Scale matters: genome-wide signatures of local adaptation to high-resolution environmental variation in an alpine plant

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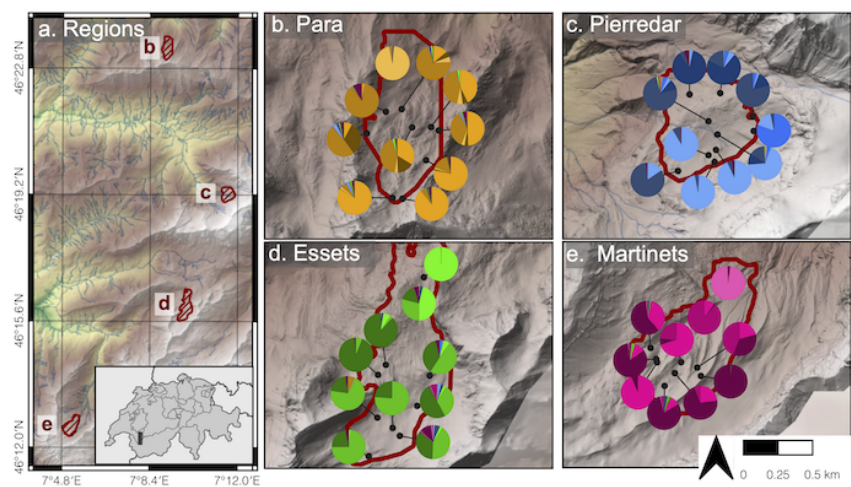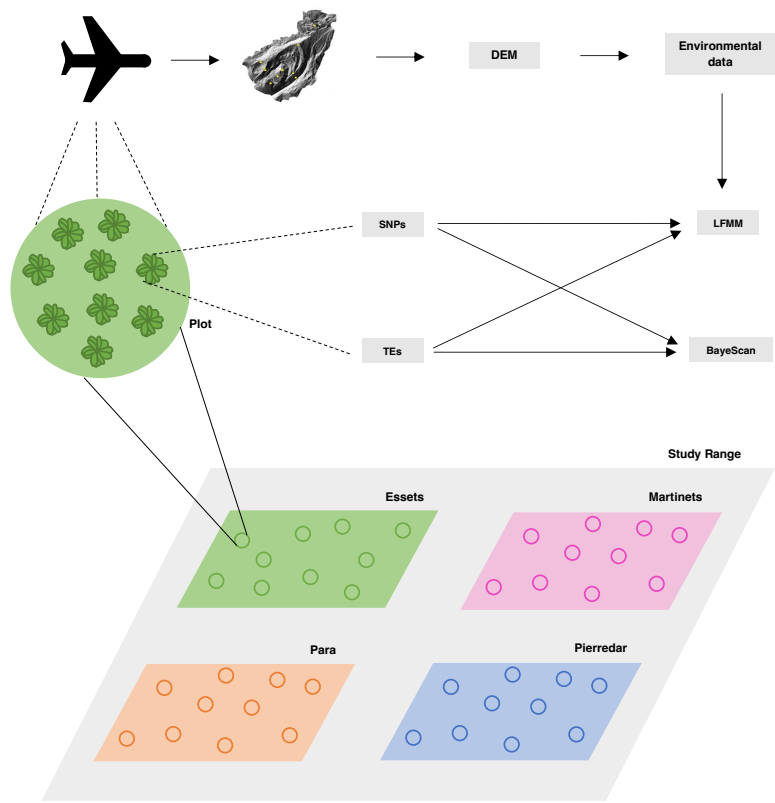[5]Musée et Jardins Botaniques Cantonaux
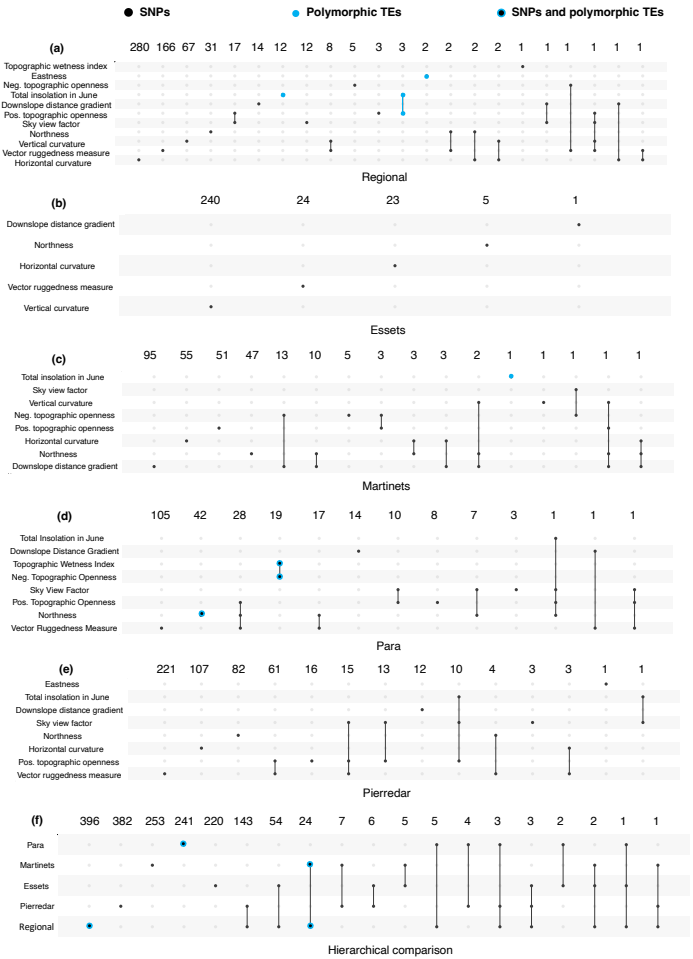[6]Haute Ecole d'Ingénerie et de Gestion (HEIG)
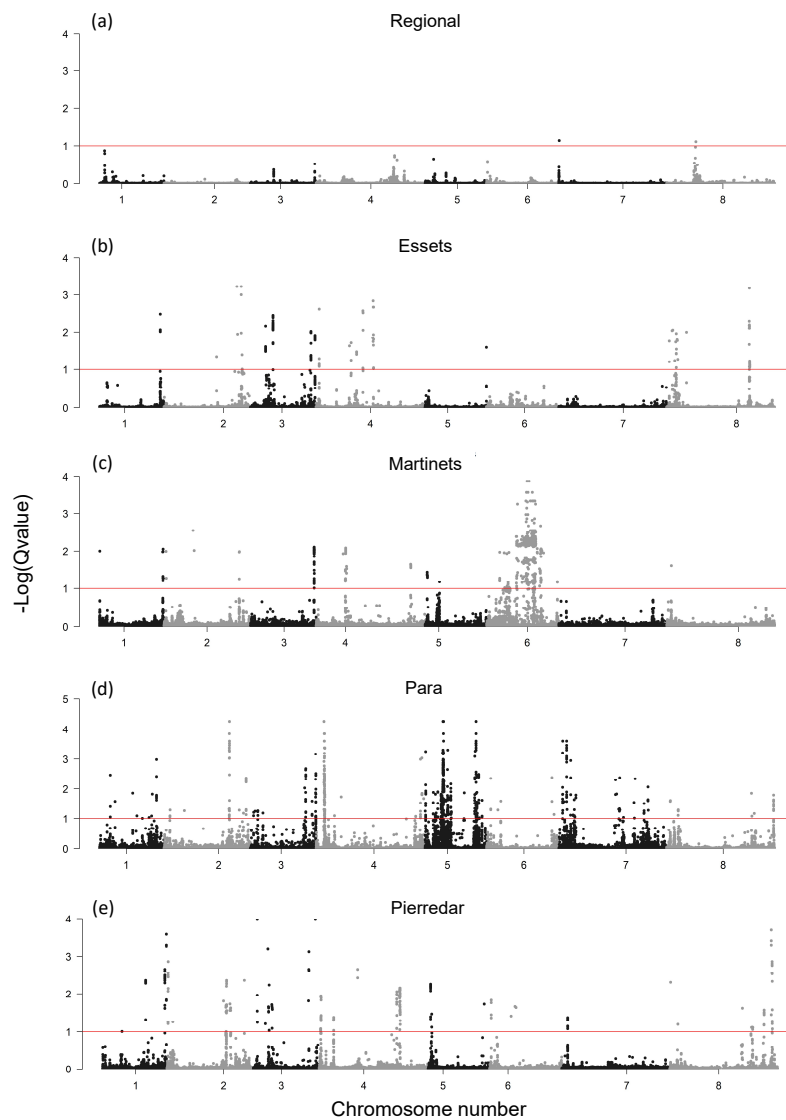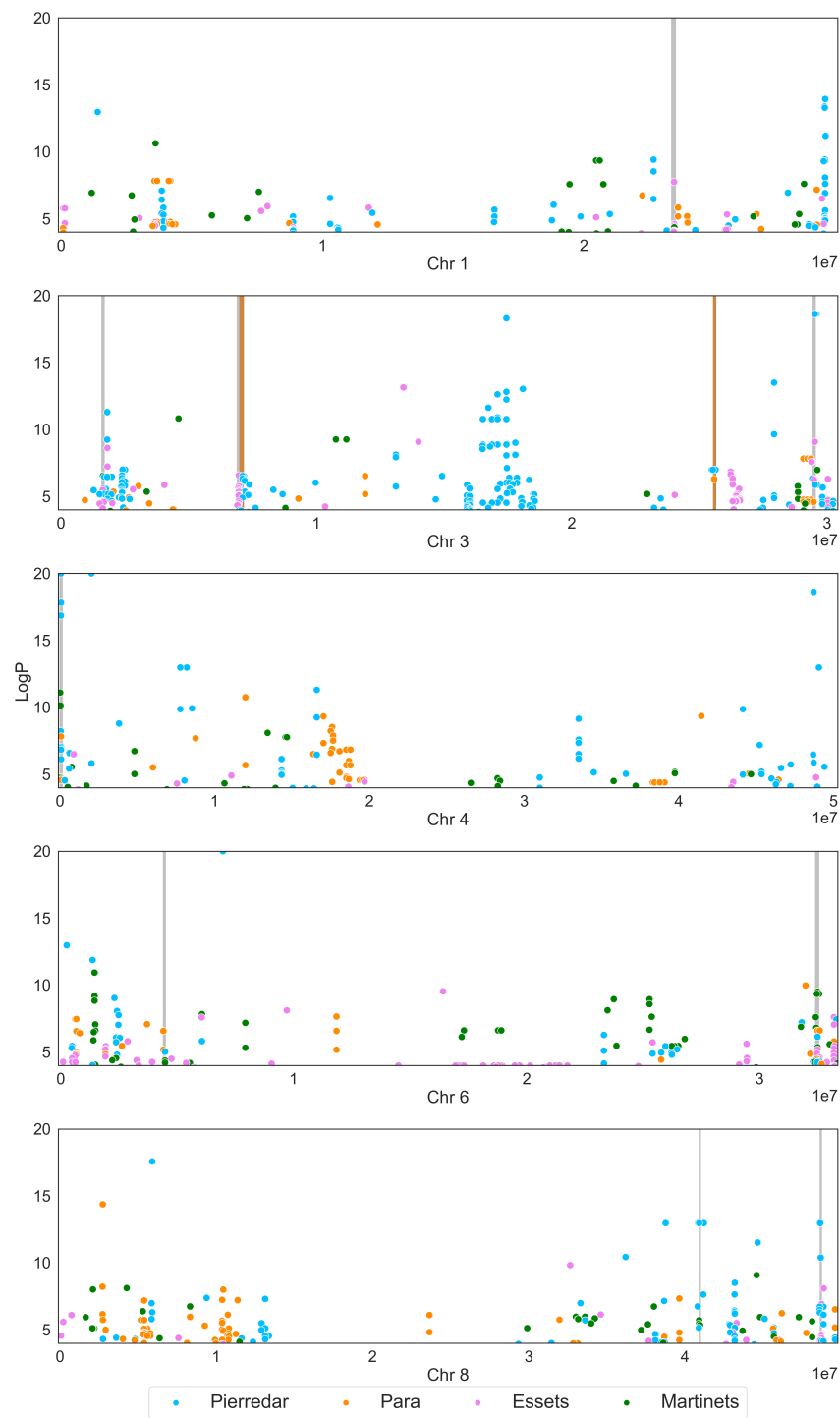[7]WSL Swiss Federal Research Institute

