The acquisitive-conservative axis of leaf trait variation emerges even in homogeneous environments

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- **Background and Aims**The acquisitive-conservative axis of plant ecological strategies results in a pattern of leaf trait covariation that captures the balance between leaf construction costs and plant growth potential. Studies evaluating trait covariation within species are scarcer, and have mostly dealt with variation in response to environmental gradients. Little work has been published on intraspecific patterns of leaf trait covariation in the absence of strong environmental variation.
- **Methods** We analysed covariation of four leaf functional traits (SLA: specific leaf area, LDMC: leaf dry matter content, F_t: force to tear, and N_m: leaf nitrogen content) in six Poaceae and four Fabaceae species common in the dry Chaco forest of Central Argentina, growing in the field and in a common garden. We compared intraspecific covariation patterns (slopes, correlation and effect size) of leaf functional traits with global interspecific covariation patterns. Additionally, we checked for possible climatic and edaphic factors that could affect the intraspecific covariation pattern.
- **Key Results** We found negative correlations for the LDMC-SLA, F_t-SLA, LDMC-N_m, and F_t-N_m trait pairs. This intraspecific covariation pattern found both in the field and in the common garden and not be explained by climatic or edaphic variation in the field follows the expected acquisitive-conservative axis. At the same time, we found quantitative differences in slopes among different species, and between these intraspecific patterns and the interspecific ones. Many of these differences seem to be idiosyncratic, but some appear consistent among species (e.g.all the intraspecific LDMC-SLA and LDMC-N_m slopes tend to be shallower than the global).

- **Conclusions** Our study indicates that the acquisitive-conservative leaf functional trait covariation pattern occurs at the intraspecific level even in the absence of relevant environmental variation in the field. This suggests a high degree of variation-covariation in leaf functional traits not driven by environmental variables.

Key words: leaf functional traits, acquisitive syndrome, conservative syndrome, leaf economics spectrum, intraspecific trait variation, common garden experiment, Fabaceae, Poaceae.

INTRODUCTION

Leaf functional traits mediate plant responses to environmental conditions and in turn influence plant effects on ecosystem properties (Reich *et al.*, 1997; Cornelissen *et al.*, 1999; Díaz *et al.*, 2004; Wright *et al.*, 2004; Shipley *et al.*, 2006b; Violle *et al.*, 2007; Cornwell *et al.*, 2008). Leaf traits related to resource use strategy have been found to consistently correlate with each other. Most of the variation in such traits can be characterized by a single acquisitive-conservative axis. The position of any plant species on this axis is related with its resource use strategy (Wright *et al.*, 2004) and describes a gradient from "fast" or "acquisitive" species—species with a fast recovery of foliar investment and fast turnover of matter and energy—to "slow" or "conservative" species with traits associated with slow return on investment. This gradient is manifested as a negative correlation between traits related to high net assimilation rate per unit of leaf mass on the one hand, and traits related to long leaf lifespan on the other. Specific leaf area (SLA=1/LMA, where LMA is the leaf dry mass per unit leaf area) and leaf nitrogen content per leaf mass (N_m) are intimately (and positively) related to the net assimilation rate both empirically (Wright *et al.*, 2004, 2005a) and theoretically (Shipley *et al.*, 2006a; Onoda *et al.*, 2017). On the other hand, leaf mechanical resistance (to herbivores, wind and other sources of physical damage; often measured as the force to tear) and dry matter content (LDMC) are positively related to leaf lifespan. Leaf dry matter content is a proxy for the cell cytoplasm (V_c) to cell wall volume (V_w) ratio ($V_c/V_w \sim W_m$; $LDMC^{-1}=1-W_m$, where W_m is the mass of water per dry leaf mass), which could be a key variable explaining covariation patterns among leaf functional traits (Shipley *et al.*, 2006a). A low cytoplasm to cell wall volume ratio (i.e. high LDMC) is associated with well-defended, long-lived leaves, whereas a high ratio (i.e. low LDMC) enables the high metabolic activity in "fast" species. Mechanical resistance is considered one of the main causes of leaf lifespan variability (Wright *et al.*, 2004). Leaf thickness, fibre content and density affect leaf mechanical resistance, which enhances leaf lifespan in the face of herbivory and physical damage (Onoda *et al.*, 2011; Kitajima *et al.*, 2012). Leaf mechanical resistance depends on leaf thickness, density and the specific toughness per unit of density. Therefore leaf mechanical resistance is expected to be correlated with SLA (negatively) and LDMC (positively). However, because most of the variability in leaf mechanical resistance (55-74%) depends on specific toughness per unit of density (Onoda *et al.*, 2011), an important degree of independence remains between leaf mechanical resistance and SLA or LDMC (see also Grubb, 2016 for a discussion of departures from these general trends among leaf functional traits).

All the proposed causal hypotheses for the acquisitive-conservative axis are at the level of the leaf and are based on biophysical and physiological principles that determine relations among traits (Wright *et al.*, 2004; Shipley *et al.*, 2006a; Blonder *et al.*, 2011, 2013, 2015; Onoda *et al.*, 2017, but see Grubb 2016). As a consequence, covariation patterns should be independent of scale or level of organization. In other words, the covariation pattern among leaf functional traits at the intraspecific level is expected to mirror the global interspecific pattern.

The acquisive-conservative axis was originally observed within global databases of diverse taxa collected across broad environmental gradients (Reich *et al.*, 1997; Wright *et al.*, 2004; Díaz *et al.*, 2004, 2016). Also, leaves from different populations of the same species distributed across broad geographical scales (e.g. its entire range of distribution), or under contrasting growing conditions, usually reproduce the interspecific global patterns (Albert *et al.*, 2010a; Jackson *et al.*, 2013; Richardson *et al.*, 2013; Niinemets, 2015; Hu *et al.*, 2015; Martin *et al.*, 2017; Fajardo and Siefert, 2018; Xiong and Flexas, 2018; Hayes *et al.*, 2019;

Sartori *et al*., 2019). At these broad scales, climatic and soil properties have been shown to drive the leaf functional trait variation (Reich and Oleksyn, 2004; Wright *et al.*, 2005b; Ordoñez *et al.*, 2009; Hidaka and Kitayama, 2011; Moles *et al.*, 2014).

This strong, consistent leaf functional trait covariation pattern at both interspecific and intraspecific level appears to weaken or even change direction as the taxonomic (Anderegg *et al*., 2018) or organization level (Fajardo and Siefert, 2018) of analysis gets finer. At the intraspecific level and local scale (i.e. from metres to a few kilometres but certainly far smaller than the geographic distribution range of a given species), where environmental conditions are less variable, leaves from individuals of the same population do not always show a covariation pattern similar to the global interspecific pattern (Blonder *et al.*, 2013; Hu *et al.*, 2015). These observations, together with some patterns of genetic correlations (i.e. the proportion of variance that two traits share due to genetic causes), have led to the suggestion that natural selection has played a bigger role than genetic constraints in the evolution of the acquisitive-conservative covariation pattern (e.g. Donovan et al., 2011). Also, it has been proposed that the acquisitive-conservative covariation pattern in leaf traits might not consistently hold at local scales and, at the population level, this pattern should be present among ecotypes within species only when these ecotypes span bioclimatic zones (Messier *et al*., 2017). However, none of the previous studies has explicitly addressed the leaf functional trait covariation pattern under constant environmental conditions. If selection is the main driver in the evolution of the acquisitive-conservative covariation pattern, then homogeneous environmental conditions should lead to stabilizing selection on each trait, and the intraspecific leaf functional trait covariation pattern should become weaker and more prone to deviation from the global interspecific pattern. Exploring variation in the absence of environmental variation (at lower levels of organization) thus helps elucidate whether biophysical constraints on leaf properties are a product of, or independent from, the environment.

Whether or not the leaf functional trait covariation pattern at the intraspecific level reproduces the global interspecific pattern is also a relevant question beyond plant functional biology. The global interspecific acquisitive-conservative axis is a powerful concept to link vegetation and ecosystem processes (Grime, 2001; Díaz *et al.*, 2004; Garnier *et al.*, 2004; Suding *et al.*, 2008; Funk *et al.*, 2017) and predict plant community changes (Shipley *et al.*, 2006b; Shipley, 2015; Warton *et al.*, 2015). If the leaf functional trait covariation pattern underlying the considerable intraspecific trait variability (now documented by many authors, such as Albert *et al.*, 2010a,b; Messier *et al.*, 2010; Siefert *et al.*, 2015) does not mirror the global interspecific covariation pattern, it follows that the acquisitive-conservative framework could not integrate plant ecology across all organization levels.

In the present study, we ask: At the intraspecific level and when the leaf functional trait variation is not mainly driven by environmental conditions, is the covariation pattern of leaf functional traits consistent with the global interspecific acquisitive-conservative covariation pattern? To address this question we studied the leaf functional trait covariation patterns in six grasses and four woody legumes. We complemented the study of plants from a field area with small environmental (climatic and edaphic) variation with their descendants grown under common conditions. Growing plants in a common garden removes environmentally-induced phenotypic plasticity and its effects on covariation patterns, but not local adaptation (i.e. population genetic change due to environmental conditions) that may still be present among genotypes. Therefore, to rule out climatic and edaphic variables as explanatory factors for genetic trait variation and covariation patterns, we selected a narrow study area with little environmental variability. Additionally, we analysed the intraspecific leaf functional trait variation as a function of these environmental variables to test if the remaining environmental variability is relevant to the leaf functional trait variation, and could affect the leaf functional trait covariation pattern, in our study. We analysed the intraspecific covariation of leaf functional traits and compared them with the global interspecific covariation pattern. We focused on two speciose, locally abundant and well represented plant families within the study area: Fabaceae and Poaceae. These families differ in their patterns of trait covariation (Adams *et al.*, 2016), which further motivated comparing the trait patterns observed at local intraspecific scales with those at global interspecific scale, for each family.

We measured SLA, N_m, LDMC and leaf mechanical resistance under two conditions: in the field in order to account for natural local intraspecific variability (which is partially shaped by phenotypic plasticity), and in a common garden, where the effects of phenotypic plasticity are controlled and phenotypic differences should be mostly the expression of genetic variability (maternal effects cannot be ruled out).

MATERIAL AND METHODS

Study area and species

The field study area is located in central Argentina, at the southern extreme of the South American Gran Chaco (c. 31°18’–31°32’ S and 65°23’–65°32’ W). The sampling area is approximately 25 km long N to S and 10 km wide E to W. The climate is subtropical and semiarid (Cabido *et al.*, 1994) with a mean annual precipitation of 514.8 mm concentrated to spring–late summer (October – March) and a mean annual temperature of 19.6 °C (Supplementary data Table S1). Soils vary from Torriorthents (Entisols order) to Camborthids ustolics (Aridisols order) (Cabido *et al.*, 1994). Vegetation corresponds to an open-canopy xerophytic forest with the trees *Aspidosperma quebracho-blanco* and *Prosopis flexuosa* as canopy and sub-canopy dominants, respectively. The shrub layer is often dense and dominated by *Mimozyganthus carinatus*, *Senegalia gilliesii* and *Larrea divaricata*. Land use, logging and livestock grazing result in a mosaic of communities with different relative abundances of these species and varying proportions of bare soil (Cabido *et al.*, 1994).

We measured the leaf functional traits of six perennial C_4 grasses (*Aristida mendocina, Gouinia paraguayensis, Neobouteloua lophostachya, Sporobolus pyramidatus, Leptochloa crinita*—formerly *Trichloris crinita*—, *Leptochloa pluriflora*—formerly *Trichloris pluriflora*—) and four woody legume species (*Vachellia aroma*—formerly *Acacia aroma*—, *Senegalia gilliesii*—formerly *Acacia gilliesii*—, *Prosopis flexuosa, Prosopis torquata*) (see Supplementary data Table S2 for species list including authorities). All these species are common and often abundant in the Chaco ecosystem (Cabido *et al.*, 1993, 1994).

Sampling protocol

In the study area, 39 to 49 sampling points were selected for each species. For each species, sampling points were separated by at least 100 m to avoid cross-pollination both for grasses (Bateman, 1947; Griffiths, 1950; Jain and Bradshaw, 1966; Caisse and Antonovics, 1978) and woody legumes (Vilardi *et al.*, 1988; Saidman and Vilardi, 1993; Butcher *et al.*, 1998; Bessega *et al.*, 2000, 2005; Casiva *et al.*, 2004). For grasses, each sampling point corresponded to a group of three individuals of a given species with less than 20 m distance from each other. For grasses, at each sampling point, we collected a leaf sample from each of these three individuals. For woody legumes, each sampling point corresponded to a single individual of a given species. For woody legumes, at each sampling point, we collected two leaf samples from the sun-exposed outer canopy of one reproductively mature plant, one sample from the lowest branch and one sample from the highest branch reachable (approximately 2m). Each leaf sample (both for grasses and woody legumes) consisted of 3 or more fully developed leaves. A total of 1172 leaf samples were analysed from plants in the field (850 leaf samples from 850 grass individual plants and 322 leaf samples from 161 woody individual plants).

