved from https://cran.r-project.org/web/packages/pls

Miles, J. (1985). The pedogenic effects of different species and vegetation types and the implications of succession. *Journal of Soil Science*, *36*, 571–584. https://doi.org/10.1111/j.1365-2389.1985.tb00359.x

Moore, G., Li, F., Kui, L., & West, J. (2016). Flood water legacy as a persistent source for riparian vegetation during prolonged drought: An isotopic study of *Arundo donax* on the Rio Grande. *Ecohydrology*, *9*, 909–917.

Naiman, R. J., & Decamps, H. (1997). The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics*, *28*, 621–658. https://doi.org/10.1146/annurev.ecolsys.28.1.621

National Research Council (2005). *Mineral tolerance of animals*, 2nd ed. National Academies Press.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., & van Kleunen, M. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, *15*, 684–692. https://doi.org/10.1016/j.tplants.2010.09.008

Nohara, D., Kitoh, A., Hosaka, M., & Oki, T. (2006). Impact of climate change on river discharge projected by multimodel ensemble. *Journal of Hydrometeorology*, *7*, 1076–1089. https://doi.org/10.1175/JHM531.1

Norby, R. J., Long, T. M., Hartz-Rubin, J. S., & O'neill, E. G. (2000). Nitrogen resorption in senescing tree leaves in a warmer, CO_2-enriched atmosephere. *Plant and Soil*, *224*, 15–29.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'Hara, R., Simpson, G., Solymos, P., Stevens, M. & Wagner, H. (2019). vegan: Community Ecology Package. R package version 2.5-7. Retrieved from https://cran.r-project.org/web/packages/vegan

Oliveira, R., Martínez, A., Gonçalves, A. L., & Canhoto, C. (2021). Intraspecific leaf trait variability controls leaf decomposition of *Vitis vinifera* L. cultivars in streams. *Aquatic Ecology*, 1–11. https://doi.org/10.1007/s10452-021-09891-0

Onoda, Y., Wright, I. J., Evans, J. R., Hikosaka, K., Kitajima, K., Niinemets, Ü., Poorter, H., Tosens, T., & Westoby, M. (2017). Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytologist*, *214*, 1447–1463. https://doi.org/10.1111/nph.14496

Ordoñez, J. C., Van Bodegom, P. M., Witte, J. P. M., Wright, I. J., Reich, P. B., & Aerts, R. (2009). A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, *18*, 137–149. https://doi.org/10.1111/j.1466-8238.2008.00441.x

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528.

Pérez, J., Basaguren, A., López-Rojo, N., Tonin, A. M., Correa-Araneda, F., & Boyero, L. (2021). The role of key plant species on litter decomposition in streams: Alder litter as experimental model. In C. M. Swan, L. Boyero, & C. Canhoto (Eds.), *The ecology of plant litter decomposition in stream ecosystems* (pp. 143–161). Springer.

Pérez, J., Correa-Araneda, F., López-Rojo, N., Basaguren, A., & Boyero, L. (2021). Extreme temperature events alter stream ecosystem functioning. *Ecological Indicators*, *121*, 106984. https://doi.org/10.1016/j.ecolind.2020.106984

Perry, L. G., Andersen, D. C., Reynolds, L. V., Nelson, S. M., & Shafroth, P. B. (2012). Vulnerability of riparian ecosystems to elevated CO_2 and climate change in arid and semiarid western North America. *Global Change Biology*, *18*, 821–842.

Pickett, S. T. A. (1989). Space-for-time substitution as an alternative to long-term studies. In G. E. Likens (Ed.), *Long-term studies in ecology* (pp. 110–135). Springer.

