Leaf trait records of vascular plant species in the Pannonian flora with special focus on endemics and rarities

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Introduction

In the last decade, the number of studies using plant functional traits for understanding community assembly

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patterns has grown exponentially. Simultaneously, the demand for standardized and precise trait measurements has increased, bringing about the establishment of large and comprehensive trait databases (e.g. TRY – Kattge

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et al. 2011). Functional plant traits are generally de-scribed as 'any morphological, physiological or pheno-logical features measurable at the individual level' (Violle et al. 2007) and are frequently associated with certain plant strategies (r-K strategies – MacArthur and Levins 1967; CSR strategies, Grime 1979; LHS strategy scheme, Westoby 1998).

Leaf traits in general, and specific leaf area (thereafter SLA) and leaf dry matter content (thereafter LDMC) in particular, are among the most extensively studied traits. These 'soft traits' are easy to measure and strongly related to plant fitness via affecting other 'hard traits' such as relative growth rate, photosynthetic rate and nutrient utilization efficiency (Pérez-Harguindeguy et al. 2013); moreover, they are associated with plant re source use strategies (acquisitive vs conservative) along the leaf economics spectrum (Wright et al. 2004). Studying the leaf economics spectrum is also necessary for the assessment of the whole-plant eco-nomics spectrum (i.e. 'fast–slow' plant economics spec-trum; Reich 2014). According to a global assessment on plant forms and functions (Díaz et al. 2016), size-related traits were allocated to the first main axis whereas the second independent dimension of plant functionality was running from conservative to acquisitive strategies. SLA and leaf nitrogen content were allocated to the second axis, thus the leaf economics spectrum, while LA was correlated to both axes, being partially impor-tant in both trade-offs. Although LDMC is known to be either inversely related to or independent of SLA (Pérez-Harguindeguy et al. 2013), the position of LDMC on the global trait spectrum remains unclear (Díaz et al. 2016). Both SLA and LDMC may explain plant functional variation in response to biotic and abiotic drivers ('re-sponse traits', Lavorel and Garnier 2002) and indirectly affect ecosystem functioning through covariation with several 'effect traits' (Lavorel and Garnier 2002).

There are contradictory views on how rare species relate to ecosystem functioning. According to the 'mass ratio hypothesis' (Grime 1998), dominant species are the main drivers of community productivity; thus, sus-taining ecosystem functions (Sonkoly et al. 2019). Therefore, in trait-based ecology, abundance-weighted measures are often preferred over non-weighted ones, where the importance of common species is highlighted, and that of rare species is neglected (Roumet et al. 2007). However, rare species may have a crucial role in ecosystem multifunctionality, and in the resistance to disturbance acting as keystone species (Lyons et al.

2005). The decision, therefore, whether abundant or rare species are given higher relative importance when eval-uating functional responses to the environment should be dependent on the context and the research questions.

The Pannonian ecoregion harbours a large num-ber of endemic species due to its geographical loca-tion. The majority of the ecoregion lies in a basin, which has a sheltered position surrounded by moun-tain ranges (the Carpathians, the Alps and the Dinarics) from all directions. This geographical lo-cation influences species dispersal and migration, so the Carpathian basin serves as a refugium for spe-cies with restricted distributions (Roekaerts 2002, http://ec.europa.eu/environment/nature/natura2000/biogeog_regions – last accessed on 26 April 2019). Moreover, the region is part of the Eurasian steppe zone, where a considerable amount of steppic relicts survived since the Holocene (Magyari et al. 2010). For the majority of steppic species, which have large continental distribution ranges, the Pannonian ecoregion harbours the most western occurrences (Kajtoch et al. 2016).