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Abstract

Microevolutionary processes shape adaptive responses to heterogeneous environments, where these effects vary both among and within species. However, the degree to which signatures of adaptation to environmental drivers can be detected based on spatial scale and genomic marker remains largely unknown. We studied signatures of local adaptation across different spatial extents, investigating complementary types of genomic variants–single nucleotide polymorphisms (SNPs) and polymorphic transposable elements (TEs)–in populations of the alpine model plant species Arabis alpina. We coupled high-resolution (0.5m) environmental factors, derived from remote sensing digital elevation models, with whole-genome sequenced data of 304 individuals across four populations. We demonstrate that responses of A. alpina to similar amounts of abiotic variation are largely governed by local evolutionary processes and find minimally overlapping signatures of local adaptation between SNPs and polymorphic TEs. Notably, functional annotations of high-impact genomic variants revealed several defence-related genes associated with the abiotic factors studied, which could indicate indirect selective pressure of biotic agents. Our results highlight the importance of considering different spatial extents and types of genomic polymorphisms when searching for signatures of adaptation to environmental variation. Such insights provide key information on microevolutionary processes and could guide management decisions to mitigate negative impacts of climate change on alpine plant populations.

1

● SNPs   ● Polymorphic TEs   ● SNPs and polymorphic TEs

(a) 280 166 67 31 17 14 12 12 8 5 3 3 2 2 2 2 1 1 1 1 1 1

Topographic wetness index
Eastness
Neg. topographic openness
Total insolation in June
Downslope distance gradient
Pos. topographic openness
Sky view factor
Northness
Vertical curvature
Vector ruggedness measure
Horizontal curvature

Regional

(b) 240 24 23 5 1

Downslope distance gradient

Northness

Horizontal curvature

Vector ruggedness measure

Vertical curvature

Essets

(c) 95 55 51 47 13 10 5 3 3 3 2 1 1 1 1 1

Total insolation in June
Sky view factor
Vertical curvature
Neg. topographic openness
Pos. topographic openness
Horizontal curvature
Northness
Downslope distance gradient

Martinets

(d) 105 42 28 19 17 14 10 8 7 3 1 1 1

Total Insolation in June
Downslope Distance Gradient
Topographic Wetness Index
Neg. Topographic Openness
Sky View Factor
Pos. Topographic Openness
Northness
Vector Ruggedness Measure

Para

(e) 221 107 82 61 16 15 13 12 10 4 3 3 1 1

Eastness
Total insolation in June
Downslope distance gradient
Sky view factor
Northness
Horizontal curvature
Pos. topographic openness
Vector ruggedness measure

Pierredar

(f) 396 382 253 241 220 143 54 24 7 6 5 5 4 3 3 2 2 1 1

Para
Martinets
Essets
Pierredar
Regional

Hierarchical comparison

3

1 **Scale matters: genome-wide signatures of local adaptation to**

2 **high-resolution environmental variation in an alpine plant**

3 **Running title**   Scale effects in local adaptation

4

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Abstract

Microevolutionary processes shape adaptive responses to heterogeneous environments, where these effects vary both among and within species. However, it remains largely unknown to which degree signatures of adaptation to environmental drivers can be detected based on the choice of spatial scale and genomic marker. We studied signatures of local adaptation across different levels of spatial extents, investigating complementary types of genomic variants–single nucleotide polymorphisms (SNPs) and polymorphic transposable elements (TEs)–in populations of the alpine model plant species *Arabis alpina*. We coupled environmental factors, derived from remote sensing digital elevation models at very high resolution (0.5m), with whole-genome sequencing data of 304 individuals across four populations. We demonstrate that responses of *A. alpina* to similar amounts of abiotic variation are largely governed by local evolutionary processes, and we find minimally overlapping signatures of local adaptation between SNPs and polymorphic TEs. Notably, functional annotations of high-impact genomic variants revealed several defence-related genes associated with the abiotic factors studied, which could indicate indirect selective pressure of biotic agents. Our results highlight the importance of considering different spatial extents and types of genomic polymorphisms when searching for signatures of adaptation to environmental variation. Such insights provide key information on microevolutionary processes and could guide management decisions to mitigate negative impacts of climate change on alpine plant populations.

Introduction

Local adaptation enables populations to evolve traits that confer a fitness advantage in their respective habitats (Kawecki & Ebert, 2004). Genomic variation may reveal signatures of such adaptive processes, but identifying the underlying environmental drivers and relevant spatial scale remains challenging (Savolainen et al., 2013). To improve our understanding of traits under selection and their underlying functional processes, one may decipher the imprints of local adaptation based on whole-genome patterns of variation. However, to our knowledge, fine-grained sampling of individuals and environmental data, at a resolution matching genomic variation, has never been used to assess environmental drivers of adaptation.

Studies investigating local adaptation often cover broad spatial extents (commonly referred to as scales), involving continent-wide sampling for example (Gougherty et al., 2021; Pais et al., 2017; Yeaman et al., 2016), but see (de Villemereuil et al., 2018; Eckert et al., 2015; Fischer et al., 2013). However, adaptation can be truly local (Rellstab et al., 2017), particularly in highly heterogeneous alpine landscapes where environmental conditions vary over short distances (Rellstab et al., 2020).

In their local study on the alpine Brassicaceae *Biscutella laevigata,* Leempoel et al. (2018) highlight the importance of considering the ratio between grain (spatial resolution) and extent of a study area to assess signatures of adaptation, which should match the spatial context at which selection operates (Dauphin et al., 2023). In rugged alpine terrain, an organism's habitat can be adequately described using ecological data derived from digital elevation models (DEM; Kozak et al., 2008), which correlate significantly with climatic factors measured using ground-based sensors (Leempoel et al., 2015)(Pradervand et al., 2014). Such topography-derived environmental descriptors provide continuous information across habitats, reflecting long-term patterns of local site conditions, as compared to point-based measurements acquired on-site or interpolated from local weather stations, which provide short-term and often patchy environmental information.

