

Unravelling the coordination between leaf and stem economics spectra through local and global scale approaches

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Abstract The existence of a coordination between leaf and stem economic spectra in woody species has been postulated repeatedly in the literature, with contrasting results. Here, we postulated that this coordination is conditioned by climate factors, being stronger in stressful environments. To test this hypothesis we explored the coordination between leaf and stem economic spectra in a seasonally dry forest in central Argentina and at the global scale, we analysed if the outcome of their coordination varies along a climatic gradient. At the local scale, we characterized leaf and stem economic spectra in 37 woody species by measuring six leaf and stem functional traits related to resource acquisition and use, and two functional traits used as proxies of water transport and use capacities. At the global scale, a meta-regression was performed to analyse if the outcome of the coordination among leaf and stem traits varies along gradients of the mean precipitation of the driest quarter and of the minimum temperature of the coldest month. At the local scale, we observed a high integration among the measured leaf and stem traits, and this coordination seemed to be linked to hydraulic properties. At the global scale, we found not only that the overall weighted mean effect size of the correlation between specific leaf area and wood density was significant and negative but also that the coordination between leaf and stem traits seemed to be shaped by climate and tends to become stronger under harsh climate conditions. Furthermore, although our results seem to suggest that their coordination is context-dependent, alternative strategies could be observed under stressful conditions.

Key words: functional ecology, functional traits, meta-regression, spectra of variation, woody species.

INTRODUCTION

In the last decades, comparative plant functional ecology has focused on identifying leading ecological spectra or dimensions (Grime 1977; Westoby *et al.* 2002; Reich *et al.* 2003; Reich 2014). These spectra of variation arrange species in categories or along a spectrum according to their ecological attributes (*sensu* Westoby 1998). An important goal of plant functional ecology is to figure out to what extent the different spectra are independent (Chapin *et al.* 1993; Curtis & Ackerly 2008). This is relevant for the understanding of two main factors: (i) the evolution of plant strategies (Chapin 1991; Reich *et al.* 2003); and (ii) species responses to environmental factors (Lavorel & Garnier 2002; Westoby & Wright 2006; Shipley *et al.* 2016).

In woody species, leaf and stem economics spectra are the main dimensions of variation related to resource acquisition and use that have been described until now (Westoby *et al.* 2002; Wright

et al. 2004; Chave *et al.* 2009). The leaf economics spectrum summarizes a trade-off from species with quick returns on investments in nutrients and dry mass in leaves, supported by high specific leaf area (SLA) and high carbon assimilation rate, to species with the opposite functional attributes that determine a slower rate of return (Wright *et al.* 2004). The stem economics spectrum defines a trade-off between the allocation to stem tissue (wall vessels, parenchyma and fibres), which is related to mechanical support and defence properties (Taylor *et al.* 2002; Anten & Schieving 2010; Larjavaara & Muller-Landau 2010; Poorter *et al.* 2010), and to the xylem lumen volume, which determines the relative cross-sectional area available for water transport and storage (Hacke & Sperry 2001; Bucci *et al.* 2004; Chave *et al.* 2009). Nonetheless, whether leaf and stem economics spectra are coordinated or not is still under debate, mainly due to the contrasting results observed in studies performed at local scales (Ackerly 2004; Baraloto *et al.* 2010; Méndez-Alonzo *et al.* 2012). For instance, Baraloto *et al.* (2010) did not find a relationship between stem and branches traits with leaf traits in woody species from a tropical rain forest.

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Contrarily, Méndez-Alonzo *et al.* (2012) observed that leaf and stem economics spectra are coordinated in woody species from a tropical seasonal forest, particularly in traits related to hydraulic properties. These results suggest that climatic factors (i.e. precipitation and temperature) of the study areas might have an effect on the outcome of the coordination between leaf and stem traits.

