

1 **CSRcalculator: a reproducible framework for understanding**

2 **plant ecological strategies**

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22 **Societal impact statement**

23 Understanding how plants respond to environmental change is essential for conserving
24 biodiversity and managing ecosystems under climate change. We developed
25 CSRcalculator, an open-source platform that brings together major competitor, stress-
26 tolerator, ruderal (CSR) models to make ecological strategy classification accessible,
27 reproducible, and scalable. The software enables users to rapidly translate plant trait
28 data into standardised ecological strategy classifications through a simple, user-friendly
29 interface, promoting consistent and reproducible analyses across studies. By improving
30 access to the CSR framework and supporting reproducible research, CSRcalculator
31 strengthens ecological monitoring, informs conservation and land management, and
32 enables more robust evidence for environmental policy and practice.

33 Summary

- 34 • The competitor, stress-tolerator, ruderal (CSR) theory, first proposed by John Philip
35 Grime, is a useful framework for understanding plant ecological strategies and
36 predicting responses to environmental changes and pressures. However, current
37 tools for assigning CSR strategies are limited to an Excel sheet format and have
38 yet to be integrated into modern computational platforms that enable
39 reproducible research.
- 40 • We present *CSRcalculator* (<https://github.com/TeddyGaskin/CSRcalculator>), an
41 open-source R package and shiny application that calculates CSR scores and
42 assigns strategies based on user-uploaded trait data. *CSRcalculator* supports
43 CSR assignments according to the three most prominent models: The original *soft*
44 *approach*, the global StrateFy, and a morpho-physiological model.
- 45 • The R package outputs a table including CSR scores, assigned strategies and
46 intermediate traits for the selected model. The shiny application produces this
47 same table alongside an interactive ternary plot to visualise the strategy
48 distribution and an optional summary table describing the overall CSR strategy
49 distribution, using metrics such as, the modal strategy, axis means, standard
50 deviations, and ranges. Group-level analyses calculate the same statistics across
51 user-defined categories.
- 52 • We demonstrate the utility and reliability of *CSRcalculator* by validating its outputs
53 against a published dataset and original CSR tools, as well as benchmarking its
54 performance across dataset sizes to confirm it scales efficiently to large datasets.

55

56 **Key Words:** competitive, CSR, plant strategies, ruderal, shiny application, stress-
57 tolerant, universal adaptive strategy theory.

58 **1 Introduction**

59 Understanding how plants interact with and adapt to their environment is fundamental
60 to addressing global ecological challenges, including biodiversity conservation and
61 climate change adaptation. Adaptations of a plant to their environment can be broadly
62 categorised into competitive (C), stress-tolerant (S), and ruderal (R) strategies (CSR;
63 Grime, 1974). Plants falling into the competitor category survive in relatively resource-
64 abundant and stable environments by investing resources into rapid growth for the pre-
65 emptive attainment of further resources, thus increasing competitive ability. In contrast,
66 stress-tolerant plants invest in their capacity to retain resources and repair damage
67 under stress in response to resource-limited environments. Lastly, ruderal plants survive
68 in environments that undergo repeated destructive events, such as wildfires or human
69 activity, by investing in their reproduction ability, allowing plants to regenerate despite
70 these events.

71 The CSR framework provides an effective means for interpreting the environmental
72 conditions underlying plant community structure. A classic example comes from
73 Massant et al. (2009), who showed that communities dominated by stress-tolerant
74 species are typically adapted to shaded conditions, whereas those with a higher
75 proportion of competitor species tend to persist in well-lit environments. More recent
76 work extends the utility of the framework across diverse ecological contexts. CSR
77 strategies have been used to characterise community composition along water and
78 salinity gradients and to reveal interactions with land-use practices such as grazing
79 (McIntosh-Buday et al. 2024). In parallel, CSR classifications have been shown to mirror
80 patterns of functional composition derived from community-weighted means of more

81 complex traits (Han et al 2024), highlighting their value as an efficient proxy when detailed
82 trait data are unavailable. Experimental studies further demonstrate that CSR scores can
83 predict community trajectories under imposed stress and disturbance (Li and Shippley
84 2017), underscoring the broader utility of CSR as both a diagnostic and predictive
85 framework for understanding community responses to environmental change.

86

87 Beyond describing present-day community structure, the CSR framework also provides
88 a valuable basis for predicting how species and communities will respond to
89 environmental change, helping identify potential “winners” and “losers” and informing
90 whether management intervention may be needed to preserve biodiversity. Recent
91 studies illustrate this predictive and diagnostic power across scales, as discussed below.

92 At the intraspecific level, Vasseur et al. (2018) demonstrated substantial variation in CSR
93 strategies among *Arabidopsis thaliana* ecotypes, with genotypes from colder climates
94 exhibiting more stress-tolerant strategies and many ecotypes showing plastic shifts in
95 CSR scores when grown in contrasting environments, although without strong
96 geographic structuring of these genotype-by-environment interactions. At the
97 community scale, Zhang et al. (2024) recently provided empirical support for long-
98 standing CSR theory by documenting the expected shift from ruderal toward stress-
99 tolerant strategies across 60 years of secondary succession, reinforcing the framework’s
100 ability to capture temporal trajectories in community assembly. Importantly, CSR theory
101 is now being incorporated into predictive ecosystem models: Wirth et al. (2024)
102 integrated CSR-based plant strategies into a land dynamic global vegetation model,
103 improving its ability to reproduce observed vegetation patterns and ecosystem

104 functioning under changing climate drivers. Together, these studies highlight how CSR
105 analyses enhance our capacity to interpret and forecast plant individual and community
106 responses to environment change, thereby underscoring the need for a reproducible
107 platform for their robust and consistent determination.