Ramos, S. M., Graça, M. A. S., & Ferreira, V. (2021). A comparison of decomposition rates and biological colonization of leaf litter from tropical and temperate origins. *Aquatic Ecology*, *55*(3), 925–940. https://doi.org/10.1007/s10452-021-09872-3

Read, Q. D., Moorhead, L. C., Swenson, N. G., Bailey, J. K., & Sanders, N. J. (2014). Convergent effects of elevation on functional leaf traits within and among species. *Functional Ecology*, *28*, 37–45. https://doi.org/10.1111/1365-2435.12162

Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 11001–11006. https://doi.org/10.1073/pnas.0403588101

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Rosenfield, M. V., Keller, J. K., Clausen, C., Cyphers, K., & Funk, J. L. (2020). Leaf traits can be used to predict rates of litter decomposition. *Oikos*, *129*, 1589–1596. https://doi.org/10.1111/oik.06470

Rubio-Ríos, J., Pérez, J., Salinas, M., Fenoy, E., López-Rojo, N., Boyero, L., & Casas, J. (2021). Key plant species and detritivores drive diversity effects on instream leaf litter decomposition more than functional diversity: A microcosm study. *Science of the Total Environment*, *798*, 149266. https://doi.org/10.1016/j.scitotenv.2021.149266

Salinas, M. J., Casas, J. J., Rubio-Ríos, J., López-Carrique, E., Ramos-Miras, J. J., & Gil, C. (2018). Climate-driven changes of riparian plant functional types in permanent headwater streams. Implications for stream food webs. *PLoS One*, *13*(6), e0199898.

Santonja, M., Rodriguez-Perez, H., Le Bris, N., & Piscart, C. (2019). Leaf nutrients and macroinvertebrates control litter mixing effects on decomposition in temperate streams. *Ecosystems*, *23*(2), 400–416. https://doi.org/10.1007/s10021-019-00410-9

Scafaro, A. P., Xiang, S., Long, B. M., Bahar, N. H., Weerasinghe, L. K., Creek, D., Evans, J. R., Reich, P. B., & Atkin, O. K. (2017). Strong thermal acclimation of photosynthesis in tropical and temperate wet-forest tree species: The importance of altered Rubisco content. *Global Change Biology*, *23*, 2783–2800. https://doi.org/10.1111/gcb.13566

Schindler, M. H., & Gessner, M. O. (2009). Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology*, *90*, 1641–1649. https://doi.org/10.1890/08-1597.1

Seager, R., Liu, H., Henderson, N., Simpson, I., Kelley, C., Shaw, T., Kushnir, Y., & Ting, M. (2014). Causes of increasing aridification of the Mediterranean region in response to rising greenhouse gases. *Journal of Climate*, *27*, 4655–4676. https://doi.org/10.1175/JCLI-D-13-00446.1

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., L. Dantas, V., Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*, 1406–1419. https://doi.org/10.1111/ele.12508

Soudzilovskaia, N. A., Elumeeva, T. G., Onipchenko, V. G., Shidakov, I. I., Salpagarova, F. S., Khubiev, A. B., Tekeev, D. K., & Cornelissen, J. H. (2013). Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 18180–18184. https://doi.org/10.1073/pnas.1310700110

Sun, X., Kang, H., Kattge, J., Gao, Y., & Liu, C. (2015). Biogeographic patterns of multi-element stoichiometry of *Quercus variabilis* leaves across China. *Canadian Journal of Forest Research*, *45*, 1827–1834.

Tonin, A. M., Júnior, J. F. G., Pearson, R. G., Graça, M. A. S., Pérez, J., & Boyero, L. (2021). Multi-scale biophysical factors driving litter dynamics in streams. In C. M. Swan, L. Boyero, & C. Canhoto (Eds.), *The ecology of plant litter decomposition in stream ecosystems* (pp. 7–21). Springer.

