Climate-induced plasticity in leaf traits of riparian plants

Juan Rubio-Ríos¹,² | Javier Pérez³ | María J. Salinas¹,² | Encarnación Fenoy¹,² | Luz Boyero³ | José Jesús Casas¹,²

¹Department of Biology and Geology, University of Almería (UAL), Almería, Spain
²Andalusian Centre for the Evaluation and Monitoring of Global Change, CAESCG, Almería, Spain
³Department of Plant Biology and Ecology, University of the Basque Country (UPV/EHU), Leioa, Spain

Correspondence
Juan Rubio-Ríos, Department of Biology and Geology, University of Almería (UAL), 04120 Almería, Spain.
Email: jrr812@ual.es

Funding information
FEDER Operative Program Andalusia, Grant/Award Number: FEDER-UAL18-RNM-B006-B; Ministerio de Ciencia e Innovación, Grant/Award Number: CGL2012-39635

Editor: Sabine Rumpf

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
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 & Lionello, 2008), with direct effects on hydrologic regimes (Nohara et al., 2006; Vicente-Serrano et al., 2014) and soil moisture (Manabe & Lionello, 2008). 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 fueling 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 (Boyer 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 km².
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 m² 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 x 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 x CO₂ climate change scenario).
| 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           |                   | 2.0            | 1.5              |
| 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           | 8.8               |                |                  |
| Arroyo de Aguamulas        | 38.05    | −2.82     | 689                 | Calcareous      | Midland    | 42.6                       | Semi-arid                          | 22.8           | 25.7             | 6.8            |                  |
| Río Bacares                | 37.31    | −2.44     | 943                 | Calcareous      | Midland    | 51.9                       | Sub-humid                          | 11.0           | 24.8             | 9.2            |                  |
| Río Vacal                  | 36.92    | −3.81     | 956                 | Calcareous      | Midland    | 54.5                       | Sub-humid                          | 19.3           |                  |                |                  |
| 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 Turrellas              | 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            |                  |                |                  |
| Riberas de Santa Ana       | 37.87    | −6.70     | 546                 | Siliceous       | Midland    | 62.5                       | Sub-humid                          | 66.3           |                  | 9.3            |                  |
| Arroyo Corterrangle        | 37.94    | −6.60     | 462                 | Siliceous       | Midland    | 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           |                  | 3.0            |                  |
| Río Guadalentin            | 37.89    | −2.85     | 1273                | Calcareous      | Highland   | 66.3                       | Sub-humid                          | 22.9           |                  | 5.5            |                  |
| Arroyo de Aguascuebas      | 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 Bocalesones      | 36.83    | −5.41     | 316                 | Calcareous      | Lowland    | 88.6                       | Sub-humid                          | 11.3           |                  | 9.5            |                  |
| Arroyo Gaidorvar           | 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              |
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 river-bank 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 mm² 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).

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

| Functional type       | Plant species       | Set of environmental predictors or combination | Dependent variable |
|-----------------------|---------------------|-----------------------------------------------|--------------------|
|                       |                     |                                               | PC1                | PC2                |
|                       |                     |                                               | $N$ $Q^2$ $R^2(Y)$ | $N$ $Q^2$ $R^2(Y)$ |
| Deciduous N-fixter    | *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.

**FIGURE 2** Present (open, 2000) and projected (closed, 2100) Emberger’s bioclimatic coefficient values ($Q_2$), 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.
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 nutrient concentrations. Tannins and lignin heavily loaded (0.67 and 0.80, respectively) on positive PC 2, where Salix samples were clustered.
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 predominately 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 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.