108 Plant species are arranged along CSR axes based on indexing for each strategy according
109 to specific functional traits, with classification determined by the coordinates for each
110 species within a triangular CSR space (Hodgson et al. 1999; Table 1). These functional
111 traits give insight into how a plant allocates its resources and are ideally representative
112 of the extreme trade-offs for each strategy; for example, competitive species tend
113 towards large leaf areas (LA), enabling greater resource acquisition, whilst stress-
114 tolerant species exhibit smaller specific leaf area (SLA) coupled with high leaf dry matter
115 content (LDMC) reflecting a thicker and tougher leaf to be more resistant to
116 environmental stresses (Chen et al. 2019). The original CSR framework scored plant
117 species in the C-axis according to canopy height, litter accumulation and lateral spread,
118 and in the S-axis according to the maximum relative growth rate in the seedling phase
119 (Grime, 1974). The R-axis, initially underdeveloped, was later refined to reflect the role of
120 disturbance in plant strategies (Grime, 1986), leading to a seven-type classification
121 system that included primary types (C, S, R) and intermediates (CR, SR, SC, and CSR).
122 Further acknowledgment of 12 tertiary classes resulted in the 19 CSR categories that are
123 currently used (Grime et al. 1988). Hodgson et al. (1999) later developed a model for CSR
124 classification based on measurable functional traits, including canopy height (CH),
125 lateral spread (LS), SLA, LDMC, flowering start (FS) and flowering period (FP), to provide
126 a standardised approach for classifying plant CSR strategies. To build this model, they
127 began by defining a set of “gold standard” CSR scores for plant species that had been

128 judged as C, S or R based on expert opinion and ecological data: competitiveness was
 129 quantified using a 'dominance index' derived from the relative abundance of a species
 130 within a stable environment; stress-tolerance was based on scores on the first principal
 131 component axis (PCA) from analyses of laboratory trait data for plants grown under
 132 controlled conditions designed to simulate resource-limited environments; and
 133 ruderality was estimated from co-occurrence with monocarpic species in disturbed
 134 habitats. These gold standard values were then used as dependent variables in multiple
 135 regression analyses, with combinations of transformed functional traits selected through
 136 trial and error to maximise the correlation with each axis. The resulting regression
 137 equations form the basis of the model, allowing raw C, S, and R scores to be calculated
 138 from trait data.

139 **Table 1. Required traits and their transformations per each competitor, stress-**
 140 **tolerator, ruderal (CSR) model. Conversions to these scales are provided by Hodgson**
 141 **et al. (1999).**

Trait	Abbreviation	Units	Required by	Transformation
Leaf Area	LA	mm ²	StrateFy	square root
Specific Leaf Area	SLA	mm ² /mg	StrateFy	Natural log
			Morpho-physiological	square root
			Hodgson	square root
Leaf Dry Matter Content	LDMC	%	StrateFy	Logit
			Morpho-physiological	square root
			Hodgson	square root
Canopy Height	CH	mm	Morpho-physiological	Natural log

			Hodgson	*Ordinal scale (1-6)
Flowering Period	FP	Months	Morpho-physiological	None
			Hodgson	none
Flowering Start	FS	1 = March or earlier ... 6 = August or later	Hodgson(non- Grasses only)	none
Lateral Spread	LS	*Categorical scale (1–6)	Morpho-physiological	none
			Hodgson	none
Leaf Dry Weight	LDW	mg	Morpho-physiological	Natural log + 3
			Hodgson	Natural log + 3
Net Photosynthesis	PN	mg CO ₂ /g dry weight/hour	Morpho-physiological	square root
Dark Respiration	RD	mg CO ₂ /g dry weight/hour	Morpho-physiological	square root
Leaf Nitrogen Content	LNC	mg/g	Morpho-physiological	square root
Leaf Carbon Concentration	LCC	mg/g	Morpho-physiological	square root

142

143 Two more recent models have further expanded the CSR framework. The StrateFy model
144 (Pierce et al. 2017) limits the selection of functional traits to leaf traits: specific leaf area
145 (SLA), leaf dry matter content (LDMC), and leaf area (LA), with SLA and LDMC calculated
146 from leaf fresh weight (LFW) and leaf dry weight (LDW). For this model, equations to
147 calculate CSR scores are derived from PCA of leaf trait data gathered from the TRY
148 database (www.try-db.org; Kattge et al. 2011). Specifically, the first two PCA axes are
149 used: axis 1 captured the trade-off between SLA and LDMC and represents a spectrum
150 from ruderal to stress-tolerant strategies; axis 2, influenced primarily by leaf area, helps

151 to differentiate competitive species. Transformed trait data were then regressed against
152 the PCA axis that captured the greatest variation for those traits, to generate equations
153 that estimate a species' position in CSR space. The minimal trait set makes the model
154 suitable for broad-scale ecological applications due to the easily accessible
155 measurements that are ubiquitous across a variety of plant species.