Top, S. M., Preston, C. M., Dukes, J. S., & Tharayil, N. (2017). Climate influences the content and chemical composition of foliar tannins in green and senesced tissues of *Quercus rubra*. *Frontiers in Plant Science*, *8*, 423. https://doi.org/10.3389/fpls.2017.00423

Torchiano, M. M. (2020). effsize: Efficient Effect Size. R package version 0.8.1. Retrieved from https://cran.r-project.org/web/packages/effsize

Trivedi, M. R., Morecroft, M. D., Berry, P. M., & Dawson, T. P. (2008). Potential effects of climate change on plant communities in three montane nature reserves in Scotland, UK. *Biological Conservation*, *141*, 1665–1675. https://doi.org/10.1016/j.biocon.2008.04.008

Umaña, M. N., & Swenson, N. G. (2019). Does trait variation within broadly distributed species mirror patterns across species? A case study in Puerto Rico. *Ecology*, *100*, e02745. https://doi.org/10.1002/ecy.2745

Valladares, F., Gianoli, E., & Gómez, J. M. (2007). Ecological limits to plant phenotypic plasticity. *New Phytologist*, *176*, 749–763. https://doi.org/10.1111/j.1469-8137.2007.02275.x

Vicente-Serrano, S. M., Lopez-Moreno, J.-I., Beguería, S., Lorenzo-Lacruz, J., Sanchez-Lorenzo, A., García-Ruiz, J. M., Azorin-Molina, C., Morán-Tejeda, E., Revuelto, J., Trigo, R., Coelho, F., & Espejo, F. (2014). Evidence of increasing drought severity caused by temperature rise in southern Europe. *Environmental Research Letters*, *9*, 044001. https://doi.org/10.1088/1748-9326/9/4/044001

Vicente-Serrano, S. M., Zouber, A., Lasanta, T., & Pueyo, Y. (2012). Dryness is accelerating degradation of vulnerable shrublands in semiarid Mediterranean environments. *Ecological Monographs*, *82*, 407–428. https://doi.org/10.1890/11-2164.1

Wallace, J. B., Eggert, S. L., Meyer, J. L., & Webster, J. R. (2015). Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data. *Ecology*, *96*, 1213–1228. https://doi.org/10.1890/14-1589.1

Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., Gallagher, R. V., Jacobs, B. F., Kooyman, R., Law, E. A., Leishman, M. R., Niinemets, Ü., Reich, P. B., Sack, L., Villar, R., Wang, H., & Wilf, P. (2017). Global climatic drivers of leaf size. *Science*, *357*, 917–921. https://doi.org/10.1126/science.aal4760

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827. https://doi.org/10.1038/nature02403

Yuan, Z., & Chen, H. Y. (2009a). Global trends in senesced-leaf nitrogen and phosphorus. *Global Ecology and Biogeography*, *18*, 532–542. https://doi.org/10.1111/j.1466-8238.2009.00474.x

Yuan, Z., & Chen, H. Y. H. (2009b). Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Global Ecology and Biogeography*, *18*, 11–18.

Zhang, B., Hautier, Y., Tan, X., You, C., Cadotte, M. W., Chu, C., Jiang, L., Sui, X., Ren, T., Han, X., & Chen, S. (2020). Species responses to changing precipitation depend on trait plasticity rather than trait means and intraspecific variation. *Functional Ecology*, *34*, 2622–2633. https://doi.org/10.1111/1365-2435.13675

Zhang, M., Cheng, X., Geng, Q., Shi, Z., Luo, Y., & Xu, X. (2019). Leaf litter traits predominantly control litter decomposition in streams worldwide. *Global Ecology and Biogeography*, *28*, 1469–1486. https://doi.org/10.1111/geb.12966

BIOSKETCH

The research team is made up of ecologists and botanists whose work focuses on the basic and applied aspects of the ecology of streams and riparian zones. We aim to increase our knowledge about the relationships between riparian plant communities and stream ecosystem functioning.

Author contributions: JJC and MJS connceptualized the study. JRR, MJS and JJC contributed to methodology. JRR performed analyses with help of JP and EF. JRR wrote the original draft with help of JP and JJC. All authors reviewed and edited the manuscript. JJC provided resources and performed funding acquisition.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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