In the Pannonian ecoregion, leaf traits have recent-ly been studied in the context of plant community assembly rules (Kelemen et al. 2015; Lhotsky et al. 2016a; Lukács et al. 2019), the diversity-productivity relationship (Sonkoly et al. 2019), invasion biology (Fenesi and Botta-Dukát 2012; Kelemen et al. 2016; Lukács et al. 2017), and succession (Kelemen et al. 2017; Fantinato et al. 2019) and restoration ecology (Tölgyesi et al. 2019). In the above studies, trait values were measured *in situ*, or compiled from da-tabases, which have relatively high coverage of Cen-tral European species (BiolFlor – Kühn et al. 2004; LEDA – Kleyer et al. 2008; TRY – Kattge et al. 2011). In general, database data are a good substitu-tion for time- and resource-consuming trait measure-ments; however, there is low spatial coverage for a large number of taxa (Kattge et al. 2011), and there is a severe lack of data for endemic, locally rare or red-listed species. Both of these problems could be re-solved by collecting and publishing data on under-sampled species from underrepresented regions (such as the Pannonian ecoregion).

Because of the incompleteness of trait databases, the majority of current trait-based studies have to deal with a considerable amount of missing data. Some evidence suggests that the effects of missing data can be moder-ated using careful data transformations in functional
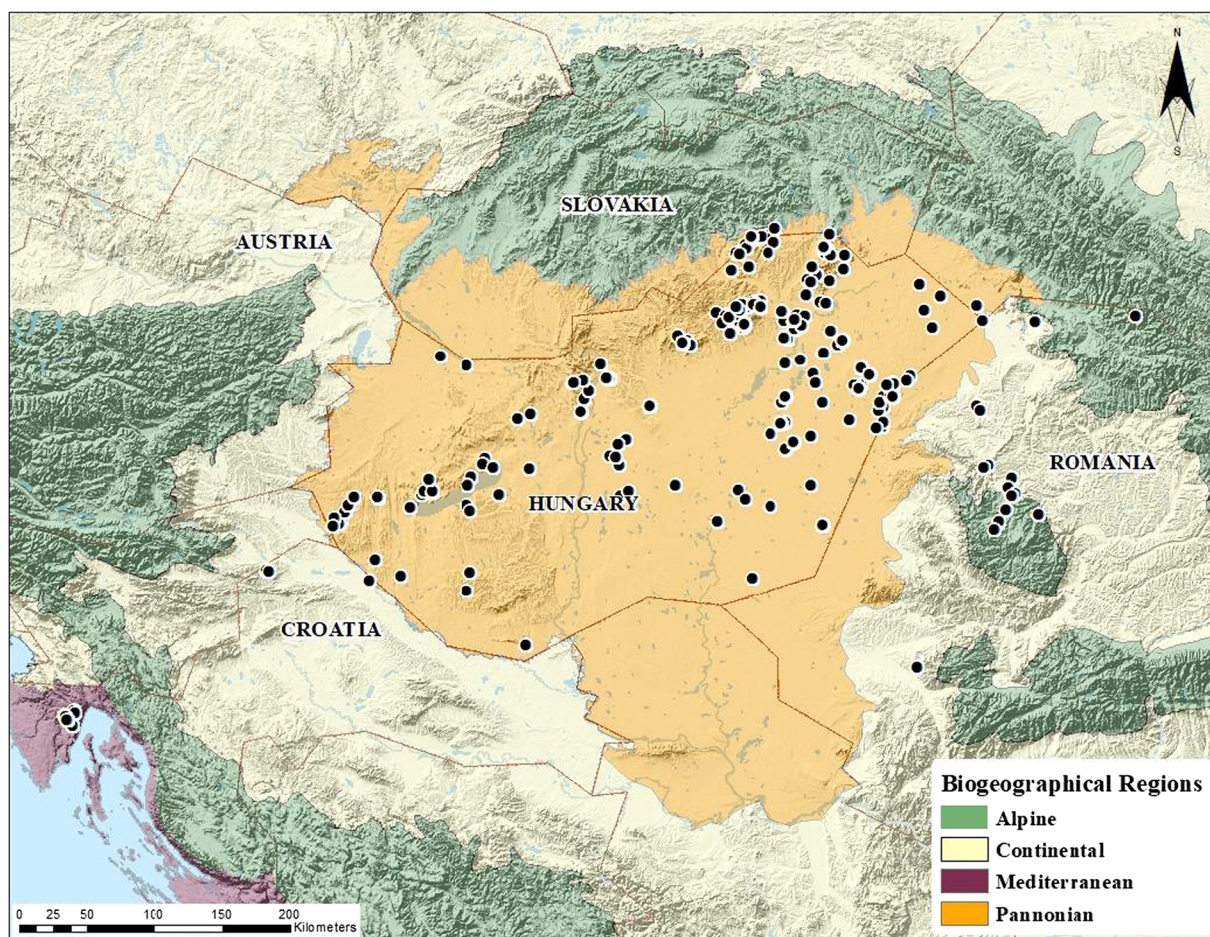
Fig. 1 Sampling sites within European ecoregions. Localities of sampling points are marked with black dots