The relationship between traits and environmental conditions have been frequently documented (Díaz *et al.* 1998; Fonseca *et al.* 2000; Lamont *et al.* 2002; Moles *et al.* 2014), supporting the idea that environmental gradients shape certain trait attributes and trait combinations (Weiher & Keddy 1995; Shipley *et al.* 2016). Wright *et al.* (2005) explored how climate influences key leaf economics traits at the global scale and reported lower SLA values at hotter, drier and higher irradiance sites. Furthermore, Swenson and Enquist (2007) observed that wood density (W_d ; the leading functional traits of the stem economics spectrum; Chave *et al.* 2009) was more related to temperature than to precipitation changes in a large dataset comprising both gymnosperms and angiosperms (see also Wiemann & Williamson 2002). However, and taking in account that plant traits are not individually affected, and since selective pressures act on individuals as a whole (Gould & Lewontin 1979; Reich 2014), we hypothesized that increasing climate harshness (e.g. low precipitation and temperature) may promote a coordination between leaf and stem plant traits. Hence, in stressful environments, where resource acquisition and use might be reduced (Grime 1977; Chapin *et al.* 1993), we will observe the tightest coordination between leaf and stem functional traits.

In the present work we first introduce a new case study in which we tested, in a highly seasonally dry forest system, whether six leaf and stem traits were related between them and to two functional traits commonly used as proxies of water transport and use capacities (leaf area to sapwood area ratio (LA/SA) and midday leaf water potential (Ψ_j ; see materials and methods for more details). Secondly, and in order to explore whether climate conditions affect the relationship between leaf and stem economics spectra, we performed a worldwide meta-regression analysis using the correlation coefficient between the leading traits of both functional spectra: SLA and wood density (W_d), along with the mean precipitation of the driest quarter and minimum temperature of the coldest month. We selected these climatic variables because temperature and precipitation extremes are considered among the main factors that limit plant growth and survival globally (Reyer *et al.* 2013; Kikuzawa *et al.* 2013). Based on the evidence from the results of the case study and the meta-regression, we argue that differences in climatic conditions between case studies could explain the lack of consensus about whether leaf and stem

functional spectra are coordinated or not (Weiher & Keddy 1995).

MATERIALS AND METHODS

Study area, species selection and trait measurements

The study was conducted in an area near the locality of Salsipuedes (31°07'18"W, 64°19'13"S), in Córdoba Mountains, central Argentina. The altitude is 750 m a.s.l., and mean annual temperature and precipitation are 15°C and 800 mm respectively (De Fina 1992). Precipitation is mainly concentrated during the warm season, from September to April. The vegetation belongs to the Chaco Serrano District of the Chaco Phytogeographical Province (Cabrera 1976), and comprises a mosaic of woodlands and shrublands in different successional stages (Zak & Cabido 2002). A total of 37 woody species, both shrubs and trees, were recorded in 192 complete vegetation surveys performed in the study area (Giorgis *et al.* 2011; Zeballos *et al.* 2014). These species encompass a large range of phylogenetic diversity at the family level (see Appendix S1 for the complete species list), representing 33 genera and 20 families. Eleven species are aliens and the rest are native to the area. Species nomenclature follows Zuloaga *et al.* (2008) and their on-line update: www2.darwin.edu.ar.

Standard protocols were used for the selection of individuals and functional trait measurements, following Pérez-Harguindeguy *et al.* (2013). In general terms, mature and healthy individuals of all species, with no sign of diseases, were selected. In the case of leaf traits, full sun expanded leaves on outer canopy branches with no signs of disease or herbivory were selected. All traits were measured in six individuals per species during the growing season.

To characterize the species according to leaf and stem economics spectra, six commonly used leaf- and stem-level functional traits related to resource acquisition and use were measured. Leaf area (LA; mm²) was measured in 10 leaves per individual which were scanned and their area was calculated with the Leaf Area© software (A. P. Askew, University of Sheffield, UK, downloadable from the Nucleo DiverSus toolbox). In species with compound leaves (13 of 37 species) both LA and the area of their individual leaflets were taken into account (LA_{efc}, effective leaf area; Ackerly 2004). The LA scanned was also used for SLA measurements and these samples were oven-dried (48 h at 70°C) and weighed to calculate SLA (mm² mg⁻¹; Wright *et al.* 2004). Additionally, leaf tensile strength (LTS; N mm⁻²) was measured using a small leaf fragment from two leaves per individual, which was cut following the leaf longitudinal axis from the central section of the leaf but away from the midrib. Leaf tensile strength (LTS) was measured using a portable apparatus described in Hendry and Grime (1993) (for more details see Pérez-Harguindeguy *et al.* 2013). In addition, one wood sample was taken per individual from the main trunk at a height of 1.5 m using an increment borer for stem functional trait measurements. Wood cores were soaked for 24 h (saturation mass), weighed, and then their volumes were calculated via the Archimedes' principle using a graduated test tube (10:0.1 mL). The samples were

