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1 **Leaf economics guides slow-fast adaptation across the geographic range of**  
2 ***A. thaliana***

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## 21 **Summary**

22           The slow-fast continuum describes how resource allocation constrains life-history  
23 strategies in many organisms. In plants, it is reflected by a trade-off at the leaf level between  
24 the rate of carbon assimilation and lifespan, the so-called Leaf Economics Spectrum (LES).  
25 However, it is still unclear how the LES is connected to the slow-fast syndrome, and reflects  
26 adaptation to climate. Here, we measured growth, morpho-physiological and life-history traits  
27 at both leaf and whole-plant levels in 384 natural accessions of *Arabidopsis thaliana*. We  
28 examined the extent to which the LES continuum parallels the slow-fast continuum, and  
29 compared trait variation to neutral genetic differentiation between lineages. We found that the  
30 LES is tightly linked to variation in whole-plant functioning, relative growth rate and life  
31 history. A genetic analysis further suggested that phenotypic differentiation is linked to the  
32 evolution of different slow-fast strategies in contrasted climates. Together, our findings shed  
33 light on the physiological bases of the slow-fast continuum, and its role for plant adaptation to  
34 climate.

35

## 36 **Keywords**

37           *Arabidopsis thaliana*, eco-physiological trade-off, genetic differentiation, intraspecific  
38 variability, plant adaptation, plant functional trait, plant performance

39

40

## 41 **Introduction**

42 Plant populations diversify geographically as a result of adaptive (e.g., natural selection) and  
43 non-adaptive (e.g., genetic drift and isolation) processes. To understand plant evolutionary  
44 responses to current and future climate variations, it is crucial to investigate the genetic and  
45 phenotypic differentiation of plant lineages along environmental gradients. As plants cannot  
46 simultaneously optimize competing eco-physiological functions, an important question is how  
47 plant adaptation occurs under the influence of major trade-offs between traits.

48 The slow-fast continuum is a pervasive trade-off between resource allocation to  
49 growth, reproduction and survival, spread across the tree of life <sup>1</sup>. The slow end of this  
50 continuum is characterized by slow growing, long-lived species and low reproductive output,  
51 while species at the fast end reach reproductive maturity faster and produce more offspring. In  
52 plants, the leaf economics spectrum (LES hereafter) <sup>2-4</sup>, is thought to reflect the physiological  
53 basis of the slow-fast continuum <sup>4</sup>. The LES arrays plant species along a continuum of leaf  
54 trait syndromes going from short-lived leaves with fast metabolism and rapid return on  
55 investment to the reverse syndrome <sup>3</sup>. Core LES traits include leaf dry mass per area (LMA),  
56 leaf lifespan and net photosynthetic rate per mass unit ( $A_{\text{mass}}$ ) <sup>3,5-7</sup>. Some of these leaf traits  
57 are broadly used in comparative ecology to infer whole-plant ecological strategies <sup>4,8-12</sup>.  
58 However, the extent to which leaf-level resource economics reflects whole-plant physiology,  
59 performance, and ultimately fitness, is still under debate <sup>13</sup>. Many processes can lead to a  
60 mismatch between LES and whole-plant functioning <sup>14</sup>, including the impact of self-shading  
61 among leaves and resource allocation patterns, such as carbon investment in non-  
62 photosynthetic tissues <sup>15,16</sup>. To gain insights into the robustness of the slow-fast continuum at  
63 different organizational levels, we need to examine how LES traits scale up to plant level  
64 resource-use strategies, life history and performance. However, it remains difficult to compare  
65 individual performance across species with different growth forms, phenology and dispersal  
66 strategies, which impedes a clear linkage between physiological and adaptive trade-offs <sup>17-19</sup>.

67 The LES has been associated with differences in the ability of plants to adapt to more  
68 or less harsh environmental conditions <sup>4,12,20,21</sup>: species displaying high photosynthetic,  
69 respiration and growth rates, short-lived, thin and nitrogen-rich leaves are preferentially found  
70 in nutrient-rich and/or growth-suitable climatic conditions. Those species are qualified as  
71 acquisitive in contrast to conservative species that exhibit the opposite set of traits. Despite

72 those observations, functional ecology has no tools to test for adaptation, and empirical  
73 evidences of the adaptive value of being at one end or the other of the continuum in a given  
74 environment remain scarce (see <sup>22</sup> for review). Furthermore, sampling procedure in field  
75 observation studies often impedes to disentangle the effects of plasticity vs. genetic  
76 differentiation on the emergence of the LES <sup>23</sup>. Thus, comparative studies looking for plant  
77 adaptation are at best incomplete <sup>22,24</sup>, and the role of selection in shaping the LES and driving  
78 adaptation to diverse environments is hardly understood. To fill this gap, intraspecific studies  
79 are encouraged since they can take benefit from tools developed in population ecology and  
80 genetics <sup>22,25,26</sup>. The LES has started to be analysed at the intraspecific level, with contrasting  
81 findings depending on the studied organism and type of study <sup>23,27-32</sup>. LES relationships  
82 appeared consistent with cross-species ones when using species with broad environmental  
83 niche spectra <sup>31,33</sup> and/or broad phenotypic variability <sup>23</sup>, but inconsistent when using species  
84 with narrow phenotypic (and genetic) diversity <sup>34</sup>. Genetic differentiation of LES strategies  
85 has been demonstrated between populations of *Helianthus anomalus* along a 400 km rainfall  
86 gradient <sup>35</sup>. However, the question whether LES diversifies because of adaptation to climate  
87 between lineages spanning large geographic distribution remains open. Overall, we still miss  
88 a comprehensive understanding of within-species LES variation and the subsequent insights  
89 they can provide to well-described interspecific patterns from an evolutionary perspective.

