



HAL
open science

Into the range: a latitudinal gradient or a center-margins differentiation of ecological strategies in *Arabidopsis thaliana* ?

Aurélien Estarague, François Vasseur, Kevin Sartori, Cristina Bastias, Denis Cornet, Lauriane Rouan, Gregory Beurier, Moises Exposito-Alonso, Stéphane Herbette, Justine Bresson, et al.

► To cite this version:

Aurélien Estarague, François Vasseur, Kevin Sartori, Cristina Bastias, Denis Cornet, et al.. Into the range: a latitudinal gradient or a center-margins differentiation of ecological strategies in *Arabidopsis thaliana* ?. *Annals of Botany*, 2022, 129 (3), pp.343-356. 10.1093/aob/mcab149 . hal-03574480

HAL Id: hal-03574480

<https://hal.science/hal-03574480>

Submitted on 29 Nov 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 ORIGINAL ARTICLE

2 **Into the range: a latitudinal gradient or a center-margins**
3 **differentiation of ecological strategies in *Arabidopsis***
4 ***thaliana*?**

5 Aurélien Estarague^{1*}, François Vasseur¹, Kevin Sartori^{1,2}, Cristina Bastias¹,
6 Denis Cornet^{3,4}, Lauriane Rouan^{3,4}, Gregory Beurier^{3,4}, Moises Exposito-
7 Alonso^{5,6}, Stéphane Herbette⁷, Justine Bresson¹, Denis Vile⁸ and Cyrille Violle¹

8

9 1. CEFÉ, Univ Montpellier, CNRS, EPHE, IRD, F-34293, Montpellier, France.

10 2. Swedish University of Agricultural Sciences, Uppsala, Sweden

11 3. CIRAD, UMR AGAP Institut, F-34398, Montpellier, France

12 4. UMR AGAP Institut, Univ Montpellier, CIRAD, INRAE, Institut Agro, F-34398, Montpellier, France

13 5. Department of Plant Biology, Carnegie Institution for Science, Stanford University, Stanford, CA 94305, USA

14 6. Department of Biology, Stanford University, Stanford, CA 94305, USA

15 7. UCA, INRAE, PIAF, Clermont-Ferrand, France

16 8. Laboratoire d'Ecophysiologie des Plantes sous Stress Environnementaux (LEPSE), INRAE, Montpellier
17 SupAgro, UMR759, F-34060, Montpellier, France

18 *: Corresponding author: a.estarague.pro@gmail.fr

19

20 **Abstract**

21 • *Background and Aims.* Determining within-species large-scale variation in phenotypic
22 traits is central to elucidate the drivers of species' ranges. Intraspecific comparisons offer the
23 opportunity to understand how trade-offs and biogeographical history constrain adaptation to
24 contrasted environmental conditions. Here we test whether functional traits, ecological
25 strategies and phenotypic plasticity in response to abiotic stress vary along a latitudinal or a
26 center- margins gradient within the native range of *Arabidopsis thaliana*.

27 • *Methods.* The phenotypic outcomes of plant adaptation at the center and margins of its
28 geographic range were experimentally examined in 30 accessions from southern, central and
29 northern Europe. The variation of traits related to stress tolerance, resource use, colonization
30 ability as well as survival and fecundity was determined in response to high temperature
31 (34°C) or frost (- 6°C), in combination with response to water deficit.

32 • *Key Results.* Both evidence for a latitudinal and a center-margins differentiation was
33 found. Traits related to the acquisitive/conservative strategy trade-off varied along a
34 latitudinal gradient. Northern accessions presented a greater survival to stress than central and
35 southern accessions. Traits related to a colonization-competition trade-off followed a center-
36 margin differentiation. Central accessions presented a higher phenotypic plasticity and trait
37 values associated with a higher colonization ability than northern and southern accessions
38 which instead had a higher competition ability.

39 • *Conclusions.* Intraspecific phenotypic variation helps us understand how the
40 distribution range has evolved in *Arabidopsis thaliana*, which is shaped both by climate and
41 the population migratory history. We advocate to consider intraspecific trait variation in
42 species range studies instead of species means only as classically done in macroecology.

43 **Keywords:** phenotypic plasticity, CSR strategies, performance, water stress, functional trait,
44 plant trait-based ecology, intraspecific variation, stress resistance-fecundity trade-off

45 **Introduction**

46 The way species deploy various ecological strategies to cope with local abiotic and biotic
47 conditions across their geographical distribution range is critical to understand the evolution
48 of distribution range (Brown, 1984; Banta et al., 2012; Schurr et al., 2012). Surprisingly
49 though, most theoretical developments on the determinants of species' ranges have focused on
50 biogeographical and evolutionary aspects linked to colonization ability (e.g., Kirkpatrick and
51 Barton, 1997; Sexton et al., 2009; Bridle et al., 2010) while overlooking the divergence of
52 populations in term of eco-physiological traits. Phenotypic adaptations along environmental
53 gradients have been widely recognized both between- and within species in functional and
54 evolutionary ecology (Reich et al., 1997, 2003; Wright et al., 2017; Dong et al., 2020;
55 Kuppler et al., 2020). However, such phenotypic adaptations have been scarcely added to the
56 long list of *usual suspects* that determine species' range size and dynamics (Brown and
57 Gibson, 1983; Gaston, 2009; Sexton et al., 2009). The ecological drivers of range size
58 variation remain largely tackled through the comparison of multiple species while considering
59 species' ecological characteristics as fixed. This is most often implicit in model species
60 distributions studies (Guisan and Thuiller, 2005), and explicit in studies dedicated to the
61 analysis of phenotypic diversity (namely functional diversity) across species and scales
62 (Violle et al., 2014). The lack of consideration of within-species ecological variation might be
63 necessary in biogeography from a pragmatic point of view, but it ignores theoretical
64 expectations of major differences in ecological performances – survival, growth and
65 reproduction – when moving from the center to the margins of the range of a given species
66 (Abeli et al., 2014; Csergő et al., 2017; Salguero-Gómez et al., 2018).

67 Plant trait-based ecology has long investigated the variability of phenotypic features
68 (functional traits hereafter) among species, and has linked it to the environments and
69 communities they live in (Violle et al., 2007; Garnier et al., 2016). The joint analysis of the

70 variability of multiple traits further led to the identification of plant ecological strategies that
71 are expected to reflect the phenotypic outcome of natural selection at a given place (Westoby
72 et al., 2002). Notably, based on the combination of a limited number of plant functional traits,
73 the CSR scheme (Grime, 1977, 1988; Hodgson et al., 1999; Pierce et al., 2013, 2017) depicts
74 alternative ecological strategies displayed by any plant species within a triangle whose three
75 summits represent plants completely invested in either competitive strategies (C), stress-
76 tolerant strategies (S), or ruderal strategies (R). Despite its simplicity, the CSR scheme has
77 successfully been used to describe plant community gradients across broad environmental
78 clines (Cerabolini et al., 2010; Rosenfield et al., 2019). However, this classification remains
79 silent regarding its underlying adaptive causes, although this was a prerequisite of plant
80 functional ecology at its infancy (Calow, 1987). The lack of consideration of the adaptive
81 value of functional strategies is partly due to a negligence of intraspecific trait variation in
82 functional ecology (Albert et al., 2010, 2011, 2012; Violle et al., 2012). Recent efforts have
83 emphasized noticeable variations of plant functional strategies across ecotypes of a given
84 species, and demonstrated their adaptive value (Vasseur, et al., 2018a). The exploration of
85 functional trait variation across species' range is promising since they can reveal the ability of
86 populations to adapt to local, potentially stressful, conditions through functional
87 specialization.

88 It is expected by definition that the populations at the edges of a species distribution
89 experience the most extreme environmental conditions the species can tolerate (Brown, 1984;
90 Holt, 2009). The contrasted environmental conditions throughout the species' distribution
91 area are expected to select for differential values of functional traits that reflect physiological
92 tolerance and plant performance as a whole, but also for different levels of phenotypic
93 plasticity. Theoretical considerations predict higher adaptive phenotypic plasticity at the
94 margins of the distribution than at the center (Chevin and Lande, 2011) as a flexible adaptive

95 response to stressful conditions (Chevin and Lande, 2009). Strikingly, the few empirical
96 studies that explicitly quantify plastic divergence across the range draw divergent
97 conclusions, depending on the trait and on the species. In some cases, phenotypic plasticity
98 was found to be higher at the margins than at the center, which was interpreted as an
99 adaptation to more stressful and fluctuating climatic conditions (Volis et al., 1998, 2001,
100 2015; Lázaro-Nogal et al., 2015; Carvajal et al., 2017). Conversely, some studies highlighted
101 lower plasticity at the margins of plant species' distribution compared to the center (eg., Mägi
102 et al., 2011), which was explained by a higher cost of maintaining environment sensors in
103 stressful conditions (van Kleunen and Fischer, 2005). Testing hypotheses linking variation
104 and plasticity of functional traits with geography will thus be key to understanding the
105 emergence of species distribution ranges.

