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## A global method for calculating plant CSR ecological strategies 2 applied across biomes worldwide

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57 Running headline: *Global plant CSR analysis*

## 58 **Summary**

59 **1.** Competitor, Stress-tolerator, Ruderal (CSR) theory is a prominent plant functional strategy scheme  
60 previously applied to local floras. Globally, the wide geographic and phylogenetic coverage of available  
61 values of leaf area (LA), leaf dry matter content (LDMC) and specific leaf area (SLA) (representing,  
62 respectively, interspecific variation in plant size and conservative *vs.* acquisitive resource economics)  
63 promises the general application of CSR strategies across biomes, including the tropical forests hosting  
64 a large proportion of Earth's diversity.

65 **2.** We used trait variation for 3068 tracheophytes (representing 198 families, six continents and 14  
66 biomes) to create a globally-calibrated CSR strategy calculator tool and investigate strategy-  
67 environment relationships across biomes worldwide.

68 **3.** Due to disparity in trait availability globally, co-inertia analysis was used to check correspondence  
69 between a 'wide geographic coverage, few traits' dataset and a 'restricted coverage, many traits' subset  
70 of 371 species for which 14 whole-plant, flowering, seed and leaf traits (including leaf nitrogen content)  
71 were available. CSR strategy/environment relationships within biomes were investigated using fourth-  
72 corner and RLQ analyses **to determine strategy/climate specialisations.**

73 **4.** Strong, significant concordance ( $RV=0.597$ ;  $p<0.0001$ ) was evident between the 14 trait multivariate  
74 space and when only LA, LDMC and SLA were used.

75 **5.** Biomes such as tropical moist broadleaf forests exhibited strategy convergence (i.e. clustered around  
76 a CS/CSR median; C:S:R=43:42:15%), with CS-selection associated with warm, stable situations (lesser  
77 temperature seasonality), with greater annual precipitation and potential evapotranspiration. Other  
78 biomes were characterised by strategy divergence: e.g. deserts varied between xeromorphic perennials  
79 such as *Larrea divaricata*, classified as S-selected (C:S:R=1:99:0%), and broadly R-selected annual  
80 herbs (e.g. *Claytonia perfoliata*; R/CR-selected; C:S:R=21:0:79%). Strategy convergence was evident  
81 for several growth habits (e.g. trees) but not others (forbs).

82 **6.** The CSR strategies of vascular plants can now be compared quantitatively within and between biomes  
83 at the global scale. Through known linkages between underlying leaf traits and growth rates, herbivory  
84 and decomposition rates, this method and the strategy-environment relationships it elucidates will help  
85 to predict which kinds of species may assemble in response to changes in biogeochemical cycles, climate  
86 and land-use.

87

88 **Key-words:** Comparative ecology, community assembly, plant economics spectrum, Grime's CSR  
89 triangle, plant functional type, survival strategy, universal adaptive strategy theory

90

91 **Data Archiving:** Data are available from the TRY database, at [www.try-db.org](http://www.try-db.org).

## 92 **Introduction**

93 A common framework for the comparison of organism function within and between ecosystems  
94 worldwide can potentially be achieved using the continuous variation evident along spectra of  
95 functional (adaptive) traits. The main plant trait spectra evident globally represent variation in  
96 plant resource economics (a trade-off between traits conferring resource acquisition and internal  
97 conservation) and the size of plants and plant organs (Díaz *et al.* 2016). These two principal  
98 functional trait spectra can be used to assign species a position within multivariate space relative  
99 to other species, and concurrently to allocate discrete ecological strategy classes (Pierce *et al.*  
100 2013). These classes are more precise than traditional life-form or ‘plant functional type’  
101 categories characterised by constant attributes (van Bodegom *et al.* 2012; Soudzilovskaia *et al.*  
102 2013). Functional trait spectra may also better reflect the acquisition, use and cycling of energy  
103 and matter within the ecosystem. For instance, plant resource economics is a particularly  
104 important determinant of photosynthetic carbon fixation, biomass production, litter  
105 decomposition and thus ecosystem nutrient availabilities (Grime *et al.* 1997; Wright *et al.* 2004;  
106 Cornwell *et al.* 2008; Reich 2014). Ecological strategies reflect viable suites of traits that impact  
107 fitness and survival and can also provide a conceptual link between ecology and natural  
108 selection. Indeed, recent studies underline the evolutionary history of functional traits  
109 (Cornelissen & Cornwell 2014; Cornwell *et al.* 2014; Flores *et al.* 2014; Díaz *et al.* 2016) and  
110 the consistent co-occurrence of particular traits and trait values (Reich 2014; Verheijen *et al.*  
111 2016). It is now clear that plant size and economics are the most prominent aspects of plant  
112 functional variation globally (Díaz *et al.* 2016), although there is currently no consensus on any  
113 particular ecological strategy scheme that can potentially explain *why* certain combinations of  
114 trait values are consistently observed under similar circumstances.

115 A prominent strategy scheme is Grime’s (1974, 1977, 2001) competitor, stress-tolerator,  
116 ruderal (CSR) theory (reviewed by Grime & Pierce 2012), in which the three principal strategies

117 represent viable trait combinations rising under conditions of competition, abiotic limitation to  
118 growth or periodic biomass destruction, respectively. Specifically, C-selected ‘competitors’ are  
119 said to survive in relatively stable, productive habitats *via* investment of resources in continued  
120 vegetative growth and rapid attainment of large individual and organ size to aid resource pre-  
121 emptation. S-selected ‘stress-tolerators’ protect metabolic performance in variable and resource-  
122 poor environments by investing mainly in capacity to retain resources and repair cellular  
123 components in dense, persistent tissues. They may be small or gradually accrue large size over  
124 a long life span. R-selection, or ruderalism, involves investment of a large proportion of  
125 resources not in the individual but in propagules from which the population can regenerate in  
126 the face of repeated lethal biomass destruction events, or disturbances. The worldwide leaf  
127 economics spectrum, itself a part of the ‘fast-slow’ plant economics spectrum (Reich 2014),  
128 and the leaf size spectrum are major components of CSR strategy variation (Pierce *et al.* 2012).

129 A number of CSR analysis methods have been developed (Grime, Hodgson & Hunt 1988;  
130 Hodgson *et al.* 1999; Pierce *et al.* 2013) and have been applied as practical tools to characterise,  
131 map and compare vegetation function (Bunce *et al.* 1999; Hunt *et al.* 2004; Schmidtlein,  
132 Feilhauer & Bruehlheide 2012). They have also been used to investigate and interpret a range of  
133 community processes, such as resistance and resilience, coexistence, succession and the  
134 relationship between species richness and productivity (Lepš, Osbornová-Kosinová &  
135 Rejmánek 1982; Caccianiga *et al.* 2006; Cerabolini *et al.* 2016). However, each CSR analysis  
136 method has drawbacks, and all have been calibrated using local floras. Application of CSR  
137 analysis is therefore typically applied to herbaceous vegetation in Europe (but see Negreiros *et*  
138 *al.* 2014 and de Paula *et al.* 2015), while the majority of plant diversity is found in tropical  
139 forests (Kreft & Jetz 2007).

140 Potential for a global system for comparative plant ecology lies in the fact that variation in  
141 leaf economics and leaf size is a ubiquitous phenomenon evident not just for temperate herbs

142 but also for trees, lianas and understory herbs in tropical forests (Santiago & Wright 2007).  
143 Indeed, other widely-used traits are not applicable across life forms: e.g. plant height cannot be  
144 measured for aquatic species, whereas leaf traits allow aquatic and terrestrial species to be  
145 compared on an equal footing (Pierce *et al.* 2012). Leaf area (LA), a key determinant of capacity  
146 to intercept light, is one of the most widely available indicators of the size spectrum (Díaz *et al.*  
147 2016). Large values of specific leaf area (SLA) and, alternatively, of leaf dry matter content  
148 (LDMC) are highly representative of the opposite extremes of the economics spectrum and are  
149 amongst the most widely available traits in the global TRY plant functional trait database (see  
150 list at [www.try-db.org/de/TabDetails.php](http://www.try-db.org/de/TabDetails.php); Kattge *et al.* 2011). Data for other key traits such as  
151 leaf nitrogen content (LNC) have a much more restricted geographic and phylogenetic coverage  
152 (Díaz *et al.* 2016).