diversity analyses (Májeková et al. 2016). However, caution should be taken with regard to species abundance structure, the distribution of trait values and the diversity indices used. Although the suggested tools (R package 'traitor'; Májeková et al. 2016) enable bypassing missing data, having more complete datasets can increase the robustness of statistical methods.

In this paper we provide original leaf trait data of vascular plant species from the Pannonian ecoregion. We place special emphasis on rare, red-listed species, species endemic to this ecoregion as well as species with continental (steppic) distribution ranges. We prioritized providing data on species that are so far missing from frequently used plant trait databases.

Table 1 Summary of differences between measurement protocols of datasets A and B

Data	Sampling	Image processing software	Drying procedure	Reference protocols
A	Each record is one sample from a single individual, 3–10 records per population	Image J, v. 1.48, Schneider et al. 2012	Oven drying at 80°C for 48 h	Pérez-Harguindeguy et al. 2013
B	Each record is the average of 3 samples from the same individual, 10 records per population	Lafore; Lehsten 2005	Drying at room temperature for 1 month	Cornelissen et al. 2003; Kleyer et al. 2008

Table 2 Basic statistics for the five leaf traits included in the dataset, with unit of measurement, number of observations), number of species according to The Plant List nomenclature and number of locations for each measured trait. Mean and standard deviation is calculated across all samples. LA - leaf area, SLA - specific leaf area; LDMC, leaf dry matter content

Trait	Unit	No. of observations	No. of species	No. of locations	Mean	SD
fresh mass	g	3,970	484	164	0	1
dry mass	mg	3,945	479	159	106	334
LA	mm^2	3,986	484	165	2,080	4,387
SLA	mm^2/mg	3,895	475	157	28	32
LDMC	mg/g	3,889	472	156	256	136

Material and methods

Altogether, 4,041 samples belonging to 491 species (27 woody, 464 non-woody) and 73 families were collected. Samples originated from 167 locations, including Hungary ($n = 3,854$), Romania ($n = 81$), Croatia ($n = 55$), Slovakia ($n = 36$) and Slovenia ($n = 15$) (Fig. 1), and were collected between 2014 and 2018. Sampling sites were situated predominantly in the Pannonian ecoregion and partly in its adjacent ecoregions (Alpine, Continental and Mediterranean; Roekaerts 2002, http://ec.europa.eu/environment/nature/natura2000/biogeog_regions)

Table 3 Structure of the dataset. The data is attached as electronic supplementary material (Table S1) and is freely available within the TRY database

Column	Description
ID	individual identifier for each entry (e.g. A_1234). For differences in measurement protocols between datasets A and B, see Table 1.
Species	species name supplied by collectors. The Taxonomic nomenclature follows Király (2009).
TPL_Sp	valid species names standardized according to The Plant List (www.theplantlist.org)
Family	according to The Plant List (www.theplantlist.org)
Status	according to the *Red list of vascular plants of Hungary* (Király 2007), (EX – extinct, EW – extinct in the wild, CR – critically endangered, EN – endangered, VU – vulnerable, NT – near threatened, DD – data deficient, non-endangered – not red-listed)
Country	abbreviation of the county where the sample was collected (Hu – Hungary, Ro – Romania, Cr – Croatia, Sk – Slovakia, Sl – Slovenia)
Location	name of the settlement closest to the sampling location
Date	date of sampling
fresh_mass_g	leaf fresh mass [g]
dry_mass_mg	leaf dry mass [mg]
LA_mm2	leaf area [mm^2]
SLA_mm2/mg	specific leaf area [mm^2/mg]
LDMC_mg/g	leaf dry matter content [mg/g]
Comment	indicating when the measured sample was larger or smaller than a single leaf (or the entire compound leaf) and when rosette and stem leaves were measured separately