90         Adaptation requires the fixation of beneficial alleles in a population, which  
91 subsequently leads to phenotypic variation and differential response to the environment.  
92 However, neutral alleles can also vary in abundance due to the effect of genetic drift. By  
93 comparing genetic and phenotypic differentiation between populations or lineages, Qst-Fst  
94 provides a powerful tool to infer adaptation in polygenic quantitative traits such as LES  
95 traits <sup>36</sup>. It notably enables to decipher neutral and adaptive demographic processes at the  
96 origin of phenotypic diversity within species. Indeed, Qst-Fst comparisons are based on the  
97 computation of genetic (Fst) and phenotypic (Qst) differentiation between populations or  
98 lineages. Hence, Qst values above neutral Fst are interpreted as a signature of diversifying  
99 selection on the underlying trait. For instance, Qst-Fst comparisons have been successfully  
100 used in the species *Campanula rotundifolia*, *Arrhenatherum elatius* and *Quercus oleoides* to  
101 investigate the role of selection in the diversification of life-history traits, growth strategies or  
102 drought resistance between lineages at both local and global scales <sup>37-39</sup>. Thus, Qst-Fst  
103 comparison appears promising in the perspective of examining how phenotypic trade-offs

104 trigger local adaptation along geographical and environmental gradients<sup>35</sup>. This method is  
105 expected to be particularly powerful in model species, with the help of modern genomics such  
106 as high-throughput genotyping and sequencing<sup>40,36</sup>.

107 The species *Arabidopsis thaliana* has been widely used in molecular biology, cell  
108 biology and quantitative genetics. Thanks to the efforts to characterize the genetic diversity in  
109 this species<sup>41-44</sup>, it is also a model in population dynamics<sup>45</sup> and evolutionary ecology<sup>46</sup>. For  
110 instance, the genetic determinism of *A. thaliana* life history has been extensively studied,  
111 notably with the discovery of genes that control major developmental transitions such as  
112 flowering time<sup>47</sup>. Allelic variation in these genes appears to be adaptive to climatic and  
113 altitudinal gradients<sup>48</sup>. A recent study in *A. thaliana* supports the hypothetic link between life  
114 history variation and the LES, highlighted by strong genetic correlations between these traits  
115<sup>28,49</sup>. However this analysis was performed on recombinants inbred lines used for genetic  
116 mapping. Made of artificial crosses, they preclude examining the relationships between LES  
117 and the natural environment. Interestingly, *A. thaliana* has recently gained a renewed interest  
118 in functional ecology and biogeography<sup>50,51</sup>, notably due to the large panel of natural  
119 accessions that have been collected from contrasting climates, and genotyped at high density  
120 (e.g.<sup>41-44</sup>). As genetic data in *A. thaliana* allows an unprecedented large-scale analysis of  
121 genetic variation between populations and lineages, this species is promising to investigate  
122 the extent of intraspecific diversity in LES traits and its role for adaptation to contrasted  
123 climates.

124 In this study, we explored the evolutionary bases of LES variation using a pan-  
125 European collection of 384 natural accessions from the RegMap panel<sup>43</sup>. Specifically, we  
126 investigated whether plant adaptation to various climates is associated with genetic  
127 differentiation along the slow-fast continuum. To test this hypothesis, we first examined how  
128 the LES shapes phenotypic diversity across contrasted accessions of *A. thaliana*, and tested  
129 whether LES traits scale up to plant level resource-use strategies, life history and  
130 performance. Secondly, we took benefit from the large genomic information available in *A.*  
131 *thaliana* to evaluate with Qst-Fst comparisons to what extent LES differences between  
132 lineages are attributable to adaptive processes such as adaptation to contrasted climates.

133

## 134 **Results**

### 135 **Geographic clustering of *A. thaliana* lineages**

136 The range of biomes experienced by the sampled genotypes covers temperate grasslands,  
137 deserts, woodlands-shrublands and temperate forests (Fig. 1b). Using the 250K SNPs data  
138 available from Horton et al.<sup>43</sup>, we performed a genetic clustering of the genotype set. A  
139 cross-validation for different numbers of clusters ( $k = 3$  to  $k = 11$ ) showed that our set of  
140 genotypes can be separated into six groups representative of different genetic lineages (cross  
141 validation error = 0.89). These lineages were moderately differentiated (mean  $F_{ST} = 0.11$ ),  
142 geographically (Fig. 1a) as well as in the Whittaker's biome classification (Fig. 1b). The  
143 analysis revealed the existence of two genetic groups exclusively located in France in our  
144 sample (French 1 and French 2 hereafter) of 73 and 45 genotypes, respectively. Among the 15  
145 genotypes of the third group, seven were defined as North Swedish in the 1001 genomes  
146 dataset<sup>44</sup>. Consistently, the 15 "Swedish" genotypes, although not all in Sweden (Fig. 1a),  
147 were mainly located in cold environments and woodland-shrubland in Whittaker's  
148 classification (Fig. 1b). We considered genotypes from group 4 as "Central European" (Fig.  
149 1a), typically living at intermediate temperatures and rainfall (Fig. 1b). 68 genotypes  
150 composed the group 5, all located in Western Europe (Fig. 1a), in a range of relatively warm  
151 environments with intermediate rainfall. Finally, only five genotypes composed group 6, all  
152 collected in USA ("American" genotypes hereafter).