156 The morpho-physiological model developed by Novakovskiy et al. (2016) extends the
157 selection of functional traits with the inclusion of physiological traits such as
158 photosynthetic capacity (PN) and dark respiration (RD) for more accurate assignment of
159 CSR strategies, offering an alternative method for CSR classification. Similar to StrateFy,
160 this model is also based on PCA, but here it is applied to a trait dataset including
161 physiological and morphological traits. Axis 1 reflected most of the variation in
162 physiological traits whilst axis 2 captured a combination of nutrient content and
163 morphological traits, allowing species' positions to be inferred within CSR space.

164 The above-described models are currently limited to Excel-based tools or require manual
165 implementation. Both the StrateFy and Hodgson models are provided as a spreadsheet
166 tool (Pierce et al., 2017; Hodgson et al. 1999). The original paper describing morpho-
167 physiological model (Novakovskiy et al., 2016) also includes a supplemental Excel
168 spreadsheet that calculates C, S, and R percentages scores but it does not automatically
169 assign strategies. The reliance on spreadsheets can present some limitations, for
170 instance: scaling for large datasets or incompatibility with modern data science tools.
171 Moreover, these fragmented implementations restrict the reproducibility for these
172 methods across datasets, which leads to inconsistent outputs depending on how the

173 user implements these methods, in turn making it difficult to compare results or build
174 upon previous studies and advance our broader ecological understanding.

175 To address these issues, we introduce an R (R Core Team, 2024) package and Shiny
176 (Chang et al., 2024) application designed to calculate CSR strategies for plants allowing
177 the user to select either/or the original Hodgson's method (Hodgson et al. 1999), the
178 morpho-physiological model (Novakovskiy et al. 2016) and the StrateFy model (Pierce et
179 al. 2017). By hosting these various models on one open-source platform, this application
180 aims to integrate and validate these principal CSR frameworks while providing an
181 accessible platform for exploring ecological strategies across both scientific and applied
182 contexts.

183 **2 Material and Methods**

184 2.1 Tool structure and implementation

185 The *CSRcalculator* was developed in R and is available as both an R package and a Shiny
186 web application (<https://portal.bethchatto.co.uk/csr.php>; local version:
187 <https://github.com/TeddyGaskin/CSRcalculator-Shiny-application>; [Supporting Code](#)
188 [S1](#)). The standalone R package is available at:
189 <https://github.com/TeddyGaskin/CSRcalculator>, local install instructions are provided in
190 the readme files of each repository for offline use. The R package includes three model-
191 specific functions, `strateFy()`, `morphoPhys()`, and `hodgson()`, each of which can be
192 applied to a data frame containing species information and the necessary trait data:

193 `strateFy()`

194 Implements the StrateFy model. Arguments:

195 • data: A data frame containing species-level trait values.

196 • calcSLA: Logical. If TRUE, calculates SLA from LA and LDW if not provided.

197 Default is TRUE.

198 • calcLDMC: Logical. If TRUE, calculates LDMC from LFW and LDW if not

199 provided. Default is TRUE.

200 morphoPhys()

201 Implements the morpho-physiological model. Arguments:

202 • data: A data frame containing species-level morphological and physiological

203 trait values.

204 • calcLDMC: Logical. If TRUE, calculates LDMC from LFW and LDW. Default is

205 FALSE.

206 hodgson()

207 Implements the Hodgson et al. (1999) model. Arguments:

208 • data: A data frame containing species-level morphological and phenological

209 trait values.

210 • calcLDMC: Logical. If TRUE, calculates LDMC from LFW and LDW. Default is

211 FALSE.

212 • calcSLA: Logical. If TRUE, calculates SLA from LA and LDW. Default is FALSE.

213 • preferNonGrasses: Logical. If TRUE, applies the non-grass equations when

214 valid flowering start (FS) values (1–6) are present. Default is FALSE.

215 These functions follow the same workflow (Fig. 1) and return a data frame with additional
216 columns for calculated intermediate traits, the CSR scores and/or percentages and the
217 assigned strategy classes.

218 Alternatively, the Shiny web application provides a user-friendly interface for CSR
219 analysis without requiring R experience. The user interface includes an “Introduction”
220 panel which details usage guidance and model descriptions. The second panel, “CSR
221 analysis”, allows the user to upload and prepare trait data. Here, users can manually
222 assign traits to columns, select an averaging option and apply the chosen CSR model.
223 Results are displayed in an interactive table and ternary plot. Lastly, there is an “Output”
224 panel with options for displaying summary statistics and a degree of table and plot
225 customisation (Fig. 2).

226

227 2.2 CSR model calculations

228 CSR model calculations are based on Pierce et al. (2017), Hodgson et al. (1999), and
229 Novakovskiy et al. (2016). Full calculations are provided in the Supporting data (Methods
230 S1). Each model requires a specific set of traits with transformations applied prior to the
231 model calculations (Table 1). Where applicable, intermediate traits (e.g. for non-
232 succulents, $LDMC = [LDW * 100] / LFW$ or $SLA = LA / LDW$) are computed automatically
233 if not provided. Trait transformations are applied internally prior to model-specific CSR
234 calculations, following the methods described in the original publications.