Leaf functional trait measurements

All leaf samples were processed independently and used to measure SLA (mm^2 mg^{-1}), LDMC (proportion), force to tear (F_t, N mm^{-1}) and N_m (%), following the protocols of Pérez-Harguindeguy *et al.* (2013). In woody legumes all measurements were performed on leaflets (excluding rachis), therefore force to tear could not be measured because leaflets were too small to be handled into our measuring device. Leaf nitrogen content per leaf mass was measured using an Elementary Analyzer Perkin Elmer 2400 Series II (USA). Due to financial limitations, we only were able to measure N_m in two species per family. We selected the most contrasting ones in terms of growth form and habit: the grasses *L. pluriflora* and *N. lophostachya* and the woody legumes *P. flexuosa* and *P. torquata*.

Soil properties and climatic variables

At each sampling point, we measured surface compaction (pocket penetrometer), compaction at 0–5 cm and 5–10 cm (dynamic cone penetrometer INTA-Villegas), volumetric soil water content at 3 inches (Field Scout TDR 100 Soil Moisture Meter, Spectrum Technologies, Inc.). Additionally, we collected a pooled soil sample (four samples 0–10 cm deep) from each sampling point to determine pH (PHS-3E pH Meter, Arcano), conductivity (PHS-3E pH Meter, Arcano), organic matter content (Walkley & Black technique, Sparks *et al.*, 1996), total nitrogen content (Elementary Analyzer Perkin Elmer 2400 Series II), extractable phosphates (Olsen technique, Sparks *et al.*, 1996), silicates (Wei-min *et al.*, 2005), and cation (Ca^{2+}, Mg^{2+}, Na^{+} and K^{+}) concentration (atomic absorption spectroscopy, Laboratorio de Edafología del Departamento de Recursos Naturales de la Facultad de Ciencas Agropecuarias, Universidad Nacional de Córdoba, Argentina). Soil samples were pooled by the closeness of the sampling points, grouping all samples into 22 composite samples. The other variables were averaged following the same grouping factor before statistical analysis. Also, we extracted 19 standard WorldClim bioclimatic variables (Supplementary data Table S1) from WorldClim 2.1 at 30 seconds resolution (approximately 1 km^2) (Fick and Hijmans, 2017).

Common garden experiment

From all sampling points, we collected seeds and produced seedlings that were grown in pots in a common garden at Córdoba National University, Argentina. For woody legumes, seeds from a given sampling point were all from a single mother plant, the same plant whose leaves were measured, so they constituted a maternal family (full or half-siblings). In the case of grasses, seeds from a sampling point were collected from several random plants (within a 20m radius circular plot) so the resulting seedlings are not necessarily maternal siblings. Nevertheless, we treated the plants produced with seeds from the same sampling point as "genetic families" for both woody and grasses. For all the pots, we used a commercial potting soil similar to field soil (Supplementary data Table S1). For grasses we used 0.79 L (10 cm diameter, 10 cm height) pots. For woody legumes we used 2.4 L (10 cm diameter, 30 cm height). All pots were weeded weekly during the growing season and monthly in winter. Herbivory by ants and aphids was controlled by applying insecticide to all plants when herbivores were detected. All plants were watered in short pulses (1 to 3 minutes) with automatic sprinklers, evenly spaced and homogenously (Christiansen's uniformity coefficient: CUC=87%) covering the whole surface where the pots were placed. Each watering day plants received four pulses. Irrigation (frequency and pulse duration) was adjusted weekly or more frequently to ensure enough moisture and avoid overwatering. We successfully obtained seedlings from the seeds from 28 to 40 sampling points per species. A year after germination, we measured the leaf functional traits of these plants, 2 to 4 individual plants per sampling point. We took one leaf sample per plant, each sample consisting of 3 or more fully developed leaves. A total of 1195 individual plants (and samples) were analysed in the common garden experiment. At that time grasses had reached maturity and reproduced sexually. In contrast, woody legumes were still juvenile.

Data analysis

If two leaf functional traits are affected by the same environmental variable, this environmental effect will produce a correlation between the two traits. Therefore, in the case of plants growing in the field, for each species separately, we tested for correlations (Pearson correlation test) between each leaf functional trait (log10-transformed) and each environmental variable. We then tested for significant correlation (p-values<0.05) among each environmental variable and two or more leaf functional traits.

We then analysed the correlation (Pearson correlation test) between pairs of leaf functional traits for each species and growing condition, both in the field and in the common garden separately, as well as correlations for the global interspecific dataset as a whole, and for the Fabaceae and Poaceae families within it (see below). To compare each of these correlations we computed Fisher's z effect size (Fisher, 1925). Additionally, we computed the overall effect size for the intraspecific correlation in our Fabaceae and Poaceae species in the field and in common garden by using "*rma*" function from the R-package "*metafor*" (Viechtbauer, 2010).

Finally, we computed the slopes of the relationships between pairs of leaf functional traits in each one of our species, in the global interspecific, in the Fabaceae interspecific, and in the Poaceae interspecific datasets. To do that, we performed standardised major axis (SMA) regressions (Warton *et al.*, 2006) where both elevation (i.e. intercept) and slope varied freely. We used the R-package "*smatr 3*" (Warton *et al.*, 2012) and the pair-wise comparisons among the resulting slopes. P-values were adjusted using the Sidak correction (Šidák, 1967) to reduce false positives among multiple comparisons. All leaf functional traits were log10-transformed to achieve normality and homoscedasticity across the whole dataset (both in correlation and slopes analyses). For multiple comparison tests among slopes, only groups with significant correlation (p-value ≤ 0.05) between leaf functional traits were included.

In common garden conditions, the whole covariation pattern (phenotypic covariation) can depend on the covariation between families (genetic correlation, i.e.: an estimate of the additive genetic effect that is shared between our pair of traits) and/or covariation within families. So, in the case of leaf functional traits for which several measurements were taken per genetic family (SLA, LDMC, F_t), we performed the same analyses (correlation and slopes comparisons) for genetic families, to assess the genetic correlation between leaf functional traits. All analyses were performed within R version 3.6.1 (R Core Team, 2019).

Interspecific leaf functional trait data

The global interspecific, Fabaceae and Poaceae covariation patterns were obtained from the publicly available data in the TRY global communal database (www.try-db.org—Kattge *et al.*, 2011; Fitter and Peat, 1994; Shipley, 1995, 2002; Cornelissen, 1996; Cornelissen *et al.*, 1996; Atkin *et al.*, 1997; Atkin *et al.*, 1999; Cornelissen *et al.*, 1999;

Medlyn *et al.*, 1999; Meziane and Shipley, 1999; Pyankov *et al.*, 1999; Castro-Diez *et al.*, 2000; Shipley and Lechowicz, 2000; White *et al.*, 2000; Wilson *et al.*, 2000; Meir *et al.*, 2002; Shipley and Vu, 2002; Cornelissen *et al.*, 2003; Loveys *et al.*, 2003; Quested *et al.*, 2003; Xu and Baldocchi, 2003; Adler *et al.*, 2004; Cornelissen *et al.*, 2004; Díaz *et al.*, 2004; Givnish *et al.*, 2004; Wright *et al.*, 2004; Craine *et al.*, 2005; Louault *et al.*, 2005; Sheremetev, 2005; Vile, 2005; Cavender-Bares *et al.*, 2006; Kazakou *et al.*, 2006; Kerkhoff *et al.*, 2006; Michaletz and Johnson, 2006; Preston *et al.*, 2006; Campbell *et al.*, 2007; Craven *et al.*, 2007; Meir and Levy, 2007; Price and Enquist, 2007; Scherer-Lorenzen *et al.*, 2007; Swaine, 2007; Kleyer *et al.*, 2008; Kraft *et al.*, 2008; Shiodera *et al.*, 2008; Craine *et al.*, 2009; Kattge *et al.*, 2009; van de Weg *et al.*, 2009; Wirth and Lichstein, 2009; Baraloto *et al.*, 2010; Freschet *et al.*, 2010; Laughlin *et al.*, 2010; Messier *et al.*, 2010; Ordonez *et al.*, 2010; Blonder *et al.*, 2011; Butterfield and Briggs, 2011; Campetella *et al.*, 2011; Chen *et al.*, 2011; Craine *et al.*, 2011; de Araujo *et al.*, 2011; Kattge *et al.*, 2011; Laughlin *et al.*, 2011; Milla and Reich, 2011; Onoda *et al.*, 2011; Prentice *et al.*, 2011; Tucker *et al.*, 2011; Sandel *et al.*, 2011; van de Weg *et al.*, 2011; Yguel *et al.*, 2011; Yu *et al.*, 2011; Adriaenssens, 2012; Beckmann *et al.*, 2012; Blonder *et al.*, 2012; Choat *et al.*, 2012; Craine *et al.*, 2012a; Craine *et al.*, 2012b; Frenette-Dussault *et al.*, 2012; Gutiérrez and Huth, 2012; Han *et al.*, 2012; Minden *et al.*, 2012; Powers and Tiffin, 2012; Rolo *et al.*, 2012; Spasojevic and Suding, 2012; Vergutz *et al.*, 2012; Williams *et al.*, 2012; Wright and Sutton-Grier, 2012; Auger and Shipley, 2013; Blonder *et al.*, 2013; Boucher *et al.*, 2013; Demey *et al.*, 2013; Dahlin *et al.*, 2013; Guy *et al.*, 2013; Kichenin *et al.*, 2013; Lukeš *et al.*, 2013; Martinez-Garza *et al.*, 2013; Adler *et al.*, 2014; Joseph *et al.*, 2014; Minden and Kleyer, 2014; Muir *et al.*, 2014; Seymour *et al.*, 2014; Siefert *et al.*, 2014; Slot *et al.*, 2014; Smith *et al.*, 2014; Takkis, 2014; van der Plas and Olff, 2014; Walker, 2014; Atkin *et al.*, 2015; Blonder *et al.*, 2015; Ciccarelli, 2015; La Pierre and Smith, 2015; Li *et al.*, 2015; Maire *et al.*, 2015; Minden and Kleyer, 2015;

Tribouillois *et al.*, 2015; Blonder *et al.*, 2016; De Vries and Bardgett, 2016; Gos *et al.*, 2016; Lhotsky *et al.*, 2016; Schroeder-Georgi *et al.*, 2016; Sharpe and Solano, 2016 *a*, *b*; Chacón-Madrigal *et al.*, 2018). Once entries with ErrorRisk (indication for outliers, distance to mean in standard deviations) greater than 4 were excluded, the dataset contained information of 10369 species from 309 taxonomic families. From these, 5403 species from 249 taxonomic families including ferns, gymnosperms and angiosperms contain information for at least two leaf functional traits. The observations are widely distributed over the world (Supplementary data Fig. S1).

RESULTS

Overall leaf functional trait variation and environmental effects

In general, the 10 Chaco species measured in this study were clustered in a relative narrow section of the global interspecific variability for each leaf functional trait (Supplementary data Fig. S2). Bioclimatic variables showed little variability among sampling points (CV < 4%) whereas some soil properties were quite variable (e.g. Soil Mg^{2+} content and Conductivity show CV of 48.3% and 43.3% respectively) (Supplementary data Table S1). However, only one correlation (between SLA and F_t) for two species (*S. pyramidatus* and *L. pluriflora*) could be partially explained by the effects of environmental variables. In *S. pyramidatus*, soil water content correlated positively with SLA ($r = 0.363$, p-value < 0.0001) and negatively with F_t ($r = -0.446$, p-value <0.0001) (Fig. 1). In *L. pluriflora*, soil conductivity correlated negatively with SLA ($r = -0.517$, p-value < 0.0001) and positively with F_t ($r = 0.523$, p-value < 0.0001) (Fig. 1). No other pair of leaf functional traits from any species correlated significantly with any other environmental variable. Therefore environmental variation within the study area could not explain most of the covariation patterns observed (presented below).

Trait-trait covariation patterns

The intraspecific covariation of the leaf functional traits generally followed the expected pattern. We observed a negative correlation for the LDMC-SLA, F_t-SLA, LDMC-N_m, and F_t-N_m trait pairs, but a positive correlation for the SLA-N_m and F_t-LDMC trait pairs (Supplementary data Table S3; Fig. S3). Only some species in some conditions showed non-significant correlations, but the effect size was always in the expected direction (e.g. *L. crinita* in common garden for F_t-SLA correlation) and the overall effect sizes for intraspecific correlations (Fabaceae intraspecific field, Fabaceae intraspecific common garden, Poaceae intraspecific field, and Poaceae intraspecific common garden) followed the expected pattern in all cases (Supplementary data Fig. S3). The intraspecific covariation pattern was similar to the global, the Fabaceae, and the Poaceae interspecific patterns for most of the pairs of leaf functional traits, but was different for the F_t-N_m and F_t-LDMC pairs of traits. For these, the interspecific patterns showed no correlation.

Trait-trait slopes

The intraspecific slopes always followed the expected qualitative trend, i.e. a negative slope for the pairs LDMC-SLA (Fig. 2A), F_t-SLA (Fig. 2C), LDMC-N_m (Fig. 3A), F_t-N_m (Fig. 3C); and a positive slope for the pairs LDMC-F_t (Supplementary data Fig. S4A), SLA-N_m (Supplementary data Fig. S4C). This pattern was observed in leaf functional traits of individuals both collected in the field and grown in the common garden (Fig. 2B, D; Fig. 3B, D; Supplementary data Fig. S4B, D). Even family means showed similar patterns (Supplementary data Fig. S5, Tables S4 and S5).

