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Title: The leaf economics spectrum emerges at the intraspecific level even under homogenous environmental conditions

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Running title: The persistence of the leaf economics spectrum in homogeneous conditions

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Abstract

- Background and Aims: The leaf economics spectrum (LES), a general trait covariation pattern that captures the balance between leaf construction costs and growth potential in vascular plants, has been extensively explored at the interspecific level. However, studies at the intraspecific level are much scarcer and have mostly dealt with variation in response to environmental gradients. Little work has been published on the relative roles of environmental and genetic variation in determining intraspecific trait covariation.

- Methods: We analyzed the covariation of four key traits involved in the LES (specific leaf area, leaf dry matter content, force to tear, and leaf nitrogen content) in 10 species common in the seasonally dry Chaco forest of Central Argentina, growing in the field and in a common garden. We then compared trait covariation at the local intraspecific level with global covariation at the interspecific level, using available data from the TRY global trait database.

- Key Results: We found that the general pattern of intraspecific covariation—both in the field and in the common garden—is qualitatively similar to that in the global interspecific LES. At the same time, we found quantitative differences among the LES covariation patterns of different species, and between these and the global interspecific LES.

- Conclusions: This indicates that the LES emerges even in the absence of environmental variation. But, there might be different underlying causes determining the LES covariation pattern at different scales, from local populations to the global flora.

Key words: Leaf economics spectrum, intra-specific covariation, local population, common garden experiment, Fabaceae, Poaceae.

1 **Introduction**

2 The leaf economic spectrum (LES—Wright *et al.*, 2004) is a covariation pattern between leaf
3 traits related to resource use strategy. The involved traits have effects at multiple levels, from
4 individual plants to ecosystems (Reich *et al.*, 1997; Cornelissen *et al.*, 1999; Díaz *et al.*, 2004;
5 Wright *et al.*, 2004; Shipley *et al.*, 2006b; Cornwell *et al.*, 2008). The functional traits
6 involved in the LES are related by a common causal structure (Shipley *et al.*, 2006 *a*; Blonder
7 *et al.*, 2013; Onoda *et al.*, 2017), and most of the variation of such traits can be characterized
8 by a single axis. The position of any plant species on this axis is related with its resource use
9 strategy (Wright *et al.*, 2004) and describes a gradient from species with a fast recovery of
10 foliar investment and fast turnover of matter and energy, to species showing the opposite.
11 This gradient is manifested as a negative correlation between traits related to high net
12 assimilation rate per leaf mass such as specific leaf area (SLA) and leaf nitrogen content per
13 leaf mass (N_m) on the one hand, and traits related to long leaf lifespan, such as leaf structural
14 resistance and dry matter content (LDMC) on the other. Structural resistance is considered
15 one of the main causes of leaf lifespan variability (Wright *et al.*, 2004). Moreover, leaf
16 thickness, fiber content and density affect leaf lifespan via the structural resistance (Onoda *et al.*
17 *et al.*, 2011; Kitajima *et al.*, 2012). Leaf dry matter content has been proposed as a direct proxy
18 for the wall to cell volume ratio, which could be a key variable in the LES (Shipley *et al.*,
19 2006 *a*). In order to gain more insight about the origin of the LES, the present study analyses
20 the intraspecific pattern of covariation of leaf functional traits in six grasses and four woody
21 legumes, and compared them with the global interspecific LES.

22 The LES covariation pattern among traits can be considered an emergent property of a group
23 of leaves. It was originally observed within global databases of leaf traits from diverse taxa
24 collected at locations spanning broad environmental gradients (Reich *et al.*, 1997; Wright *et*