106 The model species *Arabidopsis thaliana* (L.) Heynh., for which both functional traits
107 (Lasky et al., 2012; Vile et al., 2012; Vasseur et al., 2018ab; Sartori et al., 2019; Exposito-
108 Alonso, 2020) as well as biogeographic history (Lee et al., 2017; Hsu et al., 2019) are well
109 studied, presents a unique opportunity to test above hypotheses (Takou et al., 2019). The
110 native distribution of this annual selfing species extends from north Africa to the north of
111 Norway and thus its populations experience dramatically-different environmental conditions
112 (Hoffmann, 2002). Thanks to an international effort of sampling, seeds from more than a
113 thousand of fully sequenced accessions are available (1001 Genomes Consortium, 2016).
114 Taking advantage of this unique genomic database, Lee *et al.* (2017) reconstructed the recent
115 history of colonization of Europe of *A. thaliana*. They showed that the majority of actual
116 european lineages originate from the recolonization of a single lineage of Europe, from
117 central Europe to the south and to the north since the last glacial event. This central lineage
118 then admixed with southern and northern populations. Thus, comparing northern and southern
119 margins allows to compare adaptations to very contrasted climates in a similar demographic

120 context (Lee et al., 2017; Hsu et al., 2019). Moreover, single-nucleotide polymorphisms
121 (SNP) analyses suggested that recolonization of Europe may correlate with adaptations to the
122 contrasted European climates (Méndez-Vigo et al., 2011; Lasky et al., 2012). A huge
123 temperature gradient could be an intense selective strength throughout the latitudinal
124 distribution of *A. thaliana* (Kaplan et al., 2004; Swindell et al., 2007; Vile et al., 2012).
125 Furthermore, some similarities in water availability (due to summer drought or winter frost)
126 may suggest similar strategies for water use on the two opposite margins (Exposito-Alonso et
127 al., 2018). Interestingly, genomic and functional ecology studies provided contrasted evidence
128 in *A. thaliana*. On the one hand, alleles conferring resistance to extreme drought are
129 maintained at both geographical margins (Exposito-Alonso et al., 2018). On the other hand,
130 the “S” (stress-resistance) strategy seem to be displayed by northern accessions only (Vasseur
131 et al., 2018a). Again, the lack of consideration for phenotypic plasticity in functional ecology,
132 and its role in local adaptation, impedes a comprehensive understanding of variation in plant
133 ecological strategies throughout a species distribution range. Here we asked: (i) How do
134 functional traits and strategies vary across the distribution range of *A. thaliana*? (ii) Do the
135 plasticity of traits and strategies differ between the center and the margins of its distribution
136 range? (iii) Are the accessions from the margins more resistant to abiotic stresses than those
137 from the center? To answer these questions, we analyzed functional traits and performance
138 variations of 30 accessions from the south, the center and the north of Europe, grown in
139 controlled conditions under different temperature and water availability treatments.

140 **Material and methods**

141 **Plant material**

142 We chose thirty natural accessions of *Arabidopsis thaliana*, randomly selected among three
143 geographical groups (**Fig. 1, [Supplementary Information Table S1]**). Ten accessions came
144 from Iberian Peninsula and from Cape Verde, ten accessions from central Europe and ten

145 accessions from Scandinavia (namely hereafter South, Center and North, respectively). All
146 the seeds originated from multiplication realized at the Center of Evolutionary and Functional
147 Ecology (CEFE, Montpellier, France) from original stocks of the 1001Genome Project (1001
148 Genomes Consortium, 2016). These accessions covered a large range of climatic conditions
149 where *A. thaliana* can grow [**Supplementary Information Fig. S1**]. This set of thirty
150 accessions represents 86.4% of allelic diversity of *A. thaliana*.

151 **Experimental design**

152 Seeds of the 30 accessions were sown in November 2018. We used 25 alveolate culture plates
153 containing 120 individual pots of 130mL each filled with peat soil (Neuhaus Humin substrat
154 N2). Each accession was replicated four times in every plate and distributed randomly within
155 and among plates (n = 100 replicates per accession). We stratified seeds by placing plates at 4
156 °C during for four days. Then, the plates were placed in a greenhouse at 10 °C average
157 temperature during 40 days for vernalization. During vernalization period, we irrigated the
158 pots by osmosed water dipping for 30 minutes once a week. Thereafter, we settled the
159 temperature at 15 °C until the end of January 2019. We then applied five environmental
160 conditions during two weeks (**Table 1**). These five environmental conditions were composed
161 of five culture plates each, for a total of 20 individuals per accession and per condition (n =
162 600 individuals in each condition). The control condition consisted of a temperature of 15 °C
163 day and night without any water limitation. These conditions are considered as non-stressful
164 for *A. thaliana*. The cold (LT) treatment consisted of a nocturnal temperature of -6 °C and 15
165 °C during the day. We set up the nocturnal temperature in a refrigeration enclosure where
166 temperature was homogenous inside (Platinum PLAT7BT, Franstal, France). The Hot (HT)
167 treatment consisted of a daily temperature of 35 °C and of 15 °C during the night. For this
168 treatment, we moved the plants in another compartment at 35 °C. Light and air humidity were
169 kept identical both in LT and HT treatments. In each temperature condition, half of the plates

170 was sub-irrigated at field capacity once a week for 30 minutes (WW) while the second half
171 was not watered during 15 days (WD) (**Table 1**). At the end of the two weeks of the five
172 differential treatments, temperature was settled back at 15 °C day and night and all pots were
173 sub-irrigated during 30 minutes once a week until the end of the experiment when plants
174 reproduced and completed their life cycle or otherwise died.

175 **Survival measurement**

176 We estimated survival directly after the temperature treatments. An individual was considered
177 as alive if at least the center of its rosette was still green. We estimated pre-treatment
178 mortality by analyzing pictures of the plate the day before treatment settlement. Individuals
179 that did not germinate or died before the treatments were discarded from the analysis.

180 **Leaf trait measurements and CSR scores**

181 Two days after the end of the temperature and watering treatments, we selected 270 leaves
182 among living individuals (2 individuals per accession and per treatment). Each leaf was
183 rehydrated during 24 hours at 4 °C in demineralized water then weighted (Balco ME2355,
184 France) and scanned (Epson Perfection V800, 300dpi). Then leaves were dried in an oven at
185 60 °C for three days and leaf dry weight determined using a balance (10^{-5} g resolution, Balco
186 ME2355, France). We measured the leaf area (LA, mm²) from leaf scans using ImageJ
187 (Schneider et al., 2012). We calculated specific leaf area (SLA, mm².g⁻¹) as the ratio of leaf
188 area to leaf dry mass. We calculate the leaf dry mass content (LDMC, mg.g⁻¹) as the ratio of
189 leaf dry mass to leaf rehydrated mass (Pérez-Harguindeguy et al., 2013). From these three leaf
190 traits, we calculated the CSR scores from the algorithm provided by Pierce et al (2017). This
191 algorithm implies a multivariate regression among LA, SLA and LDMC. The CSR scores
192 obtained through this method is in accordance with scores using more traits (see Pierce et al.,
193 2017 for more details).

194 **Near-infrared spectra predictions**

195 At the end of the treatment, we acquired spectra of near-infrared reflectance of green leaves,
196 non-destructively, using a portable spectrometer (ASD LabSpec, Malvern Panalytical,
197 Holland, wavelength range: [780; 2500 nm]). Spectra were taken on leaves dedicated for leaf
198 traits measurements just before harvesting and on additional individuals in order to get 12
199 spectra per accession and per treatment. Acquired spectra were used to predict SLA, LDMC,
200 leaf nitrogen concentration (LNC, %), R scores and C scores for 2,160 individuals. Predictive
201 models based on convolutional neural networks (CCNs) were developed using an independent
202 database gathering more than 20,000 spectra and their respective reference. We evaluated the
203 robustness of our predictions by testing their correlation with values obtained with the
204 traditional destructive methods [**Supplementary Material S1; TableS2**]. Afterward, we
205 considered predicted values superior or inferior to three median absolute values as outliers for
206 each trait, each accession, in every treatment (Hampel, 1974). Final dataset contains traits
207 values for 6 to 12 individuals of each of the 30 accessions in each treatment.

208 **Phenology and fecundity measurements**

209 We monitored the 2,365 surviving individuals from germination to the date of the first mature
210 and dehiscent fruit. The age at maturity was calculated as the number of days from
211 germination to the date at which the first fruit became dehiscent. At this date, we took a
212 picture of the inflorescence of every individual to estimate the number of fruits. We took all
213 the pictures at the same distance from the floral stem. Based on Vasseur et al. (2018c), we
214 first segmented the images and then shrank them in lines of crossed pixels (“skeleton”) using
215 ImageJ (Schneider et al., 2012). Thanks to nine variables describing these skeletons and
216 automatically measured by ImageJ, we built a linear model to estimate fecundity ($n = 100$, R^2
217 $= 0.92$). This method detects aborted or non-fecundated fruits from mature and fecundated
218 fruits (Vasseur et al., 2018c).

219 **Statistical analyses**

220 We compared means of traits observed in control condition and coefficients of variation of
221 NIRS-predicted values of traits in all treatments thanks to Tukey tests ('Multcomp' package,
222 Hothorn et al., 2008). We compared cross-treatment plasticity of geographical groups through
223 Tukey tests comparisons of the coefficient of variation across all treatments. The coefficient
224 of variation (CV) is calculated as the total standard deviation of traits of each group across
225 treatments divided by the cross-treatment mean. We analyzed trait plasticity in response to the
226 treatments using linear mixed-effects models that test log-response ratios (log ratios hereafter)
227 of traits and CSR scores as a function of geographical groups, treatments, and their
228 interactions. Accession identity and plate identity were considered as random effects in the
229 models. Log ratios were calculated as the logarithm of the ratio of an individual value in a
230 given treatment and the mean value of its accession in control condition.