While the intraspecific patterns of leaf functional trait covariation in this study matched those expected on a global scale, many of the intraspecific slopes significantly differed from the global interspecific slope as well as from the slopes of its respective taxonomic family (Fig. 2B, Fig. 3B and Supplementary data Fig. S4D). Specifically, for the LDMC vs SLA relationship, 10 out of 20 cases (species × growing condition) and 3 out of 10 species have slopes shallower than the global interspecific slope (Fig. 2B, Supplementary data Table S6). Within Fabaceae, three species (*P. flexuosa* field, *P. flexuosa* c. garden, *P. torquata* field, *V. aroma* field) showed shallower slopes than the interspecific Fabaceae slope (Fig. 2B, Supplementary data Table S6). Within Poaceae, two species (*N. lophostachya* field, *N. lophostachya* common garden, *S. pyramidatus* field) showed slopes steeper than the interspecific Poaceae slope (Fig. 2B, Supplementary data Table S6). For the F_t vs SLA relationship, 3 out of 12 cases and 1 out of 6 grasses have slopes steeper than the global interspecific slope (Fig. 2D, Supplementary data Table S7). But, none of the grasses (F_t was no measured for woody legumes) was different from the interspecific Poaceae slope. For the LDMC vs N_m relationship, 3 out of 8 cases had slopes shallower than the global interspecific pattern (Fig. 3B, Supplementary data Table S8). Within Fabaceae, one species (*P. flexuosa* field, *P. flexuosa* c. garden) showed shallower slopes than the interspecific Fabaceae slope, which is in turn steeper than the global interspecific (Fig. 3B, Supplementary data Table S8). Within Poaceae, just one case (*L. pluriflora* field) showed a slope shallower than the interspecific Poaceae slope (Fig. 3B, Supplementary data Table S8). For the N_m vs SLA relationship, three out of eight cases and one out of four species (all grasses) have steeper slopes than the global and Poaceae interspecific slopes (Supplementary data Fig. S4, Table S9). For the F_t vs N_m and the F_t vs LDMC relationships, at the intraspecific level, there were strong correlations for most cases (Supplementary data Table S3, Fig. S3). Moreover, the intraspecific slopes of all cases with significant correlation were similar (Fig. 3D, Supplementary data Fig. S4A).

Field vs. common growing conditions

For a given species, the relationship between a pair of leaf functional traits sometimes differed depending on whether the plants were grown in the field or in the garden. These differences appeared more common for the LDMC vs SLA pair of traits (Fig. 2B), than others (e.g. F_t vs SLA; Fig. 2D). The slopes of the relationship between leaf functional traits never changed sign under different growth conditions (even in genetic family analysis), however, in some cases the correlation became nonsignificant. This was more common in pairs of traits involving N_m, in the common garden and in woody legumes (Supplementary data Table S3). For the rest, only F_t vs SLA for *L. crinita* in the common garden showed a nonsignificant correlation (Supplementary data Table S3). The correlation between a pair of leaf functional traits was significant in the common garden but not in the field only in the case of SLA and N_m in *P. flexuosa* (Supplementary data Table S3).

DISCUSSION

If the acquisitive-conservative axis arises from biophysical constraints on leaf functional traits, it should be present across levels of organization and be independent from the magnitude of environmental variation. Yet patterns at the intraspecific level have been reported to deviate from the global interspecific pattern (Donovan *et al.*, 2011; Niinemets, 2015; Martin *et al.*, 2017; Anderegg *et al.*, 2018; Xiong and Flexas, 2018; Hayes *et al.*, 2019). We sought to test whether phenotypic plasticity or local (genetic) adaptation might explain such deviation. We found that the intraspecific leaf functional trait covariation pattern within each of the 10 selected species, belonging to two contrasting taxonomic families and growth forms, are consistent with the theoretically expected acquisitive-conservative axis. These covariation patterns are also similar to the interspecific trait covariation pattern, although the strengths of the correlations are variable. This suggests that the trade-off between resource acquisition and conservation, which has been extensively documented among species, also operates within species. This is in accordance with previous studies at the intraspecific level (Albert *et al.*, 2010a; Vasseur *et al.*, 2012; Blonder *et al.*, 2013; Jackson *et al.*, 2013; Richardson *et al.*, 2013; Niinemets, 2015; Hu *et al.*, 2015; Martin *et al.*, 2017; Anderegg *et al.*, 2018; Fajardo and Siefert, 2018; Xiong and Flexas, 2018; Hayes *et al.*, 2019; Sartori *et al.*, 2019). However, those studies focused on trait covariation along environmental gradients, and/or under contrasting growing conditions (Supplementary data Table S3). We gained further insight by focusing on intraspecific covariation patterns under less variable conditions in the field to avoid the effect of major environmental gradients like rainfall and temperature (i.e. local adaptation), as well as in a common garden experiment to capture the genetic rather than environmental underpinning (phenotypic plasticity) of leaf functional trait correlations. Although we detected some environmentally-driven variation in SLA and F_t for two species, this was an exception rather than a commonality and does not influence the study conclusions.

We found that the pattern of covariation related to the acquisitive-conservative axis persists at the intraspecific level, both in the field and in a common garden experiment, even when environmental variation among sampling points (in the field) cannot explain such covariation. This suggests that, in our dataset, plastic responses or local adaptation (in response to selection) are not the primary determinants of the intraspecific acquisitive-conservative covariation pattern, as previously posed (Donovan *et al.*, 2011). On the contrary, it seems that the same trade-offs shaping the global interspecific acquisitive-conservative axis operate at the intraspecific level.

Donovan *et al.* (2011) showed that the genetic correlation between leaf functional traits may be variable among species and even between populations of the same species. They showed that such genetic correlations may be opposite to what is expected on the basis of the global acquisitive-conservative interspecific axis, leading them to conclude that natural selection should be the main force shaping the acquisitive-conservative covariation pattern. However, covariance among leaf functional traits is modulated by plasticity (Sherrard *et al.*, 2009). In our work, field conditions are different from common garden conditions in many ways, e.g. water availability. These differences induced variable effects in the slopes according to the leaf functional trait pair considered, i.e. there is some degree of plasticity in such covariance structure and some trait-trait correlations may be more plastic than others. So, even when the main trends in the acquisitive-conservative pattern were independent of environmental variation, this heterogeneity could modulate the strength and slope of the covariation pattern.

The relationship between SLA and LDMC is mediated by leaf thickness and leaf density (Vile *et al.*, 2005). Moreover, there is a link between leaf morphology and chemical composition such that the thicker the leaf is, the greater LDMC (Roderick *et al.*, 1999). It follows that the steeper the negative LDMC-SLA slope, the more steeply positive the LDMC-thickness slope would be. With respect to the LDMC-N_m slopes, if leaf nitrogen is assumed to be located mostly in the cytosol (the liquid phase) and not in the extracellular matrix (Roderick *et al.*, 1999), N_m is inversely proportional to LDMC (Shipley *et al.*, 2006a), and the log-log relationship should have a slope equal to -1. While the less steep the negative slope, the less nitrogen should be (proportionally) in the extracellular matrix (the solid phase). Leaf N allocation to cell walls ranges from 2.8% to 25% (90% quantile range) (Onoda *et al.*, 2017). This N allocation trade-off may have important functional consequences because of its effect on the photosynthetic N use efficiency. Among our studied cases, grasses tend to show a shallower slope than legume species in the LDMC-N_m relationship. This indicates that the N content of the cytoplasm per unit of N content of the cell wall (N_{cyt}:N_{wall}) is greater in grasses than in legumes

The acquisitive-conservative axis (and its variants, like the leaf economics spectrum) has proven to be a useful concept to understand vegetation dynamics and ecosystem processes, as well as being relevant to functional and comparative plant ecology (McGill *et al.*, 2006, Reich, 2014). The evidence presented here confirms that, in general, the acquisitive-conservative covariation pattern is valid from the global level to the local population level, which has been already demonstrated in a number of other studies (Blonder *et al.*, 2013; Hu *et al.*, 2015; Fajardo and Siefert, 2018). Our study goes further by showing that the pattern occurs at the intraspecific level even when environmental conditions do not explain it, and it also holds in the absence of environmental variation. This is strongly suggests that natural selection, while clearly modulating this pattern (e.g. Wright *et al.*, 2005b) is not indispensable for its emergence. Our findings also reinforce the idea of one underlying cause for the pattern across scales and levels of organization. However, all the different causal hypotheses for the leaf economics spectrum (Wright *et al.*, 2004; Shipley *et al.*, 2006a; Blonder *et al.*, 2011, 2013, 2015; Onoda *et al.*, 2017) have found empirical support at some levels of organization, but failed when tested out of their domains (Blonder *et al.*, 2015). Among all the new studies that could be carried out to further elucidate the causes of these patterns, operating across levels of organization, the combination of phenotypic integration—i.e. the study of complex patterns of covariation among functionally related traits in a given organism—and pleiotropy—i.e. the phenomenon of a single gene affecting multiple traits—frameworks (Pigliucci, 2003; Paaby and Rockman, 2013; Geiler-Samerotte *et al.*, 2020) is arguably the most promising. For example, the fact that the leaf functional trait covariation pattern holds in the absence of environmental variation could be explained by the fact that highly integrated phenotypes (stronger co-variation among traits) have higher adaptive value (Damián *et al.*, 2020) and therefore are selected for. But, different types of pleiotropy (Paaby and Rockman, 2013; Geiler-Samerotte *et al.*, 2020) could also explain the covariation pattern even if no selective advantage rises from integrated phenotypes. An experimental design combining both theoretical frameworks could bring light on the mechanisms driving the acquisitive-conservative axis at different levels.

CONCLUSIONS

Our study indicates that the acquisitive-conservative leaf functional trait covariation pattern occurs at the intraspecific level, in a similar way to the well-known global interspecific pattern, even in the absence of relevant environmental variation in the field. This pattern remains mostly consistent even when the possible plastic responses were removed by common growing conditions. This suggests a high degree of variation-covariation in leaf functional traits not driven by environmental variables, i.e. not shaped by selection or plasticity. Our study supports the idea that genetic (or developmental/biophysical) constraints are the main determinants in the evolution of the acquisitive-conservative axis in the leaf functional traits; natural selection then operates modulating it.

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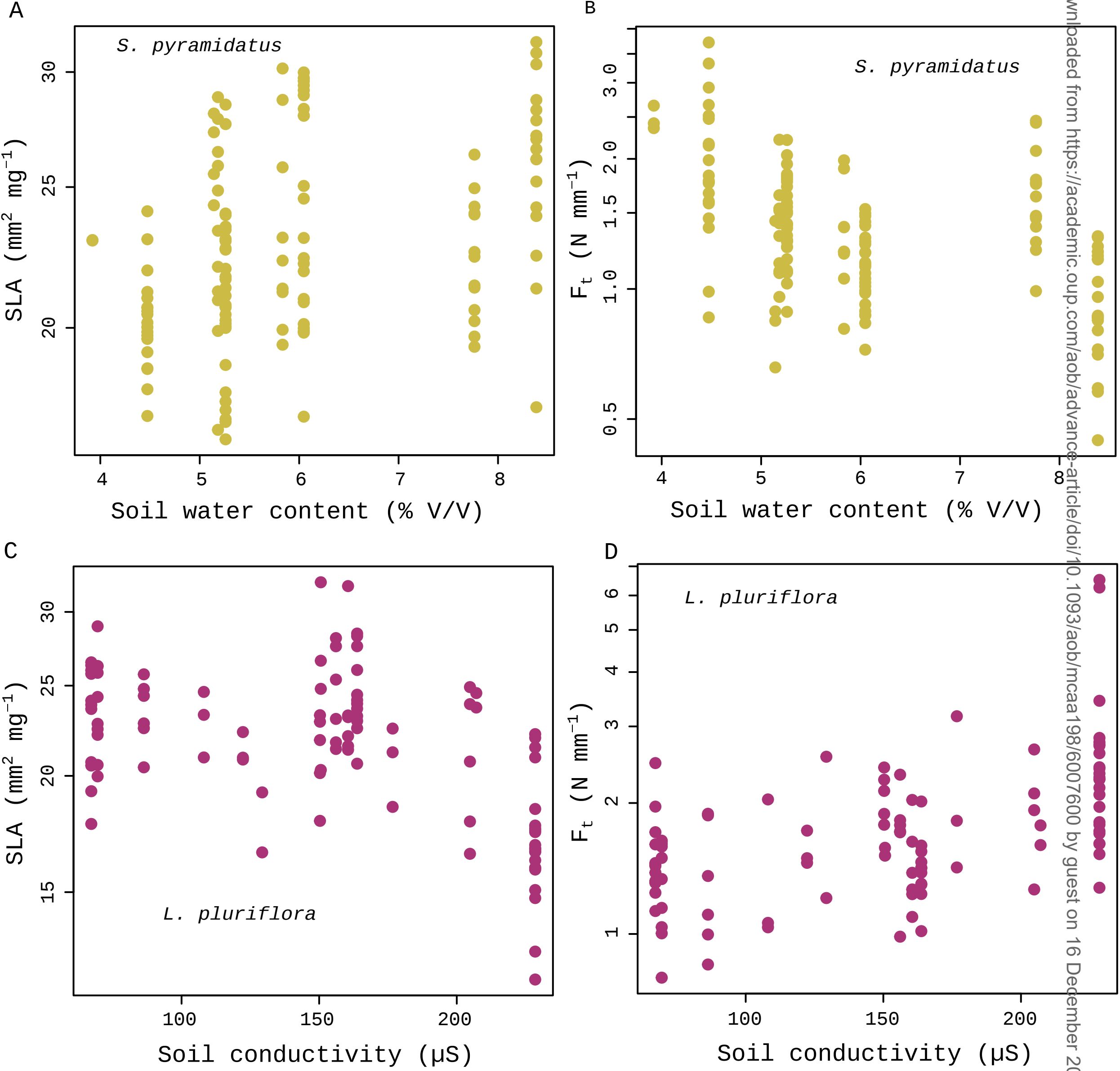
Figure legends