235 Rather than accepting SLA and LDMC as direct inputs, the original StrateFy tool
236 calculates them from LA, LFW and LDW, allowing it to correct LDMC values for succulent
237 species before they enter the model. A succulence index is calculated for each species,

238 and where this value exceeds a threshold of 5, the LDMC calculation is adjusted to
239 prevent distortion from high water content leaves. After trait transformations, these
240 values are used in principal component analysis (PCA)-based equations to gather axis
241 scores for each CSR strategy. These scores are normalized and converted to percentages
242 for strategy assignment based on the minimum Euclidean distance between CSR
243 percentages of 19 predefined categories.

244 The morpho-physiological model, similarly, relies on two PCA-derived equations. Each
245 PCA axis represents a weighted linear combination of all transformed input traits. The
246 resulting PCA1 and PCA2 values are then projected onto CSR axes by measuring the
247 position of each species along lines that connect the origin point of PCA1 and 2 to the
248 centroid of known C, S and R groups. The species position along these lines is considered
249 their new coordinates in CSR space, or their C, S and R scores. A strategy class is
250 assigned based on the minimum Euclidean distance to one of 19 predefined CSR
251 categories, following the same classification method as the other models, the
252 `morphoPhys()` function will then convert these scores into percentages to be plotted onto
253 a ternary plot to visualize these results, any negative percentages are clipped to zero and
254 the remaining positive percentages are proportionally renormalized.

255 The Hodgson model is not based on PCA and instead calculates each axis score directly
256 from transformed trait values using two sets of algebraic equations, one for grasses and
257 one for non-grasses, they differ in trait inclusion as well as coefficients, affecting the
258 contribution of each trait to each axis score. Although the authors do not provide
259 rationale for this approach, it is likely due to shared morphological and phenological
260 traits that necessitate different trait weightings to ensure accurate strategy assignment

261 between these two groups. A C score is derived from squared values of CH and LS; the
262 non-grass version additionally includes squared log-transformed LDW. S score is
263 calculated from combining the squared transformations of LDMC, SLA, CH and LS.
264 Again, the non-grasses version diverges with the inclusion of the squared transformed
265 LDW. R score is calculated by applying a linear equation to FP, log-transformed LDW, and
266 square root-transformed SLA, the non-grass version includes FS as well. The resulting
267 axis scores are scaled to a coordinate space bounded between -2.5 and 2.5, then
268 classifying each species by identifying the nearest predefined strategy.

269 2.3 Model comparison and validation

270 All validation and cross-model comparisons used the dataset published by Novakovskiy
271 et al. (2021), which provides trait data and CSR outputs for 74 boreal and tundra species.
272 This dataset was uploaded to *CSRcalculator* and each model applied using default
273 parameters.

274 To validate the package, each function's output was compared against the corresponding
275 original tool: the StrateFy and Hodgson Excel spreadsheets, and the published CSR
276 percentages (Novakovskiy et al. 2021). We ran the same validation specifically for the
277 StrateFy model using a larger, more diverse dataset retrieved from TRY (Kattge et al.
278 2011), selecting species with the leaf traits required by the StrateFy model (LA, LFW and
279 LDW). Agreement between each model's *CSRcalculator* output and the corresponding
280 reference values was quantified using the R^2 and the root mean squared error (RMSE),
281 calculated separately for the C, S, and R axes of each model.

282 2.4 *CSRcalculator* performance benchmarking

283 To assess the performance of the *CSRcalculator* package, we benchmarked the three
284 model functions across randomly generated datasets ranging from 10 to 100,000
285 species, where the upper limit far exceeds a realistic dataset. Trait values were randomly
286 generated across biologically plausible ranges, with LDW constrained to a fraction of LFW
287 so that calculated LDMC remained valid. Runtimes were measured using the
288 microbenchmark package (Mersmann, 2024), repeating each evaluation 100 times, and
289 median runtime and throughput (samples processed per second) were calculated for
290 each model at each dataset size. Benchmarking was performed within R 4.4.2 (R Core
291 Team 2024) on a desktop computer (AMD Ryzen 7 9800X3D, 32 GB RAM) and repeated on
292 a laptop (Intel Core Ultra 5 235U, 16 GB RAM) for runtime comparison.

293 **3 Results**

294 3.1 Comparison and validation of CSR classification across models

295 Across all three models, *CSRcalculator* outputs showed close agreement with the
296 original tools and published values (Fig. S1). For both the grass and non-grass Hodgson
297 models, agreement was exact ($R^2 = 1.000$, RMSE = 0.00 for all three axes), as it was for
298 *StrateFy* ($R^2 = 1.000$, RMSE = 0.01). The morpho-physiological model also showed near-
299 exact agreement ($R^2 = 1.000$), with RMSE of 0.00, 0.11, and 0.12 for the C, S, and R axes
300 respectively. The small deviation on the S and R axes arose from a single species (*Ledum*
301 *decumbens*), the model produces a negative ruderal score; *CSRcalculator* clips this to
302 zero, whereas the reference assigns a small positive value instead. As for the additional
303 validation of the *StrateFy* function against the spreadsheet tool on a large, taxonomically
304 diverse dataset retrieved from TRY ($n = 6,913$ species) showed near-exact agreement,
305 with $R^2 = 1.000$ and RMSE = 0.03 across all three axes.