231 We analyzed the variability of performance traits (survival and number of fruits) using
232 generalized mixed models ('lme4' package, Bates et al., 2015). We performed a binomial
233 regression for survival models (logit as a link function) and a Poisson regression for fecundity
234 models (log as a link function). We considered three fixed effects in these models:
235 geographical origin (3 levels), treatment effect (5 levels) and their interaction. Two random
236 effects were considered: accession identity and plate. Only one plant died in the control
237 condition. Because most values were at the extreme of the binomial distribution in this
238 condition, the model suffered from convergence issues. Consequently, this treatment was not
239 compared to the others in the survival analysis.

240 In every model, we calculated means and standard errors of estimates with the
241 'emmeans' package (Lenth et al., 2019). We compared means between groups and between
242 treatments with Tukey post-hoc tests ('Multcomp' package, Hothorn et al., 2008). We
243 analyzed the relationship between survival and fruit production using a linear model with
244 mean values per accessions.

245 **Results**

246 **Variation of functional traits and ecological strategies across the geographical range**

247 Under control condition, traits can be categorized into two groups: those that tend to exhibit a
248 latitudinal gradient and those that tend to exhibit a center-margins gradient. Within the former
249 group, geographical origin had a significant effect on age at maturity: southern accessions had
250 a shorter lifespan than central and northern accessions (both $P < 0.001$), while northern
251 accessions had a longer lifespan than central accessions ($P < 0.001$, **Fig. 2A**). A trend for a
252 latitudinal gradient existed for SLA, LDMC and LNC, but no significant differences were
253 found across geographical groups for these traits (**Fig. 2BCD**). Central accessions had
254 significantly smaller leaves than southern accessions ($P = 0.046$), and non-significantly
255 smaller leaves than northern accessions (**Fig. 2E**). Consistent with their lower leaf area,
256 central accessions tend to exhibit smaller C-scores and higher R-scores than southern and
257 northern accessions, but these variations were not significant (**Fig. 2FG**). All accessions had a
258 null S-score. Central accessions produced on average more fruits than southern and northern
259 accessions, but the difference was only significant with northern accessions ($P < 0.001$; **Fig.**
260 **2H**).

261 **Variation of plasticity of functional traits and ecological strategies across the** 262 **geographical range**

263 We first estimated cross-treatment trait plasticity with the coefficient of variation across five
264 contrasted environmental conditions (control, WW-HT, WD-HT, WW-LT, WD-LT). The
265 four traits that tended to exhibit a latitudinal gradient for trait values under control condition
266 (age at maturity, SLA, LDMC and LNC) globally had a center-margins differentiation for trait
267 plasticity (**Fig. 3ABCD**). For instance, central accessions had a higher plasticity of SLA
268 across treatments than southern accessions ($P = 0.048$) and marginally higher than northern
269 accessions ($P = 0.054$, **Fig. 3B**). Yet, the response of SLA to individual treatments exhibited

270 more a latitudinal gradient than a center-margins gradient (**Fig. 4B**), with both southern and
271 central accessions being more similar in their SLA log-ratio than northern accessions.
272 Northern accessions had a higher decrease in SLA in low temperature whereas central and
273 southern accessions had a higher increase in SLA in hot temperature conditions. Cross-
274 treatment plasticity was not significantly different across geographical groups for age at
275 maturity (**Fig. 3A**). Yet, the response of age at maturity to individual stress displayed a
276 latitudinal gradient with decreasing plasticity toward the north (**Fig. 4A**). In particular, the
277 three geographical groups differed significantly in plasticity of age at maturity in response to
278 WD-LT. Other traits displayed more a center-margins differentiation than a latitudinal
279 gradient. For instance, central accessions had a higher but not significant cross-treatment
280 plasticity of LDMC (**Fig. 3C**). Central accessions had a higher coefficient of variation of LNC
281 than northern accessions ($P = 0.01$) but did not differ significantly with southern accessions
282 for this trait ($P = 0.08$, **Fig. 3D**). This center-margins gradient was mainly driven by the
283 response of LNC to WD-HT (**Fig. 4D**).

284 Among the four traits that tended to exhibit a center-margins gradient in non-stressing
285 conditions (LA, C and R scores, and fruit number), only fruit number also had a center-
286 margins gradient for trait plasticity (**Fig. 3H**). Central accessions had a significantly higher
287 coefficient of variation of fruit number than southern accessions ($P = 0.04$) and slightly higher
288 than northern accession even if not significantly different ($P = 0.15$). Central accessions are
289 the only accessions to produce less fruits in WD-HT and in WW-LT conditions than in
290 control. (**Fig. 4H**). In contrast to fruit number, LA and C-scores exhibited a significant
291 latitudinal gradient for cross-treatment plasticity. Northern accessions had a significantly
292 lower plasticity of LA than southern accessions ($P = 0.009$), central accessions having an
293 intermediate but not significantly different coefficient of variation on this trait (**Fig. 3E**). Yet,
294 this cross-treatment plasticity pattern hides contrasted responses to individual stresses:

295 plasticity of LA displayed a clear center-margins gradient only in WW-HT and WD-LT, but it
296 exhibited a latitudinal gradient in response to WD-HT and WW-LT (**Fig. 4E**). Similar to LA,
297 C-scores had a smaller coefficient of variation in northern than in southern accessions across
298 treatments ($P = 0.006$), central accessions having an intermediate but not significantly
299 different coefficient of variation for this trait (**Fig. 3G**). Yet, only northern accessions
300 exhibited a significantly different response of C-scores to WW-LT when looking at individual
301 treatment effect (**Fig. 4G**). The cross-treatment plasticity of R-scores exhibited no differences
302 between geographical groups (**Fig. 3F**), although it exhibited significantly different response
303 of northern accessions to WD-LT (**Fig. 4F**). All accessions had a null S-score in every
304 treatment.

305 **Geographical origin effects on survival**

306 Survival of accessions varied significantly among treatments ($P < 0.001$). In particular, WW-
307 LT (79.9% of survival), WD-HT (72.2% of survival) and WD-LT (52.4% of survival) were
308 associated with a significantly weaker probability of survival than WW-HT (99.2% of
309 survival) ($P = 0.02$; $P = 0.0003$; and $P < 0.001$ respectively). A single individual died in
310 Control (99.8% of survival), likely unrelated to adaptation to such conditions. Survival of
311 accessions varied significantly across geographical groups ($P < 0.001$), which globally
312 exhibited a latitudinal gradient. Among all treatments, northern accessions survived
313 significantly more than central ($P = 0.01$) and southern accessions ($P = 0.001$), consistent
314 with the significant interaction between geographical group and treatment ($P < 0.001$). In
315 WW-LT, central accessions survived more than southern accessions ($P = 0.007$). Northern
316 accessions survived significantly more than the central and southern accessions in the cold
317 treatments (WW-LT and WD-LT, resp. $P < 0.001$). Moreover, northern accessions survived
318 significantly more than central accessions ($P = 0.046$) in WD-HT, but they were not different
319 from southern accessions ($P = 0.06$) (**Fig. 5A**).

320 Survival was significantly negatively related to fruit number under WD-HT and WD-
321 LT ($R^2 = 0.75$; $P < 0.001$) but the slope of the relationship was not significantly different from
322 zero under control, WW-HT and WW-LT. In other words, under WD conditions, accessions
323 with low fecundity survived more than accessions with high fecundity (**Fig. 5B**,
324 **[Supplementary Information Fig. S2]**).

325 **Discussion**

326 This study dissects functional variation at the intraspecific level within different environments
327 and across the distribution range of a widespread species. We expected two main types of
328 geographic mean trait variation patterns across *A. thaliana* distribution; either a latitudinal
329 gradient or a differentiation between the center and the margins of the distribution. The
330 studied traits and their plasticity were correlated but they exhibited various patterns of
331 geographic variation. We discuss the consequences for variation in individual performance
332 and local plant adaptation across the range.

333 In Europe, *Arabidopsis thaliana* faces very contrasted climates (Hoffmann, 2002),
334 which are expected to constitute strong yet variable natural selection pressures throughout its
335 distribution range (Kaplan et al., 2004; Swindell et al., 2007; Vile et al., 2012). Coherently,
336 part of our results supports a latitudinal gradient in functional variation across the distribution
337 range of *A. thaliana*. In non-stressful conditions for plant growth, age at maturity, specific leaf
338 area, leaf dry matter content, and leaf nitrogen concentration vary along this latitudinal
339 gradient. These traits are closely associated with the leaf economics spectrum (Wright et al.,
340 2004). Our results support a latitudinal gradient in resource-use strategies, from acquisitive
341 resource-use strategy for southern accessions (characterized by short lifespan, thin leaves with
342 high LNC and photosynthetic rate) to conservative resource-use strategy in northern
343 accessions (characterized by long lifespan, thick leaves with low LNC and photosynthetic
344 rate). An abundant literature in *A. thaliana* supports this functional gradient associated with