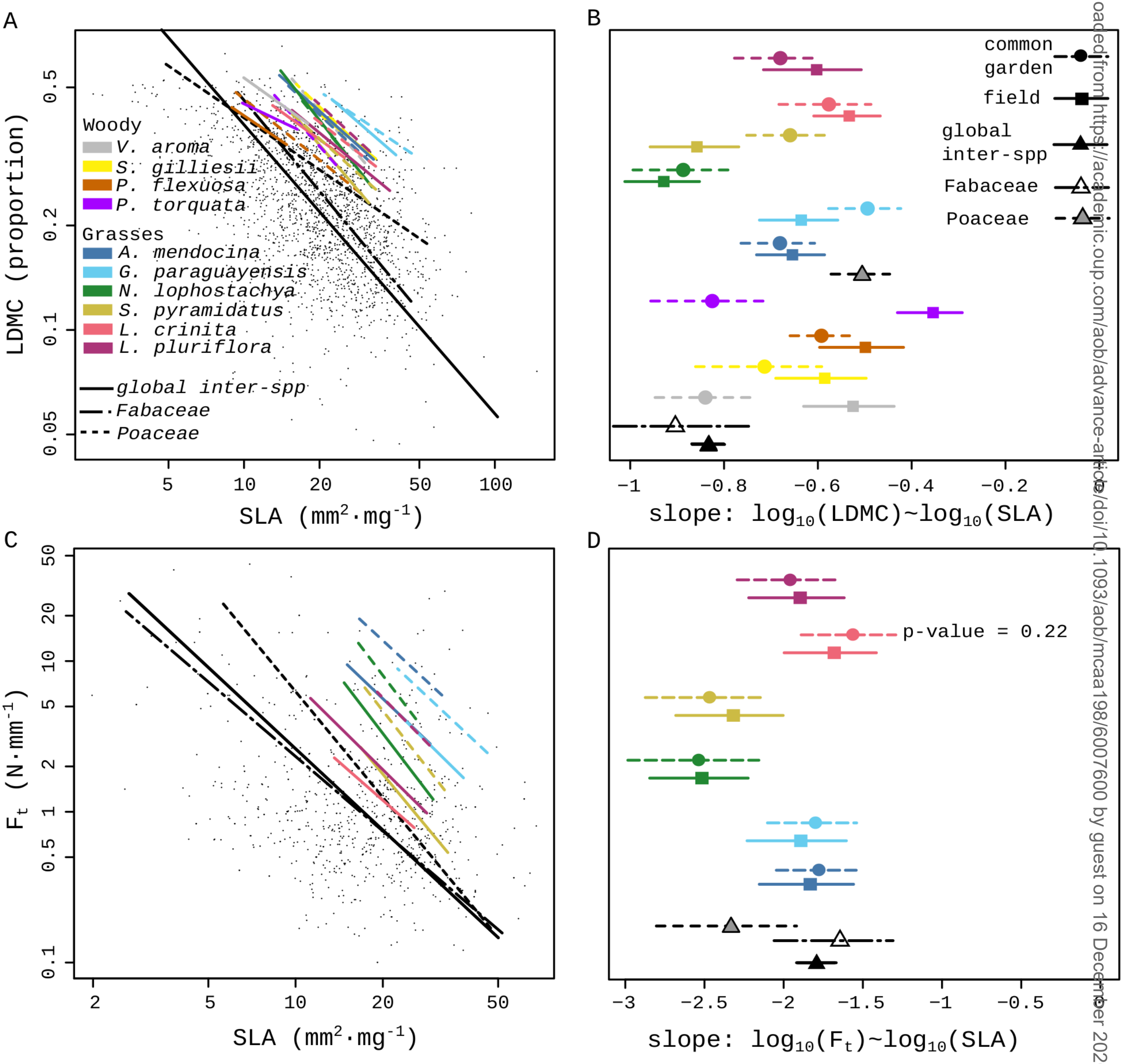
Figure 1. Relationship between leaf functional traits and environmental variables. Here we show the only two cases were an environmental variable (Supplementary data Table S1) affects simultaneously two leaf functional traits within a species. SLA: specific leaf area. Ft: force to tear.

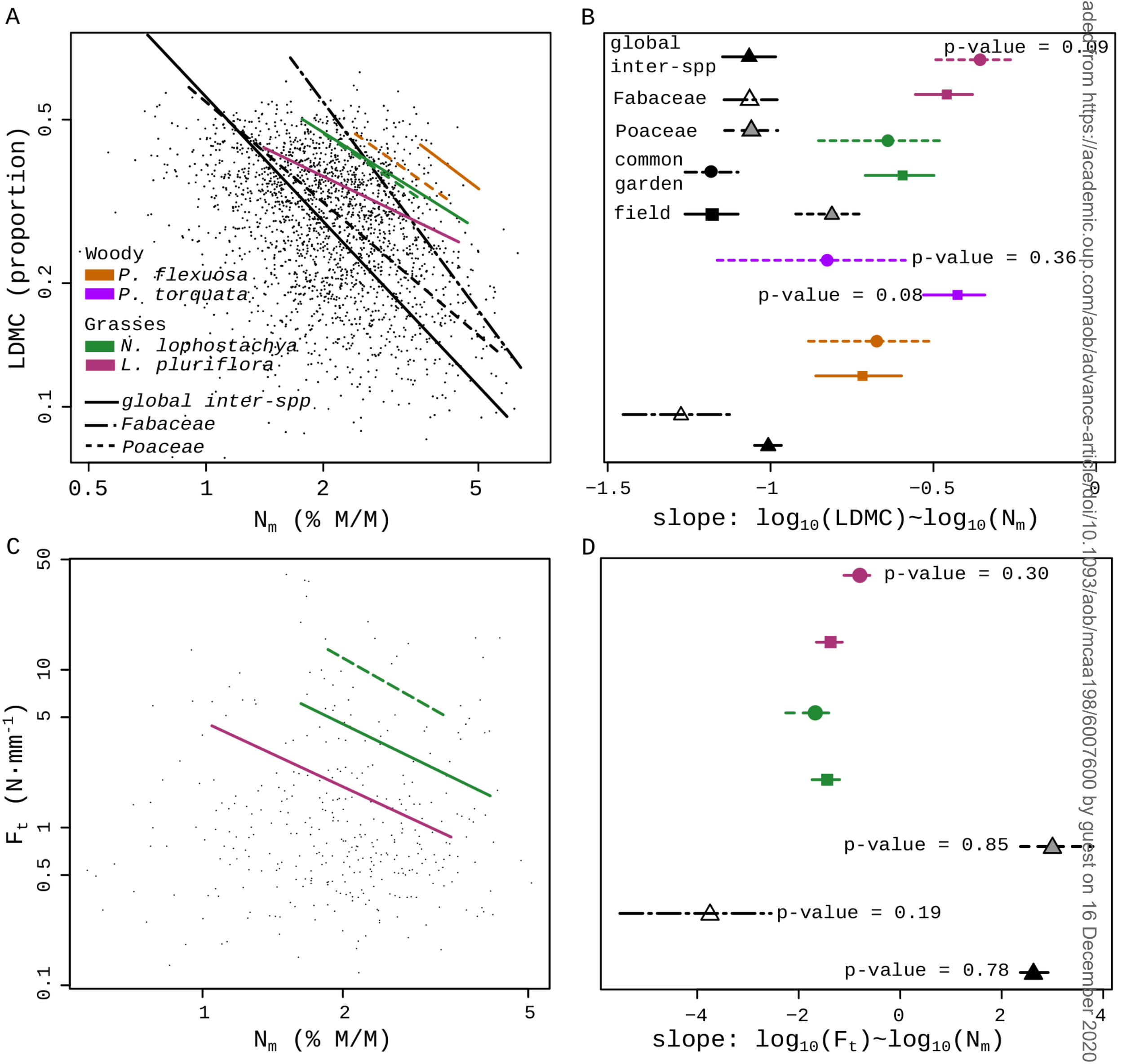
Figure 2. Relationship between leaf dry matter content (LDMC), force to tear (F_t) and specific leaf area (SLA). Different colours represent different species, continuous lines and squares represent field condition and dashed lines and circles the common garden condition. Black lines and dots shows the same analysis and data for the global, Fabaceae and Poaceae interspecific dataset obtained from the TRY datasets. Left panels (A and C) show the SMA lines for each species at each condition, the global interspecific data, the Fabaceae and Poaceae interspecific data. Each dot represents one species, intraspecific data (individual plants) are not shown. Right panels (B and D) show the estimated slope and 95% confidence interval for each group. When an estimated slope comes from a non-significant correlation, it is indicated at the right panel by reporting the corresponding p-value and it is not shown at the left panel. LDMC: leaf dry matter content. SLA: specific leaf area. F_t: force to tear. Results from multiple comparisons of the slopes are shown in Supplementary data Tables S6 and S7.

Figure 3.

Relationship between leaf dry matter content (LDMC), force to tear (F_t) and leaf nitrogen content (N_m). Different colours represent different species, continuous lines and squares represent field condition and dashed lines and circles the common garden condition. Black lines and dots shows the same analysis and data for the global, Fabaceae and Poaceae interspecific dataset obtained from the TRY datasets. Left panels (A and C) show the SMA lines for each species at each condition, the global interspecific data, the Fabaceae and Poaceae interspecific data. Each dot represents one species, intraspecific data (individual plants) are not shown. Right panels (B and D) show the estimated slope and 95% confidence interval for each group. When an estimated slope comes from a non-significant correlation, it is indicated at the right panel by reporting the corresponding p-value and it is not shown at the left panel. Results from slopes multiple comparison test are shown in Supplementary data Table S8. In the F_t vs N_m relationship there were no significant differences in slopes among those with correlation different from zero. There are only two species per taxonomic family in the intraspecific analyses.


A
S. pyramidatus
SLA (mm^2 mg^{-1})
20
25
30
4
5
6
7
8
Soil water content (% V/V)
B
S. pyramidatus
F$_t$ (N mm^{-1})
0.5
1.0
1.5
2.0
3.0
4
5
6
7
8
Soil water content (% V/V)
C
L. pluriflora
SLA (mm^2 mg^{-1})
15
20
25
30
100
150
200
Soil conductivity (µS)
D
L. pluriflora
F$_t$ (N mm^{-1})
1
2
3
4
5
6
100
150
200
Soil conductivity (µS)


A
LDMC (proportion)
0.5
0.2
0.1
0.05
5
10
20
50
100
SLA (mm^2·mg^{-1})
Woody
V. aroma
S. gilliesii
P. flexuosa
P. torquata
Grasses
A. mendocina
G. paraguayensis
N. lophostachya
S. pyramidatus
L. crinita
L. pluriflora
global inter-spp
Fabaceae
Poaceae
B
common garden
field
global inter-spp
Fabaceae
Poaceae
−1
−0.8
−0.6
−0.4
−0.2
slope: log$_{10}$(LDMC)~log$_{10}$(SLA)
C
F$_t$ (N·mm^{-1})
50
20
10
5
2
1
0.5
0.1
2
5
10
20
50
SLA (mm^2·mg^{-1})
D
p-value = 0.22
−3
−2.5
−2
−1.5
−1
−0.5
slope: log$_{10}$(F$_t$)~log$_{10}$(SLA)


A
LDMC (proportion)
0.5
0.2
0.1
0.5
1
2
5
Nm (% M/M)
Woody
P. flexuosa
P. torquata
Grasses
N. lophostachya
L. pluriflora
global inter-spp
Fabaceae
Poaceae
B
global inter-spp
Fabaceae
Poaceae
common garden
field
p-value = 0.09
p-value = 0.36
p-value = 0.08
−1.5
−1
−0.5
0
slope: log10(LDMC)~log10(Nm)
C
Ft (N·mm-1)
50
10
5
1
0.5
0.1
1
2
5
Nm (% M/M)
D
p-value = 0.30
p-value = 0.85
p-value = 0.19
p-value = 0.78
−4
−2
0
2
4
slope: log10(Ft)~log10(Nm)

Supplementary information.

Figure S1. Geolocation of the entries in the TRY public dataset.