### 153 **Leaf economics of *A. thaliana***

154 Assimilation rate was the most variable trait among the leaf economics traits in our dataset  
155 (18-fold; from 34.8 to 608.9  $\mu\text{mol g}^{-1} \text{s}^{-1}$ ) while LMA and LLS varied 5 and 3.5 times (from  
156 18.7 to 101  $\text{g m}^{-2}$ , and from 15 to 53.5 d), respectively. Representing the dataset within this 3-  
157 dimension space revealed that the LES constrains the covariation of *A. thaliana* leaf traits.  
158 Consistent with interspecific comparisons, genotypes are ranked from low  $A_{\text{mass}}$  and high  
159 LMA and LLS, toward high  $A_{\text{mass}}$  and low LMA and LLS (Fig. 2). A principal component  
160 analysis (PCA) showed that 78% of the covariation between these three traits was explained  
161 by a single Principal Component (Fig. S1a). Hereafter, we assigned a position along the LES  
162 for each genotype with its score on PC1.  $A_{\text{mass}}$  was highly negatively correlated with PC1 ( $r =$   
163  $-0.91$ ) while LMA and LLS were positively correlated with PC1 ( $r = 0.93$  and  $0.81$ ,

164 respectively). Thus, high and low PC1 values are representative of genotypes located at the  
165 conservative and acquisitive side of the LES, respectively.

#### 166 From the leaf economics spectrum to the plant slow-fast continuum

167 Trait measurement at the plant level revealed that assimilation rate was again the most  
168 variable trait with a 68-fold variation (from 8.4 to 578.1  $\mu\text{mol g}^{-1} \text{s}^{-1}$ ), while plant mass per  
169 area and age of maturity varied 5 times (from 17.7 to 85.4  $\text{g m}^{-2}$  and 22 to 111 d,  
170 respectively). Standardized major axis regressions between traits measured at the leaf and  
171 plant levels were highly significant. Leaf and plant-level LMA were highly correlated ( $r =$   
172 0.78;  $P < 0.001$ ; Fig. S1c) and the slope was close to, but significantly different from 1 (95%  
173 CI slope = [1.07, 1.17]), as well as for leaf-level and plant-level net photosynthetic rate ( $r =$   
174 0.84;  $P < 0.001$ ; Fig. S1d, 95% CI slope = [0.79, 0.9]). Similarly, leaf life-span and plant age  
175 of maturity were significantly correlated with a slope below 1 (slope = 0.58 [0.53; 0.63],  $r =$   
176 0.47,  $P < 0.001$ ; Fig. S1e). A single principal component explained 87% of the trait  
177 covariation at the plant level (Fig S1b) and was highly correlated with the PC1 of the PCA on  
178 leaf traits ( $r = 0.87$ ,  $p < 0.001$ ). Indeed, life history and performance at the plant level were  
179 strongly related to PC1, as illustrated by the correlation between relative growth rate (RGR)  
180 and PC1 ( $r = -0.33$ ) and age of maturity (AM) and PC1 ( $r = 0.76$ ) (Fig. 3a,b), highly  
181 significant when including or not the kinship matrix as a covariate ( $p < 0.001$ ). Conservative  
182 leaf strategies are thus associated with slow plant growth and late reproduction, whereas  
183 acquisitive leaf strategies are associated with fast plant growth and early reproduction.

#### 184 Adaptation cues of the slow-fast continuum

185 We performed  $Q_{ST}$ - $F_{ST}$  comparisons for both RGR and AM to assess the adaptability of the  
186 slow-fast strategies. Pairwise comparisons based on the whole genetic data indicated a strong  
187 genetic divergence between French2 and the other groups ( $F_{ST} > 0.19$ ), as well as between  
188 American and other groups ( $F_{ST} > 0.43$ ), although the low number of accessions belonging to  
189 the American group can bias the latter. French1 group was genetically closer to Western  
190 European group ( $F_{ST} = 0.13$ ) than French2 group ( $F_{ST} = 0.20$ ). Interestingly, North Swedish  
191 lines showed strong phenotypic and genetic differentiation with other lineages (Fig. S2).  
192 While the average genetic differentiation between genetic groups was moderate (mean  $F_{ST} =$   
193 0.11), phenotypic differentiation was remarkably high for RGR and AM compared to the  $F_{ST}$   
194 distribution. Further, the high skewness of the  $F_{ST}$  distribution (1.46) suggested that the large

195 majority of SNPs can be considered as neutral while the RGR and AM  $Q_{ST}$  fell on the upper  
196 5% of the  $F_{ST}$  distribution (Fig. 3c,d). We performed a parametric bootstrap analysis to  
197 generate confidence intervals around  $Q_{ST}$  values and showed that the lowest estimates of the  
198 relative growth rate (age of maturity)  $Q_{ST}$  fell on the upper 10% (5%) of the  $F_{ST}$  distribution.  
199 Similarly, we showed that all LES traits but leaf lifespan, exhibited extreme  $Q_{ST}$  values (Fig.  
200 S1f). This suggests that slow-fast traits at both leaf and plant levels behaved like outlier  
201 variants that strongly diverged between lineages due to the effect of diversifying selection.