345 latitude in Europe (Stenøien et al., 2002; Stinchcombe et al., 2004; Hopkins et al., 2008;
346 Vasseur et al., 2012; Debieu et al., 2013; Vasseur et al., 2018a; Exposito-Alonso, 2020). By
347 contrast, Sartori et al., (2019) found that both southern and northern accessions displayed a
348 conservative resource-use strategy. Here, we show that northern accessions had a higher
349 survival rate at low temperature than central and southern accessions. This suggests that
350 conservative resource-use strategies selected in cold climates in northern areas of Europe is
351 associated with an optimization of survival to freeze. Surprisingly though, northern accessions
352 had also a higher survival rate than southern and central accessions in the hot temperature
353 treatment. We can hypothesize that the metabolic pathways associated to a better survival in
354 dehydration caused by freeze could also be efficient for a better survival under water deficit
355 conditions (Sanada et al., 2007; Suprasanna et al., 2016; Gillespie and Volaire, 2017; Bristiel
356 et al., 2018). However, the inverse is not true, southern accessions being the most vulnerable
357 to nocturnal freezing. A possible explanation is that stress escaping (Ludlow, 1989) is closely
358 associated with acquisitive resource-use strategies that are selected in the southern area of the
359 distribution range of *A. thaliana*. However, in southern populations, the two opposite
360 strategies are coexisting with four southern accessions surviving more than the other southern
361 accessions. Interestingly, these four accessions are from the same genetic lineage: the relict
362 group ([**Supplementary Information Table S1**], 1001 Genomes Consortium, 2016). This
363 ancient genetic lineage is associated with stress-tolerance in Spain (Lee et al., 2017). Modern
364 Spanish accessions present a short life cycle following spring germination (our results;
365 Assmann, 2013; Exposito-Alonso, 2020) that is strongly associated with an acquisitive
366 resource-use strategy. Oppositely, northern accessions from Scandinavia where low
367 temperatures and short spring season do not allow for a rapid life cycle strategy, plants are
368 selected for high tolerance strategy to resist winter conditions (Bartlett et al., 2014; Delzon,
369 2015; Exposito-Alonso, 2020). Underpinning this tolerance/avoidance trade-off, southern

370 survivors under stressful conditions increased more their life duration than central and
371 northern accessions. This corroborates the study of Exposito-Alonso et al. (2020) who showed
372 that Spanish accessions had a more plastic life cycle than Scandinavian strict winter cyclus
373 accessions. These results also corroborate the genetic correlation between water use efficiency
374 and life span found in previous studies (Mckay et al., 2003): increasing water use efficiency
375 through phenotypic plasticity may constrain the life cycle of individuals to be longer.

376 The center-margins gradient of abiotic stress hypothesis, which posits that less suitable
377 environments occur at the peripheries (Holt, 2009), has been discussed on numerous species
378 (Sexton et al., 2009; Pironon et al., 2017). In *A. thaliana*'s distribution range, mean annual
379 precipitation exhibits a bell-shaped curve with latitude. Northern and southern populations
380 encountering less precipitations than central populations [**Supplementary Information Fig.**
381 **S1**]. Low precipitations are expected to reduce the variance of phenotypes associated with
382 water-stress resistance and may limit phenotypic plasticity (Valladares et al., 2007; Palacio-
383 López et al., 2015; Stotz et al., 2021). In parallel, northern and southern parts of the
384 distribution range of *A. thaliana* encounter more seasonal variation of temperature and
385 precipitation [**Supplementary Information Fig. S1**]. Fluctuating conditions, when
386 predictable, are expected to select for plastic phenotypes (Lázaro-Nogal et al., 2015; Leung et
387 al., 2020; Stotz et al., 2021). Our results show a general trend for a weaker cross-treatment
388 plasticity in peripheral accessions than central accessions. This could be explained by the cost
389 of phenotypic plasticity, being higher in stressful conditions associated with fewer
390 precipitations (van Kleunen and Fischer, 2005; Molina-Montenegro and Naya, 2012; Nicotra
391 et al., 2015). A weaker or an absence of phenotypic plasticity as well as a stronger genetic
392 determinism independent of the climate at ecological margins may be adaptive (Ghalambor et
393 al., 2007; Murren et al., 2015; Palacio-López et al., 2015; Acasuso-Rivero et al., 2019;
394 Pfennig, 2021). Indeed, only the central populations showed a significant fecundity reduction

395 in stress conditions. This result is also in accordance with Exposito-Alonso et al. (2018) who
396 showed that similar alleles involved in drought resistance are under selection at both
397 latitudinal margins of Europe in *A. thaliana*. Our results demonstrate stress-tolerance in *A.*
398 *thaliana* whereas all of the accessions had a null S-score in our estimations, based on Pierce et
399 al.'s methodology (2017). This result questions the use of such classification at the
400 intraspecific level. We suggest improving the CSR classification by using phenotypic traits
401 and performances actually measured under competition, disturbance and stress conditions.

402 The reduction of plasticity at both margins of the distribution range may also be
403 associated with the evolutionary history of the species. Actual marginal populations of *A.*
404 *thaliana* derived from the European colonization of a genetic lineage from central Europe and
405 its admixture with northern and southern populations (Lee et al., 2017). The colonization of
406 margins may have been accompanied with both high cumulative foundation effects and
407 directional selection, limiting thus the phenotypic variability at both opposite margins
408 (Kirkpatrick and Barton, 1997; Sagarin and Gaines, 2002; Bridle and Vines, 2007; Eckert et
409 al., 2008; Sexton et al., 2009; Luo et al., 2015; Pironon et al., 2017; Hämälä et al., 2018).
410 Accordingly, leaf area, C-scores, R-scores and fruit number are more similar among the two
411 opposite margins than with the central accessions. Our results suggest that trait values
412 associated with colonization (number of fruits and R-scores) are higher in central accessions
413 than peripheral ones. Moreover, traits related to competitive ability (leaf area and C-scores)
414 are lower in central accessions than peripheral ones. This result is quite counter-intuitive
415 regarding theoretical expectations that abundance in central populations should be higher than
416 in marginal populations, selecting thus for a higher competition ability at the center than at the
417 margins of a distribution range (Brown, 1984; Brown et al., 1995; Holt, 2009; Sexton et al.,
418 2009; but see Pironon et al., 2017). We show that central accessions invest more in fecundity
419 than peripheral accessions who invest more in resistance to stress. Grounded on ecological

420 theories regarding the existence of a colonization/competition trade-off (Levins and Culver,
421 1971; Hastings, 1980; Turnbull et al., 1999; Yu and Wilson, 2001; Cadotte et al., 2006), we
422 can thus hypothesize that central accessions exhibit traits that optimize seed dispersal and
423 colonization, perhaps also at the expense of competitive or stress-coping ability. Indeed, we
424 confirm the classical trade-off described at the interspecific level between survival to stress
425 and fecundity (Muller-Landau, 2010; D’Andrea et al., 2013). It may be thus interesting to
426 experimentally test this competition/colonization ability differentiation across the distribution
427 range in order to better understand how phenotypes evolved through the evolutionary history
428 of *A. thaliana* (e.g. Lorts and Lasky, 2020).

429 All in all, our work confirmed hypothesized trends on how ecological strategies vary
430 across the geographic distribution of a species. More importantly, we show that both climate
431 variations and evolutionary history shaped the actual phenotypic diversity in this model
432 species, leading to a latitudinal and a center-margins differentiation respectively depending on
433 the nature of the traits. The latitudinal gradient was associated with an
434 acquisition/conservation trade-off, tightly linked to a temperature gradient along european
435 latitudes. At the opposite, the center-margins differentiation was more associated with a
436 competition/colonization trade-off potentially due to the demographic history of this species.
437 Our findings thus point out the importance of considering the structured phenotypic
438 variability of species to understand the ecology and evolution of species’ ranges rather than
439 comparing species using their mean trait values only. This is particularly important to better
440 predict distribution range future evolution.

441 **Acknowledgements**

442 We are very grateful to Justine Floret and Amelie Emmanuel for their help on measurements.
443 We also thank the technical platform “Plateforme des Terrains d’Expérience du LabEx
444 CeMEB,” (CEFE, CNRS) in Montpellier and particularly Pauline Durbin and Thierry

445 Matthieu for their precious advices. This work was supported by the European Research
446 Council (ERC) Starting Grant Project “Ecophysiological and biophysical constraints on
447 domestication in crop plants” (Grant ERC-StG-2014- 639706-CONSTRAINTS).

448 **Supplementary Information**

449 **Table S1.** List of accessions and their geographical coordinates. **Figure S1.** Description of
450 climate of origin of the three geographical groups compared to the diversity of climate from
451 the complete set of 1135 accessions available in the 1001genome project. Data were
452 downloaded from <https://chelsa-climate.org/> **Supplementary Material S2.** Predictive
453 models' development. **Table S2.** Performances of models predicting leaf traits from near
454 infrared spectroscopy predictive models for in-sample and cross-validation sets of (N: number
455 of samples, RMSE: Root Mean Square Error, R²: Coefficient of Determination). **Figure S2.**
456 Relationship between survival of accessions among geographical groups in WD-HT and WD-
457 LT. Labels referred to accessions ID (see Table S1).

458 **Caption for figures**

459 **Figure 1.** Geographical origin of the 30 accessions of *Arabidopsis thaliana*. The southern
460 group is represented with orange dots, the central group in green and the northern group in
461 purple. Accessions were chosen randomly in each geographical group.

462 **Figure 2.** Phenotypic variation in *Control* condition across the distribution range of *A.*
463 *thaliana*. Different letters indicate significant differences between geographical groups
464 following Tukey tests at $P < 0.05$.

465 **Figure 3.** Coefficient of variation of traits across the distribution range of *A. thaliana*.
466 Different letters indicate significant differences between geographical groups following
467 Tukey tests at $P < 0.05$.

468 **Figure 4.** Plasticity of functional traits and CSR scores across geographical groups and
469 treatments. Difference between mean values of Log Ratios following Tukey tests within and
470 across treatments are indicated with lowercase letters and capital letters, respectively. Log
471 ratios significantly different from zero following Student tests, corrected by Holm's method,
472 are indicated with stars (*: $P < 0.05$, **: $P < 0.01$; ***: $P < 0.001$). WW: well-watered; WD:
473 Water deficient; HT: Hot temperature; LT: Low temperature.