153 Any generally-applicable method for calculating CSR strategies must include ubiquitous  
154 traits that can represent the extremes of a trade-off between large size and conservative vs.  
155 acquisitive economics. Leaf size and economics traits are widely available, applicable to a range  
156 of life-forms and are highly representative of plant functional trade-offs. Specifically, in the  
157 European flora species characterised by high LA do not exhibit high SLA or high LDMC,  
158 species exhibiting high LDMC all have small, dense leaves, and species with high SLA are  
159 small and exhibit low LDMC (Cerabolini *et al.* 2010). These trade-offs at the level of the leaf  
160 are associated with whole-plant and reproductive trade-offs (e.g., species with large leaves tend  
161 to have large seeds; Pierce *et al.* 2014a; Díaz *et al.* 2016), and it is reasonable to expect leaf-  
162 level variation to reflect a substantial portion of overall plant variation (Díaz *et al.* 2016).

163 The **main** aim of the current study was to examine the trade-off between LA, LDMC and  
164 SLA variation worldwide in order to assign combinations of leaf traits within the triangle of  
165 CSR strategies, **and to use this to produce a readily-applicable practical tool. This builds on the**  
166 **previous CSR classification system of Pierce *et al.* (2013) but up-scaling of the method using a**

167 global calibration has a number of advantages. By using the absolute limits of plant functional  
168 trait spectra evident in the world flora, rather than local data ranges, the method is essentially  
169 altered from one that compares species relative to one another to become a method bounded by  
170 the entire range of plant size and economics currently known for vascular plants (i.e. species  
171 are compared against absolute limits). This means that ecologists working in biogeographically  
172 distinct contexts worldwide will have a common reference frame. As CSR theory predicts that  
173 strategies arise consistently in response to particular conditions, lessons learned in one location  
174 are potentially transferable to functionally similar vegetation found on different continents.

175 At local scales, an average CSR strategy for a plant community can be used to provide a  
176 'functional summary' of vegetation and allow comparison of contrasting circumstances (e.g.  
177 Caccianiga *et al.* 2006). A global methodology could similarly provide functional summaries  
178 at larger scales and allow investigation of general relationships between plant functioning and  
179 broad-scale environmental parameters operating within and between biomes. There is good  
180 reason to expect that a plant functional signal should be apparent even at the scale of biomes.  
181 For example, as woody species vary between C- and S-selected but no ruderal tree species are  
182 apparent (at least in Europe; Pierce *et al.* 2013) biomes dominated by woody species should  
183 exhibit clustering of species around the CS-selected region of the CSR triangle (whereas  
184 herbaceous species in Europe exhibit a much wider range of strategies; Pierce *et al.* 2013).  
185 Furthermore, strategies can be expected to be mediated by climatic factors such as temperature,  
186 potential evapo-transpiration and water availability, which are principal determinants of plant  
187 survival and vegetation distribution. However, the relationship between plant primary strategies  
188 and climate has not previously been investigated, despite the potential importance of plant  
189 responses to climatic changes in shaping future vegetation. For the present study, a general  
190 prediction can be made that biomes characterized by climatic extremes should include species  
191 with a greater degree of functional specialisation. For example, in the desert biome plants



192 survive using contrasting life histories that can be summarized as essentially ‘ephemeral  
193 therophyte’ or ‘long-lived and durable’ (Chesson *et al.* 2004). We can thus predict that the CSR  
194 signature of the desert biome will be polarized between extreme R- and S-selected strategies,  
195 and that these too are correlated with climatic factors, particularly precipitation seasonality.  
196 Montane grasslands and alpine herbaceous vegetation are known to exhibit CSR strategies that  
197 range between R- and S-selection, with C-selection relatively rare (Caccianiga *et al.* 2006;  
198 Pierce *et al.* 2007a,b), but these studies have investigated specific plant communities and have  
199 not enjoyed the opportunity for comparison with the range of strategies evident within the  
200 biome as a whole, or indeed with other biomes. Certain biomes, such as tropical moist broadleaf  
201 forest, have yet to be interpreted in a plant functional strategy/climate context. Thus a secondary  
202 aim of the present study was to apply the global CSR analysis tool to determine whether it is  
203 possible to discern broad patterns of plant functional variability and specialisation in response  
204 to climatic factors operating in biomes worldwide.

205

## 206 **Materials and methods**

### 207 TRAIT DATA

208 A total of 116979 plant functional trait records, composed of 38835 individual measurements  
209 of leaf area (LA; mm<sup>2</sup>), 48468 measurements of SLA (mm<sup>2</sup> mg<sup>-1</sup>), and 29676 of LDMC (%),  
210 measured from plants growing in nature were obtained from the TRY global trait database  
211 ([www.try-db.org](http://www.try-db.org); Kattge *et al.* 2011). This included traits from preceding databases such as the  
212 LEDA traitbase ([www.leda-traitbase.org](http://www.leda-traitbase.org); Kleyer *et al.* 2008). The dataset included records  
213 from all continents except Antarctica, from 16 countries and several biogeographical regions  
214 within many of these countries (species native range and typical biome information is  
215 summarised in Appendix Table S1, Supporting information). A total of 3068 species growing

216 in a wide range of biomes, including tropical woody vegetation of various types, were  
217 represented by complete sets of LA, LDMC and SLA data. Of these species, a subset of 371  
218 species was available for which sets of 14 whole-plant, leaf, flowering and seed traits were  
219 available, including the additional traits leaf nitrogen concentration (LNC), leaf carbon  
220 concentration (LCC), leaf dry weight (LDW), canopy height (CH), lateral spread (LS),  
221 flowering start (FS), flowering period (FP), seed mass (SM), seed volume (SVo), total mass of  
222 seeds (TMS) and seed variance (SVa) (these data are available from the TRY database and are  
223 also published as an appendix to Pierce *et al.* 2014a).

224 The number of replicate values for each trait of each species was typically between 10 to 15,  
225 but varied from a minimum of 3 to a maximum of 349. Nomenclature is reported in Appendix  
226 Table S1 (Supporting information) and follows the Missouri Botanical Garden Tropicos system  
227 ([www.tropicos.org](http://www.tropicos.org)). Additional taxonomic and growth habit information was obtained from the  
228 Encyclopedia of Life ([www.eol.org](http://www.eol.org)) and GBIF ([www.gbif.org/species/search](http://www.gbif.org/species/search)).

229

## 230 PRODUCTION OF A GLOBAL CSR ANALYSIS TOOL

231 Global calibration of the CSR tool involved an initial multivariate analysis (PCA) of the key  
232 leaf traits (as a method of determining the three-way relationship between traits rather than as  
233 an analysis of plant adaptation *per se*), regression of trait values against PCA axes, and the use  
234 of these regression equations to produce a Microsoft Excel spreadsheet. This spreadsheet aims  
235 to allow novel target species to be compared against the multivariate space over which the  
236 global dataset was ordinated.

237 First, a centred Pearson PCA was performed using XLSTAT 2012.5.01 software  
238 (Addinsoft, New York, USA) and Varimax rotation applied to the first two axes. As a small  
239 number of species with disproportionately large leaves are evident in the world flora, with most

240 species exhibiting smaller leaves, trait values were transformed to constrain the most extreme  
241 values and to provide distributions as close as possible to normality prior to PCA. In this case,  
242 LA data were standardised using the maximum value, followed by square root transformation  
243 (Podani 2007). LDMC data were logit transformed (logit transformation is considered a more  
244 appropriate method for proportion data with respect to traditional arcsine transformation;  
245 Warton & Hui 2011) and SLA data were log transformed.

246 Transformed trait values were regressed against values of the PCA axis along which the  
247 trait exhibited maximum variance (e.g. logSLA against PCA1). The regression equation  
248 describing the curve of best fit was then incorporated into a Microsoft Excel spreadsheet that  
249 used the equation to compare trait values for any given target species against the global  
250 spectrum for that trait. This effectively assigned target species three co-varying dimensions: a  
251 “LA dimension” based on PCA2, a “LDMC dimension” based on positive variability along  
252 PCA 1, and a “SLA dimension” based on negative variation along PCA1. As PCA values may  
253 be negative or positive, the minimum (i.e. the most negative) values along PCA axes were then  
254 determined for each trait and these were used as a constant, added to all values of each trait in  
255 order to translate the trait dimensions into an entirely positive space. The next spreadsheet  
256 function determined the maximum values, giving the range of values for each trait. In order to  
257 produce ternary coordinates (i.e. three coordinates for a triangular graph), a function was then  
258 added to the spreadsheet that summed the three dimensions and divided by 100, allowing  
259 determination of the proportional contributions of LA, LDMC and SLA for each species. Thus  
260 the resulting triangular ordination of species represented a “trade-off triangle” against which  
261 target species can be compared.