Whole-genome studies of adaptation in natural plant populations mostly remain restricted to model organisms like *Arabidopsis thaliana* (Exposito-Alonso et

83   al., 2018; Fournier-Level et al., 2011; Hancock et al., 2011) or crop wild relatives (e.g.,

84   Yoder et al., 2014). Additionally, they are often based on pooled sequencing (Fischer

85   et al., 2013; Rellstab et al., 2020; Turner et al., 2010), or only consider a few

86   individuals that do not necessarily represent the local populations (Laenen et al.,

87   2018). Moreover, structural variants, often involved in adaptation beyond what can

88   be captured by commonly analysed single-nucleotide polymorphisms (SNPs), have

89   been largely ignored in these studies. Transposable elements (TEs), for example,

90   represent a major fraction of many plant genomes (Bennetzen & Wang, 2014;

91   Quesneville, 2020) and are known to induce adaptive responses to abiotic stress

92   (Baduel et al., 2021; Kalendar et al., 2000), yet have remained largely overlooked in

93   studies of local adaptation. Indeed, biallelic SNPs and TEs are expected to have

94   complementary effects on the adaptive responses of plants to local conditions. For

95   example, polymorphic TEs are known to affect recombination along chromosomes,

96   such that they may promote entire blocks of linked loci to reveal signatures of

97   selection along chromosomes (Choudhury et al., 2019), while genomic variation in

98   non-synonymous SNPs may induce rather subtle changes in the respective proteins.

99   Therefore, it is expected that these marker types identify few common, but rather

100   complementary signals of local adaptation.

101   It is commonly assumed that similar environmental contrasts across sites

102   leave consistent signatures of selection in plants with a common genomic background

103   (Booker et al., 2021; Lotterhos & Whitlock, 2015) (Rellstab et al., 2020). However, for

104   populations with limited gene flow, particularly in species with mixed mating systems

105   or selfing, one may expect population-specific adaptive responses with limited

106   convergence (Rellstab et al., 2017; 2020).

107   *Arabis alpina* (Brassicaceae) has recently emerged as a model species for

108   ecological genomics (Wötzel et al., 2022). Studies have provided empirical evidence

109   of how local adaptation acts on the species' genome (Laenen et al., 2018; Lobréaux &

110   Miquel, 2020; e.g., Poncet et al., 2010), with notable effects on phenotypes (Chopra

111   et al., 2019; de Villemereuil et al., 2018; Vayssières et al., 2020; Wang et al., 2009). As

112   detailed in (Wötzel et al., 2022), several field studies, including reciprocal transplant

113   experiments, substantiate the potential of *A. alpina* to adapt on small spatial scales,

114   e.g., in response to elevational differences (Buckley et al., 2019; de Villemereuil et al.,

4

115   2018; Wingler et al., 2015). Due to this species' responsiveness to environmental

116   conditions, and the availability of a high-quality reference genome, it is an intriguing

117   organism to further investigate whether signatures of selection to fine-scale

118   environmental drivers are found across the whole genome.

119   Here, we re-sequenced 304 individuals of *A. alpina,* sampled in local

120   populations with a common history, using a spatially explicit, hierarchical design

121   (individuals in plots nested within four local populations, Figures 1 and 2). We

122   computed the environmental factors at a very high resolution (0.5 m) to describe the

123   local habitat for each individual. Through associations with genomic variation, we

124   inferred drivers of local adaptation (i) at the regional level, i.e., among the four local

125   populations, and (ii) at the local level, i.e., among plots within each local population.

126   In parallel, we performed outlier detection analyses to identify possible genomic

127   signatures of local adaptation irrespective of underlying environmental drivers. We

128   focused on whether signals of adaptation between regional and local spatial extents,

129   as well as between types of genomic markers (SNPs vs. TEs), show common or

130   different patterns and functions, and to what degree patterns of local adaptation are

131   driven by particular environmental factors at different spatial extents.

132   **Materials and Methods**

133   **Study species and sampling**

134   *Arabis alpina* L. has a broad ecological niche covering a large altitudinal and

135   latitudinal range, making it suitable for investigating adaptation to variation across

136   heterogeneous environments (Wötzel et al., 2022). This perennial Brassicaceae is

137   found throughout the Northern Hemisphere, predominantly on calcareous bedrock.

138   In the European Alps, *A. alpina* is found across an elevation range of 400 m to 3200 m

139   a.s.l. This species reproduces sexually, predominantly via selfing (Ansell et al., 2008;

140   Buehler et al., 2012; Laenen et al., 2018; Tedder et al., 2011), though outcrossing

141   populations can be found in parts of its range (e.g., Ansell et al., 2008; Tedder et al.,

142   2011). SNP-based estimates of individual inbreeding coefficients (*F*), as well as

143   positive F_{IS} values for both SNPs and polymorphic TEs, suggest substantial inbreeding

144 in the studied populations, likely due to extensive selfing (Choudhury et al., 2019;

145 Rogivue et al., 2019b).

146   We sampled four local populations of *A. alpina* from the western Swiss Alps in

147 summer 2014 (Figure 1 and 2), from temperate alpine climates with generally

148 abundant rain and snowfall (Drake et al., 2006). Individuals were sampled

149 predominantly from calcareous bedrock in the alpine vegetation zone above 2000 m

150 a.s.l. in the regions Para (N = 69), Pierredar (N = 69), Essets (N = 70) and Martinets

151 (N = 96) (Table S1; see also Rogivue et al., 2019b). The four studied populations are

152 considered descendants from the same refugial population and share a similar

153 genomic background (Rogivue et al., 2018). Each population is situated within a

154 different catchment valley (Figure **1**a), presumably preventing regular gene flow

155 between these populations. However, mating within each population can occur over

156 large distances, as insects may transport pollen up to 1 km (Buehler et al., 2012) and

157 their small, light seeds can be disseminated by wind. Within each population, we

158 selected ten plots from contrasting habitat types to encompass large ecological

159 gradients, within which we sampled the leaves of six to ten plants at least 1 m apart

160 to avoid sampling families (Figure 1 and Table S1). We stored the samples in silica gel

161 and extracted DNA as described elsewhere (Rogivue et al., 2019b). The precise

162 geographic coordinates of each individual (± 2 cm) were obtained with a differential

163 global positioning system (DGPS) receiver, using information provided by Real Time

164 Kinematik (RTK) Global Navigation Satellite System (GNSS) (Table S1).

165

166 **Environmental factors**

167 Using SAGA GIS (Conrad et al., 2015), we computed 13 topography-derived

168 environmental factors (Table S2) from a precise and high-resolution DEM at 0.5 m

169 pixel resolution, based on light detection and ranging (LiDAR) data obtained from the

170 regional authorities (Canton Vaud, Switzerland). These topographic factors are known

171 proxies for ecologically relevant descriptors, including elevation (and therefore

172 temperature), climate, hydrology, soil conditions, light availability and exposure

173 (Guillaume et al., 2021; Lecours et al., 2017; Leempoel et al., 2015; Wilson & Gallant,

174 2000).

175   Primary terrain attributes including slope, aspect as northness (AspC – cosine

176   of aspect) and eastness (AspS – sine of aspect), and curvature are often used in

177   species distribution models at local and regional scales, as they underlie multiple

178   biophysical processes (such as water flow, snow movement, erosion and solar

179   radiation (Guisan & Zimmermann, 2000; Lyon et al., 2008; Moore et al., 1991). Slope

180   (Slo) describes the steepness of the terrain and aspect describes its orientation. Both

181   are good proxies for solar radiation and temperature, especially when the

182   surrounding relief is of minor importance (Leempoel et al., 2015). Horizontal

183   curvature (Hcu) affects the convergence and the divergence of the water flow, while

184   vertical curvature (Vcu) describes the acceleration and the deceleration of the water

185   flow (Wilson & Gallant, 2000).

186   Over the last two decades, more elaborate secondary terrain attributes have

187   been developed as proxies to model specific biophysical features. Vector ruggedness

188   measure (VRM) describes the degree of terrain unevenness and distinguishes

189   between rocky and smooth terrain (Sappington et al., 2007). This descriptor

190   correlates with soil moisture and is a surrogate for stony soil in the western Alps

191   (Leempoel et al., 2015). Positive topographic openness (TOP) and negative

192   topographic openness (TON) express the protection of a focal point from the

193   surrounding relief (Yokoyama et al., 2002). These factors are based on the maximum

194   angle found at the zenith (TOP) or nadir (TON) from the point over a defined radius.

195   By describing the terrain convexities and concavities, these two factors reflect soil

196   drainage as well as protection from wind (Doneus, 2013).