### 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
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; Ordonez 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

| Climatic predictor | *Alnus glutinosa* PC1 | Standardized coefficient | VIP | *Salix atrocinerea* PC1 | Standardized coefficient | VIP | *Nerium oleander* PC1 | Standardized coefficient | VIP | *Rubus ulmifolius* PC1 | Standardized coefficient | VIP |
|--------------------|-----------------------|--------------------------|-----|-------------------------|--------------------------|-----|------------------------|--------------------------|-----|-------------------------|--------------------------|-----|
| 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                    |     | 1.00                    | -0.10                    |     |
| TColdestQ          | 1.03                  | -0.04                    |     | 1.11                    | 0.05                     |     | 1.04                   | -0.04                    |     | 1.00                    | -0.10                    |     |
| TWettestQ          | 0.95                  | -0.05                    | 1.33| -0.21                   |                          |     |                        |                          |     |                        |                          |     |
| TDriestQ           |                       |                          |     | 0.79                    | -0.53                    |     |                        |                          |     |                        |                          |     |
| PDrriestM          | 0.99                  | 0.04                     |     |                         |                          |     |                        |                          |     |                        |                          |     |
| PPSseasonality     | 1.14                  | 0.14                     |     |                         |                          |     |                        |                          |     |                        |                          |     |
| PWettestQ          | 0.97                  | -0.06                    |     | 0.92                    | 0.04                     |     | 0.92                   | -0.06                    |     | 1.00                    | 0.10                     |     |
| PDrriestQ          | 0.47                  | 0.04                     |     |                         |                          |     |                        |                          |     |                        |                          |     |
| PWarmestQ          | 0.95                  | 0.04                     |     |                         |                          |     |                        |                          |     |                        |                          |     |

| Soil predictor     |                       |                          |     |                         |                          |     |                        |                          |     |                        |                          |     |
| EC                 | 1.25                  | -0.21                    |     |                         |                          |     |                        |                          |     |                        |                          |     |
| pH                 | 1.15                  | -0.08                    |     |                         |                          |     |                        |                          |     |                        |                          |     |
| CaCO<sub>3</sub>   | 0.93                  | -0.07                    | 1.16| 0.12                    |                          |     |                        |                          |     |                        |                          |     |
| Organic C          |                       |                          |     |                         |                          |     |                        |                          |     |                        |                          |     |
| CEC                | 1.00                  | -0.15                    |     |                         |                          |     |                        |                          |     |                        |                          |     |
| BasSat             | 0.80                  | -0.05                    |     | 0.99                    | -0.07                    |     | 0.7                    | -0.09                    |     | 1.28                    | -0.15                    |     |
| ESP                | 0.64                  | -0.02                    | 0.90| 0.06                    | 1.11                     | -0.1 | 1.23                   | 0.16                     |     |                        |                          |     |
| P                  | 1.40                  | 0.27                     |     |                         |                          |     |                        |                          |     |                        |                          |     |

Notes: Isothermality (%); TSeasonality, 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); PPSseasonality, Precipitation Seasonality (%); PWettestQ, Precipitation of Wettest Quarter (mm); PDriestQ, Precipitation of Driest Quarter (mm); PWarmestQ, Precipitation of Warmest Quarter (mm); EC, Soil Electric conductivity (µS cm<sup>-1</sup>); pH, Soil pH; CaCO<sub>3</sub>, Soil CaCO<sub>3</sub> (%); Organic C, Soil Organic Carbon (%); CEC, Soil Cation exchange capacity (cmol<sup>+</sup> kg<sup>-1</sup>); BasSat, Soil Base saturation (%); ESP, Soil Exchangeable Sodium Percentage (%); P, Soils Phosphorus (%). Relevant variables (VIP > 1) are in bold.
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

**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.
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 (Boyer 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 (Rosenfeld 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 (Garcia-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-fixers 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.

ACKNOWLEDGEMENTS
This study was funded by grants to JJC from the Spanish Ministry of Science and Innovation, project RIBARID (CGL2012-39635; MICINN; EU FEDER), and from the 2014-2020 FEDER Operative Program Andalusia, project RIOVEGEST (FEDER-UAL18-RNM-B004-B). JRR was supported by a FPU grant from the Spanish Ministry of Education, Culture and Sports (ref. FPU16/03734). We thank Associate Editor Sabine Rumpf and 2 anonymous referees for feedback that significantly improved this manuscript.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

PEER REVIEW
The peer review history for this article is available at https://pubons.com/publon/10.1111/ddi.13493.