306

307 Here we present example results which can be reproduced by using the example trait
308 data embedded within the *CSRcalculator* application (Fig. 3; Table 2; Supporting Dataset
309 S1; Novakovskiy et al. 2021). A substantial number of species classified as
310 predominantly stress-tolerant by the morpho-physiological model are instead placed in
311 the CR region by the StrateFy and Hodgson models, which assign these same species an
312 S score of 0%. For example, *Paris quadrifolia* is classified S/CSR by the morpho-
313 physiological model (C 11.92 %, S 52.81 %, R 35.27 %), driven largely by its relatively slow
314 dark-respiration rate ($RD = 0.42 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$; Supporting Dataset S1). Both StrateFy
315 and Hodgson classify it R/CR with S = 0 %. Likewise, *Primula matthioli* is classified S/CSR
316 (C 15.79 %, S 56.55 %, R 27.66 %) by the morpho-physiological model, likely due to a low
317 net photosynthetic rate indicating a slower metabolism, a characteristic of other stress-
318 tolerating species ($PN = 1.93 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$; Supporting Dataset S1), yet the other
319 models place it in CR (S = 0 %). A further interesting observation was the shift of many
320 species towards more extreme positions, mainly towards the CS or CR boundaries within
321 the CSR triangle, when switching from the grass to the non-grass version of the Hodgson
322 model. This highlights the importance of incorporating the flowering period in defining
323 CSR of non-grasses where the inclusion of this trait is the only major difference between
324 grass and non-grass equations.

325

326 **Table 2. Summary table of competitor, stress-tolerator, ruderal (CSR)_analysis for**
327 **each model including the most common strategy types, the averages and standard**

deviation of CSR scores. Analysis based on trait data included in the supplementary data of Novakovskiy et al. (2021).

Statistic	Hodgson (grasses)	Hodgson (non-grasses)	StrateFy	Morpho-physiological
Modal Strategy	CR	CR	CR	C/CSR
Mean C%	45.98	51.92	33.18	33.00
Mean S%	20.25	10.17	24.55	35.48
Mean R%	33.77	37.90	42.27	31.52
SD C%	15.08	15.01	19.22	17.22
SD S%	19.51	17.92	25.34	18.03
SD R%	18.47	21.09	20.89	17.39
Min C%	22.67	26.09	1.02	0.00
Min S%	0.00	0.00	0.00	0.89
Min R%	2.74	0.00	0.00	0.00
Max C%	87.50	88.46	83.93	64.66
Max S%	68.49	68.18	98.98	74.15
Max R%	73.91	72.22	86.34	81.00

3.2 CSRcalculator Performance

For the R package, we assessed how runtime scales with dataset size by benchmarking each function across datasets from 10 to 100,000 samples (Fig. 4). For all three functions, runtime was near constant for small datasets and increased approximately linearly above roughly 1,000 samples, with throughput stabilising above this size; no abrupt changes in scaling were observed across the range tested. The three functions

performed near-identically, with minor differences likely due to the number of traits processed. A dataset of approximately 6,000 samples, comparable to a trait dataset retrieved from the TRY database (Kattge et al. 2011; Supporting Dataset S2), was processed in approximately 0.05–0.06 seconds for each model. Absolute runtimes will vary with hardware, but the scaling indicates that processing time remains proportional to dataset size at scale rather than degrading disproportionately as data volume grows. Benchmarking on a second, lower-specification machine produced the same scaling, with absolute runtimes approximately 1.3–1.4× longer across the tested range; for example, the 6,000-sample dataset was processed in approximately 0.08 seconds per model versus 0.055 seconds on the desktop.

4 Discussion

4.1 *CSRcalculator*: reproducibility, accessibility, and insight

The *CSRcalculator* tool was designed with three major goals in mind: reproducibility and accessibility of plant ecological analysis and integration of multiple CSR models into one platform. By implementing each model directly from its published equations and classification rules, the tool ensures that outputs are consistent with the original model sources. The open-source nature of *CSRcalculator* and the inclusion of any calculated intermediates in the table output further support transparency and reproducibility.

The tool is provided in two complementary forms. The Shiny interface allows users to upload their dataset, select a model, and immediately view CSR scores, strategy assignments, and ternary plots without requiring any coding or manual spreadsheet

manipulation. The accompanying R package provides the same workflow in scripted form up to the table output, ensuring that analyses can be repeated reliably across any dataset with the required plant traits and incorporated into larger analytical pipelines. Users can also reproduce the ternary plots using the plotly package (Sievert, 2020), with the exact plotting options available in the Shiny application code.

Although both forms implement the same underlying calculations, they suit different uses. Our benchmarking showed that the model functions scale approximately linearly with dataset size, with runtime ultimately bounded by available memory rather than by the calculations themselves. In practice, for very large datasets, the total runtime will likely be driven more by reading in the data rather than by the model calculations. The R package is therefore well suited to large datasets and to integration within scripted, reproducible workflows, where it can be applied to datasets as large as a user's hardware permits. This represents a marked practical improvement over the original spreadsheet tools, which require trait data to be entered or pasted manually and are not designed for application to large numbers of species at once. The Shiny application comfortably accommodates realistically sized datasets, but has a fixed upload limit of 30 MB, for the largest datasets, the R package will process the data more quickly and is the more practical choice.

The intuitive interface and immediate visual outputs of *CSRcalculator* make it particularly well suited for teaching trait-based ecology and for demonstrating how simple leaf traits can be translated into ecological strategies. For example, the tool could readily support an undergraduate practical in which students sample leaf traits across functional or phylogenetic diversity, or across contrasting environments, and analyse their data using

382 *CSRcalculator* to generate a dataset suitable for a scientific paper-style assignment.
383 Beyond formal teaching, the application also provides a practical resource for outreach
384 groups, garden practitioners, and conservation teams seeking to explore species'
385 functional strategies without the need for specialist software. In a conservation context,
386 CSR assignments at both individual and community levels offer valuable insights into
387 ecosystem function and resilience (as highlighted in the Introduction); readers interested
388 in broader applications are directed to the recent review of CSR theory and practice by Li
389 et al. (2025).