then oven-dried (48 h at 70°C) and weighed. Wood density (W_d) was determined as the dry mass per volume (g mL^{-1}) (Jacobsen *et al.* 2007, 2008), and wood saturated water content (WC_{sat} ; %) was calculated as: ((saturation mass – dry mass) per dry mass) \times 100 (Borchert 1994).

The functional traits taken as proxies of water-use capacity were the leaf area to sapwood area ratio (LA/SA) and midday leaf water potential (Ψ_l) (Andrade *et al.* 1998; Tausend *et al.* 2000; Santiago *et al.* 2004; Meinzer *et al.* 2008). On the one hand, LA/SA (the inverse of Huber value) was measured in two terminal branches per individual that were cut at the level where the twigs had a diameter of approximately 1 cm. All the leaves of each twig were oven-dried (48 h at 70°C) and weighed, and then the total leaf area per twig was calculated by multiplying total leaf dry mass per SLA (Wright *et al.* 2006). Stem cross-sectional area was calculated using the diameter of the twig from where it was cut and was measured with a digital calliper after the bark and pith had been removed. Then, the LA/SA was calculated as the total leaf area per twig per stem cross-sectional area ($\text{mm}^2 \text{mm}^{-2}$). The LA/SA has been used as a potential proxy for the whole-plant leaf area-specific conductance because it is considered a good indicator of potential transpiration demand relative to water transport capacity (Vander Willigen & Pammenter 1998; Tausend *et al.* 2000; Bucci *et al.* 2004). On the other hand, minimum leaf water potential (Ψ_l ; MPa) measurements were performed in two leaves per individual that were cut and measured with a pressure chamber (Scholander *et al.* 1965). The two measurements per individual were then averaged. Measurements were performed at midday on sunny days (samples were collected from 12:30 to 13:00 hours) during the wet season (Méndez-Alonzo *et al.* 2012). The Ψ_l reflects the water status of transpiring leaves, which is the result of biophysical constraints affecting the water transport system through the coordination effects of plant hydraulic architecture, xylem properties, whole-plant water storage and stomatal response (Bhaskar & Ackerly 2006; McDowell *et al.* 2008; Sperry *et al.* 2008; Manzoni *et al.* 2013). Furthermore, some studies have reported that Ψ_l is tightly linked to cavitation/embolism resistance (Hacke & Sperry 2001; Choat *et al.* 2012).

Meta-regression: literature search and data collection

With the purpose of assessing how climate conditions the outcome of the relationship between leaf and stem economics spectra, a meta-regression was performed (Mengersen *et al.* 2013; Rodríguez-Castañeda 2013; Koricheva & Gurevitch 2014), considering the correlation coefficient between SLA and W_d as an indicator of leaf and stem economics spectra association. An extensive literature survey was performed in Scopus and Google Scholar using the keywords: ‘specific leaf area’ OR ‘leaf mass area’ OR ‘wood density’ OR ‘stem specific density’ AND ‘woody species’ (see Appendix S2 for the list of selected studies). Then, we examined the references cited in the retrieved articles. For this survey, we selected only those studies that compared inter-specific functional traits, restricting only to those studies that characterized functional traits of mature woody

species within a specific site/community, as indicated in the standard protocols (Pérez-Harguindeguy *et al.* 2013). From each of the 40 studies selected in the literature search, we used the correlation coefficient (Pearson’s, Kendall’s or Spearman’s) of the relationship between SLA and W_d . Data from graphs were obtained using the Data Thief III software (Tummers 2006; <http://www.datathief.org/>). In the case of studies that did not report the correlation coefficients but did provide the mean functional trait values for each species, we calculated the Pearson correlation coefficient between SLA and W_d . Some studies provided data from more than one specific site/community; therefore, we included them as independent data. That is, some studies that characterized functionally different woody communities across a vast geographical area allowed us to obtain different independent correlation coefficients. We finally obtained 54 data points, each one corresponding to one correlation coefficient value at a specific site or community encompassing a wide range of climatic conditions, from -10 to 23°C of the minimum temperature of the coldest month and from 4 to 638 mm of the mean precipitation of the driest quarter (Fig. 1).