197   Other factors have been designed to specifically model hydrological

198   processes. The downslope distance gradient (DDG) quantifies the influence of slope

199   on local water drainage (Hjerdt et al., 2004). The topographic wetness index (TWI)

200   quantifies the topographic control of hydrological processes and is formulated as the

201   logarithm of the ratio between the catchment area and the tangent of slope. It has

202   been used to predict soil pH, snow cover and ambient humidity (Beven & Kirkby,

203   1979; Böhner & Selige, 2006), where negative values were correlated with mean and

204   minimum air temperature, while positive values were correlated with the daily range

205   of air temperature (Leempoel et al., 2015).

206   Light availability and temperature can be described by secondary terrain

207 attributes that account for surrounding terrain. The sky view factor (SVF) expresses

208 the ratio of the radiation received by a planar surface to the radiation emitted by the

209 entire hemispheric environment (Böhner & Antonić, 2009), such that SVF proxies for

210 water and light availability. At a microclimatic level, SVF also describes wind

211 protection. Finally, total insolation (Ti6, direct and diffuse radiation) and direct solar

212 insolation in the growing month of June (Di6, direct radiation) account for sun angle,

213 surrounding relief and the SVF. DEM-derived solar radiation is a direct proxy for light

214 availability affecting photosynthesis rates and indirectly accounts for air and soil

215 temperature, influencing evapotranspiration, snow melt and soil moisture (Tovar-

216 Pescador et al., 2006).

217   As environmental factors often covary, we applied Spearman correlation tests

218 to pairs of factors and retained only one factor of the pair if Spearman's $\rho > |0.8|$.

219 Finally, we performed a principal component analysis (PCA) on the retained 12

220 standardised environmental factors at the locations of the 304 sampled individuals,

221 using the 'prcomp' function in the *stats* package in R 4.1.0 (R Development Core

222 Team, 2021).

223

224 Genomic data

225 We used genomic data described elsewhere (Rogivue et al., 2019a, b), representing

226 SNPs and polymorphic TEs (presence/absence). In short, we sequenced each

227 individual with Illumina HiSeq2500 (ATLAS Biolabs GmbH, Berlin, Germany; 125-bp

228 paired-end reads). After filtering and mapping (BWA 0.7.12; Li & Durbin, 2010) to the

229 high-quality, chromosome-level reference genome (Jiao et al., 2017), the remaining

230 reads corresponded to an average coverage of 11.7x. We performed SNP calling with

231 FreeBayes 1.0.2 (Garrison & Marth, 2012), with 291,396 biallelic SNPs remaining at

232 the regional extent (across all four sites) after stringent filtering (excluding SNPs

233 within TE sequences; Rogivue et al., 2019b). At the local extent, the number of SNPs

234 retained were 220,214 in Essets, 113,900 in Martinets, 287,261 in Para and 160,322

235 in Pierredar (minor allele frequency < 0.025). To describe the spatial genetic structure

236 of the sampled individuals, we carried out an analysis of model-based ancestry,

237 implemented in the program Admixture (Alexander et al., 2009), on the retained

238 SNPs at the regional level (N = 291,396) for K = 1–20.

239   For the TEs, we genotyped presence/absence of polymorphic copies of long

240 terminal repeat retrotransposons (LTR-RTs) using TEPID (Stuart et al., 2016) and

241 inferred their zygosity from read coverage at breakpoints to treat them similarly to

242 SNPs. Of the 20,548 identified polymorphic TEs (Rogivue et al., 2019b), 3,874 loci with

243 no missing data were retained for subsequent environmental association analyses

244 and outlier detection.

245

246 **Genotype–environment association analyses (GEA)**

247 We performed GEA analyses (Lasky et al., 2022; Rellstab et al., 2015) at two

248 hierarchical levels (Figure **1**): (i) the regional level, i.e., among the four studied

249 populations; and (ii) the local catchment level, i.e., among plots within each

250 population. We applied latent factor mixed models (LFMM; Frichot et al., 2013)

251 implemented in the R package *LFMM2* (Caye et al., 2019), a univariate GEA method in

252 which neutral genetic structure is intrinsically considered.

253   We used the 'snmf' function in the R package *LEA* to replace the missing

254 observations (10%) in the SNP dataset with imputed data based on the population

255 structure from the sNMF analysis (K = 1–10, entropy = T, and 10 repetitions). We then

256 imputed the data with the 'impute' function in LEA, where latent factors (K) were

257 obtained using the lowest genomic inflation factor (gif) value (method = 'mode').

258 Once the SNP datasets were complete, we ran the LEA function 'lfmm_ridge' for

259 latent factors K = 1–8 for each environmental factor.

260   We defined the best number of latent factors (K) as the value with the

261 genomic inflation factor (λ, averaged over the 12 environmental factors) closest to 1

262 (Table S3), as suggested by Caye et al. (2019). We did not choose a specific K for each

263 environmental factor, as K has no specific biological meaning. Therefore, for the SNP

264 dataset at the regional level (i) we used K = 6, and at the local level (ii) we used K = 2

265 for Essets, K = 3 for Martinets, K = 6 for Para, and K = 2 for Pierredar. For the TE

266 dataset, we used K = 1 for all analyses. Following Rogivue et al. (2019b), we treated

267 the two marker types (SNPs and polymorphic TEs) with different K values, reflecting

268   the differential patterns of variation observed among populations (e.g., 6% of SNPs

269   were shared among populations, compared with 90% of polymorphic TEs; SNPs had

270   higher pairwise F_{ST} values (0.09–0.18) than those for polymorphic TEs (0.03–0.09)).

271   We ran the 'lfmm_test' function in *LFMM2* (Caye et al., 2019) to calculate the *z* scores

272   and *p* values based on the λ and χ^2 distributions. To control for false positives, we

273   applied the Benjamini-Hochberg algorithm (Benjamini & Hochberg, 1995) with a false

274   discovery rate (FDR) of 1%.

275

276   **Outlier analysis**

277   To complement the GEA analyses, we used BayeScan 2.1 (Foll & Gaggiotti, 2008) to

278   identify outlier SNPs and polymorphic TEs putatively under divergent selection, i.e.,

279   showing genetic differentiation above that expected for neutral markers. BayeScan is

280   an F_{ST}-based approach that considers differences in allele frequencies between the

281   common pool and each population. Outlier loci are those resulting from divergent

282   selection beyond the level of what demographic processes, such as random genetic

283   drift, may impose in terms of genetic differentiation.

284   Like with LFMM, we ran BayeScan (i) at the regional level among the four

285   populations, and (ii) at the local level among plots within each local population. We

286   converted the SNP and TE datasets from LFMM to BayeScan format using a custom R

287   script. We defined the prior odd at 100, with 5,000 outputted iterations, a thinning

288   interval size of 10, 20 pilot runs of length 5,000, and a burn-in of 50,000. We

289   visualised BayeScan results using Manhattan plots created with the R package *qqman*

290   (Turner, 2018).

291

292   **GO term enrichment analyses among levels of spatial extent, statistical methods,**

293   **and marker types**

294   We characterised the putative functions of candidate loci identified in the above

295   analyses using the same annotation as in Rogivue et al. (2019b). For simplicity, we

296   considered only the SNPs with a high impact on their respective protein based on

297   SnpEff (Cingolani et al., 2012), where high-impact SNPs were those identified as

298   missense, splice acceptor and splice donor variants, as well as start/stop codon loss

299 or gain. For similar reasons, we retained only polymorphic TEs located within 2 kb

300 upstream or downstream of annotated genes as possibly high-impact due to either

301 gene disruption or spreading of epigenetic marks lowering gene expression (Hollister

302 & Gaut, 2009).

303   We performed a gene ontology (GO) term enrichment analysis of the

304 significantly associated SNPs and polymorphic TEs with topGO 2.44.0 (Alexa et al.,

305 2006). We established the significance of the terms according to Fisher's exact tests

306 (*p* value cut off at 0.01 and not adjusted for multiple testing, as recommended by the

307 topGO authors).

308   We compared the annotated genes and enriched GO terms between

309 hierarchical levels (regional vs. local extents), statistical methods (GEA vs. outlier

310 analyses), and marker types (SNPs vs. polymorphic TEs) to identify analogous signals

311 of adaptation. We searched for common high-impact SNPs and clusters (see below)

312 among local populations and between levels of spatial extent, which we visualised

313 using upset plots created with the R package *UpSetR* (Conway et al., 2017).

314

315 **Clusters of loci identified as adaptive**

316 We further compared common clusters of high-impact SNPs across the genome by

317 defining 6228 blocks of 100 kbp, with a step of 50 kbp. We counted the number of

318 high-impact SNPs, identified using either LFMM or BayeScan, per block and per

319 region, where a cluster was assigned if a block or region contained at least two

320 significant SNPs. We note that we summed all the LFMM-derived high-impact SNPs,

321 irrespective of their associated environmental factors.