390 These advantages come with some limitations. As *CSRcalculator* applies each published
391 model directly to the trait data provided, the reliability of its outputs depends on the
392 quality and appropriateness of the input data, including the use of expected trait units.
393 As noted above, the Shiny application is best suited to interactive exploration, while very
394 large datasets are more efficiently handled through the R package. More broadly, strategy
395 assignments remain dependent on the model selected, an issue explored in detail in the
396 following section; *CSRcalculator* is intended to make these differences explicit rather
397 than to identify any single model as definitive.

398 4.2 Comparing CSR models

399 Analysis of the example dataset embedded within *CSRcalculator* revealed clear
400 differences in strategy assignment among the CSR models, driven by contrasting trait
401 selection and model structure. StrateFy represents the most parsimonious approach,
402 relying on three widely available leaf traits, making it well suited to large-scale analyses
403 where data availability is limited. However, this simplicity may constrain its ability to
404 capture the full range of ecological strategies. In contrast, the morpho-physiological

405 model incorporates a broader suite of traits, including gas exchange and nutrient
406 content, allowing it to resolve physiological trade-offs and distinguish species with
407 similar morphology but differing metabolic strategies.

408 Although both models derive CSR scores using principal component analysis, the
409 interpretation of their axes differs. In StrateFy, PCA axis 1 captures a trade-off between
410 ruderal and stress-tolerant strategies, with opposing loadings of SLA and LDMC, while
411 axis 2 is driven largely by leaf area and helps identify competitive species. In the morpho-
412 physiological model, axis 1 reflects physiological performance and axis 2 integrates
413 nutrient and morphological traits. Consistent with these differences, agreement
414 between models was highest for the ruderal axis (Spearman's $\rho = 0.68$) and substantially
415 lower for the competitive and stress-tolerant axes ($\rho = 0.28$ and 0.26 , respectively).

416 The Hodgson model occupies an intermediate position, relying on morphological and
417 phenological traits but excluding physiological variables. In the example dataset, it
418 frequently aligns with StrateFy, assigning zero stress-tolerance scores to species such
419 as *Oxalis acetosella*, despite the morpho-physiological model classifying them as
420 predominantly stress-tolerant. Unlike the PCA-based approaches, CSR scores in the
421 Hodgson model are derived from regression equations calibrated against “gold
422 standard” benchmarks for each strategy (Hodgson et al. 1999), based on dominance in
423 stable communities (C), responses to nutrient stress (S), and association with disturbed
424 habitats (R). As these benchmarks were developed largely from British flora, their
425 broader applicability may be limited. In addition, the use of separate equations for
426 grasses and non-grasses can substantially alter strategy assignments, underscoring the
427 need for careful model selection based on species identity and available trait data.

428 Taken together, these comparisons highlight that CSR strategy assignments are
429 inherently model-dependent and sensitive to both trait selection and underlying
430 analytical assumptions. *CSRcalculator* makes these differences explicit by allowing
431 users to apply and directly compare multiple CSR frameworks within a single,
432 reproducible platform.

433 4.3 Conclusion

434 This study introduces two tools that streamline analysis of ecological strategies via the
435 CSR framework: the open-source *CSRcalculator* R package and the accompanying shiny
436 web application. These tools offer a more accessible and reproducible approach to CSR
437 analysis. We have integrated the most prominent CSR models into one platform allowing
438 researchers to choose the most appropriate model for their dataset and scale of study.
439 In addition to facilitating current methods, the R package, and by extension shiny
440 application, provide a foundation for future model development. New CSR models can
441 be readily integrated into both tools, supporting the advancement and standardisation of
442 CSR analysis in modern plant ecology. *CSRcalculator* offers a reproducible, validated
443 platform for quantifying ecological strategies while supporting broader applications in
444 plant ecology, education, and sustainable landscape design.

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448 awarded to TG.

449 **Data Availability Statement**

450 All trait data used in this study were sourced from previously published materials
451 (Novakovskiy et al. 2021). An adapted data set from this source is included in the
452 *CSRcalculator* package (Supporting Dataset S1; Supporting Code S1). The TRY dataset is
453 included in the supporting material (Supporting Dataset S2).

454 The Shiny application is available at <https://portal.bethchatto.co.uk/csr.php>. Source
455 code is available on GitHub [https://github.com/TeddyGaskin/CSRcalculator-Shiny-](https://github.com/TeddyGaskin/CSRcalculator-Shiny-application)
456 [application](https://github.com/TeddyGaskin/CSRcalculator); <https://github.com/TeddyGaskin/CSRcalculator> as well as the tables used
457 in the app, a readme file with instructions of use and the code to run an example case.
458 See also an archived version in Zenodo (<https://doi.org/10.5281/zenodo.20673030>;
459 <https://doi.org/10.5281/zenodo.20673018>).