The complete dataset was collected during several sampling campaigns. Differences in sampling and measurement protocols between 'dataset A' and 'dataset B' are summarized in Table 1. 'Sample identity' indicating the original dataset – either A or B – can be found in the column 'ID' (Table S1).

Species listed in the *Red list of the vascular flora of Hungary* (Király 2007) are considered 'endangered' (*n* = 230); otherwise they are treated as 'non-endangered' (*n* = 261). Conservation status based on the IUCN categories published in Király (2007) is indicated in the dataset in the column 'Status'.

Only healthy, undamaged, young and fully developed leaves were collected and kept in plastic bags to maintain natural water saturation. All fresh leaf samples were stored in a fridge at 3–6°C and measured no later than 24 h after collection. Leaves were scanned using a flatbed scanner, and the one-sided leaf area was measured using Image J (v. 1.48, Schneider et al. 2012, available at www.imagej.net) and Lafore (Lehsten 2005) image processing software (Table 1). The area of compound leaves was measured as a whole, not as leaflets. Fresh mass was measured on fully saturated but not wet leaves using analytical scales up to the accuracy of four digits. The same scales were used to measure leaf dry mass (Table 1). SLA (leaf area/dry mass) and LDMC (dry mass/fresh mass) were calculated for all samples, and basic statistics (mean and standard deviation) were computed for all five traits (Table 2). Exceptions, where the measured sample was either larger or smaller than a single leaf (or compound leaf), are indicated in the data file, under the heading 'Comment'.

Data accessibility

The data are available as a single '.csv' file provided as electronic supplementary material to this paper (Table S1; see metadata in Table 3) and they are publicly available within the TRY database (www.try-db.org/TryWeb/Home.php; Kattge et al. 2011).

Future prospects and applications

There are several potential applications for these data in trait-based ecology. An especially important research question revolves around the concept of functional rarity, considering the large number of records about red-listed species published in this paper. Species may be locally rare but widely distributed, or they may occur in very few sites but in big populations, and they can also be functionally rare (Rabinowitz 1981). The connection between scarcity and functional rarity might shed new light on the drivers of biodiversity loss. Rare species have a special role in diverse ecosystems (Leitão et al. 2016), having the potential to be the least functionally redundant (Mouillot et al. 2013). Rare species tend to provide the most vulnerable functions (Jain et al. 2014) or aggregate in a restricted part of the functional trait space occupied by common species (Ames et al. 2017). However, the issue of functional rarity has just started to be investigated more thoroughly, and the studies have done so far reported contradictory results (Carmona et al. 2017; Violle et al. 2017).

We stress that our data have the potential to be a useful gap-filler in trait-based studies, and we hope that further data will be published in the near future, representing rare species from other geographical regions. Having a more complete coverage of species in trait databases can help us better understand not only the role rare species play in ecosystem functioning, but also more general questions in functional ecology. Moreover, publishing locally measured plant trait data are of uttermost importance for well-founded local and regional analyses. Our data are well compatible with other local trait datasets (Török et al. 2013, 2016; Lhotsky et al. 2016b) and herbaria (Molnár et al. 2012; Takács et al. 2014; E-Vojtkó et al. 2014; Takács et al. 2015; Nótári et al. 2017) from the Pannonian ecoregion and can be amalgamated in a large plant trait and life history database in the future.