## 202 Climatic drivers of *A. thaliana* phenotypes

203 We investigated whether 19 climatic variables ([www.worldclim.org/bioclim](http://www.worldclim.org/bioclim)) at the collecting  
204 sites of the genotypes explain *A. thaliana* slow-fast strategies. Stepwise regressions revealed  
205 that both RGR and AM are best predicted by a subset of climatic variables ( $r^2 \sim 0.16$  in both  
206 cases,  $p < 0.001$ ). More precisely, the annual mean temperature, annual mean precipitation,  
207 and temperature seasonality of the collecting sites had a positive (negative) effect on RGR  
208 (AM), while the mean temperature of the warmest quarter had a negative (positive) effect.  
209 The best predictor model of RGR (AM) variation included as well the minimal temperature of  
210 the coldest month (positive effect), and the best predictor model of the AM included the  
211 maximum temperature of the warmest month (negative effect). Using the WorldClim  
212 database, we predicted a theoretical map of the slow-fast continuum for *A. thaliana*. We  
213 showed that slow strategies, characterized by slow growth and late reproduction, were  
214 favoured in North Europe and Central East of Spain and in the highest European reliefs. In  
215 addition, fast strategies characterized by fast growth and early reproduction were found in  
216 Central Europe and near the coasts.

## 217 Discussion

218 The comparison of multiple species based on a few traits is the historical approach of  
219 functional ecology<sup>52</sup>. While fruitful<sup>12</sup>, such an approach impedes a deeper investigation of  
220 how evolutionary forces and trade-offs operate together to shape the observable phenotypic  
221 diversity<sup>24,26</sup>. Notably, several trait-trait covariations have been discussed in functional  
222 ecology in the light of trade-off theories. One of the most prominent phenotypic pattern  
223 discussed in the last decades, the so-called Leaf Economics Spectrum (LES), is thought to  
224 reflect a trade-off between metabolic rate and lifespan at the leaf level<sup>3,5,53,54</sup>. Plant species

225 that exhibit long-lived leaves have been referred to nutrient conservative species. They  
226 optimize long-term carbon gain and extended nutrient time residence, as well as nutrient use  
227 efficiency<sup>55</sup>. By contrast species with short-lived leaves sacrifice nutrient retention to  
228 maximize the rate of carbon fixation. The LES is expected to reflect an adaptive trade-off  
229 between fast and slow growth strategies across plant species<sup>4</sup>. Two assumptions underline  
230 this assertion: (i) the negative correlation between leaf photosynthetic rate and leaf lifespan is  
231 translated into a negative correlation between plant growth rate and the duration of the life  
232 cycle, (ii) particular combinations of slow-fast traits are selected in different environments.  
233 Both assumptions are difficult to test at the interspecific level. This has generated a living  
234 debate about the evolutionary causes of the LES<sup>22,28,56-59</sup>. Taking benefit from a large  
235 collection of sequenced ecotypes in a model species, our results show that LES traits are  
236 correlated with slow-fast strategies at the plant level, and that trait divergence between genetic  
237 lineages is non-neutral. This supports the idea that plant populations evolve different slow-  
238 fast strategies along with different LES traits in order to adapt to contrasting climates.

239 We showed that LES trait correlations in *A. thaliana* follow the interspecific pattern  
240<sup>3,5</sup>: individuals that invest a large amount of biomass per unit leaf area have a lower leaf  
241 assimilation rate and a longer leaf lifespan than plants that invest less biomass per unit leaf  
242 area. Moreover, the economics spectrum is conserved when scaling from leaf to whole-plant  
243 traits. This gives strong support to the idea that a trait value obtained on a single leaf using a  
244 standardized method, reflects the average phenotypic value expressed by all the leaves of an  
245 individual plant<sup>60,61</sup>. Furthermore, our results showed that carbon economy at the leaf level is  
246 connected to the slow-fast strategies at the plant level: the LES explained variations in growth  
247 rate and age of maturity in *A. thaliana*, two core traits of the slow-fast continuum. This  
248 suggests that the strong coordination between leaf assimilation rate, leaf lifespan and LMA  
249 act as a guide for the slow-fast strategies at the whole plant level. However, the correlations  
250 between leaf-level and whole-plant traits are presumably strongly variable between species. It  
251 is notably expected to be weaker in woody species because of the varying proportion of non-  
252 photosynthesizing tissues<sup>62</sup>. Our results illustrate this statement; the assimilation rate  
253 decreases faster and the mass per unit area increases faster at the plant level than the leaf  
254 level. Similarly, leaf lifespan varied less and increased more slowly than plant age of  
255 maturity, which gives room for a decoupling between leaf and plant life history. Nonetheless,  
256 the ranking between genotypes is conserved and allows a scaling of strategies. Although our

257 study is a first step in this direction, further explorations of how leaf level trade-offs  
258 constrains plant functioning in herbaceous and woody species are needed. In this perspective,  
259 several studies reported positive covariations between leaf carbon assimilation rate and plant  
260 relative growth rate in young trees <sup>63,64</sup>.