262 As no species exhibited zero leaf area or mass it was not possible for species to be ordinated  
263 along the axes themselves nor at the apices of the trade-off triangle. Thus a spreadsheet function  
264 was implemented that essentially expanded, along the three axes, the space occupied by species

265 to fill the entire ternary plot, resulting in full occupation of the triangle and thus positioning of  
266 species within the CSR triangle. This was achieved by multiplication of all values by a rescaling  
267 constant that allowed the maximum and minimum values to fully occupy the available range.  
268 The final spreadsheet (Appendix Table S2: ‘StrateFy’) is available online as Supporting  
269 Information, and incorporates all functions to easily allow the CSR analysis of novel plant  
270 species from leaf traits.

271

## 272 CORRESPONDENCE BETWEEN VARIATION IN 3 AND 14 FUNCTIONAL TRAITS

273 To test whether the three key leaf traits (i.e., LA, LDMC and SLA) can provide a reliable  
274 multivariate structure for assigning general ecological strategies to plants, we used the subset  
275 of species for which 14 vegetative and reproductive trait data were available without any  
276 missing data (see Pierce *et al.* 2014a). To this end, a co-inertia analysis (hereafter, COIA) is a  
277 general and flexible method that measures the concordance (i.e. co-structure) between two  
278 multivariate datasets that share the same objects (in this case, species; Dray *et al.* 2003). This  
279 approach was applied to quantify and test the association between two matrices: *i*) three traits  
280 per 371 species; and *ii*) fourteen traits for the same 371 species. The COIA provides a  
281 correlation coefficient (‘RV’) that measures the strength of the association between matrices.  
282 This coefficient is bounded between zero (i.e. no association) and one (i.e. maximum  
283 association), with significance (*p*-value) accessed by a Monte Carlo test (with 100,000  
284 permutations). To implement the COIA, a PCA was used for both matrices after data  
285 transformation to improve normality. Analyses were carried out using R software (R  
286 Development Core Team 2013) with the ade4 package (Dray & Dufour 2007).

287

## 288 COMPARISON WITH A LOCALLY-CALIBRATED METHOD

289 In addition to the new globally-calibrated method, CSR ternary triplets were also calculated  
290 using the local tool of Pierce *et al.* (2013; calibrated with six traits for the Flora of Italy) and  
291 regression of values obtained using both methods was also performed in order to allow  
292 comparison between the locally and globally-calibrated techniques.

293

#### 294 A TEST USING KNOWN VEGETATION CHANGES ALONG SUCCESSION

295 In order to test whether the CSR analysis method agreed with expectations of vegetation  
296 responses to an environmental gradient, the StrateFy tool was used to calculate CSR strategies  
297 for the species characteristic of four phytosociological syntaxa (i.e. plant communities *sensu*  
298 Braun-Blanquet 1925) associated with a sequence of vegetation development encompassing a  
299 primary succession and related pasture vegetation. Specifically, in the European Alps, mobile  
300 screes represent highly disturbed environments where vegetation is composed of annual  
301 therophytes (phytosociological syntaxon *Thlasietea rotundifolii* Br.-Bl. *et al.* 1947). With the  
302 development of the vegetation and stabilisation of scree debris (and where topography and  
303 aspect result in long-lying snow cover) snowbed vegetation arises and is characterised by a  
304 mixture of nano-phanerophytes and hemicryptophytes (*Salicetea herbaceae* Br.-Bl. *et al.* 1947;  
305 Tomaselli 1997). This can develop further on acid, nutrient poor soils into a climax vegetation  
306 dominated by slow-growing graminoids such as the sedge *Carex curvula* and the grass *Festuca*  
307 *halleri* (phytosociological alliance *Caricion curvulae* Br.-Bl. 1925) (Tomaselli & Rossi 1994).  
308 When these unproductive siliceous grasslands experience grazing by large domestic livestock  
309 dominance shifts towards the rhizomatous mat-grass *Nardus stricta* and the vegetation alliance  
310 is characterised by greater floristic richness than that evident for *Caricion curvulae* (i.e.  
311 syntaxon *Nardion strictae* Br.-Bl. in Br.Bl. & Jenny 1926; Gennai *et al.* 2014). Grazing of  
312 alpine pastures increases nutrient turnover rates and selective grazing and the patchy

313 concentration of nutrients following defecation are thought to provide contrasting microsites  
314 for a range of life histories, fostering species richness, but with dominant grass species  
315 nonetheless exhibiting conservative leaf economics and stress-tolerance (Pierce et al. 2007a,b).  
316 We expected that along this vegetation sequence plant communities would shift from R-  
317 selection towards S-selection and ultimately, in the *Nardion* pasture, to an intermediate,  
318 relatively C-selected mean strategy with greater range of strategies apparent.

319

## 320 GLOBAL FOURTH-CORNER AND RLQ ANALYSES OF CSR

### 321 STRATEGY/ENVIRONMENT RELATIONSHIPS

322 Globally, the combined fourth-corner and RLQ method of Dray *et al.* (2014) was used to test  
323 the relationship between CSR strategies and environmental variation within biomes. Fourteen  
324 biomes were defined according to Olson *et al.* (2001), and are listed as part of Appendix Table  
325 S1 (Supporting information). Information regarding the biome(s) within the native range of  
326 each species was obtained from the comparison of the global distribution of biomes with the  
327 georeferenced records of each species (from GBIF) occurring inside its native range. The native  
328 range of each species was obtained from sources such as GRIN taxonomy for plants ([www.ars-grin.gov/cgi-bin/npgs/html/tax\\_search.pl?language=en](http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl?language=en)), eMonocot (<http://emonocot.org>) and  
329 Catalogue of Life ([www.catalogueoflife.org/col/search/all](http://www.catalogueoflife.org/col/search/all)). Additionally, we investigated the  
330 CSR strategies evident for life-form categories (tree, shrub, liana, graminoid, forb (i.e.  
331 herbaceous dicot), herbaceous vine, annual and biennial herb, perennial herb) and for  
332 taxonomic families that were represented by a minimum of 30 species in the dataset.

334 The fourth-corner and RLQ approach involved the simultaneous use of three matrices: *i*) a  
335 ‘community’ matrix with sample sites in rows and species in columns; *ii*) an environmental  
336 matrix with sample sites in rows and environmental variables in columns; and *iii*) a functional

337 matrix with traits in rows and species in columns. The fourth-corner approach tests the  
338 relationship between each species trait and each environmental variable, while the RLQ  
339 analysis tests the co-structure between all species traits with all environmental variables (Dray  
340 *et al.* 2014).

341 The functional matrix was defined by the 3068 species with three traits (i.e., C, S, R  
342 percentages). The 14 world biomes (defined by Olson *et al.* 2001) were treated as sampling  
343 sites, and the presence (incidence) of the 3068 species in these biomes was equivalent to a  
344 community matrix. To generate the environmental matrix, we assessed average environmental  
345 characteristics for each biome using bioclimatic variables (temperature seasonality, annual  
346 mean temperature, precipitation seasonality, and annual precipitation) for the recent half-  
347 century (1950-2001) obtained from the WorldClim project (Hijmans *et al.* 2005), in addition to  
348 global potential evapo-transpiration (Trabucco & Zomer 2009), at a spatial resolution of  
349  $0.0083^\circ$  ( $\sim 1 \text{ km}^2$ ). Temperature and precipitation seasonality was calculated as the standard  
350 deviation of monthly values multiplied by 100, and precipitation seasonality as the coefficient  
351 of variation of monthly values (Hijmans *et al.* 2005). In order to obtain unbiased averages for  
352 each biome, we created 200,000 uniformly random points for the entire globe, covering all  
353 terrestrial biomes, using the package *gismo* for R (R Development Core Team 2013). To  
354 conduct the RLQ analysis, a correspondence analysis was used for the community matrix, while  
355 a PCA was used for the functional and environmental matrices. For the PCA applied to the  
356 functional matrix, species were weighted by their overall relative frequency across biomes (i.e.  
357 the number of biomes in which each species occurred), whereas for the PCA applied to the  
358 environmental matrix, biomes were weighted by the overall frequency of species observed  
359 (Dray & Dufour 2007). Separate fourth corner and RLQ analyses were conducted for each  
360 biome, each analysis involving only species occurring in that biome. Significance was obtained  
361 through a Monte Carlo test based on the total co-inertia, using the combined null models 2

362 (permutation of sampling sites) and 4 (permutation of species) with 50,000 permutations per  
363 test (Dray *et al.* 2014). Analyses were carried out using R software (R Development Core Team  
364 2013) with the ade4 package (Dray & Dufour 2007).