1 *al.*, 2004; Díaz *et al.*, 2004, 2016). An unresolved question is: How should this group of
2 leaves be to produce the LES pattern? Even if the mechanisms driving the LES are not
3 completely understood (Wright *et al.*, 2004; Shipley *et al.*, 2006a; Blonder *et al.*, 2011, 2013,
4 2015; Donovan *et al.*, 2011; Onoda *et al.*, 2017), all the proposed causal hypotheses are at the
5 level of the leaf, and are based on physical and physiological principles that determine
6 relations among traits, which should be independent from scale or level of organization. In
7 other words, the covariation pattern in the LES traits at the intraspecific level is expected to
8 mirror the global interspecific LES. Indeed, collections of leaves from different populations of
9 the same species across its range of distribution, usually show the canonical patterns (Albert
10 *et al.*, 2010a; Jackson *et al.*, 2013; Richardson *et al.*, 2013; Niinemets, 2015; Hu *et al.*, 2015;
11 but see Anderegg *et al.*, 2018). However, most of the studies analysing covariation of leaf
12 traits at the intraspecific level have focused on phenotypic variability across sites in relation to
13 environmental gradients such as precipitation, temperature, soil nutrients or elevation. At the
14 local scale, leaves from individuals of the same population of a species measured in the field
15 show a similar LES covariation pattern only sometimes (Blonder *et al.*, 2013; Hu *et al.*,
16 2015). So far, as far as we know, only the studies of Blonder *et al.* (2013) and Anderegg *et al.*
17 (2018) have raised the question of the biological scale at which the LES covariation pattern
18 emerges. They showed that the smaller the taxonomic level of analysis, the more variable the
19 covariation pattern (Anderegg *et al.*, 2018), but that the LES covariation pattern could emerge
20 even within a genet (Blonder *et al.*, 2013). May be additional evidence, which we do not
21 know, has been produced in plant breeding programs.

22 Whether the leaf trait covariation pattern at the intraspecific level reproduce the global
23 interspecific LES or not is a relevant question in at least three ways. First, it provides clues
24 about the organization level and scale at which the LES covariation pattern emerges (leaves

1 within an individual, local intraspecific, regional intraspecific, regional-global interspecific).

2 Second, it has been found that the global interspecific LES is a powerful concept to link

3 vegetation and ecosystem processes (Grime, 2001; Díaz *et al.*, 2004; Garnier *et al.*, 2004;

4 Suding *et al.*, 2008; Funk *et al.*, 2017), as well as to understand and predict plant community

5 changes (Shipley *et al.*, 2006 *b*; Shipley, 2015; Warton *et al.*, 2015). If the leaf trait

6 covariation pattern underlying the considerable intraspecific trait variability (now documented

7 by many authors, such as Albert *et al.*, 2010 *a* , *b*; Messier *et al.*, 2010; Siefert *et al.*, 2015)

8 does not mirror the global interspecific LES, it follows that the LES framework could not

9 integrate plant ecology across all organization levels. Third, it has profound evolutionary

10 implications. The product of leaf lifespan and assimilation rate gives the lifetime carbon gain,

11 and given the importance of carbon gain for fitness, there should be strong selection on these

12 traits to maximize lifetime carbon gain. However the global interspecific LES shows a trade-

13 off between these two traits (Kikuzawa, 1991; Kikuzawa *et al.*, 2013). If the intraspecific

14 pattern of covariation is qualitatively different from the global interspecific LES, i.e. if there

15 is no trade-off between assimilation rate-related traits and leaf lifespan-related traits, it should

16 be easier to evolve in the direction of improving the total leaf assimilation.

17 Despite all the progress in the LES theoretical framework, a number of fundamental questions

18 still remains. In the present study, we ask: (i) is the covariation pattern of LES traits at the

19 local population level consistent with the global interspecific LES?; and (ii) does this

20 canonical pattern still hold once environmental variability has been controlled? In order to

21 address these questions, we analysed the covariation of leaf functional traits in six grasses and

22 four woody legumes, and compared them with the global interspecific LES. We measured

23 these traits under two conditions: in the field in order to account for natural local intraspecific

24 variability (which is partially shaped by phenotypic plasticity), and in a common garden,

where the effects of phenotypic plasticity are homogenized and phenotypic differences should be mostly the expression of genetic variability (maternal effects cannot be ruled out).

Material and Methods

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). Field sampling area is approximately 25 km N to S and 10 km E to W, and there were no temperature, precipitation or altitude gradients. The climate is subtropical and semiarid (Cabido *et al.*, 1994) with a mean annual precipitation of 533 mm concentrated to spring–late summer (October – March) and a mean annual temperature of 18.07 °C (López Lauenstein *et al.*, 2012). Topography corresponds to an undulating plain. Soils vary from Torriorthents (Entisols order) to Camborthids ustolics (Aridisols order) (Cabido *et al.*, 1994). Vegetation corresponds to a 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 *Mimozyanthus carinatus*, *Senegalia gilliesii* and *Larrea divaricata*. Land use, logging and livestock grazing, produces a gradient from this primary forest to communities with less tree coverage and more bare soil (Cabido *et al.*, 1994).

We measured leaf traits of six perennial C₄ 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*). A species list with reference to their authorities is included in Table S1 [**Supplementary information**]. All

these species are common and often abundant in the different plant communities of the system (Cabido *et al.*, 1993, 1994).