460 **Conflict of Interest Statement**

461 The authors declare no conflicts of interest.

462 **Author Contributions**

463 JF designed the research. TG developed the application with assistance from BC, MW and
464 JF. TG wrote the paper with assistance from JF. JF, BC, AC, KH, and ZN supervised the
465 research and discussed and approved the final version of the manuscript.

466 **Figure Legends**

467 Figure 1. Workflow summarising the functions in the *CSRcalculator* package for assigning
468 plant ecological strategies given trait data as input.

469 Figure 2. Overview of the competitor, stress-tolerator, ruderal (CSR) Calculator shiny
470 application. (A) model guides, (B) analysis panel with column selection, averaging

471 options and model application, (C) output panel with table and plot options, (D) main
472 panel presenting result

473 Figure 3. A comparison of ternary plot outputs for each competitor, stress-tolerator,
474 ruderal (CSR) model using the Novakovskiy, et al. (2021) supplementary data set. (A)
475 Hodgson (grasses) (B) Hodgson (non-grasses) (C) StrateFy and (D) morpho-physiological.
476 Plot points are drawn towards each corner based on their CSR scores, competitive
477 species to the top, stress-tolerators to the bottom left and ruderals to the bottom right.
478 Point colours are blended based on their CSR scores, blue is competitive, orange is
479 stress-tolerating and green is ruderal.

480 Figure 4. Runtime of the three CSRcalculator model functions (StrateFy, Hodgson, and
481 morphoPhys) across dataset sizes ranging from 10 to 100,000 samples. Points show
482 median runtime over repeated evaluations, with shaded bands indicating the
483 interquartile range. Both axes are log-scaled. Runtimes were measured using the
484 microbenchmark package.

485 **Supporting information**

486 Supporting Figure S1: Comparison of CSR scores produced by model sources and the
487 *CSRcalculator* application. R^2 and root mean square error (RMSE) are provided for each
488 comparison.

489 Supporting Dataset S1: Trait data and *CSRcalculator* output with reference outputs

490 Supporting Dataset S2: TRY dataset after processing through the *CSRcalculator* app,
491 appended with the excel tool output.

492 Supporting Methods S1: Equations and methods used for each model function in the
493 *CSRcalculator* R package.

494 Supporting Code S1: R code text files used in the *CSRcalculator* R package and shiny
495 application.

496 **References**

497 Chang, W., Cheng, J., Allaire, J., Sievert, C., Schloerke, B., Xie, Y., Allen, J., McPherson, J.,
498 Dipert, A. & Borges, B. (2024) *shiny: Web application framework for R*. R package version
499 1.10.0. Available at: <https://CRAN.R-project.org/package=shiny> [Accessed 3 May 2025].

500 Chen, H., Huang, Y., He, K., Qi, Y., Li, E., Jiang, Z., Sheng, Z. & Li, X. (2019) Temporal
501 intraspecific trait variability drives responses of functional diversity to interannual aridity
502 variation in grasslands. *Ecology and Evolution*, 9, 5731–5742.

503 Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*, 250, 26–31.

504 Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its
505 relevance to ecological and evolutionary theory. *The American Naturalist*, 111(982),
506 1169–1194.

507 Grime, J.P. (1986) Manipulation of plant species and communities. In: Bradshaw, A.D.,
508 Goode, D.A. & Thorpe, E. (eds.) *Ecology and design in landscape*. Oxford: Blackwell
509 Scientific, pp. 175–194.

510 Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative plant ecology: A functional*
511 *approach to common British species*. Dordrecht: Springer. Available at:
512 <https://doi.org/10.1007/978-94-017-1094-7>

513 Grime, J.P. (2001) *Plant strategies, vegetation processes, and ecosystem properties*. 2nd
 514 edn. Chichester: John Wiley & Sons.

515 Grime, J.P. & Pierce, S. (2012) *The evolutionary strategies that shape ecosystems*.
 516 Chichester: Wiley-Blackwell.

517 Han, X., Yao, J., Wang, R., Xu, Y., Huang, J., Ding, Y. & Zang, R. (2024) Effects of functional
 518 composition on plant competitors, stress-tolerators, ruderals ecological strategies in
 519 forest communities across different climatic zones. *Ecology and Evolution*, 14, e11580.

520 Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P. & Thompson, K. (1999) Allocating C-S-R
 521 plant functional types: A soft approach to a hard problem. *Oikos*, 85, 282–294.

522 Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönsch, G., et al. (2011) TRY – a
 523 global database of plant traits. *Global Change Biology*, 17, 2905–2935.

524 Kenney, A.M., McKay, J.K., Richards, J.H. & Juenger, T.E. (2014) Direct and indirect
 525 selection on flowering time, water-use efficiency (WUE, $\delta^{13}\text{C}$), and WUE plasticity to
 526 drought in *Arabidopsis thaliana*. *Ecology and Evolution*, 4(23), 4505–4521.

527 Kumarathunge, D.P. et al. (2018) ‘Acclimation and adaptation components of the
 528 temperature dependence of plant photosynthesis at the global scale’, *New Phytologist*,
 529 222(2), pp. 768–784.

530 Li, Y. & Shipley, B. (2017) An experimental test of CSR theory using a globally calibrated
 531 ordination method. *PLOS ONE*, 12(4), e0175404.

532 Liu, R.L., van Kleunen, M., Pierce, S., Chytrý, M., Guo, K., Pyšek, P. & Guo, W.Y. (2025)
 533 Grime’s CSR theory revisited: A whole-plant view of vascular plant functioning across
 534 contrasting environments. *Journal of Ecology*, 113(10), 3019–3036.