261 Using  $F_{ST}$ - $Q_{ST}$  comparisons, we demonstrated how a whole plant syndrome guides the  
262 *A. thaliana* phenotypic differentiation across contrasted climates. The predicted distribution of  
263 slow-fast strategies across Europe revealed differential selection between roughly Norway,  
264 Sweden and Spain on one side, and central and Western Europe on the other. Selection for  
265 slow ecotypes toward higher latitude in *A. thaliana*, specifically in North Swedish accessions,  
266 is supported by previous findings on flowering time <sup>65,66</sup>. More surprisingly however, our  
267 results suggest that similar trait combinations representative of slow strategies are selected in  
268 two contrasted climates: Spain and Scandinavia, which are at the opposite edges of the *A.*  
269 *thaliana* latitudinal range. This clustering of *A. thaliana* genotypes echoes a recent study  
270 showing drought related allele fixation in both Scandinavian and Spanish *A. thaliana*  
271 populations <sup>67</sup>. If we consider together the absence of significant effect of the kinship matrix  
272 on trait-trait relationships tested, the globally low average differentiation between genetic  
273 groups ( $F_{ST} = 0.11$ ), and the phenotypic similarity observed at two distant locations, it  
274 suggests that genetic determinism of slow strategies as well as phenotypic differentiation  
275 could have occurred by convergence through adaptive processes. Thus, slow strategies could  
276 be selected in response to water limitation in regions from nonetheless very different climates:  
277 low average temperature at Scandinavian sites, high altitude at Spanish sites (between 300  
278 and 1100 m). Interspecific studies at global scale revealed a negative relationship between  
279 conservative strategies and rainfall <sup>3,68</sup>, possibly linked to a higher investment in cell wall  
280 complex macromolecules to face drought stress <sup>69</sup>. Large-scale interspecific studies also  
281 reported a bias toward acquisitive strategies with increasing temperature in herbaceous  
282 species <sup>70,71</sup>. Together, this suggests a general selection pressure for slow strategies in dry  
283 environments, opposed to selection for fast strategies in non-stressing environments <sup>23</sup>.

284 Using a model species, with large collections of well-characterized genetic material,  
285 appears particularly successful to go deeper into the evolutionary underpinning of major eco-  
286 physiological trade-offs, such as the LES and the slow-fast continuum. Combined with global  
287 climatic data, our findings notably revealed the role of selection for drought on slow-fast

288 strategies in *A. thaliana*. Next steps will be to merge approaches, and fully benefit from what  
289 a model species can provide both genetically and eco-physiologically. For instance, the  
290 climatic cues detected here despite the lack of climate data precision, is encouraging for the  
291 future of functional biogeography<sup>72</sup>. There is also evidence that the connection between  
292 functional trait and environmental adaptation requires a better characterisation of plant fitness  
293 through demographic measures<sup>26</sup>. Comparative studies integrating demographic approach at  
294 population level are promising to understand how selection and macro-ecological gradient  
295 shape the evolutionary responses of plants to climate variation<sup>24,26</sup>.

296

## 297 **Materials and methods**

### 298 **Plant material**

299 We used a total of 384 natural genotypes of *Arabidopsis thaliana* L. Heynh sampled  
300 from the worldwide lines of the RegMap population ([http://bergelson.uchicago.edu/wp-](http://bergelson.uchicago.edu/wp-content/uploads/2015/04/Justins-360-lines.xls)  
301 [content/uploads/2015/04/Justins-360-lines.xls](http://bergelson.uchicago.edu/wp-content/uploads/2015/04/Justins-360-lines.xls)), which were genotyped for 250K bi-allelic  
302 SNPs (Horton *et al.*, 2012).

### 303 **Growth conditions**

304 Phenotype characterization was performed under controlled conditions in the high-  
305 throughput PHENOPSIS phenotyping platform (Granier *et al.* 2006) to track daily growth.  
306 Seeds were kept in the dark at 4 °C for at least one week before sowing. Four to six seeds per  
307 genotype were sown at the soil surface in 225 ml pots filled with a 1:1 (v:v) mixture of loamy  
308 soil and organic compost (Neuhaus N2). The soil surface was moistened with one-tenth  
309 strength Hoagland solution, and pots were kept in the dark during 48 h under controlled  
310 environmental conditions (20 °C, 70% air relative humidity). Then, pots were placed in the  
311 PHENOPSIS growth chamber at 20 °C, 12 h photoperiod, 70 % relative humidity, 175  $\mu\text{mol}$   
312  $\text{m}^{-2} \text{s}^{-1}$  PPFD. Pots were sprayed with deionized water three times per day until germination,  
313 and then soil water content was adjusted to 0.35 g H<sub>2</sub>O g<sup>-1</sup> dry soil (-0.07 MPa soil water  
314 potential) to ensure optimal growth (Aguirrezábal *et al.* 2006; Vile *et al.* 2012). After  
315 emergence of the fourth leaf, one plant individual was left in each pot.

### 316 **Measurements of plant traits**

317 In order to standardize measurements at an ontogenic stage for all genotypes, all traits  
318 were quantified when flower buds were macroscopically visible (i.e. bolting stage), and leaf  
319 traits were measured on the last adult leaf, fully exposed to light.