322 **Results**

323 **Spatial genetic structure**

324 The 291,396 SNPs retained at the regional level were used to determine the genetic

325 structure across the studied populations. Using the program *Admixture* with *K* = 1–20,

326 we found substantial genetic differentiation among populations despite the common

327 genomic background reported in a phylogeographic study across the Alps (Rogivue et

328 al., 2018). Admixture converged to a minimum cross-validation for 15 clusters, to

329   which 60% of individuals could be unambiguously assigned (membership coefficient

330   > 0.8), whereas admixed individuals were typically found in a single population. All

331   clusters were well nested within the four populations (3 in Essets, 4 in Martinets, 4 in

332   Para, 4 in Pierredar) and contained < 4% of the variants originating from other

333   populations (Figure 1).

334

335   **Environmental factors and genotype–environment association (GEA) analysis**

336   We evaluated 13 environmental factors derived from LiDAR-acquired DEMs at 0.5 m

337   resolution. This spatial resolution matches our sampling grain, i.e., individuals' sites

338   within plots (minimum distance between sampled plants > 1 m). Among these

339   environmental factors, direct insolation in June was highly positively correlated with

340   total insolation in June (ρ = 0.99; Table S4), so we discarded it to reduce collinearity

341   between explanatory variables in subsequent analyses. A principal component

342   analysis (PCA) on the retained 12 environmental factors indicated that the

343   environmental conditions across the four sampled populations were similar overall,

344   with the habitat conditions of sampled individuals spanning similar gradients along

345   the environmental factors considered (Figure S1). This finding substantiates the

346   reasoning that our sampling scheme provides optimal premises for investigating

347   convergent signatures of adaptation across populations (Rellstab et al., 2020) based

348   on genomic and environmental variation.

349   In GEA analyses (Figure S2), horizontal curvature was most prominently

350   associated with genomic variation across all analyses, while eastness (with only a few

351   significant associations) and slope (with none) seemed to be uninformative regarding

352   signatures of selection (Table 1, Table S5). Notably, the environmental factors with

353   the largest number of significant associations differed substantially among the local

354   populations (Table S5).

355   The specificity of the environmental descriptors in driving local adaptation

356   was assessed through patterns of interaction between the markers and the

357   environmental factors. The majority of loci were associated with only one

358   environmental factor, while up to 32.8% showed an association with multiple

359   environmental factors in either the regional or local analyses (Figure 3a–e). The

12

360 spatial extent considered in the GEA analyses had a considerable effect on the

361 number and relative frequency of significant associations per environmental factor;

362 notably, each local population showed a distinct frequency distribution (Table 1,

363 Tables S5 and S6). Accordingly, only 260 high-impact SNPs and polymorphic TEs were

364 found to be significant between the regional and the four local analyses (Figure 2f).

365 These were located in 209 candidate adaptive genes shared among the two levels of

366 spatial extent (Figure S3a). Only one gene was identified in all five GEA analyses.

367 However, no ortholog of this gene is known from *A. thaliana* and, hence, its function

368 remains unknown.

369   For the two marker types, SNPs and polymorphic TEs, we found similar

370 percentages of loci that were significantly associated with at least one environmental

371 factor at the regional level: 2.46% of the SNPs and 2.48% of the polymorphic TEs.

372 Despite such broad variation, only one candidate gene (Aa_G559430), homologous to

373 the terpenoid cyclase AT3G14490 in *A. thaliana*, was highlighted by both SNPs and

374 polymorphic TEs.

375

376 **Outlier analysis**

377 At the regional level, BayeScan identified only two outlier SNPs, of which only one

378 was identified as high-impact. Conversley, between 15 (Essets) and 134 (Martinets)

379 high-impact SNPs significantly exceeded the neutral expectation at the local level (q

380 values < 0.1; Figure 4, Figure S4, Table 2, Table S7), though only one SNP was

381 detected across all local populations. Most of the outlier SNPs identified were tightly

382 flanked by other SNPs in linkage disequilibrium, which is known to extend across a

383 considerable physical distance (Rogivue et al., 2019b). Conversley, outlier analyses for

384 polymorphic TEs showed an inverted trend: few significant outliers were identified at

385 the local level (between zero in Essets and three in Martinets), while 108 significant

386 outliers were detected across the regional level (Table 2 and Figure S5). Comparing

387 the two statistical methods, GEA and outlier analyses, found neither common SNPs

388 nor genes at the regional level, with a few SNPs detected with both analyses at the

389 level of local populations (Table 2).

390

GO term enrichment

To substantiate the functional relevance of the loci putatively involved in divergent selection, we performed tests for gene ontology (GO) term enrichment. We followed the advice of the authors of topGO and did not apply any correction for multiple testing to avoid excessive false negatives, at the cost of obtaining false positives. Accordingly, the results of the enrichment analyses point towards, but do not necessarily substantiate, genes of interest for being involved in adaptive processes. Of the 7,180 associated SNPs identified by GEA at the regional level, we found 653 high-impact SNPs across all 12 environmental factors occurring within 519 annotated genes (Table 1, Table S8), highlighting 42 significantly enriched GO terms (Table S9). In turn, the 15 polymorphic TEs occurring within 2 kb upstream or downstream of annotated genes highlighted 11 significantly enriched GO terms (Table 1, Tables S9 and S10). At the local level, high-impact SNPs and genes highlighted 22 significantly enriched GO terms that were shared among three or four local populations (Figure S3b). No gene flanking an associated polymorphic TE was identified in Essets or Pierredar, whereas one was detected in Martinets and 62 in Para (Table S5). GO term enrichment analyses were not considered for polymorphic TEs, as only a few linked genes were identified.

At the regional-level, GEA analyses identified only two enriched GO terms based on more than five genes comprising of at least one high-impact SNP, and these were therefore considered top candidates (Table 1, highlighted in Table S9): 'defence response' (GO:0006952) and 'innate immune response' (GO:0045087). The remaining 40 SNP-based significant GO terms and all 11 TE-based ones indicated a weaker signal of selection (Table S9). Of the two outliers detected at the regional level, the SNP at position 145,431 on chromosome 7 is a missense variant located in the gene Aa_G219310 (orthologous to AT4G38420 in *A. thaliana*), encoding a 'copper ion binding' protein involved in the oxidation–reduction process (GO:0055114, http://atgenie.org/transcript?id=AT4G38420.1). The outlier SNP located on chromosome 8 is a synonymous variant situated in the gene Aa_G499380 (orthologous to AT5G16970 in *A. thaliana*; Table S11) involved in responses to oxidative stress; however, as a synonymous SNP it is likely not the locus directly

14

422   under selection, but may be linked to the causative variation (i.e., not captured

423   possibly for statistical reasons). No GO term analysis was possible because only one

424   high-impact SNP was annotated (Table 2).

425   At the local level, few GO terms were classified as top candidates: two in

426   Essets ('defence response' (GO:0006952) and 'innate immune response'

427   (GO:0045087)), one in Martinets ('protein phosphorylation' (GO:0006468)), three in

428   Para (three times 'protein phosphorylation' (GO:0006468)), and none in Pierredar

429   (Tables S5a and S9). Among the 134 identified high-impact outlier SNPs in Martinets

430   (Table S11), we found two top candidate GO terms: 'response to oomycetes'

431   (GO:0002239) and 'defence response to fungus, incompatible interaction'

432   (GO:0009817); Table S12). The three other regions presented no top candidate GO

433   terms (Table S12), despite the occurrence of several high-impact outliers (Table S11).

434

435   **Common clusters of adaptive loci**

436   We identified 12 common blocks (genomic regions spanning 100 kbp, with a step of

437   50 kbp) of high-impact SNPs detected by GEA analyses, most of which were shared

438   between at least two local populations (Figure 5). Only one genomic block was

439   common among three populations, and two (consecutive) genomic blocks were

440   shared between all four populations. Based on the outlier loci identified with

441   BayeScan, we found three common blocks, two of which were consecutive on

442   chromosome 3, which were common to the same two populations (Essets and

443   Pierredar) and in common with one population based on LFMM (Pierredar). The

444   remaining block was shared between Para and Pierredar. These 15 common blocks

445   comprised 211 significant associations in GEA analyses for 94 SNPs.

446   **Discussion**

447   Investigating the genes and functions that are under selection and identifying the

448   factors driving selection are essential for understanding local adaptation, particularly

449   in view of global change. The high-quality and high-resolution genomic and

450   environmental data now available provide increasing insights into the evolution of

451   species and how environmental conditions can shape evolution. By assessing genomic

452   variation at the whole-genome level at both single nucleotides (SNPs) and TE markers

453   for 304 individuals, and by characterising each individual's micro-habitat, we found

454   that environmental factors describing soil water availability and solar radiation are

455   important drivers of local adaptation in *A. alpina*. While we detected loci showing

456   signals of local adaptation in the genic (high-impact SNPs and polymorphic TEs) and

457   non-genic (polymorphic TEs near to genes) genome regions, the detected signals

458   differed substantially among the four local populations, with inconsistencies across

459   the regional and local spatial extents. These findings highlight the specificity of local

460   adaptation for populations, despite these populations sharing a common genomic

461   background and experiencing similar environmental conditions (Fig. S1; Rogivue et

462   al., 2018). Such truly local responses to abiotic environmental cues may reflect in part

463   the high frequency of selfing observed in Alpine populations of *A. alpina* (Buehler et

464   al., 2012; Tedder et al., 2011), which could reinforce genomic imprints of local

465   adaptation once they have become established (Trickovic & Glémin, 2022). This

466   finding provides evidence that convergent signatures of selection, even within closely

467   situated populations of a given species, may only be expected under particularly

468   strong selective pressure and, thus, are rarely realised in populations of mostly selfing

469   individuals, as investigated here.