DATA AVAILABILITY STATEMENT
Data openly available in a public repository https://doi.org/10.5061/dryad.bzk8h1899h.

ORCID
Juan Rubio-Ríos https://orcid.org/0000-0002-5335-1766

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 alni complex: Projected consequences for stream ecosystems. Freshwater Biology, 61, 565–579.
Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Johnson, 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., Swafford, A., Ferreira, V., Landeira-Dabarca, A., Alexandrou, M., Gessner, M. O., McKie, B. G., Albariño, R. J., Barmuta, L. A., Callisto, M., Chará, J., Chauvet, E., Colón-Gaud, C., Dudgong, 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/s41598-017-06400-3
Carnicer, J., Coll, M., Nineryola, 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. Ecology, 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.
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.0026-664x.2001.00239.x

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

Gli, C., Boluda, R., & Ramos, J. (2004). Determination and evaluation of cadmium, lead and nickel in greenhouse soils of Almeria (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. A., 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 shredder consumption? Tree Physiology, 20, 165–175. https://doi.org/10.1007/s10236-999-01219-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-Sabawi, 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

Cornwell, W. K., Cornelissen, J. H. C., Pérez-Harguindeguy, N., Díaz, S., Grime, J. P., Marzano, E., Beuk, W., Humbert, M., Ruiz, J., & Correa, M. (2018). Functional traits explain species distributions across 118 biomes worldwide. Ecology Letters, 11, 1065–1071. https://doi.org/10.1111/1461-0248.2008.01219.x

Cornelissen, J. H. C., Pérez-Harguindeguy, N., Díaz, S., Grime, J. P., Marzano, E., Beuk, W., Humbert, M., Ruiz, J., & Correa, M. (2018). Functional traits explain species distributions across 118 biomes worldwide. Ecology Letters, 11, 1065–1071. https://doi.org/10.1111/1461-0248.2008.01219.x

Cornell, H. S., 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

Cornell, H. S., 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
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., Mathiesius, 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, CO₂-enriched atmosphere. 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

Olivera, R., Martínez, A., Gonzáles, 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/s10542-021-09891-0

Onoda, Y., Wright, I. J., Evans, J. R., Hikosaka, K., Kitajima, K., Niinemets, Ü., Poorter, H., Tonsor, T., & Westoby, M. (2017). Physiological and structural tradeoffs underlying the leaf economics spectrum. New Phytologist, 214, 1447–1463. https://doi.org/10.1111/nph.14946

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 CO₂ 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 Oikos, 129, 165–159. https://doi.org/10.1111/oik.06470

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

Rüb-Rios, J., Pérez, J., Salinas, M., Fenoy, E., López-Rojo, N., Boyero, L., & Casas, J. (2021). Key plant species and detritivores drive diversity effects on in-stream 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

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

Scateno, S. M., Graça, M. A. S., & Ferreira, V. (2021). A comparison of 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

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

Sieniawski, A., Elumeeva, N. A., Elumeeva, N. A., Onipchenko, V. G., Shidakov, I. I., Salpagarova, F. S., Khubiev, A. B., Tekeev, D. K., & Cornellissen, J. H. (2013). Functional traits predict relationship between plant abundance 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

Son, Y., 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.

Son, Y., 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.

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., Azorín-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., Zoubir, 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., Kooymans, 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., Guillas, 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 conceptualized 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.

**How to cite this article:** Rubio-Ríos, J., Pérez, J., Salinas, M. J., Fenoy, E., Boyero, L., & Casas, J. J. (2022). Climate-induced plasticity in leaf traits of riparian plants. *Diversity and Distributions*, 28, 859–876. [https://doi.org/10.1111/ddi.13493](https://doi.org/10.1111/ddi.13493)