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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 [specific leaf area (SLA) leaf dry matter content (LDMC), force to tear (F_t) and leaf nitrogen content (N_m)] 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 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 pattern).
• **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.*, 2006*b*; 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 to 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 life span 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, 2005*a*) and theoretically (Shipley *et al.*, 2006*a*; 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; F_t) and leaf dry matter content (LDMC) are positively related to leaf life span. Leaf dry matter content is a proxy for the cell cytoplasm (V_c) to cell wall volume (V_w) ratio ($V_c/V_w{\sim}W_m$; $\mathrm{LDMC^{-1}} = 1 - W_m$, 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.*, 2006*a*). 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 life span variability (Wright *et al.*, 2004). Leaf thickness, fibre content and density affect leaf mechanical resistance, which enhances leaf life span 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 relationships among traits (Wright *et al.*, 2004; Shipley *et al.*, 2006*a*; 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.*, 2010*a*; Jackson *et al.*, 2013; Richardson *et al.*, 2013; Hu *et al.*, 2015; Niinemets, 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.*, 2005*b*; Ordoñez *et al.*, 2009; Hidaka and Kitayama, 2011; Moles *et al.*, 2014).

This strong, consistent leaf functional trait covariation pattern at both the 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 predicts plant community changes (Shipley *et al.*, 2006*b*; 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.*, 2010*a*, 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 the following question. 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 a comparison of the trait patterns observed at local intraspecific scales with those at the 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).

MATERIALS 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 (approx. 31°18′–31°32′S and 65°23′–65°32′W). The sampling area is approx. 25 km long north to south and 10 km wide east to west. The climate is sub-tropical and semi-arid (Cabido *et al.*, 1994) with a mean annual precipitation of 514.8 mm concentrated in 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* and *Prosopis torquata*) (see Supplementary data Table S2 for the 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, 39–49 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 for 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 <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 (approx. 2 m). Each leaf sample (for both grasses and woody legumes) consisted of three 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), 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 F_t 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) and 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 and 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 s resolution (approx. 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 20 m 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 legumes 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) pot. 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 (1–3 min) 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 28–40 sampling points per species. A year after germination, we measured the leaf functional traits of these plants, 2–4 individual plants per sampling point. We took one leaf sample per plant, each sample consisting of three 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 (log$_{10}$-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 next 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 the common garden by using the '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 standardized 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 log$_{10}$-transformed to achieve normality and homoscedasticity across the whole dataset (in analyses of both correlation and slopes). 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 and 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; Fitter and Peat, 1994; Shipley, 1995, 2002; Cornelissen, 1996; Cornelissen *et al.*, 1996, 1999, 2003, 2004; Atkin *et al.*, 1997, 1999, 2015; 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; Loveys *et al.*, 2003; Quested *et al.*, 2003; Xu and Baldocchi, 2003; Adler *et al.*, 2004, 2014; Díaz *et al.*, 2004; Givnish *et al.*, 2004; Wright *et al.*, 2004; Craine *et al.*, 2005, 2009, 2011, 2012, 2013; 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; Kattge *et al*., 2009, 2011; van de Weg *et al.*, 2009, 2011; Wirth and Lichstein, 2009; Baraloto *et al.*, 2010; Freschet *et al.*, 2010; Laughlin *et al.*, 2010, 2011; Messier *et al.*, 2010; Ordonez *et al.*, 2010; Blonder *et al.*, 2011, 2012, 2013, 2015, 2016; Butterfield and Briggs, 2011; Campetella *et al.*, 2011; Chen *et al.*, 2011; de Araujo *et al.*, 2011; Milla and Reich, 2011; Onoda *et al.*, 2011; Prentice *et al.*, 2011; Tucker *et al.*, 2011; Sandel *et al.*, 2011; Yguel *et al.*, 2011; Yu *et al.*, 2011; Adriaenssens, 2012; Beckmann *et al.*, 2012; Choat *et al.*, 2012; 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; 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; 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; Ciccarelli, 2015; La Pierre and Smith, 2015; Li *et al.*, 2015; Maire *et al.*, 2015; Minden and Kleyer, 2015; Tribouillois *et al.*, 2015; De Vries and Bardgett, 2016; Gos *et al.*, 2016; Lhotsky *et al.*, 2016; Schroeder-Georgi *et al.*, 2016; J. M. Sharpe and N. Solano, unpubl. res.; E. Chacón-Madrigal *et al.*, 2018). Once entries with ErrorRisk (indication for outliers, distance to mean in standard deviations) >4 were excluded, the dataset contained information on 10 369 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 ten Chaco species measured in this study were clustered in a relatively narrow section of the global interspecific variability for each leaf functional trait (Supplementary data Fig. S2). Bioclimatic variables showed little variability among sampling points [coefficient of variation (CV) <4 %], whereas some soil properties were quite variable (e.g. soil Mg^{2+} content and conductivity show a 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 the 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) and F_t–N_m (Fig. 3C), and a positive slope for the pairs LDMC–F_t (Supplementary data Fig. S4A) and 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 (Figs 2B, D and 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 (Figs 2B and 3B; Supplementary data Fig. S4D). Specifically, for the LDMC vs. SLA relationship, ten out of 20 cases (species × growing condition) and three out of ten species have slopes shallower than the global interspecific slope (Fig. 2B; Supplementary data Table S6). Within Fabaceae, three species (*P. flexuosa* field, *P. flexuosa* common garden, *P. torquata* field and *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 gardenand *S. pyramidatus* field) showed slopes steeper than the interspecific Poaceae slope (Fig. 2B, Supplementary data Table S6). For the F_t vs. SLA relationship, three out of 12 cases and one out of six grasses have slopes steeper than the global interspecific slope (Fig. 2D; Supplementary data Table S7). However, none of the grasses (F_t was not measured for woody legumes) was different from the interspecific Poaceae slope. For the LDMC vs. N_m relationship, three out of eight cases had slopes shallower than the global interspecific pattern (Fig. 3B; Supplementary data Table S8). Within Fabaceae, one species (*P. flexuosa* field, *P. flexuosa* common garden) showed shallower slopes
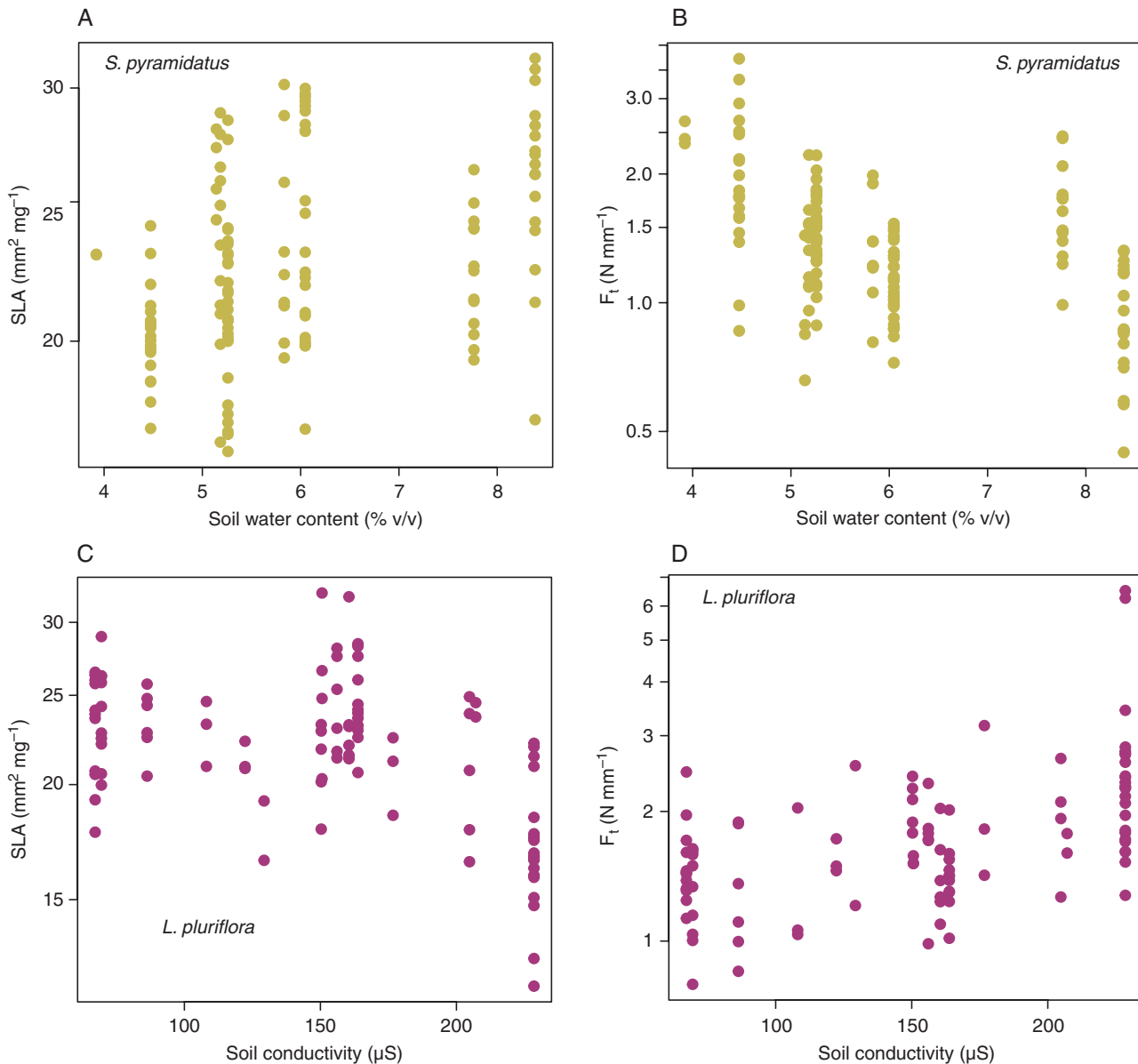
FIG. 1. Relationship between leaf functional traits and environmental variables. Here we show the only two cases where an environmental variable (Supplementary data Table S1) affects simultaneously two leaf functional traits within a species. SLA, specific leaf area. F_t, force to tear.