535 Massant, W., Godefroid, S. & Koedam, N. (2009) Clustering of plant life strategies on
536 meso-scale. *Plant Ecology*, 205, 47–56.

537 McIntosh-Buday, A., Sonkoly, J., Molnár, A., Szél-Tóth, K., Törő-Szijgyártó, V., Madar, S.,
538 Károlyi, E., Díaz Cando, P.E., Kovacsics-Vári, G., Tóthmérész, B. & Török, P. (2024) Grime's
539 ecological strategies reveal contrasting patterns in alkaline and loess grasslands. *Global*
540 *Ecology and Conservation*, 54, e03132.

541 Mersmann, O. (2024) *microbenchmark: accurate timing functions*. R package version
542 1.5.0. Available at: <https://CRAN.R-project.org/package=microbenchmark> [Accessed: 9
543 June 2026].

544 Novakovskiy, A.B., Maslova, S.P., Dalke, I.V. & Dubrovskiy, Y.A. (2016) Patterns of
545 allocation CSR plant functional types in Northern Europe. *International Journal of*
546 *Ecology*, 2016, 1323614.

547 Novakovskiy, A.B., Dubrovskiy, Y.A., Dalke, I.V. & Maslova, S.P. (2021) Plant CSR types in
548 the north: Comparing the morphological and morpho-physiological approaches.
549 *Physiology and Molecular Biology of Plants*, 27, 665–673.

550 Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P.,
551 Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J.,
552 Reich, P.B., Poorter, J., Wright, I.J., Ray, P., Enrico, A., Pausas, J.G., de Vos, A.C.,
553 Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter
554 Steege, H., van der Heijden, M.G.A., Sack, T., Blonder, B., Poschlod, P., Vaieretti, M.V.,
555 Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C. (2013) *New handbook for*

556 *standardised measurement of plant functional traits worldwide*. Australian Journal of
 557 Botany, 61(3), pp.167-234.

558 Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B.,
 559 Wright, S.J., Soudzilovskaia, N.A., Onipchenko, V.G., van Bodegom, P.M., Frenette-
 560 Dussault, C., Weiher, E., Pinho, B.X., Cornelissen, J.H.C., Grime, J.P., Thompson, K., Hunt,
 561 R., Wilson, P.J., Buffa, G., Nyakunga, O.C., Reich, P.B., Caccianiga, M., Mangili, F., Ceriani,
 562 R.M., Luzzaro, A., Brusa, G., Siefert, A., Barbosa, N.P.U., Chapin III, F.S., Cornwell, W.K.,
 563 Fang, J., Fernandes, G.W., Garnier, E., Le Stradic, S., Peñuelas, J., Melo, F.P.L., Slaviero,
 564 A., Tabarelli, M. & Tampucci, D. (2017) A global method for calculating plant CSR
 565 ecological strategies applied across biomes world-wide. *Functional Ecology*, 31, 444–
 566 457.

567 Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. and Villar, R. (2009) ‘Causes and
 568 consequences of variation in leaf mass per area (LMA): a meta-analysis’, New
 569 Phytologist, 182(3), pp. 565–588.

570 R Core Team (2024) *R: A language and environment for statistical computing*. Vienna,
 571 Austria: R Foundation for Statistical Computing. Available at: <https://www.R-project.org/>
 572 [Accessed 3 May 2025].

573 Sievert, C. (2020) *Interactive Web-Based Data Visualization with R, plotly, and shiny*.
 574 Chapman and Hall/CRC. ISBN 9781138331457. Available at: <https://plotly-r.com>

575 Vasseur, F., Sartori, K., Baron, E., Fort, F., Kazakou, E., Segrestin, J., Garnier, E., Vile, D. &
 576 Violle, C. (2018) Climate as a driver of adaptive variations in ecological strategies in
 577 *Arabidopsis thaliana*. *Annals of Botany*, 122, 935–945.

578 Wirth, S.B., Poyda, A., Taube, F., Tietjen, B., Müller, C., Thonicke, K., Linstädter, A., Behn,
 579 K., Schaphoff, S., von Bloh, W. & Rolinski, S. (2024) Connecting competitor, stress-
 580 tolerator and ruderal (CSR) theory and Lund Potsdam Jena managed Land 5 (LPJmL 5) to
 581 assess the role of environmental conditions, management and functional diversity for
 582 grassland ecosystem functions. *Biogeosciences*, 21, 381–410.

583 Wright, I.J. et al. (2004) ‘The worldwide leaf economics spectrum’, *Nature*, 428, pp. 821–
 584 827.

585 Zhang, Y.-s., Meiners, S.J., Meng, Y., Yao, Q., Guo, K., Guo, W.-Y. & Li, S.-p. (2024) Temporal
 586 dynamics of Grime’s CSR strategies in plant communities during 60 years of succession.
 587 *Ecology Letters*, 27, e14446.

588 Zhang, H., Wang, H., Wright, I.J., Prentice, I.C., Harrison, S.P., Smith, N.G., Westerband,
 589 A.C., Rowland, L., Plavcová, L., Morris, H., Reich, P.B., Jansen, S., Keenan, T. & Nguyen,
 590 N.B. (2025) Thermal acclimation of stem respiration implies a weaker carbon-climate
 591 feedback. *Science*, 388(6750), 984–988.