Since productivity loss, growth reduction and mortality are related to extremes of temperature and precipitation (Engelbrecht *et al.* 2007; McDowell *et al.* 2008; Reyer *et al.* 2013); we selected the mean precipitation of the driest quarter and the minimum temperature of the coldest month as independent continuous moderator variables for the meta-regression. Both climatic variables can be used as indicators of plant stressful conditions (e.g. Choat *et al.* 2012; Reyer *et al.* 2013). For instance, low values of these variables promote plant drought or freezing-induced cavitation (Hacke & Sperry 2001). The individual values of these variables were extracted from bioclimatic data at a scale of 2.5 arcmin for each study, using Worldclim (<http://www.worldclim.org/>). To accomplish this, we recorded the locations of each data point from the selected studies and geo-referenced them in decimal degrees. All mapping and data extraction were conducted using Qgis 2.6.1.

Statistical analysis

Correlations were performed to test for relationships among all functional traits; the Spearman’s rank correlation coefficient was used because most traits did not meet the requirements for parametric statistics. Then, a descriptive multivariate analysis was conducted to analyse the overall pattern of trait variation among the 37 woody species, using Principal Components Analysis (PCA).

To perform the meta-regression analysis, a Fisher’s z transformation was used to calculate one effect size for each vegetation community taking the individual correlation coefficients (Gurevitch & Hedges 2001), which were weighted by the species number of each study. This measurement is considered an advantageous effect size statistic because it is easy to interpret (Koricheva 2002; Koricheva *et al.* 2004). Unlike r , which must lie between $+1$ and -1 , z ranges from $+\infty$ to $-\infty$. For instance, a positive z value implies that there is a positive correlation between SLA and W_d , and a high z value indicates a strong association between both functional traits. Additionally, a random-effect model analysis was chosen to

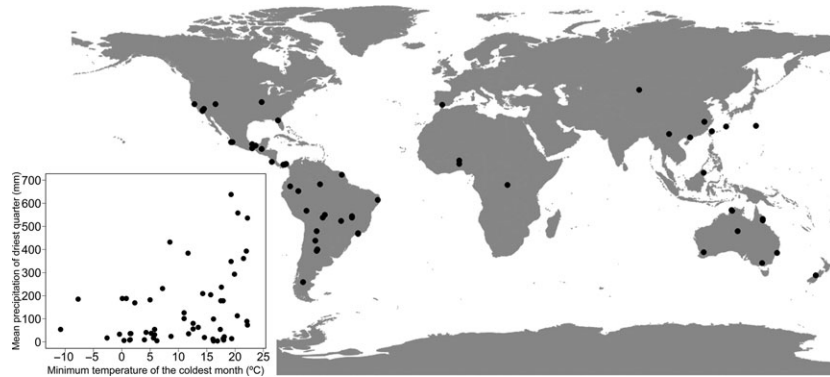


Fig. 1. World map showing the distribution of 54 studies included in this meta-regression. The inset show the spread of mean temperature of the coldest months and mean precipitation of the driest quarter spanned by these studies.

perform the meta-regression; this kind of analysis has been reported as appropriate for ecological data, since random-effect models analysis assumptions are most likely to be satisfied (Gurevitch & Hedges 2001; Mengersen *et al.* 2013). The effect of publication bias was tested through a rank correlation test for funnel plot asymmetry, which examines the relationship between the standardized effect size and the sample size across studies (Begg 1994), and by calculating Rosenthal's fail-safe number (Palmer 1999). If the fail-safe number is larger than five times the sample size plus 10, it is safe to conclude that results are robust regardless of publication bias (Rosenthal 1979).