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 non-significant. 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 non-significant
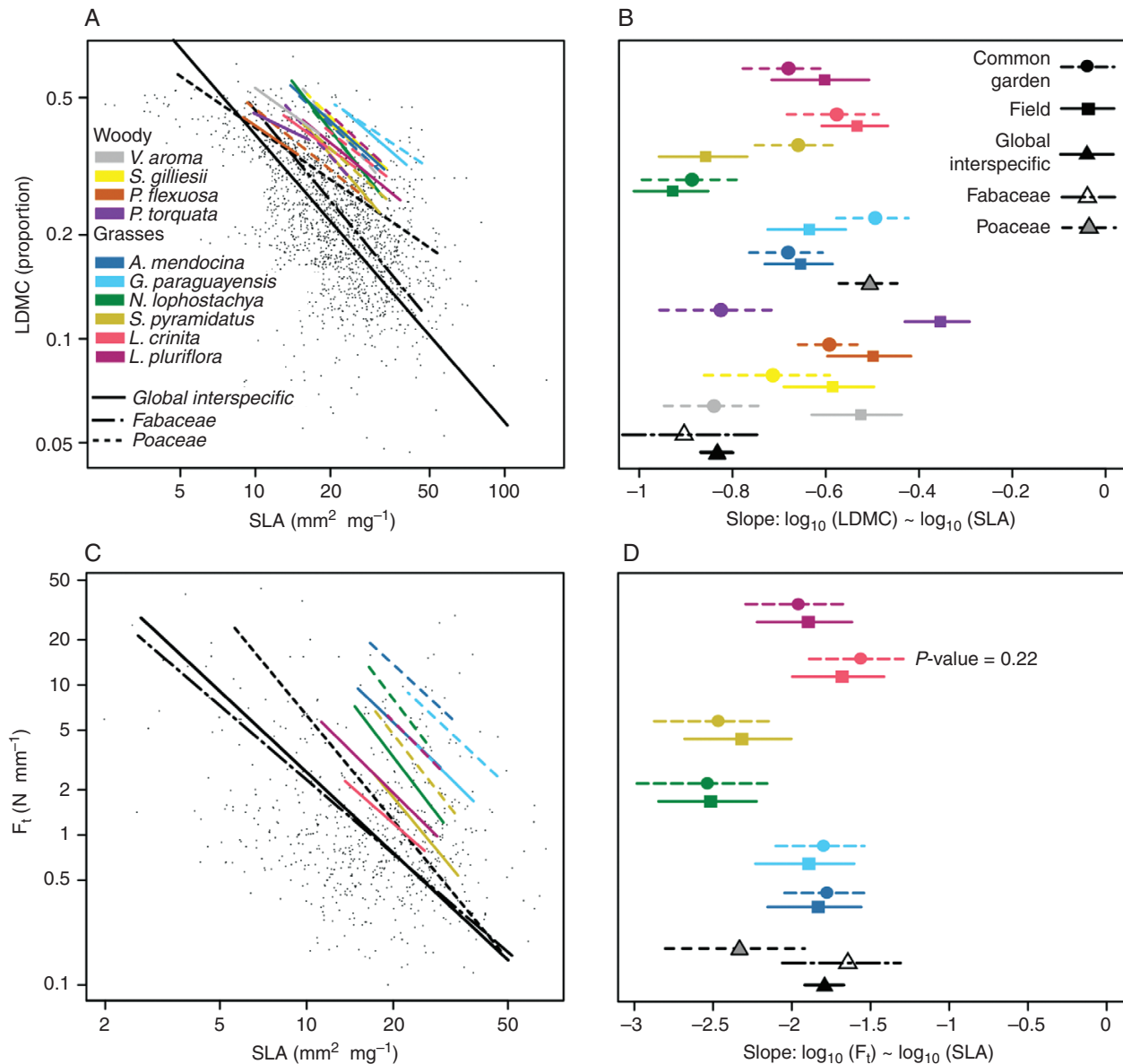
Fig. 2. Relationship between leaf dry matter content (LDMC), force to tear (F_t) and specific leaf area (SLA). Different colours represent different species, continuous lines and squares represent the field condition, and dashed lines and circles represent the common garden condition. Black lines and dots show 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 and 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 in the right panel by reporting the corresponding *P*-value and it is not shown in the left panel. Results from multiple comparisons of the slopes are shown in Supplementary data Tables S6 and S7.