In the study area, 39 to 49 sampling sites were selected for each species. For each species, sites 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 species (Vilardi *et al.*, 1988; Saidman and Vilardi, 1993; Butcher *et al.*, 1998; Bessega *et al.*, 2000, 2005; Casiva *et al.*, 2004). For grasses each site correspond to a group of three individuals of a given species with less than 20 m distance from each other. At each site we collected leaf samples from these three individuals. For woody species each site correspond to a single individual of a given species. At each site we collected two leaf samples of the outer canopy of one mature individual, one sample from the lowest branch and one sample from the highest one reachable (approximately 2m). Each sample consisted of at least three leaves. A total of 1172 leaf samples were analyzed from plants in the field (850 leaf samples from 850 grass individual plants and 322 leaf samples from 161 woody individual plants). All samples were processed independently and used to measure SLA ($\text{mm}^2 \text{mg}^{-1}$), LDMC (proportion), force to tear (F_t , N mm^{-1}) and N_m (%), following the protocols of Pérez-Harguindeguy *et al.* (2013). In woody species all measures were performed in the leaflets (excluding rachis). Force to tear 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 per leaf mass was measured using an Elementary Analyzer Perkin Elmer 2400 Series II (USA) for two species per group (grasses and woody species), selecting 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*.

From all sites, we collected seeds and produced seedlings in pots in a common garden at the National University of Córdoba, Argentina. For woody species seeds from a given site were all from a single mother plant, the same plant whose leaves were measured, so they constituted a maternal half-siblings family. In the case of grasses, seeds from a site were collected from several random plants so the resulting seedlings are not necessarily maternal half-siblings. Nevertheless, we treated the plants produced with seeds from the same site as “genetic families” for both woody and grasses. For all pots we used commercial potting soil. For grasses we used 0.79 L (10 cm diameter, 10 height) pots. For woody species we used 2.4 L (10 cm diameter, 30 cm height). All pots were weeded weekly during the growth season and monthly in winter. Herbivory by ants and aphids was controlled by applying insecticide when herbivores were detected. All plants were watered in short pulses (1 to 3 minutes) with sprinklers. Irrigation was adjusted weekly or more frequent to ensure keeping moisture in pots but no overwater. We successfully obtained seedlings from 28 to 40 sites per species. A year later after germination, we measured leaf traits of two to four plant individuals from each site for each species. A total of 1195 individual plants were analyzed in the common garden experiment. To this time grasses had reached maturity and reproduced sexually. On contrary, woody species were still juvenile.

We analysed the correlation between pairs of traits for each species, both in the field and in the common garden. We also compared the relation between pairs of traits among species and with the global interspecific LES pattern by performing pair-wise comparisons among the resulting slopes of the standardised major axis (SMA) regressions (Warton *et al.*, 2006). Standardised major axis regressions and slopes pairwise comparisons were made with with the R-package “*smatr 3*” (Warton *et al.*, 2012). P-values were adjusted using the Sidak correction. All variables were log-transformed to achieve normality and homoscedasticity

1 across the whole dataset. For multiple comparison tests among slopes, only groups with
2 significant correlation between traits were included. Additionally, in the common garden
3 experiment, in the case of traits for which several measurements were taken per genetic
4 family (SLA, LDMC, F_t), we performed the same analysis for genetic families, to assess the
5 genetic correlation between traits. All analyses were performed within R version 3.6.1 (R
6 Core Team, 2019).