470

471   **Singular signals of genomic adaptation across levels of spatial extent**

472   In our hierarchical study design, we identified few gene candidates for local

473   adaptation common between the regional and local analyses (Figure 3f). While the

474   literature about the spatial extent of adaptation is still limited, two recent studies on

475   forest trees also showed that adaptation at different levels of spatial extent appears

476   complementary (Brousseau et al., 2021; von Takach et al., 2021). These authors

477   concluded that such scale issues are important to consider for understanding

478   genomic signatures of local adaptation, which is in line with our findings. The very

479   local adaptive response of populations reported here was already highlighted by

480   Rellstab et al. (2017) in a study on the strictly outcrossing *Arabidopsis halleri*. There,

481   only 31% of previously identified candidate adaptive SNPs were confirmed in an

482   independent set of populations, underlining the truly local nature of adaptation in

483   response to a highly heterogeneous environment.

484   The low degree of overlapping results between the two marker types, SNPs

485   and polymorphic TEs, implies that their respective variation reflects adaptive

486   responses involving complementary candidate genes and gene functions. We cannot

487   exclude potential effects of using different bioinformatic tools to characterize each

488   marker type, steming from fundamental differences between the types of

489   polymorphisms. For example, SNP-derived estimates of population-specific

490   inbreeding coefficients F_{IS} were lower than respective values calculated from

491   polymorphic TEs (Rogivue et al., 2019b). By ignoring sequence variation, we

492   underestimate heterozygosity in TEs, resulting in inflated F_{IS} values. Nevertheless, our

493   findings highlight the relevance of incorporating structural polymorphisms, such as

494   TEs and copy number variants, when studying complex evolutionary responses to

495   changing environments. Similar findings have been reported previously for

496   Brassicaceae (Niu et al., 2019; Quadrana et al., 2016), emphasising the need to

497   consider TE variation when investigating adaptation to global warming (Rey et al.,

498   2016). The present study is, to our knowledge, the first to show that SNPs within

499   genes and polymorphic TE copies indicate complementary candidates of local

500   adaptation.

501   Unsurprisingly, the two statistical methods used (GEA and outlier detection)

502   revealed complementary outcomes and did not point to the same candidate genes.

503   To some degree, this inconsistency may be attributed to the smaller number of

504   candidates found in the outlier analysis (Table 2). Such a result may be associated

505   with sampling individuals in plots of contrasting environments, rather than along

506   abiotic gradients (Richardson et al., 2014). Additionally, the fundamental differences

507   between the two methodological approaches (statistical, environment-related GEA,

508   population genomic outlier detection) suggest that one should expect

509   complementary, rather than overlapping, signals of adaptation. Our results indeed

510   integrateeffects of selection across various abiotic and (unaccounted for) biotic

511   factors. Accordingly, conditional neutrality (Mee & Yeaman, 2019) might might at

512   least partly explain the small number of outliers detected that contrasts with the

513   numerous loci associated with environmental heterogeneity. Relatively high genetic

17

514 load was indeed detected within those expending alpine populations (Zeitler et al.,

515 2023), and corresponding loci may be conditionally deleterious to a large extent,

516 hence showing limited allelic differentiation despite significant genotype-by-

517 environment interactions. As simulations show that GEA analyses have a high power

518 of detection under scenarios of weak selection and low dispersal (Forester et al.,

519 2016), such approaches may be sensitive enough to identify conditionally neutral loci

520 (Lasky et al., 2022; Yoder & Tiffin, 2018).

521

522 **Selective factors are distinct among SNPs and polymorphic TEs, and are**

523 **predominantly consistent between levels of spatial extent**

524 In our study, the type of genomic marker investigated considerably affected the

525 relative importance of the associated environmental factors (Table 1, Figure 3).

526 Horizontal curvature, a proxy for drainage and hydrological processes, detected the

527 most candidate SNPs. Conversely, GEAs using polymorphic TEs highlighted that the

528 factor with the largest number of significant candidates was total insolation in June

529 (or the highly correlated direct insolation in June), a factor representing solar

530 radiation. Although mechanistic underpinnings remain out of scope, this finding again

531 highlights the complementarity of SNPs and polymorphic TEs in revealing responses

532 to different environmental cues.

533   Across the two hierarchical levels of spatial extent, the order of importance of

534 the environmental factors differed slightly, while the top environmental factors

535 largely remained consistent (Table 1 and Table S5). This result suggests that the

536 studied populations inhabit similar environments and that our study design was

537 appropriate for detecting potentially convergent signatures of adaptation (Figure S1).

538 Nevertheless, environmental contrasts such as (indirectly accounted for) differences

539 in biotic interactions as well as restricted gene flow, and hence large effects of

540 genetic drift, likely contributed to overruling selective effects to impose a common

541 signal in the genomes of *A. alpina* individuals.

542

Defence-related functions are key in heterogeneous alpine environments

543 In alpine environments, plants must deal with harsh, highly variable conditions to

544 survive. In our study, high-impact polymorphisms in genes related to defence

545 responses are overrepresented among candidates of local adaptation (Table S9).

546 Likewise, loci identified by the outlier analyses also highlighted defence-related

547 functions under selection, though outlier loci did not directly link to any

548 environmental drivers. Biotic interactions are usually considered to play a minor role

549 when compared to abiotic environmental factors for plants at high elevations

550 (Zvereva & Kozlov, 2022). Nevertheless, despite our focus on potential abiotic drivers

551 of local adaptation, our study indicated that genes with biotic-related biological

552 functions are key in adaptive responses in alpine plants. Therefore, we advocate also

553 including biotic drivers in future environmental association analyses to better

554 represent potential environmental drivers of adaptation.

555 The two biological functions under selection at the regional level, i.e., 'defence

556 response' and 'innate immune response', were also found at the local level in Essets.

557 No other common biological function was found among the two levels of spatial extent,

558 again stressing the notion that local adaptation is truly local. Moreover, adaptive

559 functions previously described in studies on *A. alpina,* e.g., related to survival,

560 flowering and fecundity (de Villemereuil et al., 2018; Toräng et al., 2015; Wötzel et al.,

561 2022), were not found in our analyses. This discrepancy might be due to differences in

562 the spatial extent and resolution of the studies, the complementary methodological

563 approaches, and the different types of environmental factors considered. Beyond this,

564 high levels of selfing encountered in Alpine populations of *A. alpina* may amplify

565 population-specific adaptive responses, though such an effect depends on various

566 conditions such as patterns of dominance, levels of selective pressure, and migration

567 rate (Trickovic & Glémin, 2022).

568 In conclusion, by combining whole-genome re-sequencing data with high-

569 resolution descriptions of environmental factors, our study pointed to several genes

570 and biological functions potentially under selection. These findings pave the ground

571 for a better understanding of adaptive processes and could guide further

572 investigations of *A. alpina* and related (alpine) species. Further, our findings suggest

574   that signatures of local adaptation are dependent on the spatial extent of the study,

575   the type of genomic markers employed, and the statistical methods used. The

576   common genomic blocks indicative of imprints of adaptation (Figure 5) refer to

577   regions in the genome that are under sufficiently strong selection to overcome the

578   presumed high level of genetic drift induced by demography and life-history traits of

579   *A. alpina* in our study regions. Taken together, our results suggest that

580   microevolutionary processes may likely result in non-overlapping signatures of local

581   adaptation across spatial scales.

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894   patterns. *Ecology Letters, 25*(9), 2076–2087. doi:10.1111/ele.14090
895

Data Accessibility and Benefit-Sharing

All data and custom-made codes are available in the DRYAD repository at

http://doi.org/...., reference number .....

A Benefit-Sharing statement does not apply, given that all samples originated from

the country where the research was conducted.

Author contributions

A.R., K.L., R.R.C., F.F., M.K., S.J., C.P. and F.G. initiated and conceived the project. AR

performed the experiments. A.R., K.L., A.S.G. and R.R.C. analysed the data. A.R., K.L.,

R.R.C., A.S.G., M.K., S.J. and C.P. contributed analysis tools. A.R., K.L. and F.G. wrote

the initial manuscript, with contributions from all co-authors.

Conflict of interest

The authors declare that they do not have any conflict of interest.