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 ten 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.
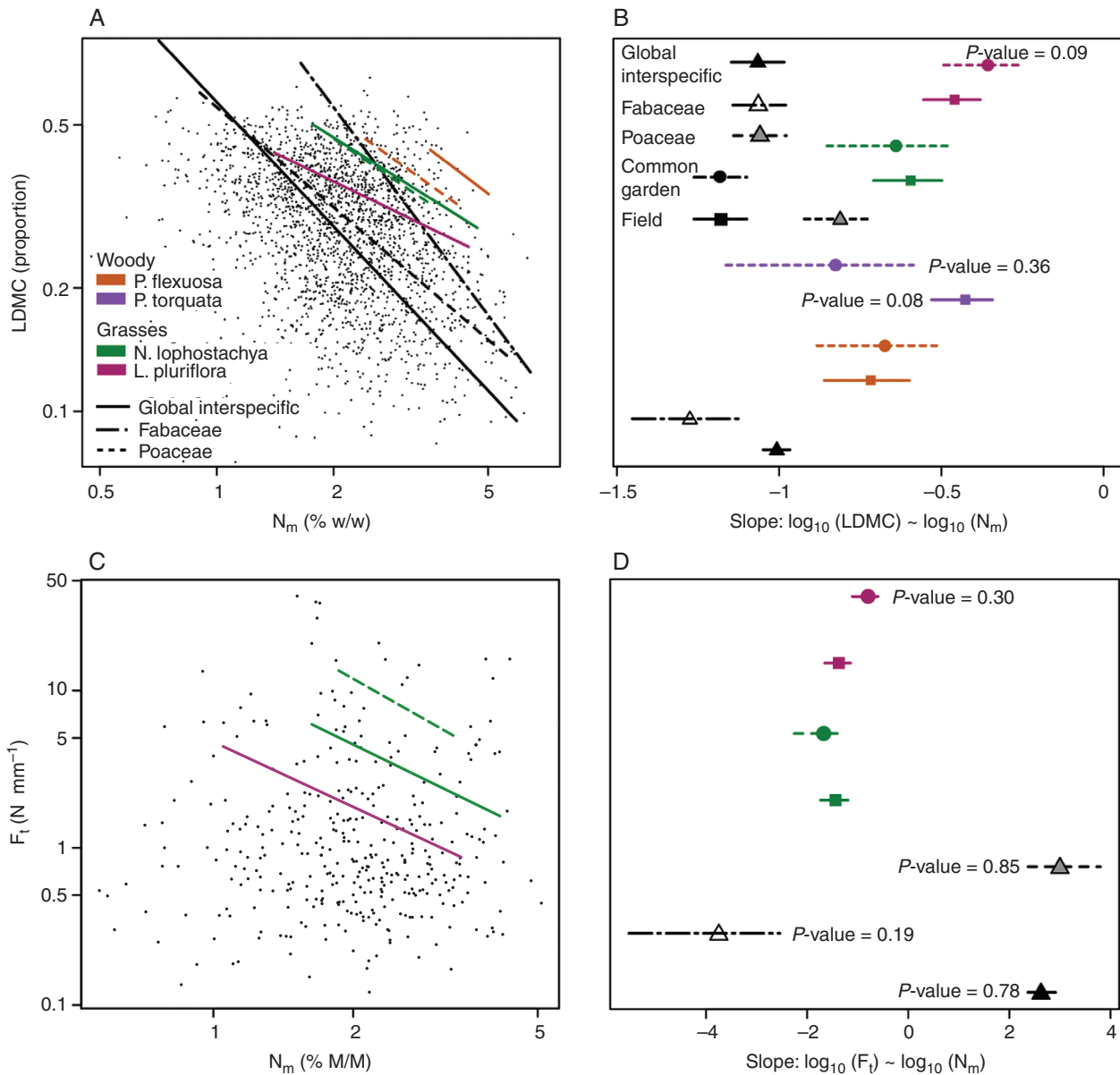
FIG. 3. Relationship between leaf dry matter content (LDMC), force to tear (F_t) and leaf nitrogen content (N_m). Different colours represent different species, continuous lines and squares represent the field condition, and dashed lines and circles represent the common garden condition. Black lines and dots show 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 and 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 in the right panel by reporting the corresponding *P*-value and it is not shown in the left panel. Results from multiple comparisons of the slopes 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.

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.*, 2010*a*; 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 such as 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 proposed (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 is the 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.*, 2006*a*), and the log–log relationship should have a slope equal to –1. While, the less steep the negative slope, the less nitrogen there 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 nitrogen 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 nitrogen content of the cell wall ($N_{cyt}:N_{wall}$) is greater in grasses than in legumes.