7 The global interspecific LES pattern was obtained from the publicly available data in the TRY
8 global communal database (www.try-db.org—Fitter and Peat, 1994; Shipley, 1995, 2002;
9 Cornelissen, 1996; Cornelissen *et al.*, 1996; Atkin *et al.*, 1997; Atkin *et al.*, 1999; Cornelissen
10 *et al.*, 1999; Medlyn *et al.*, 1999; Meziane & Shipley, 1999; Pyankov *et al.*, 1999; Castro-
11 Diez *et al.*, 2000; Shipley & Lechowicz, 2000; White *et al.*, 2000; Wilson *et al.*, 2000; Meir *et*
12 *al.*, 2002; Shipley & Vu, 2002; Cornelissen *et al.*, 2003; Loveys *et al.*, 2003; Quested *et al.*,
13 2003; Xu & Baldocchi, 2003; Adler *et al.*, 2004; Cornelissen *et al.*, 2004; Díaz *et al.*, 2004;
14 Givnish *et al.*, 2004; Wright *et al.*, 2004; Craine *et al.*, 2005; Louault *et al.*, 2005;
15 Sheremetev, 2005; Vile, 2005; Cavender-Bares *et al.*, 2006; Kazakou *et al.*, 2006; Kerkhoff *et*
16 *al.*, 2006; Michaletz & Johnson, 2006; Preston *et al.*, 2006; Campbell *et al.*, 2007; Craven *et*
17 *al.*, 2007; Meir and Levy, 2007; Price and Enquist, 2007; Scherer-Lorenzen *et al.*, 2007;
18 Swaine, 2007; Kleyer *et al.*, 2008; Kraft *et al.*, 2008; Shiodera *et al.*, 2008; Craine *et al.*,
19 2009; Kattge *et al.*, 2009; van de Weg *et al.*, 2009; Wirth and Lichstein, 2009; Baraloto *et al.*,
20 2010; Freschet *et al.*, 2010; Laughlin *et al.*, 2010; Messier *et al.*, 2010; Ordonez *et al.*, 2010;
21 Blonder *et al.*, 2011; Butterfield and Briggs, 2011; Campetella *et al.*, 2011; Chen *et al.*, 2011;
22 Craine *et al.*, 2011; de Araujo *et al.*, 2011; Kattge *et al.*, 2011; Laughlin *et al.*, 2011; Milla
23 and Reich, 2011; Prentice *et al.*, 2011; Tucker *et al.*, 2011; Sandel *et al.*, 2011; van de Weg *et*
24 *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 & 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), and from Onoda *et al.* (2011). Once excluded entries with ErrorRisk (indication for outliers, distance to mean in standard deviations) greater than 4, the dataset contained information of about 10369 species from 309 families. From these, 5403 species from 249 families including ferns, gymnosperms and angiosperms contain information for at least two traits. No pairwise traits were lost by removing outliers. The observations are widely distributed, all over the world (Fig. S1 [**Supplementary information**]).

Results

In general, the ten Chaquenian species measured in this study were clustered in a relative narrow section of the global interspecific variability for each trait (Fig. 1). The intraspecific variability for each trait showed to be as much important as variability among species (Fig. 1). The species measured in this study showed medium values for SLA (Fig. 1A), high values for

LDMC (Fig. 1B) and medium to high values for N_m and F_t (Fig. 1C, D). The most variable trait both within and among species was F_t .

The intraspecific covariation of the LES-related functional traits followed a general pattern consistent with the global interspecific LES (Fig. 2, Fig. 3 and Fig. S2 [Supplementary information]). The SMA slopes between pairs of traits 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 (Fig. S2A [Supplementary information]), SLA- N_m (Fig. S2C [Supplementary information]). This pattern was observed in plant traits from species collected both in the field and in individuals grown in the common garden (Fig. 2B, D; Fig. 3B, D; Fig. S2B, D [Supplementary information]). Even family means showed similar patterns (Fig. S3 [Supplementary information]).

Within the frame of these common general patterns, many of the intraspecific slopes significantly differed from the global interspecific slope (Fig. 1B, Fig. 2B and Fig. S2D [Supplementary information]). Specifically, for the LDMC vs SLA relationship, 10 out of 20 cases and three out of 10 species were different from the global interspecific LES (Table S3 [Supplementary information]). For the F_t vs SLA relationship, three out of 12 cases and one out of six species were different from the global interspecific LES (Table S4 [Supplementary information]). For the LDMC vs N_m relationship, three out of eight cases but no species were different from the global interspecific LES (Table S5 [Supplementary information]). For the SLA vs N_m relationship, three out of eight cases and one out of four species were different from the global interspecific LES (Table S6 [Supplementary information]). For the F_t vs N_m and the F_t vs LDMC relationships, the interspecific data showed no correlation between pairs of traits (Table S2 [Supplementary information]).

However, at the intraspecific level there was strong positive correlation between these traits for most of the species and conditions (Table S2 [**Supplementary information**]).

For a given species, the relationship between a pair of traits sometimes differed depending on whether the plants were grown in the field or in the garden. This 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 traits never reverted under different growth conditions (even in 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 condition and in woody species (Table S2 [**Supplementary information**]). For example, among structural traits, only F_t vs SLA for *L. crinita* in the common garden showed not significant correlation (Table S2 [**Supplementary information**]). In the relation between structural traits and N_m there were several cases where the correlation was not significant and this was mostly under common garden conditions (Table S2 [**Supplementary information**]). The correlation between a pair of traits was significant in the common garden but not in the field only in the case of SLA and N_m in *P. flexuosa* (Table S2 [**Supplementary information**]).