Tables and Figures

911   TABLE 1 Results of environmental association analyses in *Arabis alpina* at the
912   regional level (latent factor mixed model, LFMM). The number (#) of significant
913   single-nucleotide polymorphisms (SNPs), high-impact SNPs (i.e., missense, splice
914   acceptor and splice donor variants, as well as start/stop codon loss or gain) and
915   polymorphic transposable elements (TEs) within 2 kbp of a gene, as well as the
916   number of associated genes and significantly enriched gene ontology (GO) terms
917   associated with each environmental factor, with less (†) or more (‡) than five genes
918   significant. The three environmental factors most frequently associated with SNPs
919   and polymorphic TEs are highlighted in bold and italics, respectively.
920

Environmental factor	# associated loci			# associated genes		# significantly enriched GO terms †	
	SNPs	High-impact SNPs	TEs	From SNPs	From TEs	From SNPs	From TEs
Total insolation in June	0	0	42	0	9	0	5
Sky view factor	243	31	0	17	0	5	0
Topographic wetness index	52	1	0	1	0	0	0
Neg. topographic openness	151	6	0	6	0	0	0
Pos. topographic openness	82	21	13	9	4	7	6
Vector ruggedness measure	1767	179	3	148	0	5	0
Downslope distance gradient	224	16	0	14	0	5	0
Horizontal curvature	3355	286	36	236	0	8	0
Vertical curvature	924	78	0	62	0	6 + 2‡	0
Northness	382	35	0	26	0	4	0
Eastness	0	0	2	0	2	0	0
Slope	0	0	0	0	0	0	0
Total	7180	653	96	519	15	42	11

921   † $p < 0.01$, < 5 genes significant
922   ‡ $p < 0.01$, > 5 genes significant

923 TABLE 2 Number of outlier loci detected by BayeScan in *Arabis alpina*. The number of significant single-nucleotide polymorphisms (SNPs) and
924 polymorphic transposable elements (TEs) at the regional level and for each of the four local populations, the number of high-impact SNPs and
925 TEs, the number of genes containing SNPs or TEs, and the number of significantly enriched gene ontology (GO) terms for SNPs and TEs, with
926 less (†) or more (‡) than five genes significant.
927

Spatial extent	Local population	# outliers (q value < 0.1)		# high-impact		# genes		# enriched GO terms †		# common with LFMM		# common gene with LFMM	
		SNPs	TEs	SNPs	TEs	SNPs	TEs	SNPs	TEs	SNPs	TEs	SNPs	TEs
Regional		2	108	1	2	1	0	0	0	0	6	0	1
Local	Essets	176	0	15	0	14	0	4	0	0	0	0	0
	Martinets	2032	3	134	0	134	0	5 + 2‡	0	26	0	24	0
	Para	1193	2	100	0	100	0	6	0	1	0	2	0
	Pierredar	599	1	27	0	27	0	5	0	2	0	3	0

928 † $p < 0.01$, < 5 genes significant
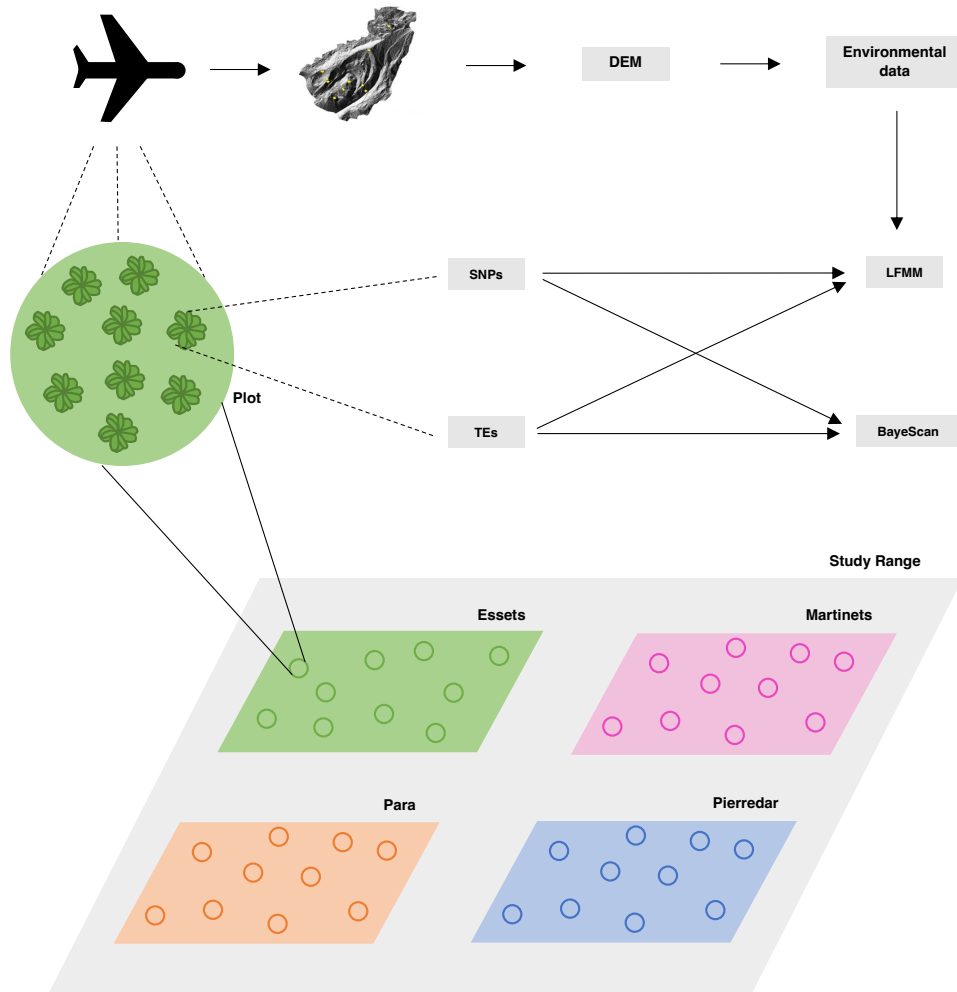929 ‡ $p < 0.01$, > 5 genes significant