320 Net photosynthetic rate, relative expansion rate, lifespan, vegetative dry weight, as  
321 well as leaf area were determined for the leaf and the plant canopy. Net photosynthetic rate  
322 was measured at leaf (leaf  $A$ ,  $\text{nmol CO}_2 \text{ s}^{-1}$ ) and whole-plant levels (plant  $A$ ,  $\text{nmol CO}_2 \text{ s}^{-1}$ )  
323 under growing conditions using, respectively, the leaf cuvette provided with the infrared gas  
324 analyser system (CIRAS 2, PP systems, USA), and a whole-plant chamber prototype designed  
325 for *A. thaliana* by M. Dauzat (INRA, Montpellier, France) and K. J. Parkinson (PP System,  
326 UK) (see Vasseur et al. 2012). Leaf and whole-plant photosynthetic rates were both expressed  
327 on dry mass basis (leaf  $A_{\text{mass}}$  and plant  $A_{\text{mass}}$ ,  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ ). Due to time constraints, we  
328 measured photosynthetic rates for 319 and 348 accessions at the leaf and whole-plant levels  
329 (306 in common), respectively. We estimated the age of maturity by the day length from  
330 germination to the appearance of the flower bud. Then, plants were harvested, and individual  
331 fresh weight was determined. The leaf used for photosynthetic measurements was identified  
332 and processed separately, and detached rosettes were kept in deionised water at 4 °C for 24 h,  
333 and water-saturated weight was determined. Individual leaves were then attached to a sheet of  
334 paper and scanned for subsequent determination of the leaf number and total leaf area using  
335 ImageJ (Schneider *et al.*, 2012). Dry weight of lamina and petioles were obtained after  
336 drying for 72 h at 65 °C. Rosette dry weight was expressed as the sum of lamina and petiole  
337 dry weights. Leaf mass per area was both calculated for the leaf used for photosynthetic  
338 measurements (LMA,  $\text{g m}^{-2}$ ) and for the whole-rosette (plant LMA,  $\text{g m}^{-2}$ ) as the ratio of  
339 lamina dry mass to lamina area. Relative growth rate (RGR,  $\text{mm}^2 \text{ mm}^{-2} \text{ d}^{-1}$ ) and leaf lifespan  
340 (LLS, d) were estimated from automated daily pictures of the rosettes. More precisely, a  
341 sigmoid curve was fitted to rosette area as a function of time in order to extract growth  
342 parameters, where RGR was calculated as the slope at the inflection point<sup>73–75</sup>. Using daily  
343 pictures, we tracked three consecutive leaves from birth (emergence) to death (full  
344 senescence). For each plant, leaf duration was calculated as the average number of days from  
345 leaf emergence to senescence.

346  $F_{\text{ST}}$  and  $Q_{\text{ST}}$  measures

347 In order to perform population genetic analyses, genetic groups were identified by  
348 genetic clustering of 384 genotypes, using the 250K SNPs data available from Horton et al. <sup>43</sup>.  
349 Clustering was performed with ADMIXTURE <sup>76</sup> after linkage disequilibrium pruning ( $r^2 <$   
350  $0.1$  in a 50 kb window with a step size of 50 SNPs) with PLINK <sup>77</sup>, resulting in 24,562  
351 independent SNPs used for subsequent analyses. Following the same approach as the 1001  
352 genomes project <sup>44</sup>, we assigned each genotype to a group if more than 60% of its genome  
353 derived from the corresponding cluster. The 123 accessions not matching this criterion were  
354 labelled “Admixed” and were not used for the  $F_{ST}$  and  $Q_{ST}$  calculation. The groups  
355 genetically defined were also geographically distinct. We calculated Weir and Cockerham  $F_{ST}$   
356 value for all the 24,562 SNPs, as well as mean  $F_{ST}$  genome-wide. We also calculated  $Q_{ST}$ , an  
357 analogue of  $F_{ST}$  measure, used to estimate the diversification of quantitative traits among  
358 populations, as the between-group variance divided by the total variance for leaf and whole-  
359 plant traits. A value of  $Q_{ST}$  higher than neutral loci  $F_{ST}$  or the 95<sup>th</sup> quantile of the  $F_{ST}$   
360 distribution means that the phenotypic differentiation between populations is larger than  
361 expected by demographic events alone, in particular genetic drift, and is thus indicative of  
362 diversifying selection on traits <sup>36,78</sup>. We used parametric bootstrap method to generate 95%  
363 confidence intervals (CI) around  $Q_{ST}$  values with the package MCMCglmm in R (10,000  
364 iterations).

## 365 Statistical analysis

366 Climate variables at the sampling sites of each genotype were extracted from the  
367 Worldclim database (<http://www.worldclim.org/bioclimate>), with a 2.5 arc-minutes resolution.  
368 The effect of climatic variables on traits was tested using linear model regressions. All  
369 analyses were performed in R 3.4.1 2017 (R Core Team, 2017). Whittaker biomes were  
370 plotted using the BIOMEplot function provided by G. Kunstler  
371 (<https://rdrr.io/github/kunstler/BIOMEplot/src/R/biomes-plot.R>). Principal component  
372 analysis (PCA) was performed using the package factominer. The package nlme was used to  
373 perform linear models and phylogenetic generalized least squares regressions. SMA  
374 regressions were performed using the package smatr <sup>79</sup>, and phylogenetic SMA regressions  
375 using the Phyl.RMA function of the Phytools package. We performed phylogenetic  
376 regressions (LM and SMA) including a relatedness matrix as covariance matrix, obtained

377 after running the PLINK --make-rel command across the 214,051 SNPs from the RegMap  
378 data.

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387

### 388 **Author contribution**

389 DV, FV and CV designed the study, KS, EB, MG, OA-G, AC, LGDJ, DM, EH,  
390 MDRG and AC conducted the experiments. KS and FV performed statistical analyses. KS  
391 wrote the first draft of the manuscript, and all authors contributed to revisions.

### 392 **Competing interests**

393 The author(s) declare no competing interests.

### 394 **Data availability statement**

395 The authors agree that the data supporting the results will be archived in an  
396 appropriate public repository and the links and identifiers will be included within the article.