All analyses and graphics were performed in R version 3.1.1 (R Core Team 2014) plus the additional R *corr.test* function in *psych* package for Spearman correlations (Revelle 2015), *rda* function in *vegan* package for PCA (Oksanen *et al.* 2015) and *escalc* and *rma* functions for meta-regression, and *ranktest* and *fsn* function to evaluate publication bias in *metafor* package (Viechtbauer 2010).

RESULTS

Local study

The analysis of all pairwise correlations among leaf, stem and water use functional traits showed 22

significant correlations out of 23 (Table 1). Since LA_{efc} and LA had the same values in simple-leaved species (24 of 37 species), the former trait was excluded from the count of significant correlations. Furthermore, the leading traits of leaf and stem economics spectra, SLA and W_d , were not only significantly and negatively correlated between them (Table 1) but also associated with the measured proxies of water transport and use capacities (Fig. 2). That is, those species with highest LA/SA and Ψ_1 values had the highest SLA values (Fig. 2a, b respectively), and the lowest W_d values (Fig. 2c, d respectively).

The first two axes of the PCA ordination of the 37 woody species based on the eight functional traits accounted for 66.51% of the total variation in trait values. Almost all leaf- and stem-level functional traits were loaded along the first PCA axis, as well as LA/SA and Ψ_1 , which were also associated with leaf and stem economic spectra (Figs 2,3). Axis 1 explained 51.46% of the variance and was related to both leaf and stem functional traits (Fig. 3). Species with positive scores along Axis 1 had higher SLA , LA/SA , Ψ_1 (less negative values), WC_{sat} and LA , as well as lower W_d . Contrarily, species with negative scores had the opposite functional attributes (Fig. 3).

Table 1. Spearman correlation coefficients for all pairwise trait comparisons

Traits	Ψ_1	SLA	W_d	WC_{sat}	LA	LA_{efc}	LA/SA
SLA	0.46***						
W_d	-0.63***	-0.59***					
WC_{sat}	0.49***	0.54***	-0.9***				
LA	0.52***	0.51***	-0.61***	0.58***			
LA_{efc}	0.76***	0.44**	-0.49***	0.43**	0.44**		
LA/SA	0.43**	0.70***	-0.47***	0.46**	0.64***	0.44**	
LTS	-0.56***	-0.54***	0.38*	-0.26	-0.43**	-0.53***	-0.47***

Significant results for coefficients are indicated with asterisks: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. LA/SA , leaf area to stem cross-sectional area ($\text{mm}^2 \text{mm}^{-2}$); LA_{efc} , effective leaf area (mm^2); LA , leaf area (mm^2); LTS , leaf tensile strength (N mm^{-1}); SLA , specific leaf area ($\text{mm}^2 \text{mg}^{-1}$); WC_{sat} , wood saturated water content (%); W_d , wood density (g mL^{-1}); Ψ_1 , midday leaf water potential (MPa).