474 **Figure 5.** A) Survival rate among treatments. Different letters indicate significant differences
475 between geographical groups following Tukey tests at $P < 0.05$ within each treatment. B)
476 Relationship between survival of accessions ($n = 30$) and fruit production across treatments.
477 Linear regression lines are indicated. Dashed lines and empty points indicate a slope not
478 significantly different from zero. The relationship under control condition was not significant
479 and is not shown. WW: well-watered; WD: water deficit; HT: hot temperature; LT: low
480 temperature.

481 **Literature cited**

- 482 1001 Genomes Consortium. 2016. 1,135 Genomes Reveal the Global Pattern of
483 Polymorphism in *Arabidopsis thaliana*. *Cell* 166: 481–491.
- 484 Abeli, T., R. Gentili, A. Mondoni, S. Orsenigo, and G. Rossi. 2014. Effects of marginality on
485 plant population performance. *Journal of Biogeography* 41: 239–249.
- 486 Acasuso-Rivero, C., C. J. Murren, C. D. Schlichting, and U. K. Steiner. 2019. Adaptive
487 phenotypic plasticity for life-history and less fitness-related traits. *Proceedings of the Royal
488 Society B: Biological Sciences* 286: 20190653.
- 489 Albert, C. H., F. de Bello, I. Boulangeat, G. Pellet, S. Lavorel, and W. Thuiller. 2012. On the
490 importance of intraspecific variability for the quantification of functional diversity. *Oikos*
491 121: 116–126.
- 492 Albert, C. H., F. Grassein, F. M. Schurr, G. Vieilledent, and C. Violle. 2011. When and how
493 should intraspecific variability be considered in trait-based plant ecology? *Perspectives in
494 Plant Ecology, Evolution and Systematics* 13: 217–225.
- 495 Albert, C. H., W. Thuiller, N. G. Yoccoz, A. Soudant, F. Boucher, P. Saccone, and S. Lavorel.
496 2010. Intraspecific functional variability: extent, structure and sources of variation. *Journal of
497 Ecology* 98: 604–613.
- 498 Assmann, S. M. 2013. Natural variation in abiotic stress and climate change responses in
499 *Arabidopsis*: implications for twenty-first-century agriculture. *International Journal of Plant
500 Sciences* 174: 3–26.
- 501 Banta, J. A., I. M. Ehrenreich, S. Gerard, L. Chou, A. Wilczek, J. Schmitt, P. X. Kover, and
502 M. D. Purugganan. 2012. Climate envelope modelling reveals intraspecific relationships

- 503 among flowering phenology, niche breadth and potential range size in. *Ecology Letters* 15:
504 769–777.
- 505 Bartlett, M. K., Y. Zhang, N. Kreidler, S. Sun, R. Ardy, K. Cao, and L. Sack. 2014. Global
506 analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology Letters* 17:
507 1580–1590.
- 508 Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models
509 Using lme4. *Journal of Statistical Software* 67: 1–48.
- 510 Bridle, J. R., J. Polechová, M. Kawata, and R. K. Butlin. 2010. Why is adaptation prevented
511 at ecological margins? New insights from individual-based simulations. *Ecology Letters* 13:
512 485–494.
- 513 Bridle, J. R., and T. H. Vines. 2007. Limits to evolution at range margins: when and why does
514 adaptation fail? *Trends in Ecology & Evolution* 22: 140–147.
- 515 Bristiel, P., L. Gillespie, L. Østrem, J. Balachowski, C. Violle, and F. Voltaire. 2018.
516 Experimental evaluation of the robustness of the growth–stress tolerance trade-off within the
517 perennial grass *Dactylis glomerata*. *Functional Ecology* 32: 1944–1958.
- 518 Brown, J. H. 1984. On the Relationship between Abundance and Distribution of Species. *The*
519 *American Naturalist* 124: 255–279.
- 520 Brown, J. H., and A. C. Gibson. 1983. Biogeography. Mosby.
- 521 Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial Variation in Abundance.
522 *Ecology* 76: 2028–2043.
- 523 Cadotte, M. W., D. V. Mai, S. Jantz, M. D. Collins, M. Keele, and J. A. Drake. 2006. On
524 Testing the Competition-Colonization Trade-Off in a Multispecies Assemblage. *The*
525 *American Naturalist* 168: 704–709.

- 526 Calow, P. 1987. Towards a definition of functional ecology. *Functional Ecology* 1: 57–61.
- 527 Carvajal, D. E., A. P. Loayza, R. S. Rios, E. Gianoli, and F. A. Squeo. 2017. Population
528 variation in drought-resistance strategies in a desert shrub along an aridity gradient: Interplay
529 between phenotypic plasticity and ecotypic differentiation. *Perspectives in Plant Ecology,
530 Evolution and Systematics* 29: 12–19.
- 531 Cerabolini, B. E. L., G. Brusa, R. M. Ceriani, R. De Andreis, A. Luzzaro, and S. Pierce. 2010.
532 Can CSR classification be generally applied outside Britain? *Plant Ecology* 210: 253–261.
- 533 Chevin, L.-M., and R. Lande. 2011. Adaptation to marginal habitats by evolution of increased
534 phenotypic plasticity: Evolving plasticity in marginal populations. *Journal of Evolutionary
535 Biology* 24: 1462–1476.
- 536 Chevin, L.-M., and R. Lande. 2009. When do adaptive plasticity and genetic evolution
537 prevent extinction of a density-regulated population? *Evolution* 64: 1143–1150.
- 538 Csergő, A. M., R. Salguero-Gómez, O. Broennimann, S. R. Coutts, A. Guisan, A. L. Angert,
539 E. Welk, et al. 2017. Less favourable climates constrain demographic strategies in plants.
540 *Ecology Letters* 20: 969–980.
- 541 D’Andrea, R., G. Barabás, and A. Ostling. 2013. Revising the Tolerance-Fecundity Trade-
542 Off; or, On the Consequences of Discontinuous Resource Use for Limiting Similarity, Species
543 Diversity, and Trait Dispersion. *The American Naturalist* 181: E91–E101.
- 544 Debieu, M., C. Tang, B. Stich, T. Sikosek, S. Effgen, E. Josephs, J. Schmitt, et al. 2013. Co-
545 Variation between Seed Dormancy, Growth Rate and Flowering Time Changes with Latitude
546 in *Arabidopsis thaliana*. *PLOS ONE* 8: e61075.
- 547 Delzon, S. 2015. New insight into leaf drought tolerance. *Functional Ecology* 29: 1247–1249.

- 548 Dong, N., I. C. Prentice, I. J. Wright, B. J. Evans, H. F. Togashi, S. Caddy-Retalic, F. A.
549 McInerney, et al. 2020. Components of leaf-trait variation along environmental gradients.
550 *New Phytologist* 228: 82–94.
- 551 Eckert, C. G., K. E. Samis, and S. C. Loughheed. 2008. Genetic variation across species'
552 geographical ranges: the central–marginal hypothesis and beyond. *Molecular Ecology* 17:
553 1170–1188.
- 554 Exposito-Alonso, M. 2020. Seasonal timing adaptation across the geographic range of
555 *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences*: 201921798.
- 556 Exposito-Alonso, M., F. Vasseur, W. Ding, G. Wang, H. A. Burbano, and D. Weigel. 2018.
557 Genomic basis and evolutionary potential for extreme drought adaptation in *Arabidopsis*
558 *thaliana*. *Nature Ecology & Evolution* 2: 352–358.
- 559 Garnier, E., M.-L. Navas, and K. Grigulis. 2016. Plant functional diversity: Organism traits,
560 community structure, and ecosystem properties. Oxford University Press.
- 561 Gaston, K. J. 2009. Geographic range limits: achieving synthesis. *Proceedings of the Royal*
562 *Society B: Biological Sciences* 276: 1395–1406.
- 563 Ghalambor, C. K., J. K. McKAY, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus
564 non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new
565 environments. *Functional Ecology* 21: 394–407.
- 566 Gillespie, L. M., and F. A. Volaire. 2017. Are winter and summer dormancy symmetrical
567 seasonal adaptive strategies? The case of temperate herbaceous perennials. *Annals of Botany*
568 119: 311–323.
- 569 Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its
570 relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169–1194.

- 571 Grime, J. P. 1988. The C-S-R model of primary plant strategies — origins, implications and
572 tests. *In* L. D. Gottlieb, and S. K. Jain [eds.], *Plant Evolutionary Biology*, 371–393. Springer
573 Netherlands, Dordrecht.
- 574 Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple
575 habitat models. *Ecology Letters* 8: 993–1009.
- 576 Hämälä, T., T. M. Mattila, and O. Savolainen. 2018. Local adaptation and ecological
577 differentiation under selection, migration, and drift in *Arabidopsis lyrata*. *Evolution* 72: 1373–
578 1386.
- 579 Hampel, F. R. 1974. The Influence Curve and its Role in Robust Estimation. *Journal of the*
580 *American Statistical Association* 69: 383–393.
- 581 Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical*
582 *Population Biology* 18: 363–373.
- 583 Hodgson, J. G., P. J. Wilson, R. Hunt, J. P. Grime, and K. Thompson. 1999. Allocating C-S-R
584 Plant Functional Types: A Soft Approach to a Hard Problem. *Oikos* 85: 282–294.
- 585 Hoffmann, M. H. 2002. Biogeography of *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae).
586 *Journal of Biogeography* 29: 125–134.
- 587 Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and
588 evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106: 19659–
589 19665.
- 590 Hopkins, R., J. Schmitt, and J. R. Stinchcombe. 2008. A latitudinal cline and response to
591 vernalization in leaf angle and morphology in *Arabidopsis thaliana* (Brassicaceae). *New*
592 *Phytologist* 179: 155–164.