365

## 366 **Results**

367

### 368 'WIDE COVERAGE, FEW TRAITS' VS. 'RESTRICTED COVERAGE, MANY TRAITS'

369 We found a strong and highly significant concordance between the multivariate space produced  
370 by three and 14 traits ( $RV = 0.597$ ;  $p < 0.001$ ; Fig. 1): i.e. there was a relatively small loss of  
371 information when only three leaf traits were used instead of 14 traits, and the multivariate plant  
372 functional space described by leaf traits alone was representative of whole plant functional  
373 variation (Fig. 1).

374

375

### 376 A GLOBAL CSR ANALYSIS METHOD

377 The three-way trade-off between LA, LDMC and SLA for the 3068 species of the main global  
378 dataset, presented in Fig. 2, confirmed that variation in LA was orthogonal to variation in SLA  
379 and LDMC in the world flora. Indeed, SLA and LDMC values ranged in opposite directions  
380 between two extremes (negative and positive, respectively) of the first axis of variability  
381 (PCA1) and thus an axis of leaf economics (Fig. 2a; for eigenvalues see Fig. 2b). The second  
382 axis of variability (PCA2) was delimited by leaf area, with large leaves evident only at  
383 intermediate leaf economics (Fig. 2a): species with extremely acquisitive or extremely  
384 conservative leaves were consistently small (Fig. 2a), confirming that high values of LA, SLA  
385 and LDMC were mutually exclusive in the global dataset. In other words, dense, tough leaves



386 were not large; soft, acquisitive leaves were not tough and conservative; only leaves with  
387 intermediate economics were large.

388 Transformed leaf area was highly and positively correlated with PCA2 ( $R^2=0.998$ ,  
389  $p<0.0001$ ) following the polynomial linear equation detailed in Fig. S1a. Transformed LDMC  
390 was strongly and positively correlated with PCA1 ( $R^2=0.794$ ,  $p<0.0001$ ) following the equation  
391 presented in Fig. S1b. Log SLA was strongly and negatively correlated ( $R^2=0.782$ ,  $p<0.0001$ )  
392 with PCA1 following the equation shown in Fig. S1c. These equations allowed comparison of  
393 target plant species with the trade-off between these traits, and thus determination of the CSR  
394 strategy (see Fig. 3 and the practical tool available as Appendix S2; 'StrateFy').

395

#### 396 COMPARISON WITH A LOCALLY-CALIBRATED METHOD

397 When the degree of C-, S- and R-selection calculated by the globally-calibrated method were  
398 regressed against C, S and R values calculated using the method of Pierce *et al.* (2013), the  
399 results were strongly and positively correlated with one another. Specifically, for the degree of  
400 C-selection determined by both methods,  $R^2=0.920$ ,  $F=9398.1$ ,  $p<0.0001$ , for S-selection  
401  $R^2=0.891$ ,  $F=24968.3$ ,  $p<0.0001$  and for R-selection  $R^2=0.866$ ,  $F=19725.1$ ,  $p<0.0001$   
402 (Supplementary Fig. S2).

403

#### 404 A TEST USING KNOWN VEGETATION CHANGES ALONG SUCCESSION

405 The CSR strategies evident for species characteristic of primary succession from scree  
406 vegetation to siliceous alpine grassland, terminating with alpine *Nardus* pasture, are evident in  
407 Fig. 4. Pioneer vegetation on screens, as expected, was characterised by mainly R-selected  
408 species and exhibited an R-selected mean strategy (C:S:R = 12:0:88 %). Species characteristic

409 of vegetation at an intermediate point along the succession exhibited a mean strategy of SR  
410 (4:58:37 %) and species of the climax vegetation exhibited a high degree of stress tolerance  
411 (mean strategy = 6:94:0 %; Fig. 4a). Under pasture, siliceous alpine grassland species exhibited  
412 a wider range of strategies encompassing C/CR-selected species such as *Gentiana punctata*, S-  
413 selected *Nardus stricta* (3:97:0 %), R/CR-selected species such as *Campanula barbata* (37:0:63  
414 %) and a mean of CR/CSR-selection (40:24:36 %; Fig. 4a). The overall trajectory of primary  
415 succession in this context is thus characterised by an initial shift from R- to S-selection, with  
416 management increasing the range of strategies present and including a higher degree of C-  
417 selection relative to the other vegetation types.

418

#### 419 CSR STRATEGIES EVIDENT WITHIN BIOMES GLOBALLY

420 The CSR strategies evident within biomes were calculated using the globally-calibrated CSR  
421 analysis tool and are shown in Fig. 5 (details of CSR strategies for each species within every  
422 biome are listed in Appendix S1, Supporting information). Tropical and subtropical broadleaf  
423 forest (both moist and dry forest biomes) exhibited a broad range of strategies but these were  
424 highly clustered around CS/CSR-selected median strategies (for both biomes, median C:S:R =  
425 43:42:15%; Fig. 5a,b). Tropical and subtropical coniferous forests also exhibited a median  
426 CS/CSR strategy that reflected a slightly greater number of S- and R-selected species at the  
427 expense of C-selection (32:46:22%; Fig. 5c). Tropical and subtropical grasslands, savannas and  
428 shrublands were highly represented by CS/CSR-selected species (34:51:15%; Fig. 5g). In  
429 contrast, biomes such as temperate broadleaf and mixed forests (Fig. 5d) and temperate  
430 coniferous forests (Fig. 5e) exhibited a SR/CSR-selected median strategy and a wide range of  
431 CSR strategies for individual species, filling the CSR triangle relatively uniformly. This  
432 denoted the presence and the even distribution of the full gamut of ecological strategies in these

433 biomes. Deserts also exhibited a range of CSR strategies, with a CSR-selected median (Fig.  
434 5m). Other biomes exhibited variation between relatively restricted strategy variation to wide  
435 variation (Fig. 5).

436 Fourth-corner and RLQ analyses for tropical and subtropical broadleaf forest (both moist  
437 and dry forest biomes) (Fig. 6a,b) showed that C- and S-selection were highly correlated with  
438 environmental variables: positively with annual mean temperature, annual precipitation and  
439 global potential evapo-transpiration, but negatively with temperature seasonality ( $p < 0.05$ , and  
440 in some cases  $p < 0.01$  or  $p < 0.001$ ). R-selection exhibited the exact opposite association with  
441 environmental variables. In contrast, no significant correlation was found between CSR  
442 strategies and environmental variables in temperate broadleaf and coniferous forests (Fig. 6d,e).  
443 A wide range of CSR strategies was evident in the desert biome that were significantly  
444 correlated with environmental variables: C- and S-selection were positively correlated with  
445 annual mean temperature, precipitation seasonality and potential evapo-transpiration, and  
446 negatively with temperature seasonality, with R-selection exhibiting contrasting correlations  
447 with these factors (Fig. 6l).

448

#### 449 CSR STRATEGIES WITHIN GROWTH HABIT CATEGORIES AND FAMILIES

450 Different growth habit categories exhibited variation in overall and median CSR strategies (Fig.  
451 S3). Trees were clustered around a CS median strategy, with no R-selected trees apparent  
452 (C:S:R = 43:47:10%; Fig. S3a) and shrubs centred around an S/CSR strategy (20:61:20%; Fig.  
453 S3b). Lianas were relatively specialised and clustered around CS/CSR-selection (52:35:14%;  
454 Fig. S3c). Graminoids exhibited a strong S-selected component, with variation around an  
455 S/CSR median strategy (14:56:29%; Fig. S3d). Forbs (herbaceous dicots) occupied the entire  
456 triangle and exhibited a comparatively generalist R/CSR strategy (30:20:51%; Fig. S3e).