The acquisitive–conservative axis (and its variants, such as 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 already been 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 strongly suggests that natural selection, while clearly modulating this pattern (e.g. Wright *et al.*, 2005*b*), 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.*, 2006*a*; 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 covariation among traits) have higher adaptive value (Damián *et al.*, 2020) and therefore are selected for. However, different types of pleiotropy (Paaby and Rockman, 2013; Geiler-Samerotte *et al.*, 2020) could also explain the covariation pattern even if no selective advantage arises from integrated phenotypes. An experimental design combining both theoretical frameworks could shed 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.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. 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 and the intraspecific variability. Figure S3: Fisher's *z* effect size for all correlations among leaf functional traits. Figure S4: relationship between force to tear and leaf dry matter content as well as specific leaf area and nitrogen content per leaf mass. Figure S5: SMA slopes of the relationship between force to tear, leaf dry matter content and specific leaf area, from plants in the field and from genetic families in the common garden. 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 covariation patterns of leaf functional traits. Table S2: full botanical names of the studied species. Table S3: correlation coefficient for each pair of leaf functional traits in each species and condition. Table S4: slopes of $\log_{10}(LDMC) \sim \log_{10}(SLA)$ for each species and condition and groups resulting from multiple comparison test. Table S5: slopes of $\log_{10}(F_t) \sim \log_{10}(SLA)$ for each species and condition and groups resulting from multiple comparison test. Table S6: slopes of $\log_{10}(LDMC) \sim \log_{10}(SLA)$ for each species and condition and groups resulting from multiple comparison test. Table S7: slopes of $\log_{10}(F_t) \sim \log_{10}(SLA)$ for each species and condition and groups resulting from multiple comparison test. Table S8: slopes of $\log_{10}(LDMC) \sim \log_{10}(N_m)$ for each species and condition and groups resulting from multiple comparison test. Table S9: slopes of $\log_{10}(N_m) \sim \log_{10}(SLA)$ for each species and condition and groups resulting from multiple comparison test.

DATA ACCESSIBILITY

The original datasets of leaf functional traits from grasses and woody legumes, both in the field and in the common garden are available at http://hdl.handle.net/11086/17167.

LITERATURE CITED

Adams MA, Turnbull TL, Sprent JI, Buchmann N. 2016. Legumes are different: leaf nitrogen, photosynthesis, and water use efficiency. *Proceedings of the National Academy of Sciences, USA* **113**: 4098–4103.

Adler PB, Milchunas DG, Lauenroth WK, Sala OE, Burke IC. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* **41**: 653–663.

Adler PB, Salguero-Gómez R, Compagnoni A, *et al.* **2014.** Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences, USA* **111**: 740–745.

Adriaenssens S. 2012. *Dry deposition and canopy exchange for temperate tree species under high nitrogen deposition*. PhD thesis, Ghent University, Belgium.

Albert CH, Thuiller W, Yoccoz NG, Douzet R, Aubert S, Lavorel S. 2010*a***.** A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology* **24**: 1192–1201.

Albert CH, Thuiller W, Yoccoz NG, *et al.* **2010***b***.** Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology* **98**: 604–613.

Anderegg LDL, Berner LT, Badgley G, Sethi ML, Law BE, HilleRisLambers J. 2018. Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters* **21**: 734–744.

de Araujo AC, Ometto JPHB, Dolman AJ, Kruijt B, Waterloo MJ, Ehleringer JR. 2011. LBA-ECO CD-02 C and N isotopes in leaves and atmospheric CO2, Amazonas, Brazil. Data set. Oak Ridge, TN: Oak Ridge National Laboratory Distributed Active Archive Center. http://daac.ornl.gov.

Atkin OK, Westbeek MHM, Cambridge ML, Lambers H, Pons TL. 1997. Leaf respiration in light and darkness. A comparison of slow- and fast-growing *Poa* species. *Plant Physiology* **113**: 961–965.

Atkin OK, Schortemeyer M, McFarlane N, Evans JR. 1999. The response of fast- and slow-growing *Acacia* species to elevated atmospheric CO2: an analysis of the underlying components of relative growth rate. *Oecologia* **120**: 544–554.

Atkin OK, Bloomfield KJ, Reich PB, *et al.* **2015.** Global variability in leaf respiration among plant functional types in relation to climate and leaf traits. *New Phytologist* **206**: 614–636.

Auger S, Shipley B. 2013. Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science* **24**: 419–428.

Baraloto C, Paine CET, Poorter L, *et al.* **2010.** Decoupled leaf and stem economics in rainforest trees. *Ecology Letters* **13**: 1338–1347.

Bateman A. 1947. Contamination in seed crops. III. Relation with isolation distance. *Heredity* **1**: 235–246.

Beckmann M, Hock M, Bruelheide H, Erfmeier A. 2012. The role of UV-B radiation in the invasion of *Hieracium pilosella*—a comparison of German and New Zealand plants. *Environmental and Experimental Botany* **75**: 173–180.

Bessega C, Ferreyra L, Julio N, Montoya S, Saidman B, Vilardi JC. 2000. Mating system parameters in species of genus *Prosopis* (Leguminosae). *Hereditas* **132**: 19–27.

Bessega C, Saidman BO, Vilardi JC. 2005. Genetic relationships among American species of *Prosopis* (Leguminosae) based on enzyme markers. *Genetics and Molecular Biology* **28**: 277–286.

Blonder B, Violle C, Bentley LP, Enquist BJ. 2011. Venation networks and the origin of the leaf economics spectrum. *Ecology Letters* **14**: 91–100.

Blonder B, Buzzard B, Sloat L, *et al.* **2012.** The shrinkage effect biases estimates of paleoclimate. *American Journal of Botany* **99**: 1756–1763.

Blonder B, Violle C, Enquist BJ. 2013. Assessing the causes and scales of the leaf economics spectrum using venation networks in *Populus tremuloides*. *Journal of Ecology* **101**: 981–989.

Blonder B, Vasseur F, Violle C, Shipley B, Enquist BJ, Vile D. 2015. Testing models for the leaf economics spectrum with leaf and whole-plant traits in *Arabidopsis thaliana*. *AoB Plants* **7**: plv049. doi: 10.1093/aobpla/plv049.

Blonder B, Baldwin B, Enquist BJ, Robichaux RH. 2016. Variation and macroevolution in leaf functional traits in the Hawaiian silversword alliance (Asteraceae). *Journal of Ecology* **104**: 219–228.

Boucher FC, Thuiller W, Arnoldi C, Albert CH, Lavergne S. 2013. Unravelling the architecture of functional variability in wild populations of *Polygonum viviparum* L. *Functional Ecology* **27**: 382–391.

Butcher P, Moran G, Perkins H. 1998. RFLP diversity in the nuclear genome of *Acacia mangium*. *Heredity* **81**: 205–213.

Butterfield BJ, Briggs JM. 2011. Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia* **165**: 477–487.

Cabido MR, González C, Acosta A, Díaz S. 1993. Vegetation changes along a precipitation gradient in Central Argentina. *Vegetatio* **109**: 5–14.

Cabido MR, Manzur A, Carranza L, González Albarracín C. 1994. La vegetación y el medio físico del Chaco Árido en la provincia de Córdoba, Argentina Central. *Phytocoenologia* **24**: 423–460.

Caisse M, Antonovics J. 1978. Evolution in closely adjacent plant populations. Evolution of reproductive isolation in clinal populations. *Heredity* **40**: 371–384.

Campbell C, Atkinson L, Zaragoza-Castells J, Lundmark M, Atkin O, Hurry V. 2007. Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *New Phytologist* **176**: 375–389.