Discussion

The ten selected species, belonging to two different growth forms and phylogenetically distant clades, represented a substantive yet partial segment of global variation in individual trait values. In this ten species we found that the intraspecific trait covariation patterns of the four leaf traits analysed were similar to the global interspecific LES. 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*

1 *al.*, 2013; Richardson *et al.*, 2013; Niinemets *et al.*, 2015; Yu-Kun Hu *et al.*, 2015; Anderegg
2 *et al.*, 2018). However, those studies focused on trait covariation along environmental
3 gradients typically spanning different populations of the same species growing in more than
4 one locality. We gained further insight by focusing on intraspecific variation at the local level
5 in order to avoid the effect of major environmental gradients like rainfall and temperature, as
6 well as in a common garden experiment in order to capture the genetic covariance between
7 traits.

8 We found that the pattern of covariation defining the global interspecific LES persists at
9 intraspecific level at the local scale, both in the field and in a common garden experiment. In
10 the latter case, it persists even among families. This suggests that plastic responses to, or
11 filtering by the environment are not, currently, the primary determinants of the intraspecific
12 LES covariation pattern. In the same way, Vasseur *et al.* (2012) showed that the correlation
13 pattern among traits in *Arabidopsis thaliana* was genetically determined. This does not mean
14 that natural selection does not matter. Donovan *et al.* (2011) showed that the genetic
15 correlation among LES traits may be variable among species and even between populations of
16 the same species, and may be opposite to the expected on the basis of the global interspecific
17 LES, leading them to conclude that natural selection should be the main force shaping the
18 LES covariation pattern. Our work provides evidence that genetic covariation among LES-
19 related traits tends to coincide with phenotypic covariation observed in the field. It seems that,
20 if some environmentally-induced change has caused such pattern, it is currently not the main
21 determinant.

22 Interestingly, by re-examining studies included in Donovan *et al.* (2011) it is made evident
23 that covariance among LES-related traits is, itself, a plastic trait (Sherrad *et al.*, 2009). Our
24 own work provides evidence of some degree of plasticity in such covariance structure (i.e.

changes in correlation and slopes between trait, between field and common garden conditions). This does not deny the potential effect of selection modulating this covariation pattern within certain limits, e.g. changing the slope or intercept of the relationship between traits (Pressoir and Berthaud, 2004), but hampers to conclude about the role of selection on the LES. Furthermore, the relevance of environmental-induced change in shaping LES covariation pattern seems to vary according to the trait pairs considered. For example, while in our study the covariation pattern between SLA and LDMC always follows the expected trend, the covariation pattern involving N_m often disappears under common garden conditions (Table S2 [**Supplementary information**]). Also the variability in slopes of the relation between traits depends on the trait pair analysed: the pair SLA vs F_t and LDMC vs F_t always kept the same intraspecific slope irrespective of the condition (field, common garden, family) (Fig. 2D, Fig. S2B [**Supplementary information**], Fig. S3B, C [**Supplementary information**]), while the pair LDMC vs SLA varied widely between species and conditions (Fig. 2B, Fig. S3A [**Supplementary information**]). The different slopes in this latter relationship could be explained by differences in leaf thickness and/or air volume proportion in the leaf among species and populations (Shipley *et al.*, 2006 *a*).

All the alternative causal hypotheses proposed for the LES (Wright *et al.*, 2004; Shipley *et al.*, 2006 *a*; Blonder *et al.*, 2011, 2013, 2015; Onoda *et al.*, 2017) have found empirical support. However, they do not explain all of the variability of the patterns reported in the literature. For example, in Blonder *et al.* (2013) some of the clones of *P. tremuloides* did not show the expected correlation between SLA and photosynthetic rate, or the lack of correlation between structural leaf functional traits and N_m found several times in different works, at intraspecific level (Jackson *et al.*, 2013; Niinemets, 2015). Hu *et al.* (2015) also found the expected correlations between leaf traits of *Phragmites australis* at site scale but not for all sites.