457 Annual herbs exhibited an R/CSR median strategy (25:14:61%), with species clustered towards  
458 R-selection (Fig. S3g). Perennial herbs had an SR/CSR median strategy (25:35:41%) and  
459 occupied the entire triangle (Fig. S3h).

460 Some plant families were predominantly R-selected (e.g. Brassicaceae, Campanulaceae,  
461 Caryophyllaceae, Plantaginaceae; Fig. S4d,e,g,p), and others were dominated by S-selected  
462 species (Cyperaceae, Ericaceae, Juncaceae, Salicaceae; Fig. S4h,i,l,w) or were clustered around  
463 a relatively S-selected point (e.g. Rosaceae; 28:49:2%, S/CSR; Fig. S4u). Poaceae exhibited a  
464 median strategy of S/CSR (15:53:33%; Fig. S4q) and varied greatly between strategy extremes.  
465 A small number of families exhibited a relatively high degree of C-selection, such as Apiaceae  
466 (47:25:28%, C/CSR; Fig. S4a).

467

468

469

## 470 **Discussion**

471 The globally-calibrated CSR analysis method allowed strategies to be determined for a wide  
472 range of vascular plant species worldwide from habitats as diverse as tropical broadleaf rain  
473 forest, desert shrublands, mangroves and alpine pasture. The use of a small number of leaf traits  
474 has the advantage that large numbers of individuals or species comprising vegetation can be  
475 rapidly measured and compared. Indeed, studies of strategy variation within and between plant  
476 communities are currently applied inconsistently due to methodological constraints and  
477 measurement issues, but many of these can now be avoided due to the simplicity of the new  
478 method. For example, Schmidtlein, Feilhauer & Bruehlheide (2012) mapped CSR strategies  
479 across landscapes as a general indicator of changes in plant function across a mosaic of  
480 environments, but the traits used, and thus the overall analysis, were limited to herbaceous

481 species and grassland vegetation. The current method will allow functional comparison of a  
482 much more inclusive set of vegetation types worldwide and will allow plant function to be  
483 considered in the broadest possible context. Despite the simplicity of the method, we have  
484 shown it to broadly represent plant functioning and to be consistent with expected patterns of  
485 plant function and along primary succession as predicted by traditional phytosociological  
486 interpretation of vegetation.

487 Application of the CSR analysis to biomes worldwide revealed that certain biomes are  
488 characterised by relatively functionally-restricted floras (i.e. clustered within particular zones  
489 of the CSR triangle), such as tropical and sub-tropical grasslands (median strategy CS/CSR;  
490 Fig. 5g). Others, sometimes despite the prevalence of extreme abiotic conditions, host  
491 comparatively uniform strategy distributions and wide variation within the CSR triangle. For  
492 example, deserts and xeric shrublands (Fig. 5m) include highly contrasting CSR strategies that  
493 reflected the presence of both xeromorphic stress-tolerators (e.g. *Larrea divaricata*; C:S:R =  
494 1:99:0 %, S) and ruderal annual herbs (e.g. *Claytonia perfoliata*, 21:0:79 %, R/CR; Appendix  
495 S1, Supporting information), some of which occupy locally humid sites (e.g. R/CR-selected  
496 *Mimulus guttatus*). The idea that biological diversity in arid environments depends on highly  
497 contrasting perennial and annual life histories, microsite differences and niche differentiation  
498 is already well established (e.g. Chesson *et al.* 2004). The value of CSR analysis is that it  
499 provides a quantitative method for comparing plant function between sites and geographic  
500 locations where equivalent ecological roles are performed by taxonomically distinct actors: for  
501 example, *L. divaricata*, *Cuphea ericoides* (C:S:R = 0:100:0 %; S) or *Sebastiania ditassoides*  
502 (1:99:0 %; S).

503 As a further example of the wide applicability of the method beyond herbaceous vegetation,  
504 a range of CSR strategies was evident in tropical and subtropical forest biomes, but strategies  
505 were particularly clustered around the CS region as predicted (Fig. 5). Furthermore, a trade-off

506 was apparent between CS- and R-selection that was correlated with environmental gradients:  
507 CS-selection was associated with relatively stable situations (i.e. with less temperature  
508 seasonality) that were warmer and wetter, with greater annual precipitation and potential evapo-  
509 transpiration. Pioneer species in tropical forests were found to be relatively C-selected, such as  
510 Neotropical *Cecropia longipes* (C), *Ficus insipida* (C/CS), and *Urera baccifera* (C/CR;  
511 Appendix Table S1, Supporting information). Indeed, although disturbances and ruderal species  
512 are present in tropical forests, disturbance is not a prevalent factor in the same way that regular  
513 grazing or cutting determine the general character of pastures or meadows. Instabilities such as  
514 gap formation in tropical forests are local events that do not shape the forest in its entirety. Gap  
515 formation in particular is characterised by a pulse of light availability, and the ensuing  
516 competition apparently favours C-selection with succession proceeding relatively uninterrupted  
517 towards a closed tree canopy. Canopy tree species in tropical moist forest were shown to exhibit  
518 a stress-tolerance component (e.g. *Brosimum alicastrum*, CS; *Platypodium elegans*, CS/CSR;  
519 *Prioria copaifera*, CS). This perhaps reflects local sequestration of resources in long-lived  
520 tissues in later successional stages (Grime 2001), or increasing adaptation to drought tolerance  
521 (Engelbrecht *et al.* 2007; Baltzer *et al.* 2008). R-selected tropical rainforest species were  
522 evident, and potentially occupy specific microsites at fine scales. The high diversity of tropical  
523 forests may also partly be related to specific, single traits operating during the life-cycle, such  
524 as flowering and fruiting characters and symbioses (Grime & Pierce 2012). The many and  
525 varied mechanisms proposed to explain higher diversity at low latitudes (discussed by Gaston  
526 2000) probably apply as much to functional diversity as they do to taxonomic diversity, with  
527 geographic area and environmental stability (both seasonal and historical) being amongst the  
528 most evident factors affecting the creation of species richness.

529 Globally, the variation in strategies within biomes is likely to be influenced by the presence  
530 of contrasting growth forms. Forbs exhibited extremely broad strategy diversity and a generalist

531 median strategy of R/CSR, while trees ranged from C to S, with a CS median strategy similar  
532 to the CS/CSR median strategies evident in tropical forests (Fig. S3). The presence or absence  
533 of particular strategies at a given location is also likely to be affected by historical and  
534 phylogenetic constraints, with restriction of CSR strategies evident in some families but not  
535 others (Fig. S4).

536 The ‘strategy of a species’ as presented here is an average calculated from individuals of  
537 each species sampled at a particular location. Ecotypic variation throughout the home range of  
538 a species and phenotypic plasticity could potentially broaden the range of strategy variation for  
539 a given species and is a complicating factor when CSR strategies measured at one site are  
540 assumed to be relevant to other situations. Thus consideration of the CSR strategy of a species  
541 across a biome worldwide, as in the present study, should be interpreted with caution and should  
542 be seen as a summary or abstract for the species *in lieu* of trait data for all **populations**  
543 throughout the geographic range: this is the best that can be managed with current global  
544 datasets. **Future detailed study of the functional differences between biomes should ideally**  
545 **involve replicated surveys within a range of habitat types, and would be a massive undertaking**  
546 **involving a great deal of international cooperation and funds. Indeed,** the biome-level analysis  
547 presented here was **limited** by the lack of available data regarding the relative abundance of  
548 species within biomes at the global scale, and could not differentiate between prevalent and rare  
549 strategies. Thus median CSR strategies for each biome were not weighted and rare species will  
550 have had a disproportionally strong influence on the median strategy. Indeed, median strategies  
551 for biomes were generally located towards the centre of the triangle (Fig. 5).