Figure S2. Distribution of the four traits considered in our analysis across the interspecific global dataset, the interspecific Fabaceae and Poaceae (black boxes) and the intraspecific variability for each one of the species measured in the field for this study (colour boxes). Boxes show median and quartiles. Whiskers show up to 1.5 times interquartiles range. Note that y-axis have been log-transformed. Force to tear (Ft) could not be measured in leaflets of the woody species because they are too small to be handled into our measuring device. Leaf nitrogen content (Nm) was measured only in four species due to high costs.

Figure S3. Fisher's z effect size for all correlations in Table S3, as well as overall effect size for intraspecific correlation in our Fabaceae and Poaceae species, at both growing conditions (i.e. Fabaceae intraspecific field, Fabaceae intraspecific common garden, Poaceae intraspecific field, and Poaceae intraspecific common garden).

Figure S4. Relationship between force to tear (F_t) and leaf dry matter content (LDMC) as well as specifics leaf area (SLA) and nitrogen content per leaf mass (N_m). Different colours represent different species, continuous lines and squares represent field condition and dashed lines and circles the common garden condition. Black lines and dots shows the same analysis and data for the global, Fabaceae and Poaceae interspecific dataset obtained from the TRY datasets. Left panels (A and C) shows the SMA lines for each species at each condition, the global interspecific data, the Fabaceae and Poaceae interspecific data. Each dot represents one species, intraspecific data (individual plants) are not shown. Right panels (B and D) shows the estimated slope and 95% confidence interval for each group. When an estimated slope comes from a non-significant correlation, it is indicated at the right panel by reporting the corresponding p-value and it is not shown at the left panel. No significant differences were found in slopes $\log_{10}(F_t)$~$\log_{10}(LDMC)$ among groups. Results of the multiple comparisons test for slopes $\log_{10}(SLA)$~$\log_{10}(N_m)$ are shown in Table S9. Slope confidence intervals non overlapping grey box in D are significantly different from the interspecific. In panel C, SMA lines for *N. lophostachya* are completely overlaped.

Figure S5. SMA slopes of the relation between force to tear (F_t), leaf dry matter content (LDMC) and specifics leaf area (SLA), from plants in the field and from genetic families in the common garden. Symbols and segments show the estimated slope and 95% confidence interval for each group. Different colours represent different species, continuous lines and squares represent field condition, dashed lines and circles the genetic families in the common garden condition. Black line and triangles represent the same analysis for the global-level interspecific dataset obtained from the TRY dataset. No significant differences were found in slopes $\log_{10}(F_t)$~$\log_{10}(LDMC)$ among groups. Results of the multiple comparisons test for slopes $\log_{10}(LDMC)$~$\log_{10}(SLA)$ and $\log_{10}(F_t)$~$\log_{10}(SLA)$ are shown in Table S4 and Table S5 respectively.

Table S1. Edaphic and climatic description of the sampling points, the common-garden potting-soil from our study, as well as the available data from previous studies about intraspecific leaf functional traits covariation patterns. Position statistics for altitude, climatic and edaphic variables, as well as coefficient of variation (CV) from field sampling points from our study (Our study field). Common-garden potting-soil (Our study CGPS) properties are also shown. Also, information about edaphic and climatic variability from previously published works about intraspecific trait covariation patterns was included when available in the works themself or could be estimated from the WorldClim database (Fick & Hijmans, 2017). Source: Albert: Albert *et al*., 2010a; Vasseur: Vasseur *et al*., 2012; Blonder: Blonder *et al*., 2013; Jackson: Jackson *et al*., 2013; Richardson: Richardson *et al*., 2013; Niinemets: Niinemets, 2015; Hu: Hu *et al*., 2015; Martin: Martin *et al*., 2017; Fajardo: Fajardo & Siefert, 2018; Sartori: Sartori *et al*., 2019.

Variable (unit)	min.	Q1	median	mean	Q3	max.	CV(%)	source
Altitude (m.a.s.l.)	304	322	359	354.5	368	430	10.5	Our study field
	455			915		1500	49.59	Martin
	5					1177	53–120	Niinemets
	39	200	356.5	433.97	679.25	1288	74.01	Richardson
	1941					3718		Blonder
	1200					3000		Albert
Soil total Nitrogen (mg g^{-1})	0.1475	0.1800	0.2260	0.2320	0.2665	0.3604	28.8	Our study field
	0.2			1.9		7.7	83.8	Hu
	6.8			13.1		19.7	24.43	Jackson
				0.85				Our study CGPS
Soil Organic Matter (%)	1.633	2.014	2.317	2.542	2.942	4.918	32.8	Our study field
				1.54				Our study CGPS
Soil pH	6.270	6.520	6.760	6.775	6.950	7.250	3.6	Our study field
	6.79			8.67		10.61	8.1	Hu
	3.3			4.34		5.49	14.74	Jackson
				7.35				Our study CGPS
Soil conductivity (µS)	67.2	70.8	135.8	134.9	176.7	228.5	43.4	Our study field
	30			5590		42120	175.6	Hu
				150				Our study CGPS
Soil PO_4^{2-} (mg kg^{-1})	14.98	27.44	31.44	31.25	33.17	42.38	17.2	Our study field
	1.5			19.2		79.0	90.3	Hu
	6.1			25.3		56.4	45.45	Jackson
Soil SiO_4^{2-} (mg kg^{-1})	171.9	218.2	244.7	258.9	286.0	414.4	21.1	Our study field
Soil Ca^{2+} (meq 100g^{-1})	6.50	9.50	11.00	11.13	13.00	20.00	25.4	Our study field
	0.4			20.4		59.6	84.31	Jackson
Soil Mg^{2+} (meq 100g^{-1})	0.500	1.000	1.500	1.743	2.500	3.000	48.3	Our study field
	3.4			7.7		14.1	40.26	Jackson
Soil K^{+} (meq 100g^{-1})	0.0435	0.0435	0.0870	0.0808	0.0870	0.1522	39.6	Our study field
	0.51			1.4		7.55	87.14	Jackson
Soil Na^{+} (meq 100g^{-1})	0.4604	1.0231	1.1126	1.1449	1.3556	1.8287	21.3	Our study field
	0.15			0.7		2.59	74.29	Jackson
Soil water content (% V/V)	3.213	4.556	5.260	5.649	6.047	8.386	23.3	Our study field

Variable (unit)	min.	Q1	median	mean	Q3	max.	CV(%)	source
Soil sup. comp. (kg cm^{-2})	0.8833	2.2473	3.1029	2.7057	3.4667	3.7262	31.1	Our study field
Soil comp. 0-5cm (kg cm^{-2})	6.070	8.185	12.929	13.457	18.525	22.532	36.6	Our study field
Soil comp. 5-10cm (kg cm^{-2})	16.37	21.15	31.83	30.15	34.95	49.75	32.1	Our study field
Annual mean temp. (°C)	19.20	19.40	19.60	19.61	19.80	19.90	1.1	Our study field
	2.0	8.2	10.6	9.83	10.8	19.1	25.4	Sartori
	8.1			8.975		10.2	9.86	Fajardo
	18.7			21.4		24	12.56	Martin
	1.6			10.6		17.4	17.4	Hu
	10.2					18.6	9.5–13	Niinemets
	5.3	8.35	10	9.51	10.875	12.4	19.54	Richardson
	8.0					22.2		Vasseur
Mean diurnal range (°C)	13.60	13.60	13.70	13.67	13.70	13.80	0.4	Our study field
	5.4	7.73	8.5	8.28	8.9	13.1	15.9	Sartori
	6.9			7.55		8.6	10.4	Fajardo
	7.0					8.5		Vasseur
Isotermality (%)	47.00	47.00	48.00	47.69	48.00	48.00	1.0	Our study field
	19	31	33	32.8	34.8	47	14.4	Sartori
	43			45.75		50	6.53	Fajardo
	32.00					62.00		Vasseur
Temp. seasonality (SD °C)	4.995	5.032	5.076	5.058	5.080	5.119	0.7	Our study field
	2.605	5.5205	6.030	6.095	6.3205	13.016	20.967	Sartori
	3.025			3.187		3.314	4.17	Fajardo
	1.456					6.507		Vasseur
Max. temp. warmest month (°C)	33.20	33.60	33.70	33.68	33.80	34.00	0.6	Our study field
	17.3	21.4	24.4	23.5	24.9	35.5	11.1	Sartori
	16.4			18.025		19.9	8.17	Fajardo
	22.2					35.6	10–4.7	Niinemets
	22.0					27.6		Vasseur
Min. temp. coldest month (°C)	4.900	5.200	5.300	5.284	5.400	5.600	3.6	Our study field
	-20.0	-2.9	-0.75	-1.7	0.3	12.8	242	Sartori
	1.2			1.75		2.8	40.81	Fajardo

Variable (unit)	min.	Q1	median	mean	Q3	max.	CV(%)	source
	-3.6					7	81–89	Niinemets
	-4.3					16.4		Vasseur
	-12			-7.5		-3		Albert
Temp. annual range (°C)	28.3	28.3	28.4	28.4	28.5	28.6	0.3	Our study field
	14.4	23.4	25.1	25.2	26.1	47.0	17.1	Sartori
	15.2			16.275		17.1	5.25	Fajardo
	16.7					34.2	6.6–10	Niinemets
	11.2					26.3		Vasseur
Mean temp. wettest quarter (°C)	25.3	25.6	25.8	25.8	26.0	26.1	0.9	Our study field
	-2.3	8.95	16.2	13.9	18.4	19.2	37	Sartori
	4.4			5.35		7.0	21.28	Fajardo
	16.1					24.1		Vasseur
Mean temp. driest quarter (°C)	12.40	12.60	12.80	12.79	13.00	13.00	1.5	Our study field
	-12.8	2.3	6.8	8.81	7.93	24.7	96.1	Sartori
	8.0			11.925		14.2	22.7	Fajardo
	7.0					21.3		Vasseur
Mean temp. warmest quarter (°C)	25.3	25.6	25.8	25.8	26.0	26.1	0.9	Our study field
	11.5	16.1	18.2	17.61	18.6	25.9	10.91	Sartori
	12.1			13.1		14.2	6.63	Fajardo
	14.82					28.507		Blonder
	16.1					24.1		Vasseur
	10					17		Albert
Mean temp. coldest quarter (°C)	12.40	12.60	12.80	12.79	13.00	13.00	1.5	Our study field
	-14.2	0.2	2.8	1.958	3.8	16.2	192	Sartori
	4.0			4.825		6.4	22.22	Fajardo
	-6.0					20.4		Vasseur
	-6.3					-1		Albert
Annual precipitation (mm)	507.0	509.0	514.0	514.8	519.0	529.0	1.3	Our study field
	134	668.3	760	765.7	798	2387	22.89	Sartori
	1747			2175.2		2460	14.05	Fajardo
	1386			2273		3200	42.56	Martin
	40			543		1702	79.9	Hu
	370.7					1484	20–27	Niinemets

Variable (unit)	min.	Q1	median	mean	Q3	max.	CV(%)	source
	668	1288	2117	2377.7	3000.2	4875	53.63	Richardson
	3500					8000		Jackson
	369					962		Vasseur
Precipitation wettest month (mm)	95.00	95.00	96.00	95.92	96.00	97.00	0.7	Our study field
	34	77	82	86.71	88	296	27.19	Sartori
	190			268.75		303	19.71	Fajardo
	123					149		Vasseur
Precipitation driest month (mm)	7.000	7.000	7.000	7.086	7.000	8.000	4.0	Our study field
	0	38	47	43.96	50	105	27.83	Sartori
	101			118.75		146	16.51	Fajardo
	0					53		Vasseur
Precipitation seasonality (VC)	72.0	74.0	75.0	74.3	75.0	75.0	1.2	Our study field
	8	13	16	21.78	27	95	54.98	Sartori
	18			28.5		38	30.92	Fajardo
	32					150		Vasseur
Precipitation wettest quarter (mm)	263.0	263.0	265.0	265.2	266.0	269.0	0.7	Our study field
	85	212	217	239	245	851	28.33	Sartori
	541			770.25		857	19.92	Fajardo
	315					357		Vasseur
Precipitation driest quarter (mm)	22.00	22.00	22.00	22.36	23.00	24.00	2.8	Our study field
	0	121.3	152	143.7	168	371	27.44	Sartori
	326			390.75		482	16.83	Fajardo
	0					165		Vasseur
Precipitation warmest quart. (mm)	263.0	263.0	265.0	265.2	266.0	269.0	0.7	Our study field
	1	184.3	212	201.1	217	479	25.37	Sartori
	326			403		500	18.27	Fajardo
	87.381					159.74		Blonder
	315					357		Vasseur
Precipitation coldest quarter (mm)	22.00	22.00	22.00	22.36	23.00	24.00	2.8	Our study field
	57	155	169	189.9	195	690	38.97	Sartori
	521			728		812	19.04	Fajardo
	5					170		Vasseur

Table S2. Full botanical names following the Instituto de Botánica Darwinion (IBODA, CONICET-ANCEFN; http://www.darwin.edu.ar/)

Species name	Family	Growth form
Aristida mendocina PHIL.	Poaceae	Grass
Gouinia paraguayensis (KUNTZE) PARODI		
Neobouteloua lophostachya (GRISEB.) GOULD		
Sporobolus pyramidatus (LAM.) HITCHC.		
Leptochloa crinita (LAG.) P.M. PETERSON & N.W. SNOW		
Leptochloa pluriflora (E. FOURN.) P.M. PETERSON & N.W. SNOW		
Vachellia aroma (GILLIES EX HOOK. & ARN.) SEIGLER & EBINGER	Fabaceae	Woody, shrub/tree
Senegalia gilliesii (STEUD.) SEIGLER & EBINGER		Woody, shrub
Prosopis flexuosa DC.		Woody, tree
Prosopis torquata (CAV. EX LAG.) DC.		Woody, shrub/tree

Table S3. Sample size and Pearson's correlation coefficient for each pair of traits in each species and condition. All traits log-transformed previous to analysis. In bold are the correlation coefficients significant at 0.05 confidence level. F_t : force to tear. LDMC: leaf dry matter content. N_m: leaf nitrogen content. SLA: specific leaf area.