1 Similarly, our results present some challenges to existing theory. Particularly in the LDMC vs
2 N_m relation, the overall interspecific slope is accurately predicted by Shipley *et al.* (2006 *a*)
3 (i.e. -1), but they cannot predict the different slopes among species (Fig. 3B). All these
4 examples ultimately indicate that the current alternative hypotheses provide only incomplete
5 explanation of the LES across different organization levels (e.g. compare Shipley *et al.*, 2006
6 *a* with Blonder *et al.*, 2015).

7 The LES has proven to be a useful concept to understand vegetation dynamics and ecosystem
8 processes, as well as being relevant to functional and comparative plant ecology (McGill *et*
9 *al.*, 2006, Reich, 2014). The present and previous evidence shows that, in general, the LES
10 covariation pattern is valid from the global to the local population levels. However, the
11 exceptions found by ourselves and other researchers alert us about the need to better
12 understand the causal mechanisms underpinning this generic pattern. Although some studies,
13 including this one, found a similar covariation pattern at intraspecific and interspecific levels,
14 more studies, particularly focusing on the unexpected patterns, are needed to elucidate causal
15 relationships operating across levels of organization. The conceptual framework of
16 phenotypic integration (Pigliucci, 2003) could be useful to assess the LES at intraspecific level.
17 Our results show that there are some degree of integration across the LES related traits and
18 that different levels of plasticity occurs in such integration, varying across species and
19 between traits. More detailed studies of phenotypic integration of LES related traits,
20 modularity and plasticity of such integration could provide better understanding of causes and
21 consequences of LES.

22 23 **Supplementary information**

Supplementary information are available online at and consist of the following. Figure S1: Geolocation of the entries in the TRY public dataset. Figure S2: Relationship between force to tear (F_t) and leaf dry matter content (LDMC) as well as specific leaf area (SLA) and nitrogen content per leaf mass (N_m). Figure S3: SMA slopes of the relation between force to tear (F_t), leaf dry matter content (LDMC) and specific leaf area (SLA), from plants in the field and from families in the common garden. Table S1: Full botanical names of the studied species. Table S2: Correlation coefficient for each pair of traits in each species and condition. Table S3: Slopes of $\log_{10}(\text{LDMC}) \sim \log_{10}(\text{SLA})$ for each species and condition (field and common garden), and groups resulting from multiple comparison test. Table S4: Slopes of $\log_{10}(F_t) \sim \log_{10}(\text{SLA})$ for each species and condition (field and common garden), and groups resulting from multiple comparison test. Table S5: Slopes of $\log_{10}(\text{LDMC}) \sim \log_{10}(N_m)$ for each species and condition (field and common garden), and groups resulting from multiple comparison test. Table S6: Slopes of $\log_{10}(N_m) \sim \log_{10}(\text{SLA})$ for each species and condition (field and common garden), and groups resulting from multiple comparison test. Table S7: Slopes of $\log_{10}(\text{LDMC}) \sim \log_{10}(\text{SLA})$ for each species and condition (field and genetic families), and groups resulting from multiple comparison test. Table S8: Slopes of $\log_{10}(F_t) \sim \log_{10}(\text{SLA})$ for each species and condition (field and genetic families), and groups resulting from multiple comparison test.

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Figure legends

Figure 1. Distribution of the four traits considered in our analysis across the interspecific global dataset (black box) 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 (F_t) 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 (N_m) was measured only in four species due to high costs.

Figure 2. Relationship between LES-structural traits. Left panels (A and C) show the SMA lines for each species at each condition. Different colours represent different species, continuous lines and squares represent field condition and dashed lines and circles the common garden condition. Black triangles and lines represent the same analysis for the global-level interspecific dataset obtained from the TRY and Onoda *et al.*'s (2011) datasets. 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. Slope confidence intervals non overlapping grey box in B and D are significantly different from the interspecific slope. Results from multiple comparisons of the slopes are shown in Table S3 and Table S4 [Supplementary information].

Figure 3. Relationship between leaf dry matter content (LDMC), force to tear (F_t) and leaf nitrogen content (N_m). Left panels (A and C) show the SMA lines for each species at each condition. Different colours represent different species, continuous lines and squares represent field condition, dashed lines and circles the common garden condition. Black triangles and lines represent the same analysis for the global-level interspecific dataset obtained from the TRY and Onoda *et al.* (2011) datasets. 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

1 and it is not shown at the left panel. Slope confidence intervals non overlapping grey box in B
2 are significantly different from the interspecific slope. Results from slopes multiple
3 comparison test are shown in Table S5 [**Supplementary information**]. In the F_t vs N_m
4 relationship there were no significant differences in slopes among those with correlation
5 different from zero.