552 Nonetheless, just as species richness and taxonomic identities are fundamental aspects of  
553 plant diversity, ‘strategy richness’ and the character of the strategies present are important  
554 aspects of ecological diversity that can now easily be quantified and compared. In local-scale  
555 studies in which relative abundance has been quantified, differing degrees of dominance

556 between CSR strategies are evident. For example, microsite differences and niche partitioning  
557 between contrasting CSR strategies have been invoked as a mechanism of coexistence and local  
558 biodiversity creation on Brazilian coastal Atlantic forest inselbergs (de Paula *et al.* 2015).  
559 Similarly, xeric sand calcareous grasslands in Europe include a mixture of relatively abundant  
560 stress-tolerator graminoids and larger numbers of infrequent ruderal or competitive-ruderal  
561 herbs, and CSR strategies are thus markedly different between dominant and subordinate plants  
562 at the centimetre scale (Pierce *et al.* 2014b). Future application of CSR analysis in further bio-  
563 geographical and ecological contexts worldwide will allow general conclusions with regard to  
564 how the equilibrium between dominant and subordinate species may change in response to  
565 environmental perturbation and with regard to the precise relationships between microsite  
566 factors and particular plant species.

567 In conclusion, the CSR analysis tool derived from 116979 records of leaf size and economics  
568 traits measured from 3068 species growing in nature worldwide has allowed a preliminary CSR  
569 analysis of major biome classes globally. The C, S and R values were in agreement with  
570 phytosociological observations of vegetation responses to an environmental gradient along a  
571 primary succession. Thus the global system is consistent with earlier locally-calibrated methods  
572 and studies of plant strategies, and can provide a functional explanation consistent with  
573 descriptive phytosociological methods of interpreting vegetation. A unified framework now  
574 exists for ecological strategy classification, using readily-determined leaf traits of plants as  
575 diverse as temperate ferns, lianas and tropical trees. The global strategy-environment  
576 relationships that the method can resolve will form a baseline for predicting which kinds of  
577 species can be expected to assemble where in response to environmental perturbation resulting  
578 from factors such as climatic or land use changes.

579



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590

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592

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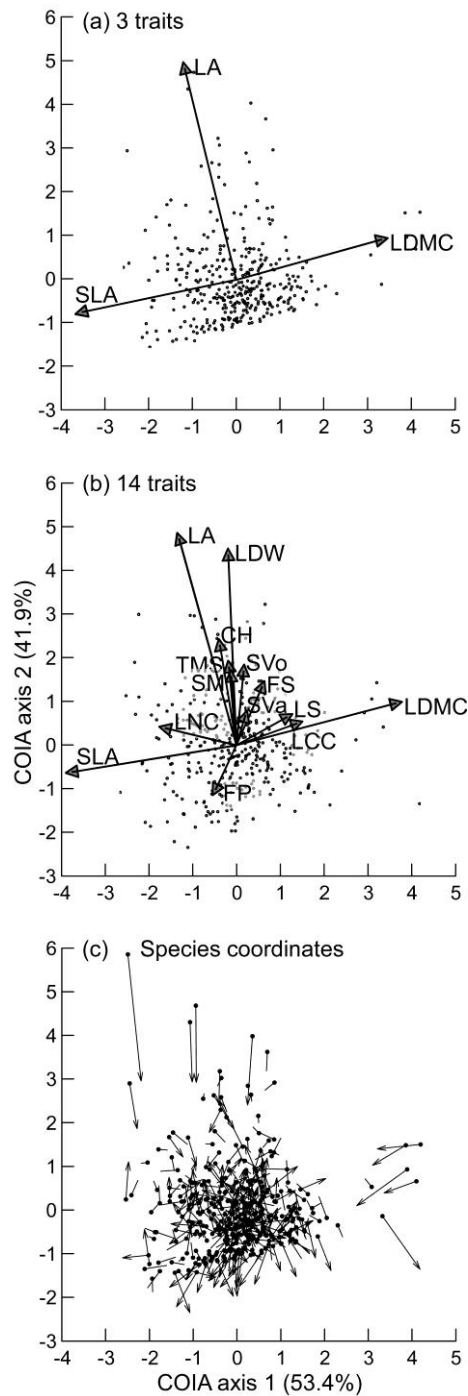
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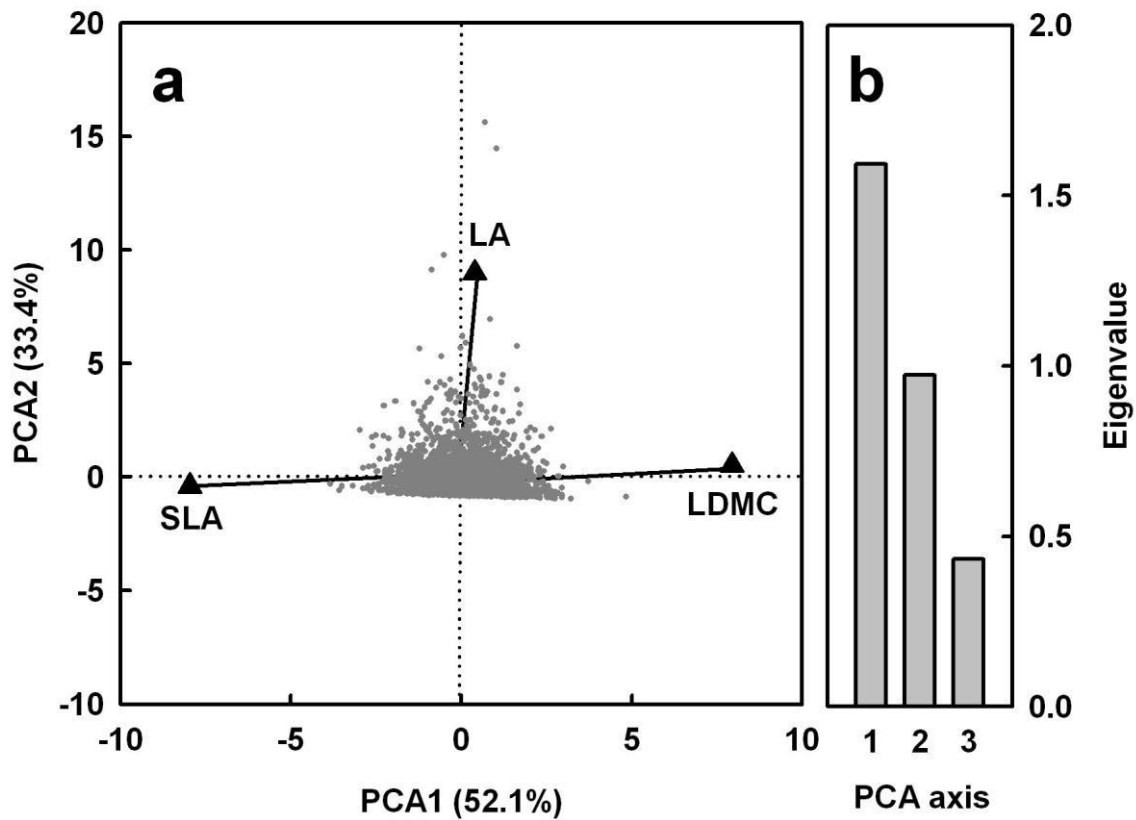
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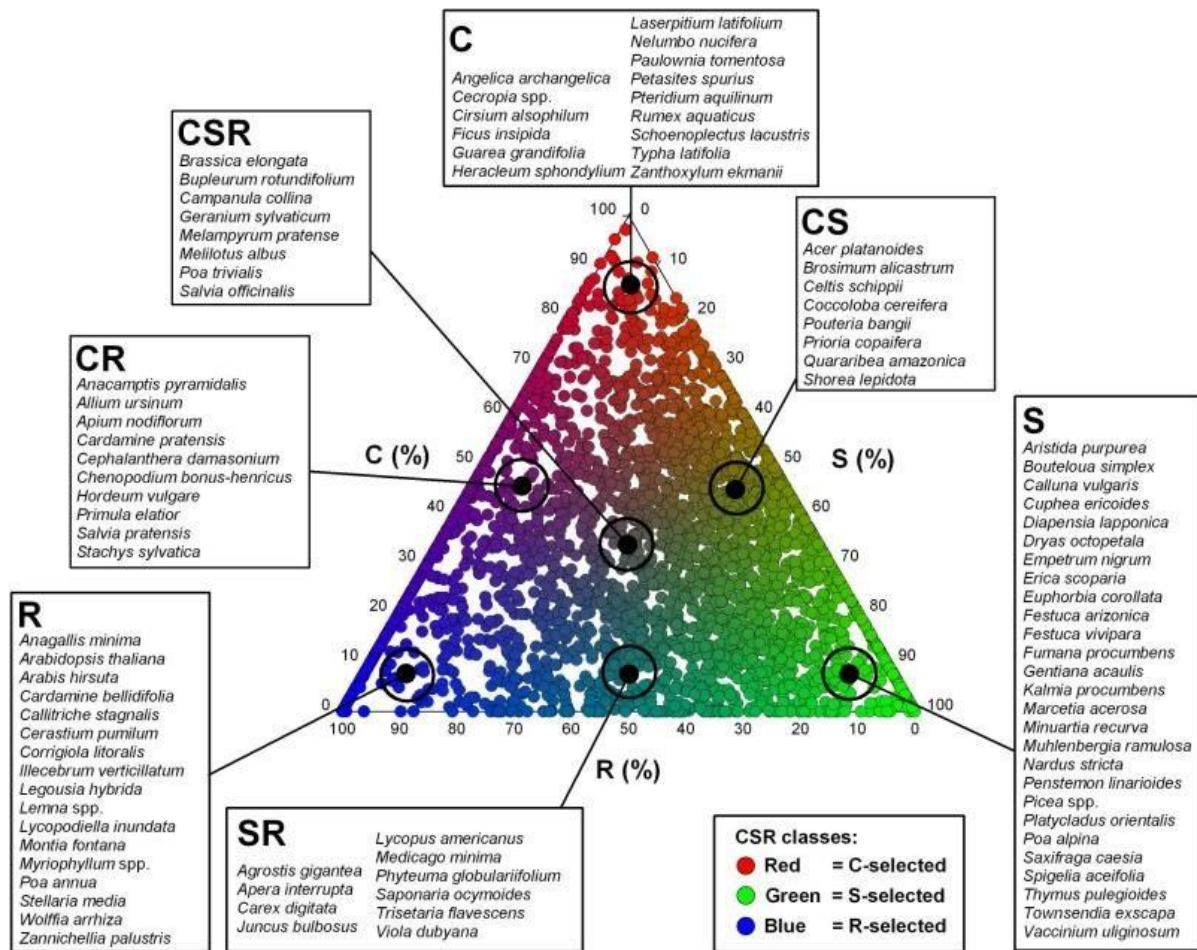
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**Fig. 1.** Projection of two main axes of co-inertia analysis (COIA) for 371 species: variable loadings for datasets including a). three traits, b). 14 traits, and c). A joint representation of species scores from the three trait (dots) and 14 trait (arrow tip) datasets. Percentage of variance explained by each axis (eigenvalues) are shown in the axis legend. Traits are CH: canopy height, FP: flowering period, FS: flowering start, LA: leaf area, LCC: leaf carbon concentration, LDMC: leaf dry matter content, LDW: leaf dry weight, LNC: leaf nitrogen concentration, LS: lateral spread, SLA: specific leaf area, SM: seed mass, SVo: apparent seed volume, SVa: seed variance, TMS: total mass of seeds. Data were log transformed to conform to normality and to constrain extreme values.