Campetella G, Botta-Dukát Z, Wellstein C, *et al.* 2011. Patterns of plant trait–environment relationships along a forest succession chronosequence. *Agriculture, Ecosystems & Environment* **145**: 38–48.

Casiva PV, Vilardi JC, Cialdella AM, Saidman BO. 2004. Mating system and population structure of *Acacia aroma* and *A. macracantha* (Fabaceae). *American Journal of Botany* **91**: 58–64.

Castro-Diez P, Puyravaud JP, Cornelissen JHC. 2000. Leaf structure and anatomy as related to leaf mass per area variation in seedlings of a wide range of woody plant species and types. *Oecologia* **124**: 476–486.

Cavender-Bares J, Keen A, Miles B. 2006. Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology* **87**: S109–S122.

Chacón-Madrigal E, Wanek W, Hietz P, Dullinger S. 2018. Traits indicating a conservative resource strategy are weakly related to narrow range size in a group of neotropical trees. *Perspectives in Plant Ecology, Evolution and Systematics* **32**: 30–37.

Chen Y, Han W, Tang L, Tang Z, Fang J. 2011. Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form. *Ecography* **36**: 178–184.

Choat B, Jansen S, Brodribb TJ, *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752–755.

Ciccarelli D. 2015. Mediterranean coastal dune vegetation: are disturbance and stress the key selective forces that drive the psammophilous succession? *Estuarine, Coastal and Shelf Science* **165**: 247–253.

Cornelissen JHC. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology* **84**: 573–582.

Cornelissen JHC, Diez PC, Hunt R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology* **84**: 755–765.

Cornelissen JHC, Perez-Harguindeguy N, Diaz S, *et al.* 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist* **143**: 191–200.

Cornelissen JHC, Cerabolini B, Castro-Diez P, *et al.* 2003. Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science* **14**: 311–322.

Cornelissen JHC, Quested HM, Gwynn-Jones D, *et al.* 2004. Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology* **18**: 779–786.

Cornwell WK, Cornelissen JHC, Dorrepaal E, *et al.* 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**: 1065–1071.

Craine JM, Lee WG, Bond WJ, Williams RJ, Johnson LC. 2005. Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology* **86**: 12–19.

Craine JM, Elmore AJ, Aidar MPM, *et al.* 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytologist* **183**: 980–992.

Craine JM, Nippert JB, Towne EG, *et al.* 2011. Functional consequences of climate-change induced plant species loss in a tallgrass prairie. *Oecologia* **165**: 1109–1117.

Craine JM, Towne EG, Ocheltree TW, Nippert JB. 2012. Community traitscape of foliar nitrogen isotopes reveals N availability patterns in a tallgrass prairie. *Plant and Soil* **356**: 395–403.

Craine JM, Ocheltree TW, Nippert JB, *et al.* 2013. Global diversity of drought tolerance and grassland climate-change resilience. *Nature Climate Change* **3**: 63–67.

Craven D, Braden D, Ashton MS, Berlyn GP, Wishnie M, Dent D. 2007. Between and within-site comparisons of structural and physiological characteristics and foliar nutrient content of 14 tree species at a wet, fertile site and a dry, infertile site in Panama. *Forest Ecology and Management* **238**: 335–346.

Dahlin KM, Asner GP, Field CB. 2013. Environmental and community controls on plant canopy chemistry in a Mediterranean-type ecosystem. *Proceedings of the National Academy of Sciences, USA* **110**: 6895–6900.

Damián X, Ochoa López S, Gaxiola A, Fornoni J, Domínguez CA, Boege K. 2020. Natural selection acting on integrated phenotypes: covariance among functional leaf traits increases plant fitness. *New Phytologist* **225**: 546–557.

Demey A, Staelens J, Baeten L, *et al.* 2013. Nutrient input from hemiparasitic litter favors plant species with a fast-growth strategy. *Plant and Soil* **371**: 53–66.

De Vries F, Bardgett RD. 2016. Plant community controls on short-term ecosystem nitrogen retention. *New Phytologist* **210**: 861–874.

Díaz S, Hodgson JG, Thompson K, *et al.* 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.

Díaz S, Kattge J, Cornelissen JHC, *et al.* 2016. The global spectrum of plant form and function. *Nature* **529**: 167–171.

Donovan LA, Maherali H, Caruso CM, Huber H, de Kroon H. 2011. The evolution of the worldwide leaf economics spectrum. *Trends in Ecology & Evolution* **26**: 88–95.

Fajardo A, Siefert A. 2018. Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. *Ecology* **99**: 1024–1030.

Fick SE, Hijmans RJ. 2017. Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**: 4302–4315.

Fisher RA. 1925. *Statistical methods for research workers*. Edinburgh: Oliver & Boyd.

Fitter AH, Peat HJ. 1994. The ecological Flora database. *Journal of Ecology* **82**: 415–425.

Frenette-Dussault C, Shipley B, Léger JF, Meziane D, Hingrat Y. 2012. Functional structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory. *Journal of Vegetation Science* **23**: 208–222.

Freschet GT, Cornelissen JHC, van Logtestijn RSP, Aerts R. 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology* **98**: 362–373.

Funk JL, Larson JE, Ames GM, *et al.* 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews* **92**: 1156–1173.

Garnier E, Cortez J, Billès G, *et al.* 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630–2637.

Geiler-Samerotte KA, Li S, Lazaris C, *et al.* 2020. Extent and context dependence of pleiotropy revealed by high-throughput single-cell phenotyping. *PLoS Biology* **18**: e3000836. doi: 10.1371/journal.pbio.3000836.

Givnish TJ, Montgomery RA, Goldstein G. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. *American Journal of Botany* **91**: 228–246.

Gos P, Loucougaray G, Colace MP, *et al.* 2016. Relative contribution of soil, management and traits to co-variations of multiple ecosystem properties in grasslands. *Oecologia* **180**: 1001–1013.

Griffiths DJ. 1950. The liability of seed crops of perennial ryegrass (*Lolium perenne*) to contamination by wind-borne pollen. *Journal of Agricultural Science* **40**: 19–38.

Grime JP. 2001. *Plant strategies, vegetation processes, and ecosystem properties.* Chichester: John Wiley & Sons Ltd.

Grubb PJ. 2016. Trade-offs in interspecific comparisons in plant ecology and how plants overcome proposed constraints. *Plant Ecology and Diversity* **9**: 3–33.

Gutiérrez AG, Huth A. 2012. Successional stages of primary temperate rain-forests of Chiloé Island, Chile. *Perspectives in Plant Ecology, Systematics and Evolution* **14**: 243–256.