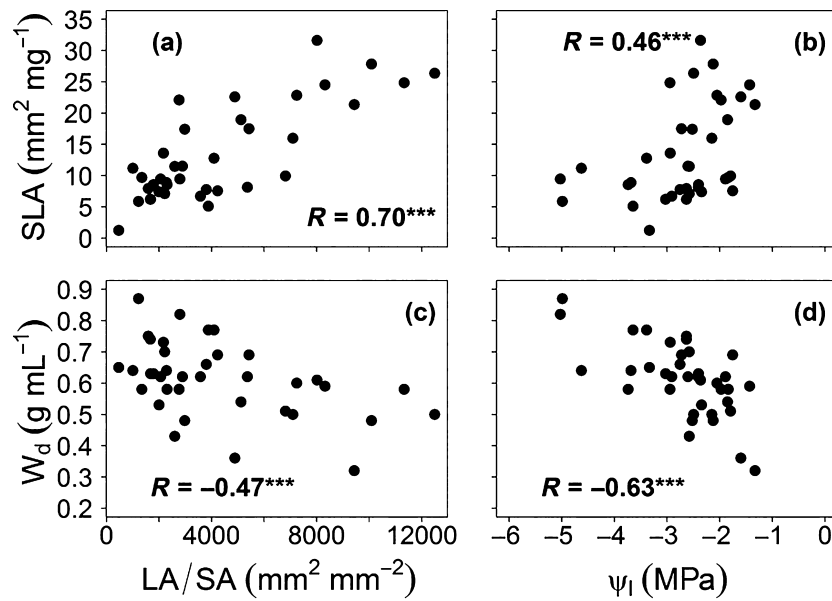


Fig. 2. Associations between the leading functional traits of leaf and stem economics spectra (SLA and W_d respectively) with the hydraulic traits measured in 37 woody species from Córdoba Mountains, central Argentina. SLA, Specific leaf area; W_d , Wood density; LA/SA; Leaf area to stem cross-sectional area; Ψ_l , Midday leaf water potential. Each dot is a species. R is the pairwise Spearman correlation coefficient value. Significant results for coefficients are indicated with asterisks; *** $P \leq 0.001$.

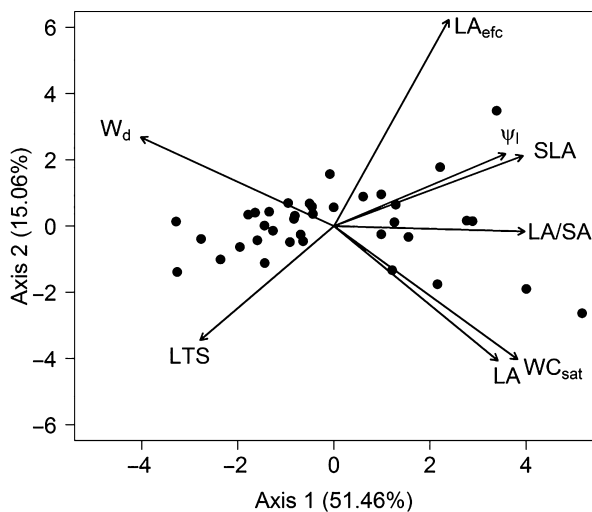


Fig. 3. Principal component analysis ordination on the basis of eight functional traits related to leaf and stem economics spectra and hydraulic properties of 37 woody species from Córdoba Mountains, central Argentina. LA/SA, leaf area to stem cross-sectional area; LA_{efc}, effective leaf area; LA, leaf area; LTS, leaf tensile strength; SLA, specific leaf area; WC_{sat}, wood saturated water content; W_d , wood density; Ψ_l , midday leaf water potential.

Axis 2 explained 15.06% of the variance and was mainly related to LA_{efc} and to a lesser extent to LA, WC_{sat} and LTS (Fig. 3).

Meta-regression analysis

Our meta-regression analysis revealed that the overall weighted mean effect size of the correlation between SLA and W_d was negative ($d = -0.31$) and significantly different from zero (95% CI = -0.42 to -0.21). Furthermore, both explanatory independent variables, mean precipitation of the driest quarter and minimum temperature of the coldest month, had significant effects on the strength of the relationship between SLA and W_d (Fig. 4a, b). Specifically, mean precipitation of the driest quarter ($\beta = 0.001$; SE = 0.0003; $Z = 3.0485$; $P = 0.002$) and minimum temperature of the coldest month ($\beta = 0.0155$; SE = 0.0061; $Z = 2.5205$; $P = 0.0117$) were positively associated with the effect size values. However, both relationships interestingly showed quite different patterns. On the one hand, a triangular relationship was observed between mean precipitation of the driest quarter and the effect size values (Fig. 4a). That is, in sites with lowest water availability we found not only the strongest negative effect size but also null and even positive effect size, whereas in sites with highest mean precipitation of the driest quarter, only positive effect size values were observed. On the other hand, a continuous high deviation was observed between minimum temperature of the coldest month and effect size (Fig. 4b).