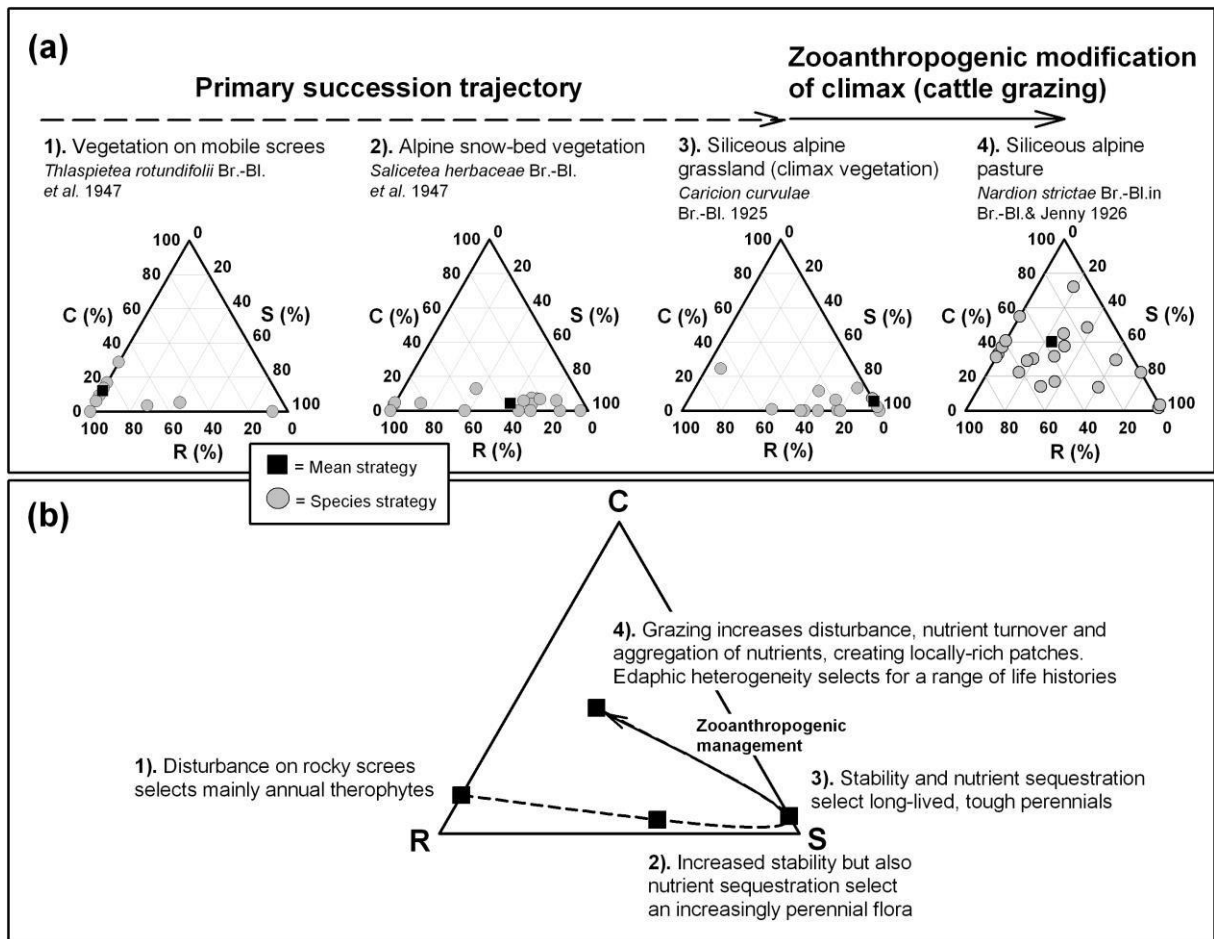
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 746 **Fig. 2. a).** Biplot showing the relationship between the three traits leaf area (LA), leaf dry matter  
 747 content (LDMC) and specific leaf area (SLA) for 3068 tracheophyte species from across the  
 748 world used as a basis for calibrating the CSR classification method (principal components  
 749 analysis; PCA), and **b).** eigenvalues for PCA axes. Data were transformed to constrain extreme  
 750 values (LA was standardized using the maximum value and then square root transformed, SLA  
 751 was log transformed, and LDMC logit transformed).  
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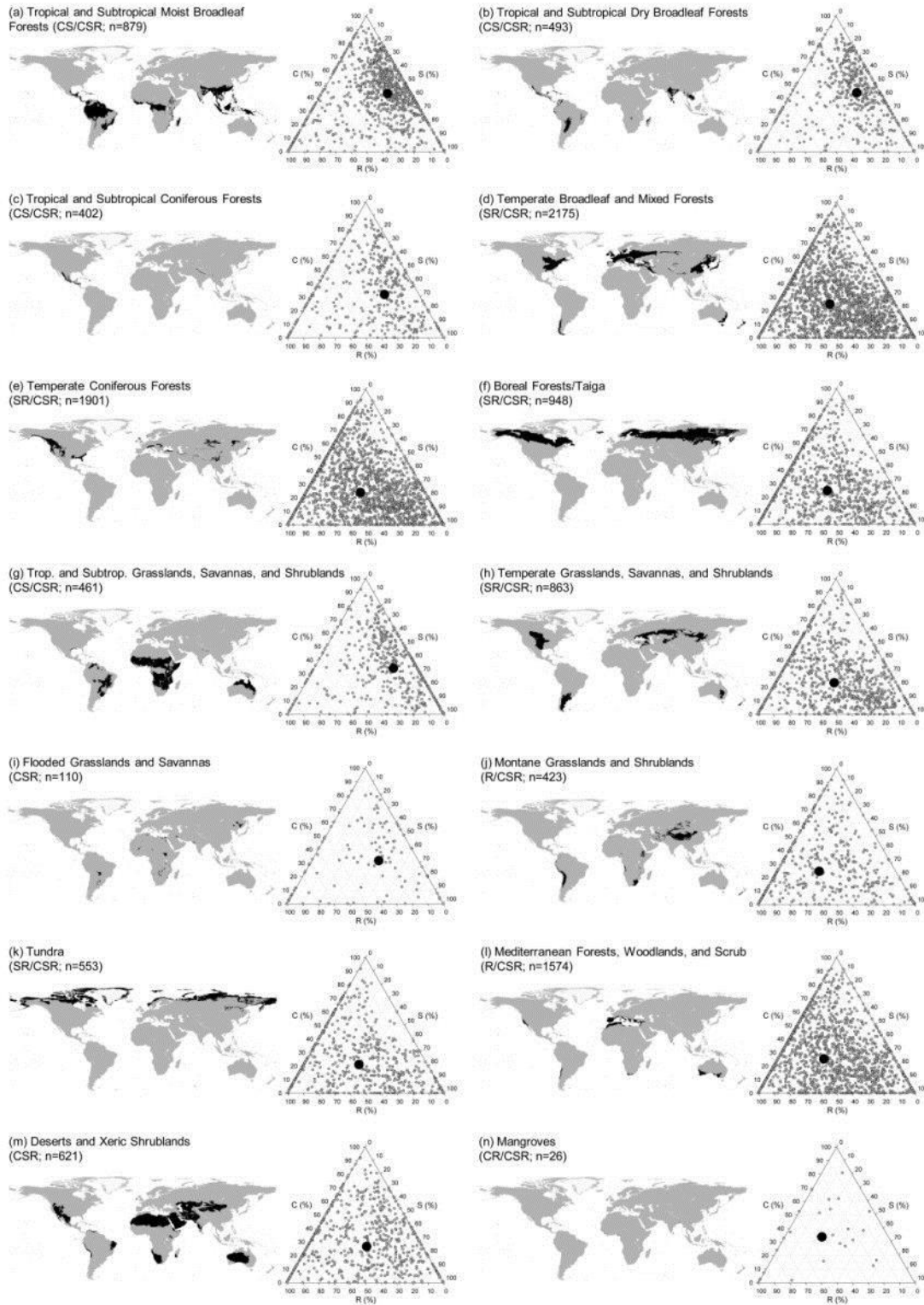
755 **Fig. 3.** Relative proportion (%) of C-, S- and R-selection for 3068 tracheophyte species  
756 measured from natural habitats across the world, using the globally-calibrated CSR analysis  
757 tool 'StrateFy'. Species names represent examples of the seven secondary CSR strategy classes  
758 (C, CS, CR, CSR, S, SR, and R) suggested by Grime (2001).