	Pearson's correlation coefficient (sample size)					
Species/Condition	LDMC-SLA	Ft-SLA	SLA-Nm	LDMC-Nm	Ft-Nm	Ft-LDMC
Global inter-spp	**-0.439 (1837)**	**-0.293 (726)**	**0.401 (3461)**	**-0.274 (2127)**	0.015 (360)	-0.021 (315)
Fabaceae inter-spp	**-0.404 (119)**	**-0.456 (60)**	**0.343 (309)**	**-0.541 (163)**	-0.259 (27)	0.188 (20)
Poaceae inter-spp	**-0.549 (174)**	**-0.372 (100)**	**0.440 (236)**	**-0.499 (179)**	0.022 (72)	0.054 (56)
V. aroma / field	**-0.541 (82)**	NA	NA	NA	NA	NA
V. aroma / c. garden	**-0.691 (140)**	NA	NA	NA	NA	NA
V. aroma / genetic family	**-0.709 (36)**	NA	NA	NA	NA	NA
S. gilliesii / field	**-0.637 (86)**	NA	NA	NA	NA	NA
S. gilliesii / c. garden	**-0.485 (85)**	NA	NA	NA	NA	NA
S. gilliesii / genetic family	**-0.541 (28)**	NA	NA	NA	NA	NA
P. flexuosa / field	**-0.441 (97)**	NA	0.129 (97)	**-0.436 (97)**	NA	NA
P. flexuosa / c. garden	**-0.729 (157)**	NA	**0.670 (40)**	**-0.550 (40)**	NA	NA
P. flexuosa / genetic family	**-0.686 (40)**	NA	NA	NA	NA	NA
P. torquata / field	**-0.448 (81)**	NA	**0.221 (80)**	-0.199 (80)	NA	NA
P. torquata / c. garden	**-0.524 (129)**	NA	0.156 (35)	-0.160 (35)	NA	NA
P. torquata / genetic family	**-0.401 (35)**	NA	NA	NA	NA	NA
A. mendocina / field	**-0.795 (116)**	**-0.489 (115)**	NA	NA	NA	**0.410 (115)**
A. mendocina / c. garden	**-0.828 (93)**	**-0.732 (93)**	NA	NA	NA	**0.636 (93)**
A. mendocina / genetic family	**-0.874 (36)**	**-0.813 (36)**	NA	NA	NA	**0.749 (36)**
G. paraguayensis / field	**-0.692 (117)**	**-0.449 (116)**	NA	NA	NA	**0.391 (116)**
G. paraguayensis / c. garden	**-0.686 (85)**	**-0.697 (85)**	NA	NA	NA	**0.384 (85)**
G. paraguayensis / genetic family	**-0.716 (31)**	**-0.755 (31)**	NA	NA	NA	**0.500 (31)**
N. lophostachya / field	**-0.831 (163)**	**-0.598 (166)**	**0.371 (106)**	**-0.410 (106)**	**-0.196 (108)**	**0.652 (163)**
N. lophostachya / c. garden	**-0.738 (136)**	**-0.287 (137)**	**0.423 (35)**	**-0.570 (35)**	**-0.518 (35)**	**0.267 (136)**
N. lophostachya / genetic family	**-0.774 (38)**	-0.202 (38)	NA	NA	NA	**0.325 (38)**
S. pyramidatus / field	**-0.775 (128)**	**-0.563 (127)**	NA	NA	NA	**0.474 (128)**
S. pyramidatus / c. garden	**-0.739 (102)**	**-0.623 (104)**	NA	NA	NA	**0.431 (102)**
S. pyramidatus / genetic family	**-0.700 (38)**	**-0.779 (38)**	NA	NA	NA	**0.541 (38)**

	Pearson’s correlation coefficient (sample size)					
Species/Condition	LDMC-SLA	Ft-SLA	SLA-Nm	LDMC-Nm	Ft-Nm	Ft-LDMC
L. crinita / field	**-0.669 (120)**	**-0.309 (120)**	NA	NA	NA	**0.225 (121)**
L. crinita / c. garden	**-0.441 (108)**	-0.119 (108)	NA	NA	NA	0.046 (108)
L. crinita / genetic family	**-0.568 (38)**	-0.181 (38)	NA	NA	NA	0.238 (38)
L. pluriflora / field	**-0.473 (101)**	**-0.619 (98)**	**0.522 (93)**	**-0.372 (95)**	**-0.447 (93)**	**0.190 (100)**
L. pluriflora / c. garden	**-0.564 (145)**	**-0.255 (145)**	0.267 (37)	-0.279 (37)	-0.176 (37)	**0.406 (145)**
L. pluriflora / genetic family	**-0.641 (38)**	**-0.325 (38)**	NA	NA	NA	**0.417 (38)**

Table S4. Slopes of $\log_{10}$(LDMC)~$\log_{10}$(SLA) for each species and condition (field and genetic families), and groups resulting from multiple comparison test.

Multiple comparisons SMA slopes $\log_{10}$*(LDMC) vs* $\log_{10}$*(SLA)*

Species/Condition	**slope**	**groups**						
N. lophostachya / field	-0.9201886	A						
Global interspecific	-0.8257997	A	B					
S. pyramidatus / field	-0.8494781	A	B	C				
N. lophostachya / family	-0.8993596	A	B	C	D			
Fabaceae interspecific	-0.8699317	A	B	C	D			
V. aroma / family	-0.8672199	A	B	C	D	E		
P. torquata / family	-0.8054150	A	B	C	D	E	F	
L. pluriflora / family	-0.6698224	A	B	C	D	E	F	
A. mendocina / family	-0.6376206	A	B	C	D	E	F	
S. gilliesii / family	-0.6498491	A	B	C	D	E	F	G
P. flexuosa / family	-0.6168681	A	B	C	D	E	F	G
L. crinita / family	-0.5771819	A	B	C	D	E	F	G
S. pyramidatus / family	-0.5620275	A	B	C	D	E	F	G
L. pluriflora / field	-0.5940442		B	C	D	E	F	
A. mendocina / field	-0.6456772			C	D	E	F	
G. paraguayensis / field	-0.6269587			C	D	E	F	
S. gilliesii / field	-0.5767890				D	E	F	
L. crinita / field	-0.5244363					E	F	G
V. aroma / field	-0.5162968					E	F	G
P. flexuosa / field	-0.4900628					E	F	G
Poaceae interspecific	-0.4968522						F	G
G. paraguayensis / family	-0.4333641						F	G
P. torquata / field	-0.3455757							G

Table S5. Slopes of $\log_{10}(F_t)$~$\log_{10}(SLA)$ for each species and condition (field and genetic families), and groups resulting from multiple comparison test.

Multiple comparisons SMA slopes $\log_{10}(F_t)$ *vs* $\log_{10}(SLA)$

Species/Condition	**slope**	**groups**	
N. lophostachya / field	-2.516028	A	
Poaceae interspecific	-2.329811	A	B
S. pyramidatus / field	-2.317633	A	B
S. pyramidatus / family	-2.273348	A	B
L. pluriflora / family	-2.083571	A	B
L. pluriflora / field	-1.895536	A	B
G. paraguayensis / field	-1.891799	A	B
A. mendocina / field	-1.832174	A	B
G. paraguayensis / family	-1.726691	A	B
Fabaceae interspecific	-1.641441	A	B
Global interspecific	-1.791179		B
L. crinita / field	-1.680648		B
A. mendocina / family	-1.631519		B

Table S6. Slopes of $\log_{10}$(LDMC)~$\log_{10}$(SLA) for each species and condition (field and common garden), and groups resulting from multiple comparison test.

Multiple comparisons SMA slopes $\log_{10}$(LDMC) vs $\log_{10}$(SLA)

Species/Condition	**slope**	**groups**						
N. lophostachya / field	-0.9201886	A						
N. lophostachya / c. garden	-0.8787146	A	B					
Global interspecific	-0.8257997	A	B					
S. pyramidatus / field	-0.8494781	A	B	C				
Fabaceae interspecific	-0.8699317	A	B	C	D			
V. aroma / c. garden	-0.8314898	A	B	C	D			
P. torquata / c. garden	-0.8167784	A	B	C	D	E		
S. gilliesii / c. garden	-0.7051413	A	B	C	D	E	F	
A. mendocina / c. garden	-0.6723132		B	C	D	E	F	
L. pluriflora / c. garden	-0.6714814		B	C	D	E	F	
S. pyramidatus / c. garden	-0.6506067		B	C	D	E	F	
L. pluriflora / field	-0.5940442		B	C	D	E	F	
A. mendocina / field	-0.6456772			C	D	E	F	
G. paraguayensis / field	-0.6269587			C	D	E	F	
S. gilliesii / field	-0.5767890				D	E	F	
L. crinita / c. garden	-0.5679364				D	E	F	G
P. flexuosa / c. garden	-0.5838521					E	F	
L. crinita / field	-0.5244363						F	G
V. aroma / field	-0.5162968						F	G
Poaceae interspecific	-0.4968522						F	G
P. flexuosa / field	-0.4900628						F	G
G. paraguayensis / c. garden	-0.4854576						F	G
P. torquata / field	-0.3455757							G

Table S7. Slopes of $\log_{10}(F_t) \sim \log_{10}(SLA)$ for each species and condition (field and common garden), and groups resulting from multiple comparison test.

Multiple comparisons SMA slopes $\log_{10}(F_t)$ *vs* $\log_{10}(SLA)$

Species/Condition	slope	groups
N. lophostachya / field	-2.516028	A
N. lophostachya / c. garden	-2.536802	A B
S. pyramidatus / c. garden	-2.466053	A B
Poaceae interspecific	-2.329811	A B C
S. pyramidatus / field	-2.317633	A B C
L. pluriflora / c. garden	-1.956062	A B C
L. pluriflora / field	-1.895536	A B C
G. paraguayensis / field	-1.891799	A B C
A. mendocina / field	-1.832174	A B C
G. paraguayensis / c. garden	-1.798912	A B C
Fabaceae interspecific	-1.641441	A B C
A. mendocina / c. garden	-1.776240	B C
L. crinita / field	-1.680648	B C
Global interspecific	-1.791179	C

Table S8. Slopes of $\log_{10}(LDMC) \sim \log_{10}(N_m)$ for each species and condition (field and common garden), and groups resulting from multiple comparison test.