References

Ames GM, Wall WA, Hohmann MG, Wright JP (2017) Trait space of rare plants in a fire-dependent ecosystem. *Conservation Biol* 31:903–911

Carmona CP, de Bello F, Sasaki T, Uchida K, Pärtel M (2017) Towards a common toolbox for rarity: a response to Violle et al. *Trends Ecol Evol* 32:889–891

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE et al (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Austral J Bot* 51:335–380

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

E-Vojtkó A, Takács A, Molnár VA, Vojtkó A (2014) Herbarium database of the vascular collection of Eszterházy Károly College (EGR). *Kitaibelia* 19:339–348

Fantinato E, Sonkoly J, Silan G, Valkó O, Tóthmérész B, Deák B et al (2019) Pollination and dispersal trait spectra recover faster than growth form spectrum during the spontaneous succession in sandy old-fields. *Appl Veg Sci* 22:435–443

Fenesi A, Botta-Dukát Z (2012) Phenotypic divergences induced by different residence time in invasive common ragweeds. *J Pl Ecol* 5174–181

Grime JP (1979) *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester, UK

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J Ecol* 86902–910

Jain M, Flynn DF, Prager CM, Hart GM, DeVan CM, Ahrestani FS et al (2014) The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecol Evol* 4104–112

Kajtoch Ł, Cieślak E, Varga Z, Paul W, Mazur MA, Sramkó G, Kubisz D (2016) Phylogeographic patterns of steppe species in Eastern Central Europe: a review and the implications for conservation. *Biodivers & Conservation* 252309–2339

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G et al (2011) TRY – a global database of plant traits. *Global Change Biol* 172905–2935

Kelemen A, Török P, Valkó O, Deák B, Tóth K, Tóthmérész B (2015). Both facilitation and limiting similarity shape coexistence in dry alkali grasslands. *Ecol Complex* 2134–38

Kelemen A, Valkó O, Kröel-Dulay G, Deák B, Török P, Tóth K, Miglécz T, Tóthmérész B (2016) The invasion of common milkweed (*Asclepias syriaca* L.) in sandy old-fields – Is it a threat to the native flora? *Appl Veg Sci* 19218–224

Kelemen A, Tóthmérész B, Valkó O, Miglécz T, Deák B, Török P (2017) Old-field succession revisited – new aspects revealed by trait-based analyses of perennial-crop-mediated succession. *Ecol Evol* 72432–2440

Király G (ed.) (2007) Vörös lista: a magyarországi edényes flóra veszélyeztetett fajai (Red list of the vascular flora of Hungary) [in Hungarian with English summary]. Private Edition, Sopron

Király G (ed.) (2009) *Új Magyar füvészkönyv. Magyarország hajtásos növényei. Határozókulcsok* (The vascular plants of Hungary. Identification key) [in Hungarian]. – Aggteleki Nemzeti Park Igazgatóság, *Jósvafő*. Available at http://anp.nemzetipark.gov.hu/?pg=news_7_1918

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M et al (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *J Ecol* 961266–1274

Kühn I, Durka W, Klotz S (2004) BiolFlor : a new plant-trait database as a tool for plant invasion ecology. *Diversity & Distrib* 10363–365

Lavorel S, Garnier, E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* 16545–556

Lehsten V (2005) *Lafore – LeafAreaFOREveryone: calculating leaf area, leaf width and length from ordinary scans*. University of Oldenburg. Available at https://uol.de/en/landeco/download-and-service/software/lafore

Leitão RP, Baraloto C, Zuanon J, Mendonça FP, Williams SE, Villéger S et al (2016) *Rare species contribute disproportionately to the functional structure of species assemblages Proc Roy Soc Biol Sci Ser B* 283:20160084

Lhotsky B, Kovács B, Ónodi G, Csecserits A, Rédei T, Lengyel A et al (2016a) Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *J Ecol* 104507–517

Lhotsky B, Csecserits A, Kovács B, Botta-Dukát Z (2016b) New plant trait records of the Hungarian flora. *Acta Bot Hung* 58397–400

Lukács BA, E-Vojtkó A, Mesterházy A, Molnár VA, Süveges K, Végvári Z et al (2017) Growth-form and spatiality driving the functional difference of native and alien aquatic plants in Europe. *Ecol Evol* 7950–963