Guy AL, Mischkolz JM, Lamb EG. 2013. Limited effects of simulated acidic deposition on seedling survivorship and root morphology of endemic plant taxa of the Athabasca Sand Dunes in well watered greenhouse trials. *Botany* **91**: 176–181.

Han W, Chen Y, Zhao FJ, Tang L, Jiang R, Zhang F. 2012. Floral, climatic and soil pH controls on leaf ash content in China's terrestrial plants. *Global Ecology and Biogeography* **21**: 376–382.

Hayes FJ, Buchanan SW, Coleman B, *et al.* 2019. Intraspecific variation in soy across the leaf economics spectrum. *Annals of Botany* **123**: 107–120.

Hidaka A, Kitayama K. 2011. Allocation of foliar phosphorus fractions and leaf traits of tropical tree species in response to decreased soil phosphorus availability on Mount Kinabalu, Borneo. *Journal of Ecology* **99**: 849–857.

Hu Y-K, Pan X, Liu G-F, *et al.* 2015. Novel evidence for within-species leaf economics spectrum at multiple spatial scales. *Frontiers in Plant Science* **6**: 901. doi: 10.3389/fpls.2015.00901.

Jackson BG, Peltzer DA, Wardle DA. 2013. The within-species leaf economic spectrum does not predict leaf litter decomposability at either the within-species or whole community levels. *Journal of Ecology* **101**: 1409–1419.

Jain S, Bradshaw A. 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity* **21**: 407–441.

Joseph GS, Seymour CL, Cumming GS, Cumming DHM, Mahlangu Z. 2014. Termite mounds increase functional diversity of woody plants in African savannas. *Ecosystems* **17**: 808–819.

Kattge J, Knorr W, Raddatz T, Wirth C. 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology* **15**: 976–991.

Kattge J, Díaz S, Lavorel S, *et al.* 2011. TRY – a global database of plant traits. *Global Change Biology* **17**: 2905–2935.

Kazakou E, Vile D, Shipley B, Gallet C, Garnier E. 2006. Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology* **20**: 21–30.

Kerkhoff AJ, Fagan WF, Elser JJ, Enquist BJ. 2006. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *The American Naturalist* **168**: E103–E122.

Kichenin E, Wardle DA, Peltzer DA, Morse CW, Freschet GT. 2013. Contrasting effects of plant inter and intraspecific variation on community level trait measures along an environmental gradient. *Functional Ecology* **27**: 1254–1261.

Kitajima K, Llorens A-M, Stefanescu C, *et al.* 2012. How cellulose-based leaf toughness and lamina density contribute to long leaf lifespans of shade-tolerant species. *New Phytologist* **195**: 640–652.

Kleyer M, Bekker RM, Knevel IC, *et al.* 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* **96**: 1266–1274.

Kraft NJB, Valencia R, Ackerly D. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* **322**: 580–582.

La Pierre KJ, Smith MD. 2015. Functional trait expression of grassland species shift with short- and long-term nutrient additions. *Plant Ecology* **216**: 307–318.

Laughlin DC, Leppert JJ, Moore MM, Sieg CH. 2010. A multi-trait test of the leaf–height–seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* **24**: 493–501.

Laughlin DC, Fule PZ, Huffman DW, Crouse J, Laliberte E. 2011. Climatic constraints on trait-based forest assembly. *Journal of Ecology* **99**: 1489–1499.

Lhotsky B, Csecserits A, Kovács B, Botta-Dukát Z. 2016. New plant trait records of the Hungarian flora. *Acta Botanica Hungarica* **58**: 397–400.

Li R, Zhu S, Chen HYH, *et al.* 2015. Are functional traits a good predictor of global change impacts on tree species abundance dynamics in a subtropical forest? *Ecology Letters* **18**: 1181–1189.

Louault F, Pillar VD, Aufrere J, Garnier E, Soussana JF. 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science* **16**: 151–160.

Loveys BR, Atkinson LJ, Sherlock DJ, Roberts RL, Fitter AH, Atkin OK. 2003. Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. *Global Change Biology* **9**: 895–910.

Lukeš P, Stenberg P, Rautiainen M, Mõttus M, Vanhatalo KM. 2013. Optical properties of leaves and needles for boreal tree species in Europe. *Remote Sensing Letters* **4**: 667–676.

Maire V, Wright IJ, Prentice IC, *et al.* 2015. Global soil and climate effects on leaf photosynthetic traits and rates. *Global Ecology and Biogeography* **24**: 706–717.

Martin AR, Rapidel B, Roupsard O, *et al.* 2017. Intraspecific trait variation across multiple scales: the leaf economics spectrum in coffee. *Functional Ecology* **31**: 604–612.

Martinez-Garza C, Bongers F, Poorter L. 2013. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *Forest Ecology and Management* **303**: 35–45.

McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21**: 178–85.

Medlyn BE, Badeck FW, De Pury DGG, *et al.* 1999. Effects of elevated CO_2 on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell & Environment* **22**: 1475–1495.

Meir P, Kruijt B, Broadmeadow M, Kull O, Carswell F, Nobre A. 2002. Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. *Plant, Cell & Environment* **25**: 343–357.

Meir P, Levy PE. 2007. Photosynthetic parameters from two contrasting woody vegetation types in West Africa. *Plant Ecology* **192**: 277–287.

Messier J, McGill BJ, Lechowicz MJ. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**: 838–848.

Messier J, McGill BJ, Enquist BJ, Lechowicz MJ. 2017. Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography* **40**: 685–697.

Meziane D, Shipley B. 1999. Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. *Plant, Cell & Environment* **22**: 447–459.

Michaletz ST, Johnson EA. 2006. A heat transfer model of crown scorch in forest fires. *Canadian Journal of Forest Research* **36**: 2839–2851.

Milla R, Reich PB. 2011. Multi-trait interactions, not phylogeny, fine-tune leaf size reduction with increasing altitude. *Annals of Botany* **107**: 455–465.

Minden V, Kleyer M. 2014. Internal and external regulation of plant organ stoichiometry. *Plant Biology* **16**: 897–907.

Minden V, Kleyer M. 2015. Ecosystem multifunctionality of coastal marshes is determined by key plant traits. *Journal of Vegetation Science* **26**: 651–662.

Minden V, Andratschke S, Spalke J, Timmermann H, Kleyer M. 2012. Plant trait–environment relationships in salt marshes: deviations from predictions by ecological concepts. *Perspectives in Plant Ecology, Evolution and Systematics* **14**: 183–192.

Moles AT, Perkins SE, Laffan SW, *et al.* 2014. Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science* **25**: 1167–1180.

Muir CD, Hangarter RP, Moyle LC, Davis PA. 2014. Morphological and anatomical determinants of mesophyll conductance in wild relatives of tomato (Solanum sect. Lycopersicon, sect. Lycopersicoides; Solanaceae). *Plant, Cell & Environment* **37**: 1415–1426.