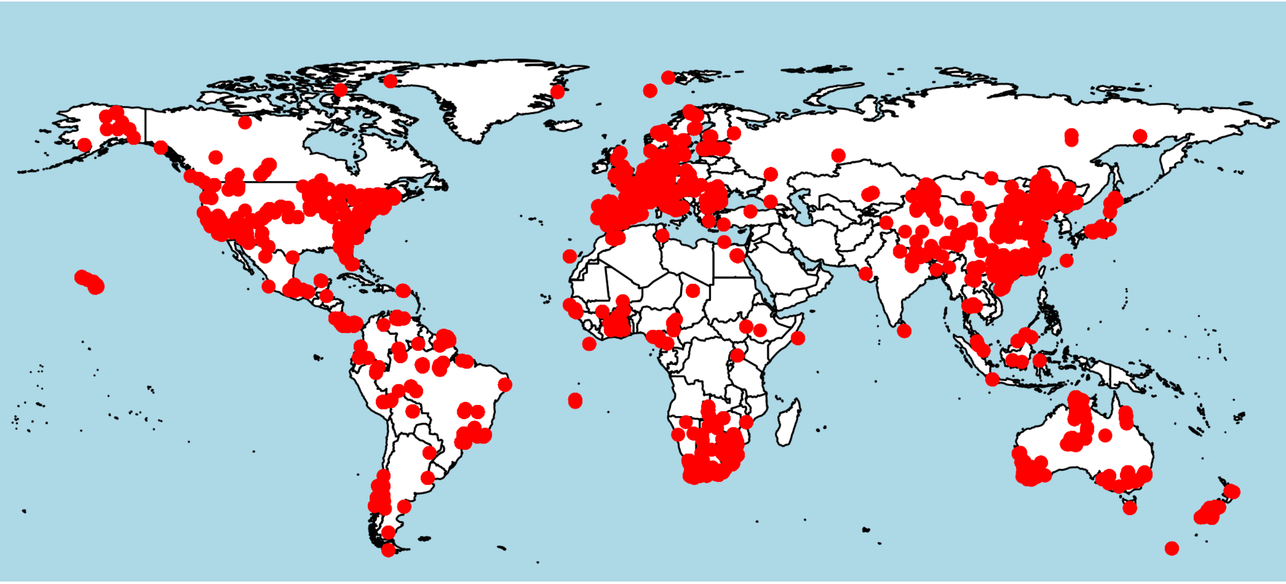
Multiple comparisons SMA slopes $\log_{10}(LDMC)$ *vs* $\log_{10}(N_m)$

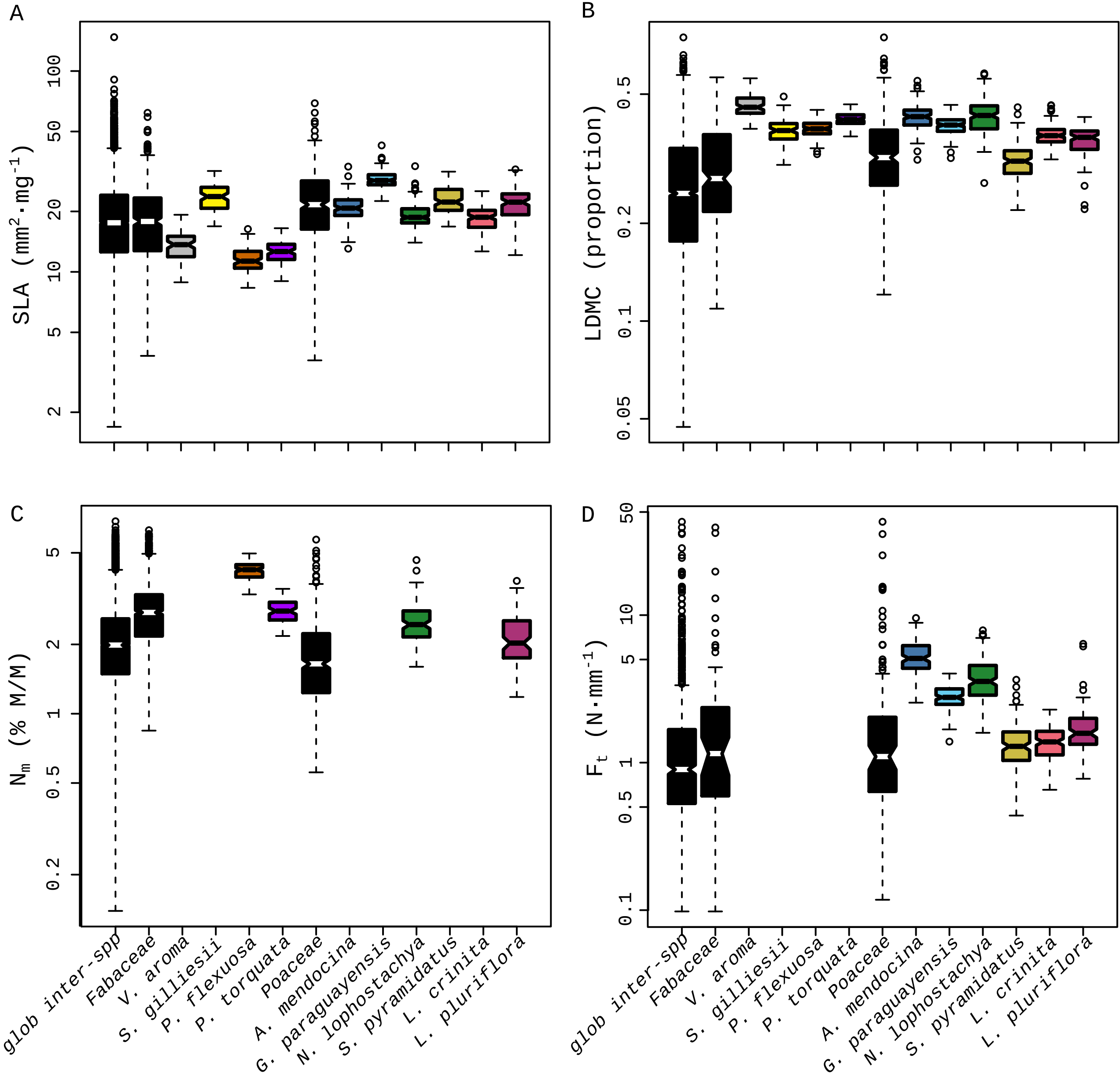
Species/Condition	slope	groups
Fabaceae interspecific	-1.2750266	A
Global interspecific	-1.0082588	B
Poaceae interspecific	-0.8116772	B C
P. flexuosa / field	-0.7177515	C
P. flexuosa / c. garden	-0.6739386	B C D
N. lophostachya / c. garden	-0.6397957	B C D
N. lophostachya / field	-0.5945122	C D
L. pluriflora / field	-0.4591987	D

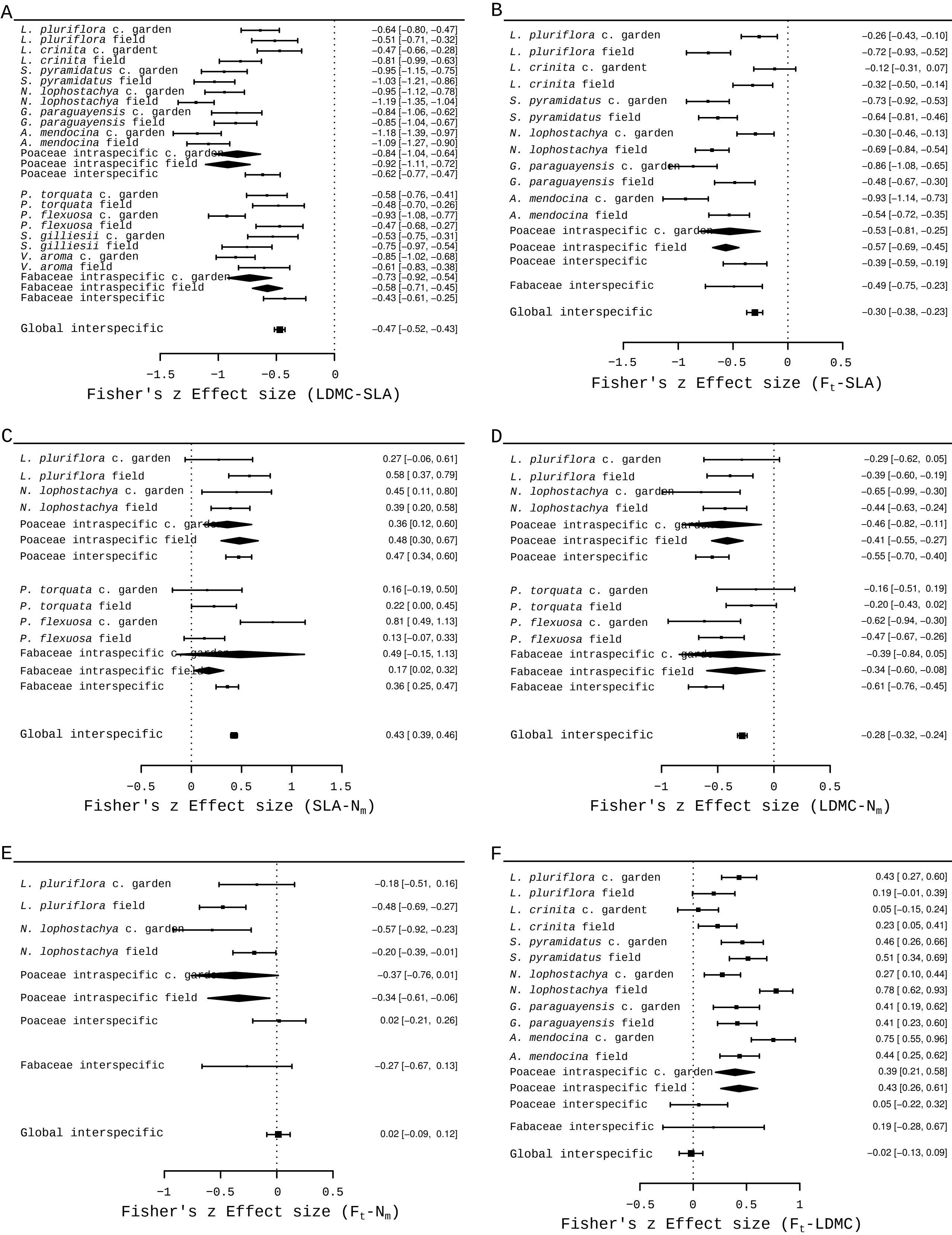
Table S9. Slopes of $\log_{10}(N_m)$~$\log_{10}(SLA)$ for each species and condition (field and common garden), and groups resulting from multiple comparison test.

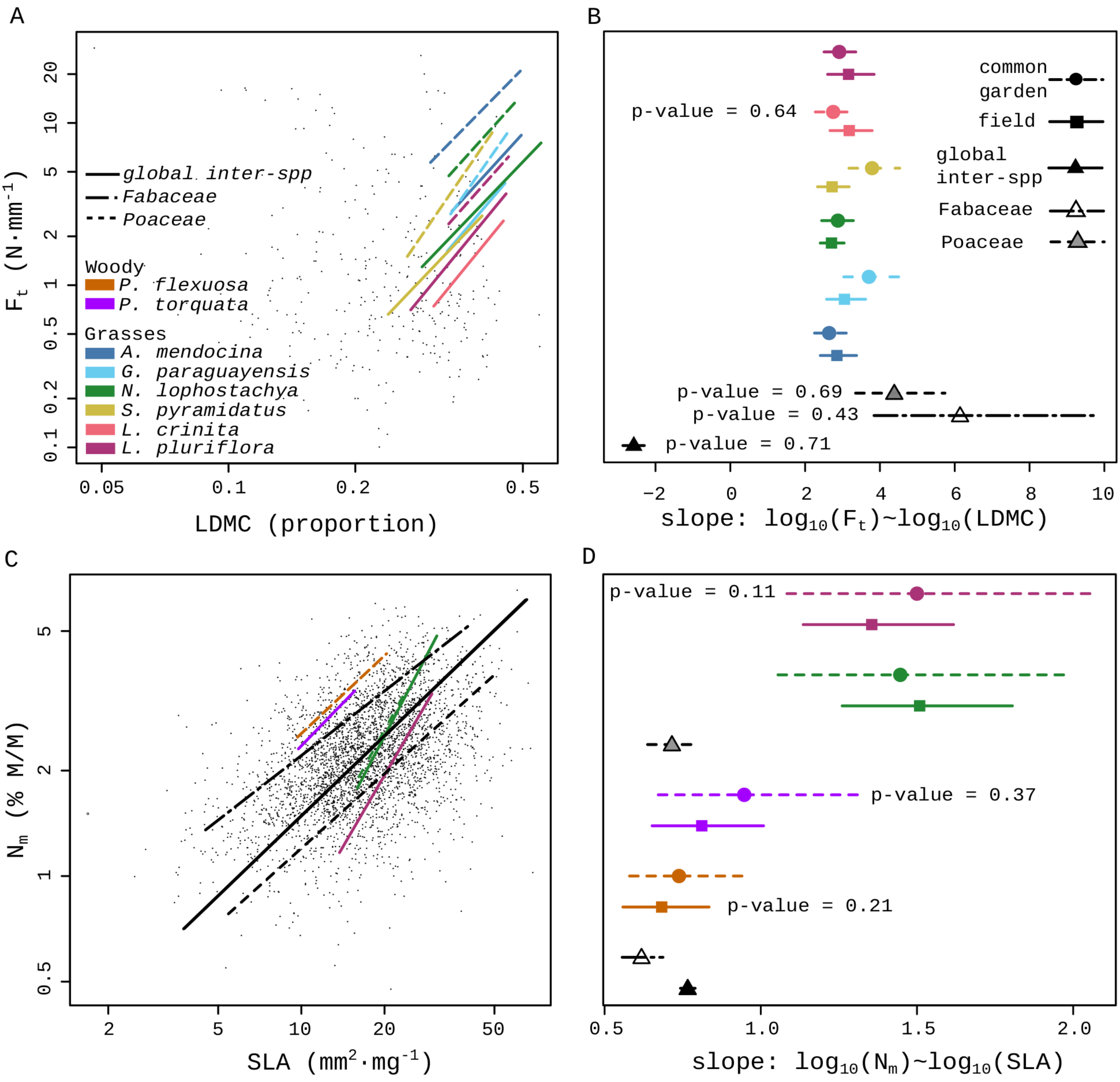
Multiple comparisons SMA slopes $log_{10}(N_m)$ vs $log_{10}(SLA)$