- 593 Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric
594 models. *Biometrical journal* 50: 346–363.
- 595 Hsu, C.-W., C.-Y. Lo, and C.-R. Lee. 2019. On the postglacial spread of human commensal
596 *Arabidopsis thaliana*: journey to the East. *New Phytologist* 222: 1447–1457.
- 597 Kaplan, F., J. Kopka, D. W. Haskell, W. Zhao, K. C. Schiller, N. Gatzke, D. Y. Sung, and C.
598 L. Guy. 2004. Exploring the Temperature-Stress Metabolome of *Arabidopsis*. *Plant*
599 *Physiology* 136: 4159–4168.
- 600 Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a Species' Range. *The American*
601 *Naturalist* 150: 1–23.
- 602 van Kleunen, M., and M. Fischer. 2005. Constraints on the evolution of adaptive phenotypic
603 plasticity in plants. *New Phytologist* 166: 49–60.
- 604 Kuppler, J., C. H. Albert, G. M. Ames, W. S. Armbruster, G. Boenisch, F. C. Boucher, D. R.
605 Campbell, et al. 2020. Global gradients in intraspecific variation in vegetative and floral traits
606 are partially associated with climate and species richness. *Global Ecology and Biogeography*
607 29: 992–1007.
- 608 Lasky, J. R., D. L. D. Marais, J. K. McKAY, J. H. Richards, T. E. Juenger, and T. H. Keitt.
609 2012. Characterizing genomic variation of *Arabidopsis thaliana*: the roles of geography and
610 climate. *Molecular Ecology* 21: 5512–5529.
- 611 Lázaro-Nogal, A., S. Matesanz, A. Godoy, F. Pérez-Trautman, E. Gianoli, and F. Valladares.
612 2015. Environmental heterogeneity leads to higher plasticity in dry-edge populations of a
613 semi-arid Chilean shrub: insights into climate change responses. *Journal of Ecology* 103:
614 338–350.

- 615 Lee, C.-R., H. Svardal, A. Farlow, M. Exposito-Alonso, W. Ding, P. Novikova, C. Alonso-
616 Blanco, et al. 2017. On the post-glacial spread of human commensal *Arabidopsis thaliana*.
617 *Nature Communications* 8: 1–12.
- 618 Lenth, R., H. Singmann, J. Love, P. Buerkner, and M. Herve. 2019. emmeans: Estimated
619 Marginal Means, aka Least-Squares Means.
- 620 Leung, C., M. Rescan, D. Grulois, and L.-M. Chevin. 2020. Reduced phenotypic plasticity
621 evolves in less predictable environments. *Ecology Letters* 23: 1664–1672.
- 622 Levins, R., and D. Culver. 1971. Regional Coexistence of Species and Competition between
623 Rare Species. *Proceedings of the National Academy of Sciences* 68: 1246–1248.
- 624 Lorts, C. M., and J. R. Lasky. 2020. Competition× drought interactions change phenotypic
625 plasticity and the direction of selection on *Arabidopsis* traits. *New Phytologist* 227: 1060–
626 1072.
- 627 Ludlow, M. M. 1989. Strategies of response to water stress.
- 628 Luo, Y., A. Widmer, and S. Karrenberg. 2015. The roles of genetic drift and natural selection
629 in quantitative trait divergence along an altitudinal gradient in *Arabidopsis thaliana*. *Heredity*
630 114: 220–228.
- 631 Mägi, M., M. Semchenko, R. Kalamees, and K. Zobel. 2011. Limited phenotypic plasticity in
632 range-edge populations: a comparison of co-occurring populations of two *Agrimonia* species
633 with different geographical distributions. *Plant Biology* 13: 177–184.
- 634 Mckay, J. K., J. H. Richards, and T. Mitchell-Olds. 2003. Genetics of drought adaptation in
635 *Arabidopsis thaliana*: I. Pleiotropy contributes to genetic correlations among ecological traits.
636 *Molecular Ecology* 12: 1137–1151.

- 637 Méndez-Vigo, B., F. X. Picó, M. Ramiro, J. M. Martínez-Zapater, and C. Alonso-Blanco.
638 2011. Altitudinal and Climatic Adaptation Is Mediated by Flowering Traits and FRI, FLC,
639 and PHYC Genes in Arabidopsis. *Plant Physiology* 157: 1942–1955.
- 640 Molina-Montenegro, M. A., and D. E. Naya. 2012. Latitudinal patterns in phenotypic
641 plasticity and fitness-related traits: assessing the climatic variability hypothesis (CVH) with
642 an invasive plant species. 7: e47620.
- 643 Muller-Landau, H. C. 2010. The tolerance–fecundity trade-off and the maintenance of
644 diversity in seed size. *Proceedings of the National Academy of Sciences* 107: 4242–4247.
- 645 Murren, C. J., J. R. Auld, H. Callahan, C. K. Ghalambor, C. A. Handelsman, M. A. Heskell, J.
646 G. Kingsolver, et al. 2015. Constraints on the evolution of phenotypic plasticity: limits and
647 costs of phenotype and plasticity. *Heredity* 115: 293–301.
- 648 Nicotra, A. B., D. L. Segal, G. L. Hoyle, A. W. Schrey, K. J. Verhoeven, and C. L. Richards.
649 2015. Adaptive plasticity and epigenetic variation in response to warming in an Alpine plant.
650 *Ecology and evolution* 5: 634–647.
- 651 Palacio-López, K., B. Beckage, S. Scheiner, and J. Molofsky. 2015. The ubiquity of
652 phenotypic plasticity in plants: a synthesis. *Ecology and Evolution* 5: 3389–3400.
- 653 Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S.
654 Bret-Harte, et al. 2013. New handbook for standardised measurement of plant functional traits
655 worldwide. *Australian Journal of Botany* 61: 167.
- 656 Pfennig, D. W. 2021. Phenotypic Plasticity & Evolution: Causes, Consequences,
657 Controversies. Taylor & Francis.

- 658 Pierce, S., G. Brusa, I. Vagge, and B. E. L. Cerabolini. 2013. Allocating CSR plant functional
659 types: the use of leaf economics and size traits to classify woody and herbaceous vascular
660 plants. *Functional Ecology* 27: 1002–1010.
- 661 Pierce, S., D. Negreiros, B. E. L. Cerabolini, J. Kattge, S. Díaz, M. Kleyer, B. Shipley, et al.
662 2017. A global method for calculating plant CSR ecological strategies applied across biomes
663 world-wide. *Functional Ecology*: 444–457.
- 664 Pironon, S., G. Papuga, J. Vilellas, A. L. Angert, M. B. García, and J. D. Thompson. 2017.
665 Geographic variation in genetic and demographic performance: new insights from an old
666 biogeographical paradigm: The centre-periphery hypothesis. *Biological Reviews* 92: 1877–
667 1909.
- 668 Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: Global
669 convergence in plant functioning. *Proceedings of the National Academy of Sciences* 94:
670 13730–13734.
- 671 Reich, P. B., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M.
672 B. Walters. 2003. The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies.
673 *International Journal of Plant Sciences* 164: S143–S164.
- 674 Rosenfield, M. F., S. C. Müller, and G. E. Overbeck. 2019. Short gradient, but distinct plant
675 strategies: The CSR scheme applied to subtropical forests. *Journal of Vegetation Science* 30:
676 984–993.
- 677 Sagarin, R. D., and S. D. Gaines. 2002. The ‘abundant centre’ distribution: to what extent is it
678 a biogeographical rule? *Ecology Letters* 5: 137–147.

- 679 Salguero-Gómez, R., C. Violle, O. Gimenez, and D. Childs. 2018. Delivering the promises of
680 trait-based approaches to the needs of demographic approaches, and vice versa. *Functional*
681 *Ecology* 32: 1424–1435.
- 682 Sanada, Y., T. Takai, and T. Yamada. 2007. Ecotypic variation of water-soluble carbohydrate
683 concentration and winter hardiness in cocksfoot (*Dactylis glomerata* L.). *Euphytica* 153: 267–
684 280.
- 685 Sartori, K., F. Vasseur, C. Violle, E. Baron, M. Gerard, N. Rowe, O. Ayala-Garay, et al. 2019.
686 Leaf economics and slow-fast adaptation across the geographic range of *Arabidopsis thaliana*.
687 *Scientific reports* 9: 1–12.
- 688 Sartori, K., F. Vasseur, C. Violle, E. Baron, M. Gerard, N. Rowe, O. Ayala-Garay, et al. 2019.
689 Leaf economics and slow-fast adaptation across the geographic range of *Arabidopsis thaliana*.
690 *Scientific Reports* 9: 10758.
- 691 Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of
692 image analysis. *Nature Methods* 9: 671–675.
- 693 Schurr, F. M., J. Pagel, J. S. Cabral, J. Groeneveld, O. Bykova, R. B. O’Hara, F. Hartig, et al.
694 2012. How to understand species’ niches and range dynamics: a demographic research agenda
695 for biogeography. *Journal of Biogeography* 39: 2146–2162.
- 696 Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and Ecology of
697 Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics* 40: 415–436.
- 698 Stenøien, H. K., C. B. Fenster, H. Kuittinen, and O. Savolainen. 2002. Quantifying latitudinal
699 clines to light responses in natural populations of *Arabidopsis thaliana* (Brassicaceae).
700 *American Journal of Botany* 89: 1604–1608.