Regarding publication bias, the non-significant rank correlation test for funnel plot asymmetry

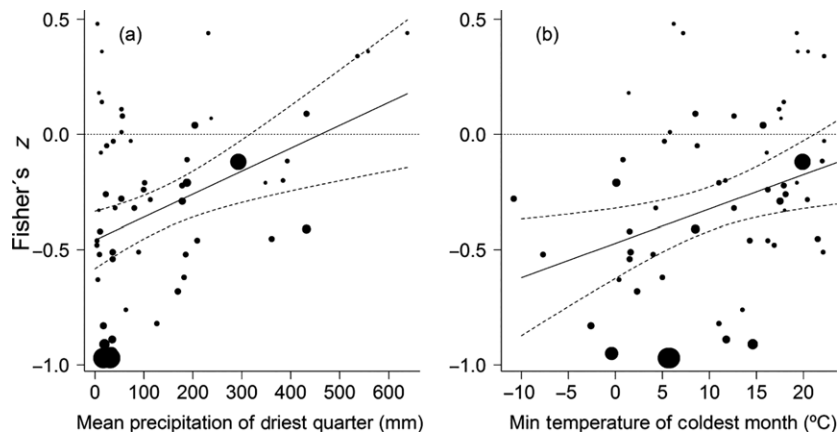


Fig. 4. Association between the effect sizes (Fisher's z) and 95% confidence intervals for the correlation coefficient between specific leaf area and wood density along mean precipitation of driest quarter ($\beta = 0.001$; $SE = 0.0003$; $Z = 3.0485$; $P = 0.002$) and minimum temperature of the coldest month ($\beta = 0.0155$; $SE = 0.0061$; $Z = 2.5205$; $P = 0.0117$). Each dot is one coefficient of correlations ($n = 54$) and their sizes are proportional to the inverse of the corresponding standard errors (i.e. lower standard errors determining higher size).

(Kendall's tau = 0.17; $P = 0.07$) suggests that there was no bias in the report of results from the studies included in this meta-regression. Furthermore, the high weighted Rosenthal's fail-safe number observed (31907) was much greater than expected (280) without publication bias, which supports the robustness of our results. Therefore, our data set does not seem to be subjected to publication bias.

DISCUSSION

The existence of a coordination between leaf and stem economics spectra in woody species has been repeatedly postulated, with contrasting results in the literature (Ackerly 2004; Baraloto *et al.* 2010; Méndez-Alonzo *et al.* 2012). Nonetheless, as far as we know, to date no study has tested how climatic factors affect the coordination between these spectra. Accordingly, at the local scale in a dry seasonal climate, we found that almost all leaf and stem functional traits were coordinated between them, and this coordination seemed to be linked to hydraulic properties. Moreover, at the global scale, our results suggest that the coordination between leaf and stem traits seems to be shaped by climate conditions and tends to become stronger under harsh conditions. That is, we found a general negative relationship between leaf and stem traits along the worldwide climatic gradient explored (i.e. mean precipitation of the driest quarter and minimum temperature of the coldest month) and the strength of this relationship increased at more stressful climatic conditions. Nonetheless, there might not be a unique relationship among leaf and stem traits along these climatic gradients.

In support of our hypothesis at the local scale in a dry seasonal climate, we observed a negative relationship between SLA and W_d as well as a high phenotypic integration among all leaf measured and stem functional traits, suggesting the existence of a common axis of resource exploitation that ranges from resource acquisitive to conservative strategies (see Díaz *et al.* 2004 for more details). These results are in agreement with the recently proposed 'whole-plant economics spectrum' (Freschet *et al.* 2010; Poorter *et al.* 2014; Reich 2014) and the global spectrum of plant form and function (Díaz *et al.* 2016). Both frameworks merge those functional traits related to resource acquisition and use in one spectrum, summarizing a trade-off between a fast and a slow growth strategy (see Reich 2014). We also observed that leaf and stem functional traits were associated with two related water use functional traits, LA/SA and Ψ_1 . Similarly, Mitchell *et al.* (2008) and Méndez-Alonzo *et al.* (2012), working in a system with a dry seasonal climate, also observed that leaf and stem functional traits were related to water transport and use traits (i.e. stomatal conductance, leaf water potentials and hydraulic conductivity). Therefore, these results suggest that one of the possible mechanisms underlying the coordination between leaf and stem traits might be linked to the trade-off between hydraulic conductivity and cavitation resistance (Markesteijn *et al.* 2011; Kröber *et al.* 2014). Nonetheless, further studies using more appropriate variables related to the 'secure-efficient' water transport trade-off are needed to test this assumption (Hacke & Sperry 2001; Sperry *et al.* 2008).