Niinemets Ü. 2015. Is there a species spectrum within the world-wide leaf economics spectrum? Major variations in leaf functional traits in the mediterranean sclerophyll *Quercus ilex*. *New Phytologist* **205**: 79–96.

Onoda Y, Westoby M, Adler PB, *et al.* 2011. Global patterns of leaf mechanical properties. *Ecology Letters* **14**: 301–312.

Onoda Y, Wright IJ, Evans JR, *et al.* 2017. Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytologist* **214**: 1447–1463.

Ordonez JC, van Bodegom PM, Witte JPM, Bartholomeus RP, van Hal JR, Aerts R. 2010. Plant strategies in relation to resource supply in mesic to wet environments: does theory mirror nature? *The American Naturalist* **175**: 225–239.

Ordoñez JC, van Bodegom PM, Witte J-PM, Wright IJ, Reich PB, Aerts R. 2009. A global study of relationships between leaf traits, climate

and soil measures of nutrient fertility. *Global Ecology and Biogeography* **18**: 137–149.

Paaby AB, Rockman MV. 2013. The many faces of pleiotropy. *Trends in Genetics* **29**: 66–73.

Pérez-Harguindeguy N, Díaz S, Garnier E, *et al.* 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167–234.

Pigliucci M. 2003. Phenotypic integration: studying the ecology and evolution of complex phenotypes. *Ecology Letters* **6**: 265–272.

van der Plas F, Olff H. 2014. Mesoherbivores affect grasshopper communities in a megaherbivore-dominated South African savannah. *Oecologia* **175**: 639–649.

Powers JS, Tiffin P. 2012. Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. *Functional Ecology* **24**: 927–936.

Prentice IC, Meng T, Wang H, Harrison SP, Ni J, Wang G. 2011. Evidence for a universal scaling relationship of leaf CO_2 drawdown along an aridity gradient. *New Phytologist* **190**: 169–180.

Preston KA, Cornwell WK, DeNoyer JL. 2006. Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist* **170**: 807–818.

Price CA, Enquist BJ. 2007. Scaling of mass and morphology in Dicotyledonous leaves: an extension of the WBE model. *Ecology* **88**: 1132–1141.

Pyankov VI, Kondratchuk AV, Shipley B. 1999. Leaf structure and specific leaf mass: the alpine desert plants of the Eastern Pamirs, Tadjikistan. *New Phytologist* **143**: 131–142.

Quested HM, Cornelissen JHC, Press MC, *et al.* 2003. Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology* **84**: 3209–3221.

R Core Team. 2019. *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Reich PB. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.

Reich PB, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences, USA* **101**: 11001–11006.

Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* **94**: 13730–13734.

Richardson SJ, Allen RB, Buxton RP, *et al.* 2013. Intraspecific relationships among wood density, leaf structural traits and environment in four co-occurring species of *Nothofagus* in New Zealand. *PLoS One* **8**: 24–26.

Roderick ML, Berry SL, Saunders AR, Noble IR. 1999. On the relationship between the composition, morphology and function of leaves. *Functional Ecology* **13**: 696–710.

Rolo V, López-Díaz ML, Moreno G. 2012. Shrubs affect soil nutrients availability with contrasting consequences for pasture understory and tree overstory production and nutrient status in Mediterranean grazed open woodlands. *Nutrient Cycling in Agroecosystems* **93**: 89–102.

Saidman BO, Vilardi JC. 1993. Genetic variability and germplasm conservación in the genus Prosopis. In: Puri S, Khosla PK, eds. *Nursery technology for agroforestry applications in arid and semiarid regions.* New Delhi: Oxford & IBH publishing Co. PVT. LTD, 187–198. .

Sandel B, Corbin JD, Krupa M. 2011. Using plant functional traits to guide restoration: a case study in California coastal grassland. *Ecosphere* **2**: doi: 10.1890/ES10-00175.1.

Sartori K, Vasseur F, Violle C, *et al.* 2019. Leaf economics and slow–fast adaptation across the geographic range of *Arabidopsis thaliana*. *Scientific Reports* **9**: 10758. doi: 10.1038/s41598-019-46878-2.

Scherer-Lorenzen M, Schulze ED, Don A, Schumacher J, Weller E. 2007. Exploring the functional significance of forest diversity: a new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology, Evolution and Systematics* **9**: 53–70.

Schroeder-Georgi T, Wirth C, Nadrowski K, Meyer ST, Mommer L, Weigelt A. 2016. From pots to plots: hierarchical trait-based prediction of plant performance in a mesic grassland. *Journal of Ecology* **104**: 206–218.

Seymour CL, Milewski AV, Mills AJ, *et al.* 2014. Do the large termite mounds of macrotermes concentrate micronutrients in addition to macronutrients in nutrient-poor African savannas? *Soil Biology and Biochemistry* **68**: 95–105.

Sheremetev SN. 2005. *Herbs on the soil moisture gradient (water relations and the structural–functional organization).* Moscow: KMK.

Sherrard ME, Maherali H, Latta RG. 2009. Water stress alters the genetic architecture of functional traits associated with drought adaptation in *Avena barbata*. *Evolution* **63**: 702–715.

Shiodera S, Rahajoe JS, Kohyama T. 2008. Variation in longevity and traits of leaves among co-occurring understorey plants in a tropical montane forest. *Journal of Tropical Ecology* **24**: 121–133.

Shipley B. 1995. Structured interspecific determinants of specific leaf-area in 34 species of herbaceous angiosperms. *Functional Ecology* **9**: 312–319.

Shipley B. 2002. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. *Functional Ecology* **16**: 682–689.

Shipley B. 2015. Describing, explaining and predicting community assembly: a convincing trait-based case study. *Journal of Vegetation Science* **26**: 615–616.

Shipley B, Lechowicz MJ. 2000. The functional co-ordination of leaf morphology, nitrogen concentration, and gas exchange in 40 wetland species. *Ecoscience* **7**: 183–194.

Shipley B, Vu TT. 2002. Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytologist* **153**: 359–364.

Shipley B, Lechowicz MJ, Wright IJ, Reich PB. 2006*a*. Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology* **87**: 535–541.

Shipley B, Vile D, Garnier E. 2006*b*. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science* **314**: 812–814.

Šidák Z. 1967. Rectangular confidence regions for the means of multivariate normal distributions. *Journal of the American Statistical Association* **62**: 626–633.

Siefert A, Fridley JD, Ritchie ME. 2014. Community functional responses to soil and climate at multiple spatial scales: when does intraspecific variation matter? *PLoS One* **9**: e111189. doi: 10.1371/journal.pone.0111189.