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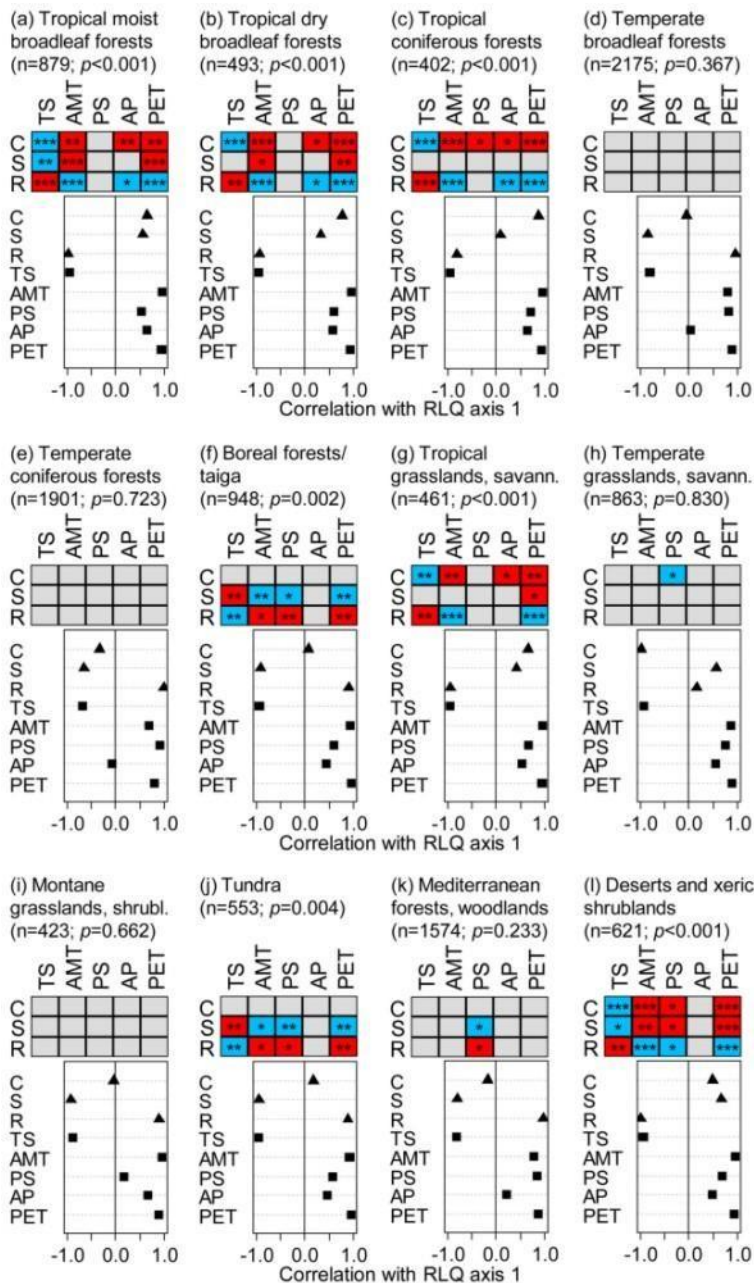
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**Fig. 4.** An example of local application of the globally-calibrated CSR analysis tool ‘StrateFy’ to species characteristic of phytosociological syntaxa undergoing primary succession following a trajectory from highly disturbed alpine scree slopes (*Thlasietea rotundifolii* Br.-Bl. et al. 1947) to siliceous grassland climax vegetation (*Caricion curvulae* Br.-Bl. 1925) further modified by cattle grazing to become alpine pasture (*Nardion strictae* Br.-Bl. in Br.Bl. & Jenny 1926). **a).** shows separate plant communities recognised by classical phytosociology as phases in the succession sequence, and **b).** a summary of the phytosociological ‘evolution’ of the vegetation represented as a trajectory in CSR space. Species data represent the mean of 10 replicate measurements for characteristic species of each syntaxon measured in the central Italian Alps.



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774 **Fig. 5.** Total (grey filled circles) and median (black filled circles) CSR strategies for 14 principal  
 775 biomes worldwide (as defined by Olson *et al.* 2001). For each biome, median CSR category  
 776 and sample size (number of species) are shown between parentheses. The distribution of each  
 777 biome in the world map is denoted by black areas.



778

779 **Fig. 6.** Global-scale fourth-corner analysis (coloured grids) and RLQ analysis (white dot charts)  
 780 of the relationship between CSR strategies and environmental variables within biomes: a).  
 781 tropical moist broadleaf forests, b). tropical dry broadleaf forests, c). tropical coniferous forests,  
 782 d). temperate broadleaf and mixed forests, e). temperate coniferous forests, f). boreal  
 783 forests/taiga, g). tropical grasslands, savannas and shrublands h). temperate grasslands,  
 784 savannas and shrublands, i). montane grasslands and shrublands, j). tundra, k). Mediterranean  
 785 forests and scrub, l). deserts/xeric shrublands. TS = temperature seasonality; AMT = annual  
 786 mean temperature; PS = precipitation seasonality; AP = annual precipitation; PET = global  
 787 potential evapo-transpiration). Fourth-corner statistic: red = positive, blue = negative, gray =  
 788 not significant, \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$  (n = number of species, p =  
 789 significance for the overall association between C-, S- and R-selection and environmental  
 790 variables).

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