In line with these findings, at the global scale we found a negative overall weighted mean effect size of the correlation between SLA and W_d . These results highlight the trade-off between a fast and a slow

growth strategy (see Reich 2014), since high SLA values promote a high carbon fixation (Wright *et al.* 2004) and low W_d values, allowing a high growth rate (Poorter *et al.* 2010). In addition, we observed that the correlation between SLA and W_d became stronger and more negative under stressing climatic conditions (i.e. lowest mean precipitation of the driest quarter and minimum temperature of the coldest month). Nevertheless, we found a homogeneous pattern of deviation along the axis of minimum temperature of the coldest month, whereas along the axis of mean precipitation of the driest quarter, we found a triangular relationship. This striking triangular relationship seems to be indicating that in systems with low stress severity there is a tendency to null or positive relationship, whereas in systems with high stress severity there is a great variation in the relationship between SLA and W_d (i.e. positive, null and negative correlation coefficients values). These contrasting patterns among studies might be related to alternative plant mechanisms of stress tolerance or avoidance strategies (Lambers *et al.* 1998), which might explain the diverse responses of plant communities found in this study. On the one hand, a stress tolerance strategy predicts stronger relationships between climate variables and plant traits (Grime 1977; Chapin *et al.* 1993), which was the general trend observed in our study. In systems with low mean precipitation of the driest quarter and minimum temperature of the coldest month, plants are prone to suffer cavitation due to drought or freezing stress (Tyree & Sperry 1989; Hacke & Sperry 2001; Sperry *et al.* 2008). Furthermore, an integrated phenotype between leaf, stem and water functional traits is needed to ensure constant water supply and maximize growth under these circumstances (McDowell *et al.* 2008; Poorter *et al.* 2010). On the other hand, an avoidance strategy allows plants to escape the climatic stress pressure by adjusting, for example, their leaf phenology (Reich & Borchert 1984; Kikuzawa 1995), taking water from the groundwater (Caldwell & Richards 1989) and/or developing a high water capacitance in their tissues (Meinzer *et al.* 2009) to avoid the dry season. This avoidance strategy might explain records reported in some studies about the lack of negative correlation between SLA and W_d under stressful climatic conditions, which allows plants to take advantage of favourable conditions. Finally, it seems that despite the strategy adopted (stress tolerance *vs.* avoidance strategy) the final aim of spectra correlations is the need for a positive carbon budget (Kikuzawa *et al.* 2013).

Despite the general trends observed among studies, the correlations between SLA and W_d with both climate variables were quite weak and showed different patterns of deviation. This powerless association between plant functional traits and climate variables is a common finding at the global scale (Wright *et al.* 2005; Swenson

& Enquist 2007; Reich 2014). As suggested by Moles *et al.* (2014), one possible explanation for this pattern could be related to the fact that both climatic variables might be poor proxies of the degree of climatic stress because particular local scale conditions, such as soil type, topography and even evolutionary history (Brown 2011; Soliveres *et al.* 2011) might ameliorate the influence of climate. Furthermore, we should not discard other alternative/independent environmental selective pressures (e.g. nutrient availability) that could act on co-variation of leaves and stems with mean precipitation of the driest quarter and minimum temperature of the coldest month, which might influence the traits independently, but in the same direction (Westoby *et al.* 2002; Wright *et al.* 2006; Patiño *et al.* 2012).

In conclusion, the use of meta-analysis together with a trait-based community ecology approach is a promising tool to understand the role of plant traits in ecosystem structure and processes (Lavorel & Garnier 2002; Westoby & Wright 2006; Reich 2014). Furthermore, future meta-analysis focused on this issue must take into account the phylogenetic non-independence. However, the lack of phylogenetic analysis in the meta-regression should not underestimate our conclusions, since this study encompasses a broad diversity of woody species from many different families and geographic localities. Moreover, our results highlight the need to evaluate the leaf and stem economics spectra coordination at wider scales and to take into account local climatic factors in order to reach a full understanding of the relationships between functional spectra and avoid misleading conclusions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Species and values of the eight functional traits from 37 woody species.

Appendix S2. Studies included in the meta-regression.