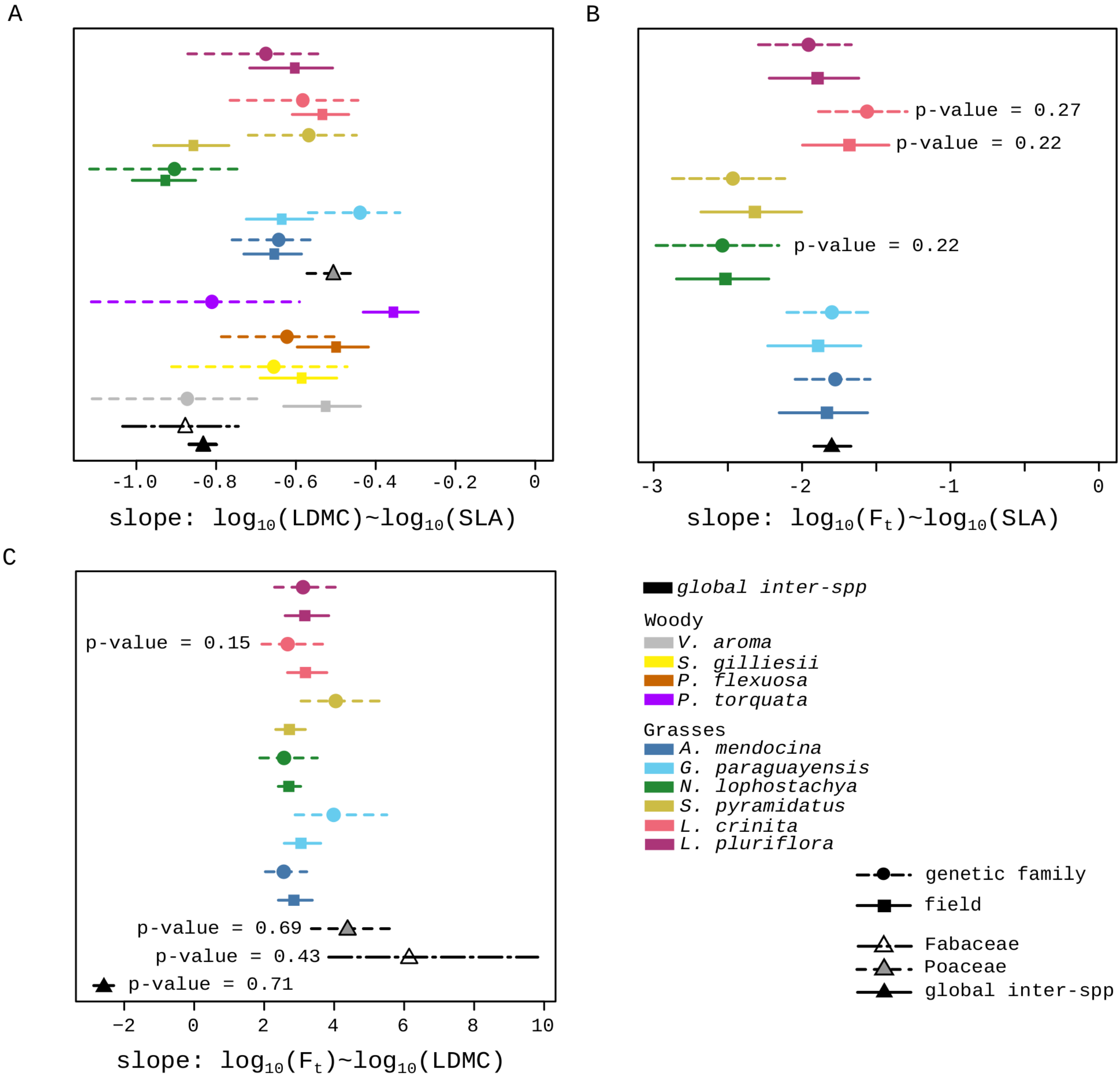
Species/Condition	**slope**	**groups**			
Fabaceae interspecific	0.6181801	A			
Poaceae interspecific	0.7156274	A	B		
P. flexuosa / c. garden	0.7381507	A	B	C	
P. torquata / field	0.8110997	A	B	C	
Global interspecific	0.7664998		B		
N. lophostachya / c. garden	1.4465750			C	D
L. pluriflora / field	1.3552130				D
N. lophostachya / field	1.5085320				D




A
SLA (mm^2·mg^{-1})
100
50
20
10
5
2
B
LDMC (proportion)
0.5
0.2
0.1
0.05
C
N_m (% M/M)
5
2
1
0.5
0.2
D
F_t (N·mm^{-1})
50
10
5
1
0.5
0.1
glob inter-spp
Fabaceae
V. aroma
S. gilliesii
P. flexuosa
P. torquata
Poaceae
A. mendocina
G. paraguayensis
N. lophostachya
S. pyramidatus
L. crinita
L. pluriflora


A
L. pluriflora c. garden −0.64 [−0.80, −0.47]
L. pluriflora field −0.51 [−0.71, −0.32]
L. crinita c. gardent −0.47 [−0.66, −0.28]
L. crinita field −0.81 [−0.99, −0.63]
S. pyramidatus c. garden −0.95 [−1.15, −0.75]
S. pyramidatus field −1.03 [−1.21, −0.86]
N. lophostachya c. garden −0.95 [−1.12, −0.78]
N. lophostachya field −1.19 [−1.35, −1.04]
G. paraguayensis c. garden −0.84 [−1.06, −0.62]
G. paraguayensis field −0.85 [−1.04, −0.67]
A. mendocina c. garden −1.18 [−1.39, −0.97]
A. mendocina field −1.09 [−1.27, −0.90]
Poaceae intraspecific c. garden −0.84 [−1.04, −0.64]
Poaceae intraspecific field −0.92 [−1.11, −0.72]
Poaceae interspecific −0.62 [−0.77, −0.47]
P. torquata c. garden −0.58 [−0.76, −0.41]
P. torquata field −0.48 [−0.70, −0.26]
P. flexuosa c. garden −0.93 [−1.08, −0.77]
P. flexuosa field −0.47 [−0.68, −0.27]
S. gilliesii c. garden −0.53 [−0.75, −0.31]
S. gilliesii field −0.75 [−0.97, −0.54]
V. aroma c. garden −0.85 [−1.02, −0.68]
V. aroma field −0.61 [−0.83, −0.38]
Fabaceae intraspecific c. garden −0.73 [−0.92, −0.54]
Fabaceae intraspecific field −0.58 [−0.71, −0.45]
Fabaceae interspecific −0.43 [−0.61, −0.25]
Global interspecific −0.47 [−0.52, −0.43]
−1.5 −1 −0.5 0
Fisher's z Effect size (LDMC-SLA)
B
L. pluriflora c. garden −0.26 [−0.43, −0.10]
L. pluriflora field −0.72 [−0.93, −0.52]
L. crinita c. gardent −0.12 [−0.31, 0.07]
L. crinita field −0.32 [−0.50, −0.14]
S. pyramidatus c. garden −0.73 [−0.92, −0.53]
S. pyramidatus field −0.64 [−0.81, −0.46]
N. lophostachya c. garden −0.30 [−0.46, −0.13]
N. lophostachya field −0.69 [−0.84, −0.54]
G. paraguayensis c. garden −0.86 [−1.08, −0.65]
G. paraguayensis field −0.48 [−0.67, −0.30]
A. mendocina c. garden −0.93 [−1.14, −0.73]
A. mendocina field −0.54 [−0.72, −0.35]
Poaceae intraspecific c. garden −0.53 [−0.81, −0.25]
Poaceae intraspecific field −0.57 [−0.69, −0.45]
Poaceae interspecific −0.39 [−0.59, −0.19]
Fabaceae interspecific −0.49 [−0.75, −0.23]
Global interspecific −0.30 [−0.38, −0.23]
−1.5 −1 −0.5 0 0.5
Fisher's z Effect size (F_t-SLA)
C
L. pluriflora c. garden 0.27 [−0.06, 0.61]
L. pluriflora field 0.58 [0.37, 0.79]
N. lophostachya c. garden 0.45 [0.11, 0.80]
N. lophostachya field 0.39 [0.20, 0.58]
Poaceae intraspecific c. garden 0.36 [0.12, 0.60]
Poaceae intraspecific field 0.48 [0.30, 0.67]
Poaceae interspecific 0.47 [0.34, 0.60]
P. torquata c. garden 0.16 [−0.19, 0.50]
P. torquata field 0.22 [0.00, 0.45]
P. flexuosa c. garden 0.81 [0.49, 1.13]
P. flexuosa field 0.13 [−0.07, 0.33]
Fabaceae intraspecific c. garden 0.49 [−0.15, 1.13]
Fabaceae intraspecific field 0.17 [0.02, 0.32]
Fabaceae interspecific 0.36 [0.25, 0.47]
Global interspecific 0.43 [0.39, 0.46]
−0.5 0 0.5 1 1.5
Fisher's z Effect size (SLA-N_m)
D
L. pluriflora c. garden −0.29 [−0.62, 0.05]
L. pluriflora field −0.39 [−0.60, −0.19]
N. lophostachya c. garden −0.65 [−0.99, −0.30]
N. lophostachya field −0.44 [−0.63, −0.24]
Poaceae intraspecific c. garden −0.46 [−0.82, −0.11]
Poaceae intraspecific field −0.41 [−0.55, −0.27]
Poaceae interspecific −0.55 [−0.70, −0.40]
P. torquata c. garden −0.16 [−0.51, 0.19]
P. torquata field −0.20 [−0.43, 0.02]
P. flexuosa c. garden −0.62 [−0.94, −0.30]
P. flexuosa field −0.47 [−0.67, −0.26]
Fabaceae intraspecific c. garden −0.39 [−0.84, 0.05]
Fabaceae intraspecific field −0.34 [−0.60, −0.08]
Fabaceae interspecific −0.61 [−0.76, −0.45]
Global interspecific −0.28 [−0.32, −0.24]
−1 −0.5 0 0.5
Fisher's z Effect size (LDMC-N_m)
E
L. pluriflora c. garden −0.18 [−0.51, 0.16]
L. pluriflora field −0.48 [−0.69, −0.27]
N. lophostachya c. garden −0.57 [−0.92, −0.23]
N. lophostachya field −0.20 [−0.39, −0.01]
Poaceae intraspecific c. garden −0.37 [−0.76, 0.01]
Poaceae intraspecific field −0.34 [−0.61, −0.06]
Poaceae interspecific 0.02 [−0.21, 0.26]
Fabaceae interspecific −0.27 [−0.67, 0.13]
Global interspecific 0.02 [−0.09, 0.12]
−1 −0.5 0 0.5
Fisher's z Effect size (F_t-N_m)
F
L. pluriflora c. garden 0.43 [0.27, 0.60]
L. pluriflora field 0.19 [−0.01, 0.39]
L. crinita c. gardent 0.05 [−0.15, 0.24]
L. crinita field 0.23 [0.05, 0.41]
S. pyramidatus c. garden 0.46 [0.26, 0.66]
S. pyramidatus field 0.51 [0.34, 0.69]
N. lophostachya c. garden 0.27 [0.10, 0.44]
N. lophostachya field 0.78 [0.62, 0.93]
G. paraguayensis c. garden 0.41 [0.19, 0.62]
G. paraguayensis field 0.41 [0.23, 0.60]
A. mendocina c. garden 0.75 [0.55, 0.96]
A. mendocina field 0.44 [0.25, 0.62]
Poaceae intraspecific c. garden 0.39 [0.21, 0.58]
Poaceae intraspecific field 0.43 [0.26, 0.61]
Poaceae interspecific 0.05 [−0.22, 0.32]
Fabaceae interspecific 0.19 [−0.28, 0.67]
Global interspecific −0.02 [−0.13, 0.09]
−0.5 0 0.5 1
Fisher's z Effect size (F_t-LDMC)


A
F_t (N·mm^{-1})
0.1
0.2
0.5
1
2
5
10
20
LDMC (proportion)
0.05
0.1
0.2
0.5
global inter-spp
Fabaceae
Poaceae
Woody
P. flexuosa
P. torquata
Grasses
A. mendocina
G. paraguayensis
N. lophostachya
S. pyramidatus
L. crinita
L. pluriflora
B
common garden
field
global inter-spp
Fabaceae
Poaceae
p-value = 0.64
p-value = 0.69
p-value = 0.43
p-value = 0.71
−2
0
2
4
6
8
10
slope: $\log_{10}(F_t) \sim \log_{10}(LDMC)$
C
N_m (% M/M)
0.5
1
2
5
SLA (mm^2·mg^{-1})
2
5
10
20
50
D
p-value = 0.11
p-value = 0.37
p-value = 0.21
0.5
1.0
1.5
2.0
slope: $\log_{10}(N_m) \sim \log_{10}(SLA)$


A
-1.0
-0.8
-0.6
-0.4
-0.2
0
slope: log10(LDMC)~log10(SLA)
B
p-value = 0.27
p-value = 0.22
p-value = 0.22
-3
-2
-1
0
slope: log10(Ft)~log10(SLA)
C
p-value = 0.15
p-value = 0.69
p-value = 0.43
p-value = 0.71
−2
0
2
4
6
8
10
slope: log10(Ft)~log10(LDMC)
global inter-spp
Woody
V. aroma
S. gilliesii
P. flexuosa
P. torquata
Grasses
A. mendocina
G. paraguayensis
N. lophostachya
S. pyramidatus
L. crinita
L. pluriflora
genetic family
field
Fabaceae
Poaceae
global inter-spp