397

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- 598

## 599 Legend of figures

600

601 **Figure 1. Location and climatic conditions of the genotype collecting sites. (a)**  
602 Distribution of the 384 natural genotypes used in this study. The small points represent the  
603 collecting sites of genotypes and bigger points give the number of collecting sites overlapped  
604 at these positions. The colours represent the six genetic groups: Admixed (grey), French1  
605 (brown), French2 (orange), Swedish (purple), Central Europe (dark blue), Western Europe  
606 (light blue), American (black). **(b)** Mean annual rainfall (MAR) and mean annual temperature  
607 (MAT) for the sites where genotypes were collected, in relation to major biome types of the  
608 world following Whittaker's classification. 1-9 : Tundra, Boreal forest, Temperate Grassland  
609 Desert, Woodland Shrubland, Temperate Forest, Temperate Rain Forest, Tropical Forest  
610 Savana, Tropical Rain Forest, and Desert.

611

612 **Figure 2. The leaf economics spectrum in *A. thaliana*.** Three-way relationships  
613 among the main leaf economics traits:  $A_{\text{mass}}$ , mass based assimilation rate ( $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ );  
614 LMA, leaf mass per area ( $\text{g m}^{-2}$ ); LLS, leaf lifespan (d).

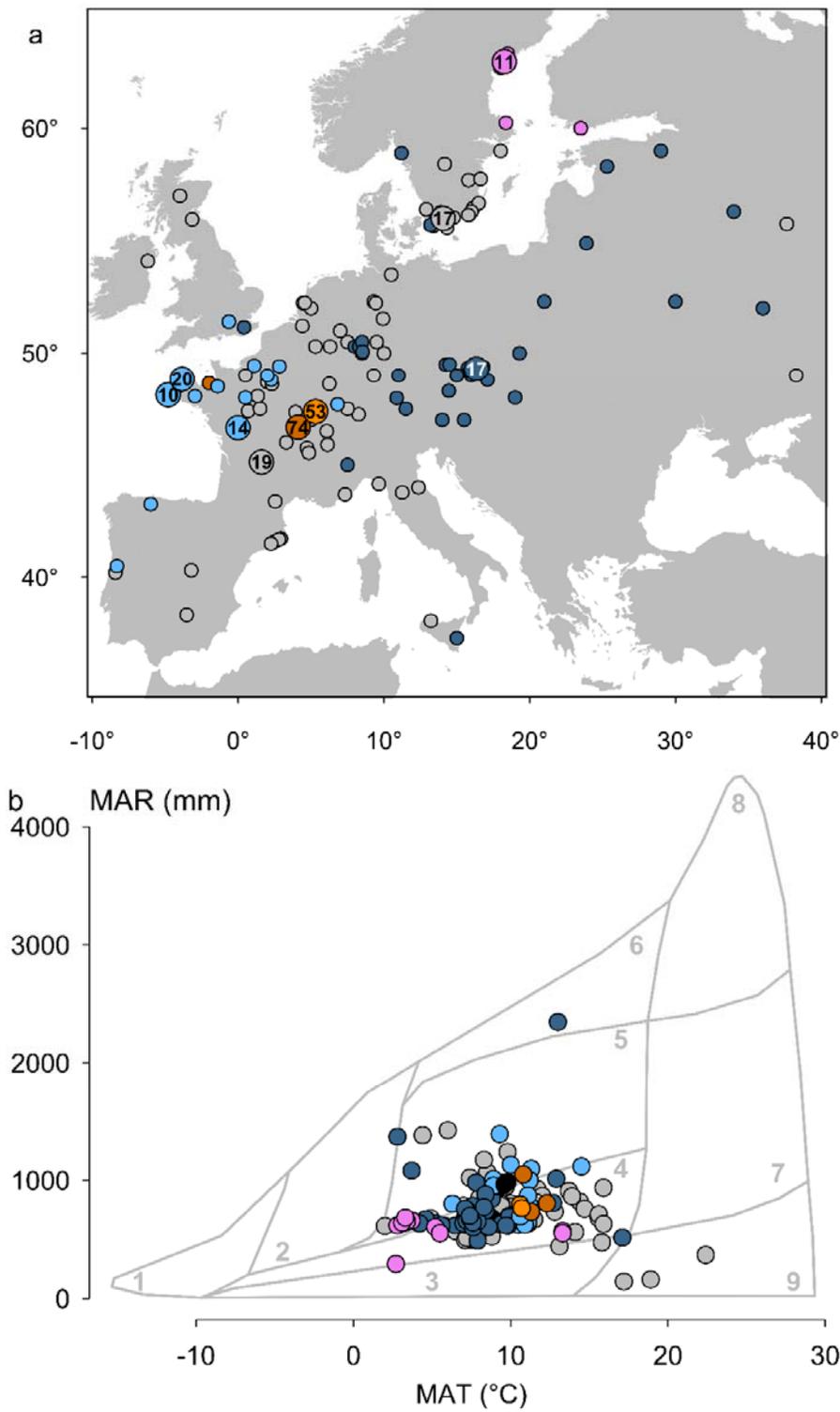
615

616 **Figure 3. The slow-fast continuum makes the bridge between leaf economics**  
617 **spectrum and plant response to climate.** (a) Relative growth rate (RGR,  $\text{mm}^2 \text{ mm}^{-2} \text{ d}^{-1}$ ) and  
618 (b) age of maturity (AM, d) as a function of the first principal component of LES traits.  
619 Regressions and phylogenetic regressions are represented by black and red lines, respectively,  
620 when significant.  $Q_{\text{ST}}$  values and 95% CI for (c) RGR and (d) AM relatively to the 95<sup>th</sup>  
621 quantile (blue area) and 90<sup>th</sup> quantile (light blue area) of the  $F_{\text{ST}}$  distribution (grey area).  
622 Representation of the climatic predictions for (e) RGR and (f) AM. Black dots represent  
623 genotypes collecting sites.