- 701 Stinchcombe, J. R., C. Weinig, M. Ungerer, K. M. Olsen, C. Mays, S. S. Halldorsdottir, M. D.
702 Purugganan, and J. Schmitt. 2004. A latitudinal cline in flowering time in *Arabidopsis*
703 *thaliana* modulated by the flowering time gene FRIGIDA. *Proceedings of the National*
704 *Academy of Sciences* 101: 4712–4717.
- 705 Stotz, G. C., C. Salgado-Luarte, V. M. Escobedo, F. Valladares, and E. Gianoli. 2021. Global
706 trends in phenotypic plasticity of plants. *Ecology Letters* 24: 2267– 2281.
- 707 Suprasanna, P., G. C. Nikalje, and A. N. Rai. 2016. Osmolyte Accumulation and Implications
708 in Plant Abiotic Stress Tolerance. In N. Iqbal, R. Nazar, and N. A. Khan [eds.], *Osmolytes*
709 *and Plants Acclimation to Changing Environment: Emerging Omics Technologies*, 1–12.
710 Springer India, New Delhi.
- 711 Swindell, W. R., M. Huebner, and A. P. Weber. 2007. Plastic and adaptive gene expression
712 patterns associated with temperature stress in *Arabidopsis thaliana*. *Heredity* 99: 143–150.
- 713 Takou, M., B. Wieters, S. Kopriva, G. Coupland, A. Linstädter, and J. De Meaux. 2019.
714 Linking genes with ecological strategies in *Arabidopsis thaliana*. *Journal of Experimental*
715 *Botany* 70: 1141–1151.
- 716 Turnbull, L. A., M. Rees, and M. J. Crawley. 1999. Seed Mass and the
717 Competition/Colonization Trade-Off: A Sowing Experiment. *Journal of Ecology* 87: 899–
718 912.
- 719 Valladares, F., E. Gianoli, and J. M. Gómez. 2007. Ecological limits to plant phenotypic
720 plasticity. *New Phytologist* 176: 749–763.
- 721 Vasseur, F., J. Bresson, G. Wang, R. Schwab, and D. Weigel. 2018. Image-based methods for
722 phenotyping growth dynamics and fitness components in *Arabidopsis thaliana*. *Plant methods*
723 14: 63.

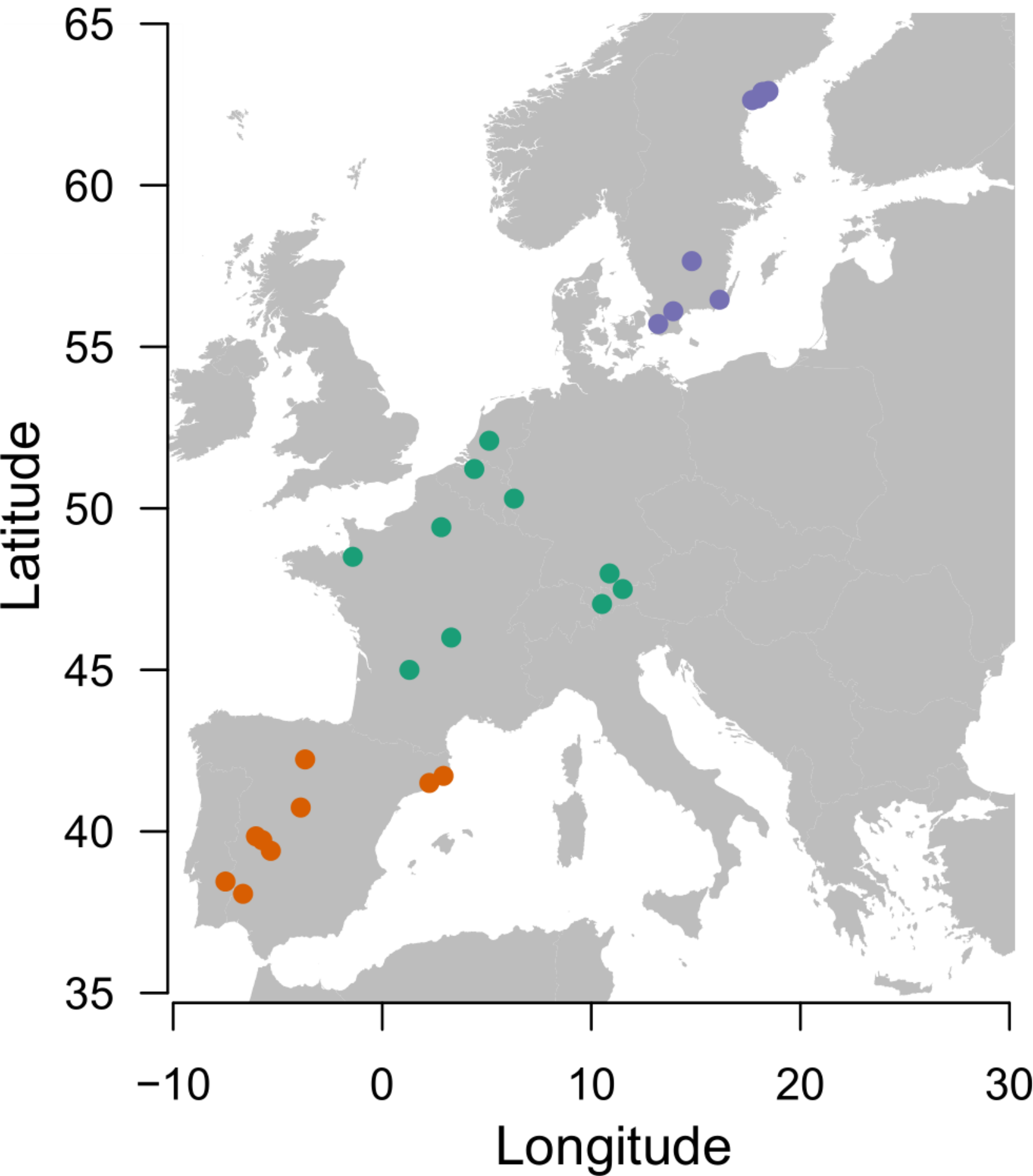
- 724 Vasseur, F., M. Exposito-Alonso, O. J. Ayala-Garay, G. Wang, B. J. Enquist, D. Vile, C.
725 Violle, and D. Weigel. 2018. Adaptive diversification of growth allometry in the plant
726 *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences* 115: 3416–3421.
- 727 Vasseur, F., K. Sartori, E. Baron, F. Fort, E. Kazakou, J. Segrestin, E. Garnier, et al. 2018.
728 Climate as a driver of adaptive variations in ecological strategies in *Arabidopsis thaliana*.
729 *Annals of Botany* 122: 935–945.
- 730 Vasseur, F., C. Violle, B. J. Enquist, C. Granier, and D. Vile. 2012. A common genetic basis
731 to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecology Letters*
732 15: 1149–1157.
- 733 Vile, D., M. Pervent, M. Belluau, F. Vasseur, J. Bresson, B. Muller, C. Granier, and T.
734 Simonneau. 2012. *Arabidopsis* growth under prolonged high temperature and water deficit:
735 independent or interactive effects? *Plant, Cell & Environment* 35: 702–718.
- 736 Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J.
737 Messier. 2012. The return of the variance: intraspecific variability in community ecology.
738 *Trends in Ecology & Evolution* 27: 244–252.
- 739 Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007.
740 Let the concept of trait be functional! *Oikos* 116: 882–892.
- 741 Violle, C., P. B. Reich, S. W. Pacala, B. J. Enquist, and J. Kattge. 2014. The emergence and
742 promise of functional biogeography. *Proceedings of the National Academy of Sciences* 111:
743 13690–13696.
- 744 Volis, S., S. Mendlinger, L. Olsvig-Whittaker, U. N. Safriel, and N. Orlovsky. 1998.
745 Phenotypic variation and stress resistance in core and peripheral populations of *Hordeum*
746 *spontaneum*. *Biodiversity and conservation* 7: 799–813.

- 747 Volis, S., S. Mendlinger, and N. Orlovsky. 2001. Variability in Phenotypic Traits in Core and
748 Peripheral Populations of Wild Barley *Hordeum Spontaneum* Koch. *Hereditas* 133: 235–247.
- 749 Volis, S., D. Ormanbekova, and K. Yermekbayev. 2015. Role of phenotypic plasticity and
750 population differentiation in adaptation to novel environmental conditions. *Ecology and*
751 *Evolution* 5: 3818–3829.
- 752 Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological
753 strategies: some leading dimensions of variation between species. *Annual review of ecology*
754 *and systematics* 33: 125–159.
- 755 Wright, I. J., N. Dong, V. Maire, I. C. Prentice, M. Westoby, S. Díaz, R. V. Gallagher, et al.
756 2017. Global climatic drivers of leaf size. *Science* 357: 917–921.
- 757 Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-
758 Bares, et al. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- 759 Yu, D. W., and H. B. Wilson. 2001. The Competition-Colonization Trade-off Is Dead; Long
760 Live the Competition-Colonization Trade-off. *The American Naturalist* 158: 49–63.