Lukács BA, E-Vojtkó A, Erős T, Molnár VA, Szabó S, Götzenberger L (2019) Carbon forms, nutrients and water velocity filter hydrophyte and river-bank species differently: a trait-based study. *J Veg Sci* 30:471–484

Lyons KG, Brigham CA, Traut BH, Schwartz MW (2005) Rare species and ecosystem functioning. *Conservation Biol* 191019–1024

MacArthur RH, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. *Amer Naturalist* 101377–385

Magyari EK, Chapman JC, Passmore DG, Allen JRM, Huntley JP Huntley B (2010) Holocene persistence of wooded steppe in the Great Hungarian Plain. *J Biogeogr* 37915–935

Májeková M, Paal T, Plowman NS, Bryndová M, Kasari L, Norberg A et al (2016) Evaluating functional diversity: missing trait data and the importance of species abundance structure and data transformation. *PLOS ONE* 11:e0149270

Molnár VA, Takács A, Horváth O, E-Vojtkó A, Király G, Sonkoly J et al (2012) Herbarium database of Hungarian orchids I. Methodology, dataset, historical aspects and taxa. *Biologia* 67:79–86

Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M et al (2013) Rare species support

vulnerable functions in high-diversity ecosystems. *PLoS Biol* 11:e1001569

Nótári K, Nagy T, Löki V, Ljubka T, Molnár VA, Takács A (2017) Az ELTE Füvészkert herbáriuma (BPU). *Kitaibelia* 22:55–59

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P et al (2013) New handbook for standardised measurement of plant functional traits worldwide. *Austral J Bot* 61:167

Rabinowitz D (1981) Seven forms of rarity. In Synge H (ed.) *The biological aspects of rare plant conservation.* John Wiley and Sons, New York, pp 205–217

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *J Ecol* 102:275–301

Roekaerts M (2002) The biogeographical regions map of Europe. Basic principles of its creation and overview of its development. European Environment Agency, Copenhagen, 17

Roumet C, Laurent G, Navas M-L, Bellmann A, Garnier E, Billès G et al (2007) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature, Meth* 9:671–675

Sonkoly J, Kelemen A, Valkó O, Deák B, Kiss R, Tóth K et al (2019) Both mass ratio effects and community diversity drive biomass production in a grassland experiment. *Sci Rep UK* 9: 1848

Takács A, Nagy T, Fekete R, Lovas-Kiss Á, Ljubka T, Löki V et al (2014) A Debreceni Egyetem Herbáriuma (DE) I.: A 'Soó Rezső Herbarium'. *Kitaibelia* 19:142–155

Takács A, Süveges K, Ljubka T, Löki V, Lisztes-Szabó Z, Molnár V (2015) A Debreceni Egyetem Herbáriuma (DE) II.: 'Siroki Zoltán Herbarium'. *Kitaibelia* 20:15–22

Tölgyesi C, Török P, Kun R, Csathó AI, Bátori Z, Erdős L et al (2019) Recovery of species richness lags behind functional recovery in restored grasslands. *Land Degrad Developm* 30: 1083–1094

Török P, Miglécz T, Valkó O, Tóth K, Kelemen A, Albert ÁJ et al (2013) New thousand-seed weight records of the Pannonian flora and their application in social behavior types. *Acta Bot Hung* 55:429–472

Török P, Tóth E, Tóth K, Valkó O, Deák B, Kelbert B et al (2016) New measurements of thousand-seed weights of Pannonian flora. *Acta Bot Hung* 58:187–198

Violle C, Vile D, Kazakou E, Hummel I, Navas M-L, Fortunel C et al (2007) Let the concept of trait be functional! *Oikos* 116: 882–892

Violle C, Thuiller W, Mouquet N, Munoz F, Kraft NJB, Cadotte MW et al (2017) Functional rarity: the ecology of outliers. *Trends Ecol Evol* 32:356–367

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Pl & Soil* 199:213–227

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F et al (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827