624

625

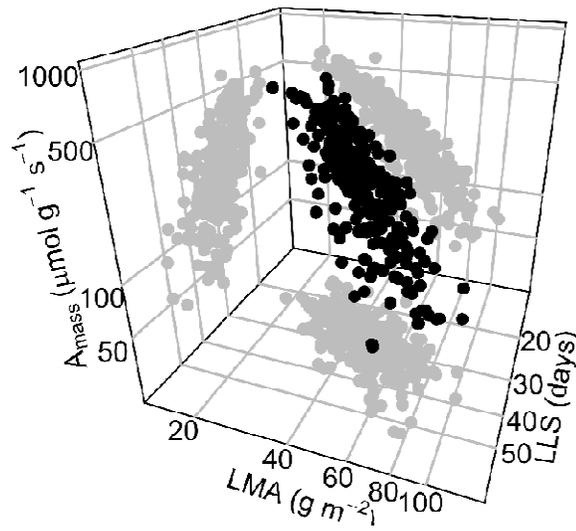
Figure 1



626

627

628            Figure 2

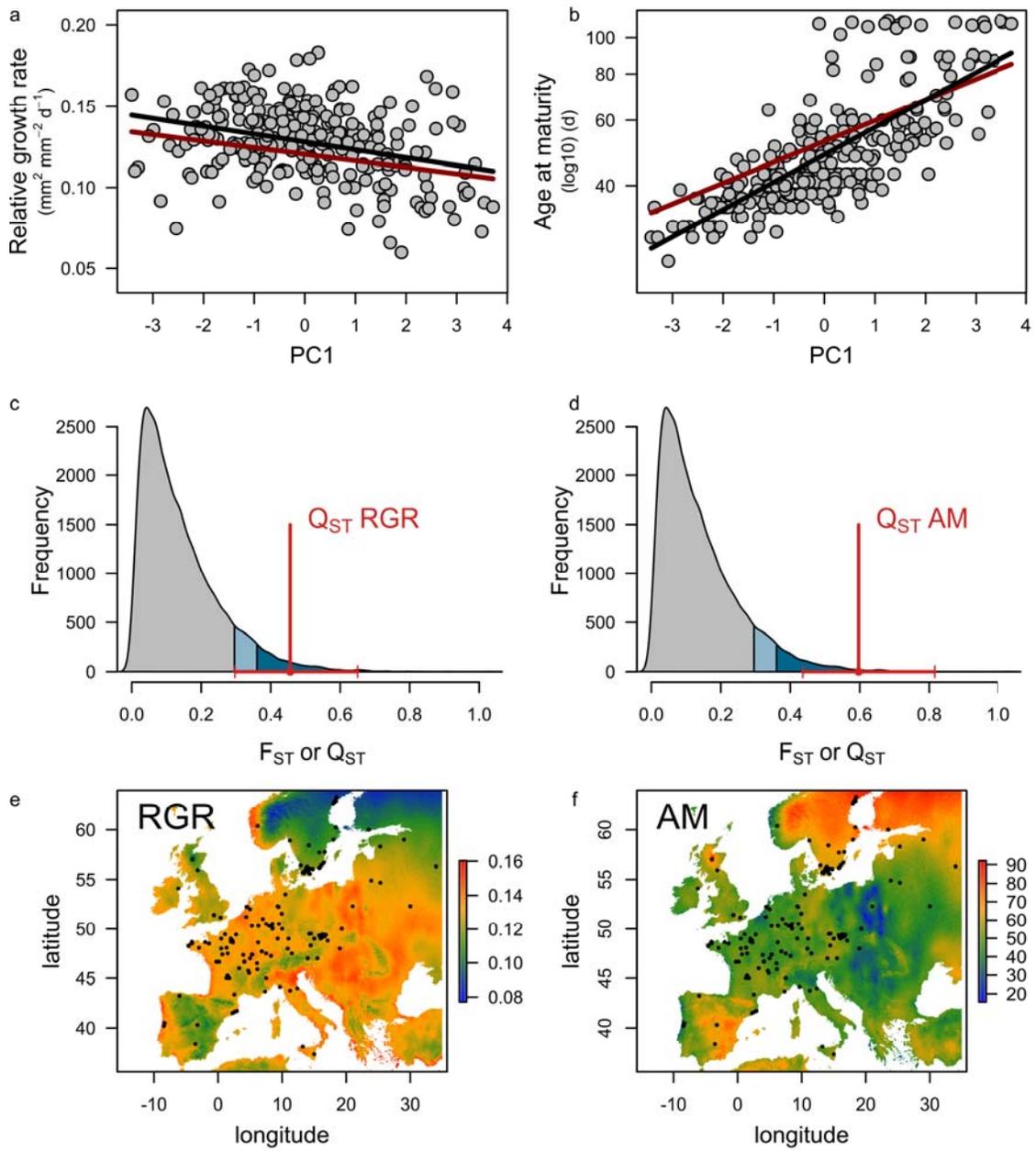


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Figure 3



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