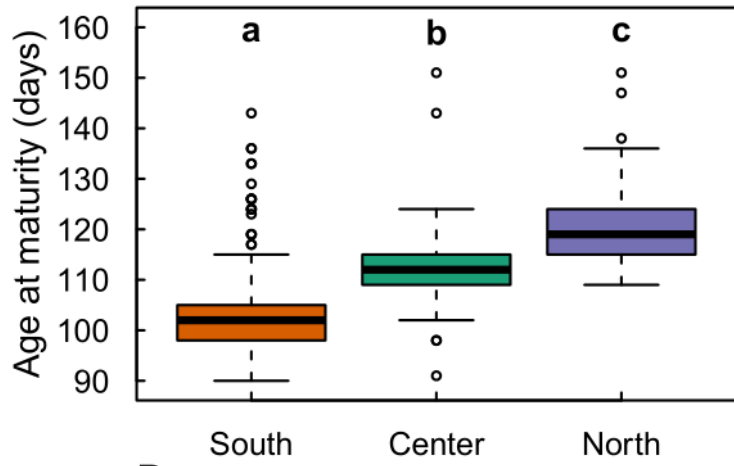
761 **Table 1.** Environmental treatments and their mean effects on plant traits and CSR scores.
 762 Traits mean and standard deviation over the 30 accessions are presented for each treatment.
 763 SLA: specific leaf area; LA: leaf area; LDMC: leaf dry matter content; C: Competitive; S:
 764 Stress-tolerance; R: Ruderal. WW: well-watered; WD: water deficit; HT: hot temperature;
 765 LT: low temperature. Temp.: mean air temperature.

Treatment	Temp. (°C)	Water deficit	LA (mm ²)	SLA (mm ² /mg)	LDMC (mg/g)	LNC (%)	C (%)	S (%)	R (%)	Age at maturity (days)	Fecundity
control	15		138.44	53.1 ±	85.57	5.65	8.05		91.04	114.34 ±	76.71 ±
			± 54.78	20.45	±	±	±	0 ±	±	10.23	37.01
					19.94	1.18	2.32		0	3.57	
WW-HT	35		142.33	54.76 ±	84.92	5.55	7.89		91.11	114.37 ±	77.57 ±
			± 62.54	12.84	±	±	±	0 ±	±	10.45	35.8
					18.96	1.23	2.28		0	2.99	
WD-HT	35	x	148.76	53.43 ±	85.96	5.52	8.02		91.19	114.25 ±	78.01 ±
			± 55	14.38	±	±	±	0 ±	±	10.28	36.04
					19.29	1.19	2.21		0	2.89	
WW-LT	-6		149.81	56.04 ±	86.61	5.52	7.97		90.9	115.34 ±	77.23 ±
			± 65.85	23.01	±	±	±	0 ±	±	10.26	38.81
					19.31	1.13	2.41		0	3.73	
WD-LT	-6	x	139.24	52.97 ±	84.91		8.05		91.06	115.21 ±	77.74 ±
			± 59.12	16.49	±	±	±	0 ±	±	10.14	37.01
					18.29		2.32		0	3.28	

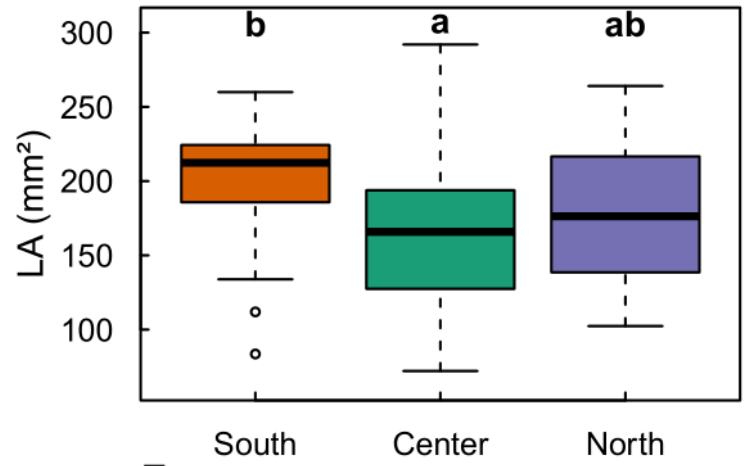
766



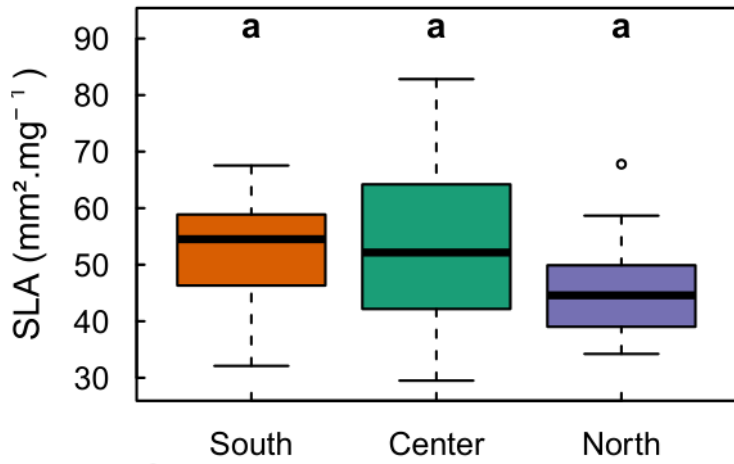
A



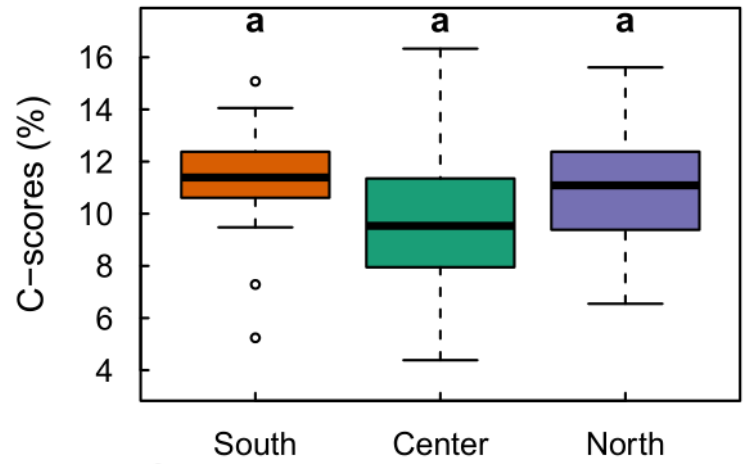
E



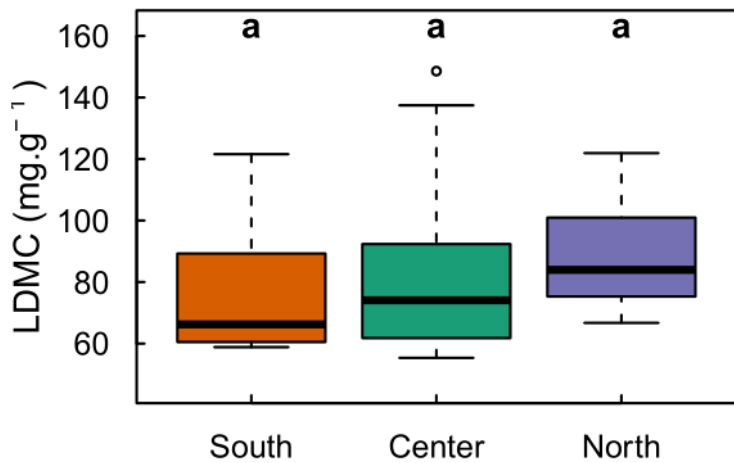
B



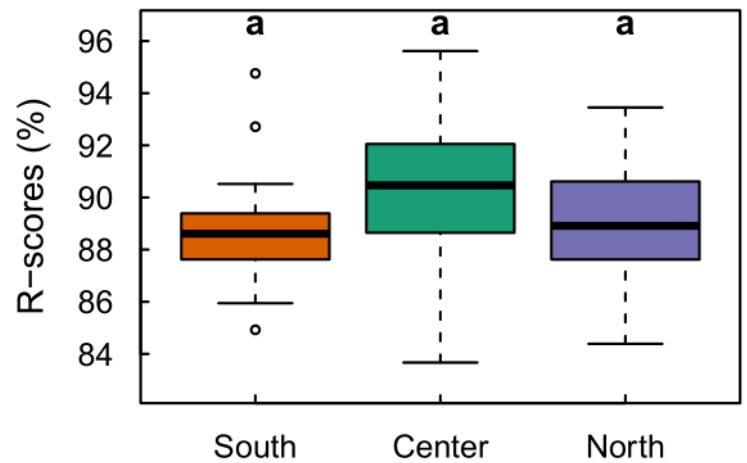
F



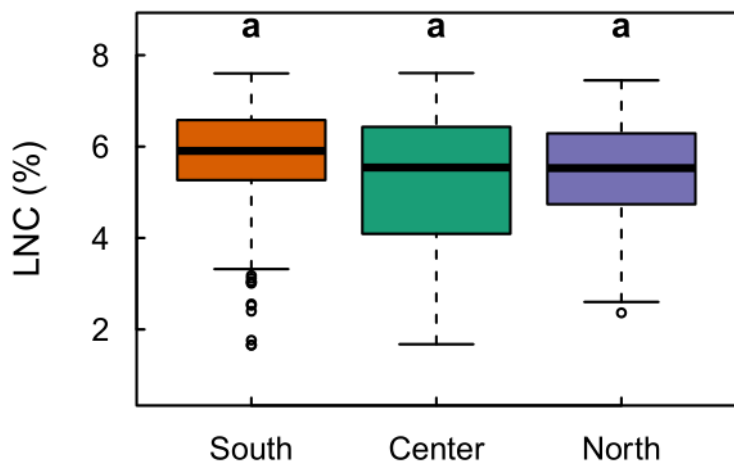
C



G



D



H