Siefert A, Violle C, Chalmandrier L, *et al.* 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**: 1406–1419.

Slot M, Rey-Sanchez C, Winter K, Kitajima K. 2014. Trait-based scaling of temperature-dependent foliar respiration in a species-rich tropical forest canopy. *Functional Ecology* **28**: 1074–1086.

Smith SW, Woodin SJ, Pakeman RJ, Johnson D, van der Wal R. 2014. Root traits predict decomposition across a landscape-scale grazing experiment. *New Phytologist* **203**: 861–862.

Sparks DL, Page AL, Helmke PA, *et al.*, eds. 1996. *Methods of soil analysis, part 3, chemical methods*, 3rd edn. Madison, WI: Soil Science Society of America, American Society of Agronomy.

Spasojevic MJ, Suding KN. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* **100**: 652–661.

Suding KN, Lavorel S, Chapin FS, *et al.* 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* **14**: 1125–1140.

Swaine EK. 2007. *Ecological and evolutionary drivers of plant community assembly in a Bornean rain forest.* PhD Thesis, University of Aberdeen, Aberdeen, UK.

Takkis K. 2014. *Changes in plant species richness and population performance in response to habitat loss and fragmentation.* PhD Thesis, Universitatis Tartuensis, Estonia.

Tribouillois H, Fort F, Cruz P, *et al.* 2015. A functional characterisation of a wide range of cover crop species: growth and nitrogen acquisition rates, leaf traits and ecological strategies. *PLoS One* **10**: e0122156. doi: 10.1371/journal.pone.0122156.

Tucker SS, Craine JM, Nippert JB. 2011. Physiological drought tolerance and the structuring of tallgrass assemblages. *Ecosphere* **2**: 48. doi: 10.1890/ES11-00023.1.

Vasseur F, Violle C, Enquist BJ, Granier C, Vile D. 2012. A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecology Letters* **15**: 1149–1157.

Vergutz L, Manzoni S, Porporato A, Novais RF, Jackson RB. 2012. *A global database of carbon and nutrient concentrations of green and senesced leaves. Data set.* Oak Ridge, TN: Oak Ridge National Laboratory Distributed Active Archive Center. doi: 10.3334/ORNLDAAC/1106.

Viechtbauer W. 2010. Conducting meta-analyses in R with the meta for package. *Journal of Statistical Software* **36**: 48. doi: 10.18637/jss.v036.i03.

Vilardi JC, Saidman BO, Palacios R. 1988. *Muestreo Según Variabilidad. Prosopis en Argentina. Primer taller internacional sobre recurso genético y conservación de germoplasma en Prosopis.* Beunos Aires: UNC-FAO, 119–124.

Vile D. 2005. *Significations fonctionnelle et ecologique des traits des especes vegetales: exemple dans une succession post-cultural mediterraneenne et generalisations*. PhD Thesis, University of Montpellier, France.

Vile D, Garnier E, Shipley B, *et al.* **2005.** Specific leaf area and dry matter content estimate thickness in laminar leaves. *Annals of Botany* **96**: 1129–1136.

Violle C, Navas M-L, Vile D, *et al.* **2007.** Let the concept of trait be functional! *Oikos* **116**: 882–892.

Walker AP. 2014. *A global data set of leaf photosynthetic rates, leaf N and P, and specific leaf area*. Data set. http://daac.ornl.gov. Oak Ridge, TN: Oak Ridge National Laboratory Distributed Active Archive Center. doi: 10.3334/ORNLDAAC/1224.

Warton DI, Wright IJ, Falster DS, Westoby M. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* **81**: 259–291.

Warton DI, Duursma RA, Falster DS, Taskinen S. 2012. smatr 3 – an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution* **3**: 257–259.

Warton DI, Shipley B, Hastie T. 2015. CATS regression – a model-based approach to studying trait-based community assembly. *Methods in Ecology and Evolution* **6**: 389–398.

van de Weg MJ, Meir P, Grace J, Atkin O. 2009. Altitudinal variation in leaf mass per unit area, leaf tissue density and foliar nitrogen and phosphorus content along the Amazon–Andes gradient in Peru. *Plant Ecology & Diversity* **2**: 243–254.

van de Weg MJ, Meir P, Grace J, Ramos GD. 2011. Photosynthetic parameters, dark respiration and leaf traits in the canopy of a Peruvian tropical montane cloud forest. *Oecologia* **168**: 23–34.

Wei-min D, Ke-qin Z, Bin-wu D, *et al.* **2005.** Rapid determination of silicon content in rice. *Rice Science* **12**: 145–147.

White MA, Thornton PE, Running SM, Nemani RR. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interactions* **4**: 3. doi: 10.1175/1087–3562(2000)004<0003:PASAOT>2.0.CO;2.

Williams M, Shimabokuro YE, Rastetter EB. 2012. *LBA-ECO CD-09 Soil and vegetation characteristics, Tapajos National Forest, Brazil*. Data set. Oak Ridge, TN: Oak Ridge National Laboratory Distributed Active Archive Center. http://daac.ornl.gov. doi: 10.3334/ORNLDAAC/1104.

Wilson K, Baldocchi D, Hanson P. 2000. Spatial and seasonal variability of photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiology* **20**: 565–578.

Wirth C, Lichstein JW. 2009. The imprint of species turnover on old-growth forest carbon balances – insights from a trait-based model of forest dynamics. In: Wirth C, Gleixner G, Heimann M, eds. *Old-growth forests: function, fate and value*. New York: Springer, 81–113.

Wright IJ, Reich PB, Westoby M, *et al.* **2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Wright IJ, Reich PB, Cornelissen JHC, *et al.* **2005a.** Assessing the generality of leaf trait of global relationships. *New Phytologist* **166**: 485–496.

Wright IJ, Reich PB, Cornelissen JHC, *et al.* **2005b.** Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* **14**: 411–421.

Wright JP, Sutton-Grier A. 2012. Does the leaf economic spectrum hold within local species pools across varying environmental conditions? *Functional Ecology* **26**: 1390–1398.

Xiong D, Flexas J. 2018. Leaf economics spectrum in rice: leaf anatomical, biochemical, and physiological trait trade-offs. *Journal of Experimental Botany* **69**: 5599–5609.

Xu LK, Baldocchi DD. 2003. Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature. *Tree Physiology* **23**: 865–877.

Yguel B, Bailey R, Tosh ND, *et al.* **2011.** Phytophagy on phylogenetically isolated trees: why hosts should escape their relatives. *Ecology Letters* **14**: 1117–1124.

Yu Q, Elser JJ, He N, *et al.* **2011.** Stoichiometric homeostasis of vascular plants in the Inner Mongolia grassland. *Oecologia* **166**: 1–10.