930

FIGURE 1 Schematic illustration of the study design and analyses. Four local populations were selected (illustrated by rectangles), each comprising ten plots (circles) with six to ten plants each. Individual plants were sampled and sequenced to identify single-nucleotide polymorphisms (SNPs) and polymorphic transposable elements (TEs). Environmental data used to characterise the habitat of each individual were computed from a regional high-resolution digital elevation model (DEM) at 0.5 m pixel resolution, based on light detection and ranging (LiDAR). Two types of analyses were performed to search for genomic signatures of selection: (i) genotype–environment association (GEA) analyses using a latent factor mixed model (LFMM; Frichot et al., 2013) and (ii) outlier analyses using BayeScan (Foll & Gaggiotti, 2008). Both types of analyses were performed at two hierarchical levels differing in spatial extent: (i) at the regional level among the four local populations and (ii) at the local level among plots within each population.
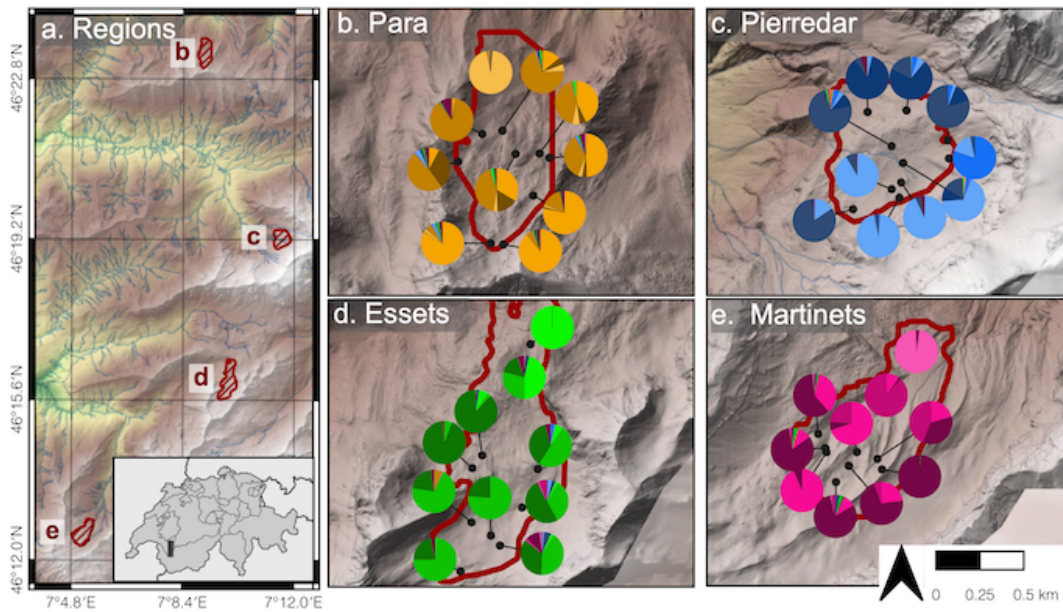
FIGURE 2 Locations of the four local populations of *Arabis alpina* and genetic assignment. (a) The study region situated in the western Swiss Alps, with four local populations (b) Para, (c) Pierredar, (d) Essets and (e) Martinets. Pie charts in (b)–(e) represent the proportions of assignment probabilities for each plot (black dot) within each studied region (delimited by a red line).
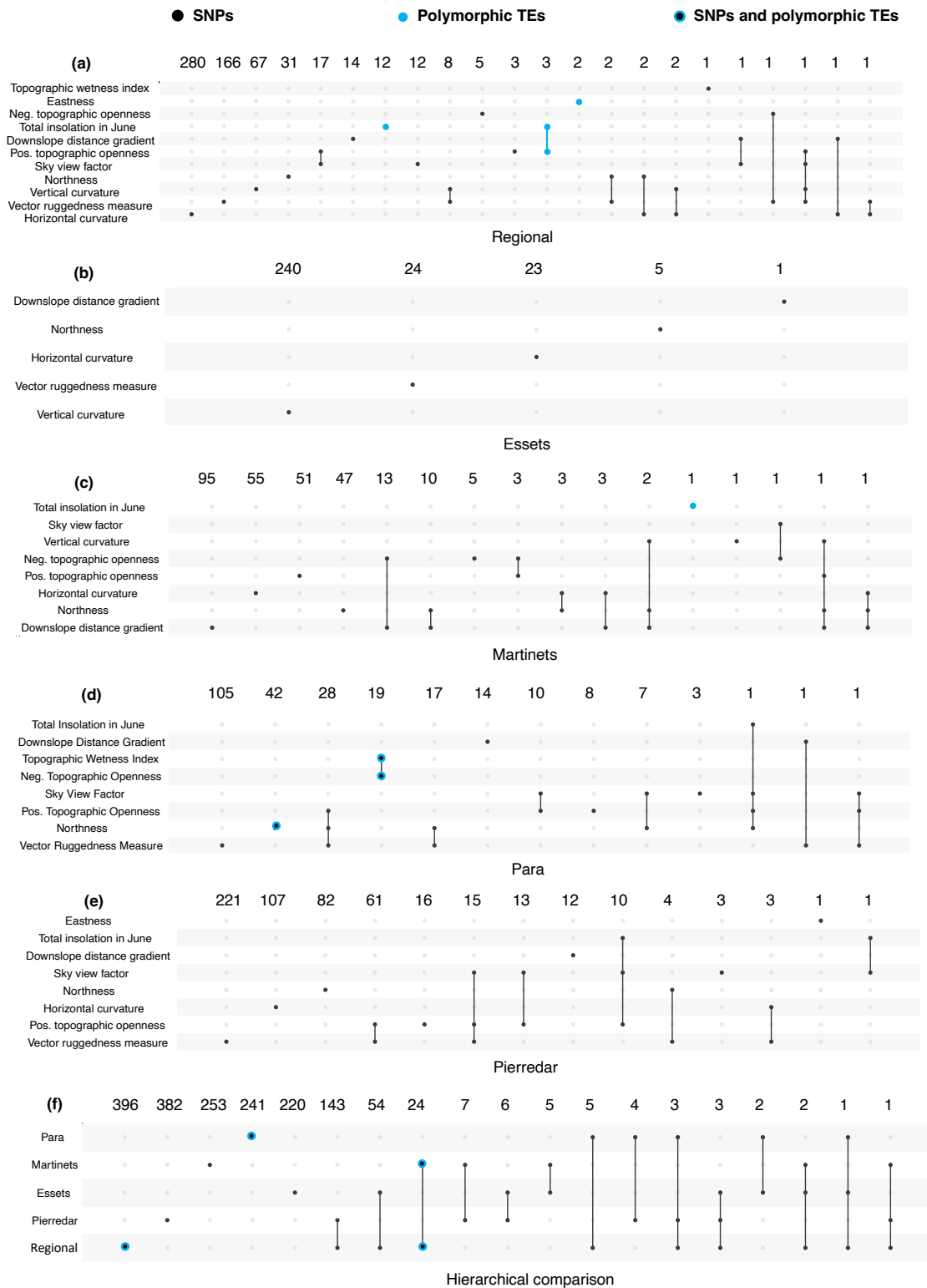
166

240

24   **23**

5

1

| Downslope distance gradient |
| Northness |
| Horizontal curvature |
| Vector ruggedness measure |
| Vertical curvature |

(c)

Essets

13 **10** **5** **3** **3** **3** **2** **1** **1** **1** **1** **1**

Total insolation in June

221

107

82

61

16 **15** **13** **12** **10** **4** **3** **3** **1** **1**

| Eastness |
| Total insolation in June |
| Downslope distance gradient |
| Sky view factor |
| Northness |
| Horizontal curvature |
| Pos. topographic openness |
| Vector ruggedness measure |

Pierredar

(f)   396 382 253 241 220 143 54 24 7 6 5 5 4 3 3 2 2 1 1

Para

Martinets

Essets

Pierredar

Regional

Hierarchical comparison

952 FIGURE 3 Common associations between environmental factors and hierarchical
953 levels. Combination and magnitude of intersections of the significantly associated
954 single-nucleotide polymorphisms (SNPs, high-impact) and polymorphic transposable
955 elements (TEs) from the latent factor mixed models (LFMM) comparing
956 environmental factors within each analysis. (a) Regional level, (b)–(e) local level, and
957 (f) between hierarchical levels. The number of loci involved in each category is given
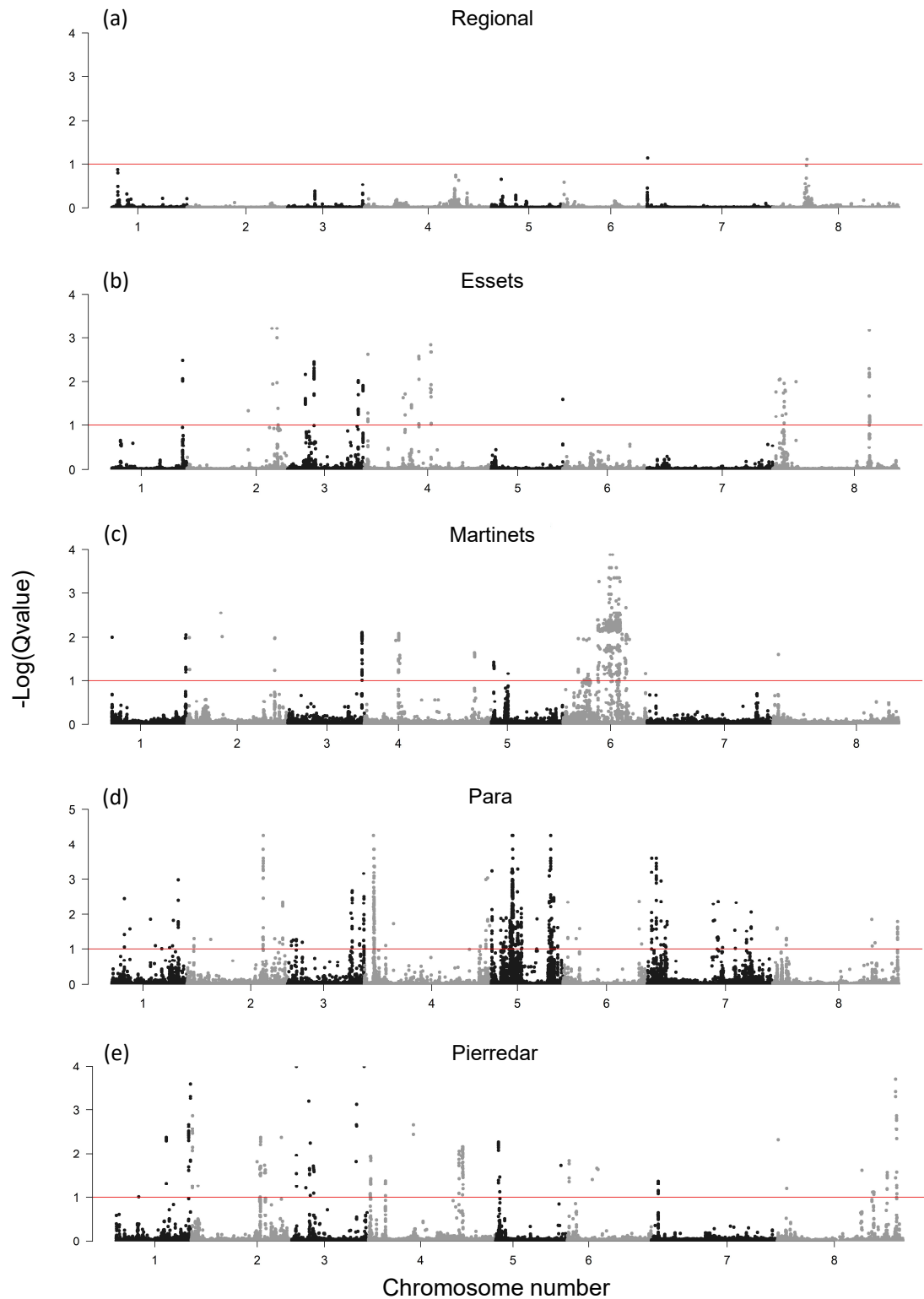958 above the corresponding plot.

959

960 FIGURE 4 Manhattan plots showing BayeScan outliers. The analysis is based on the
961 genome scan of single-nucleotide polymorphisms (SNPs) in *Arabis alpina* for the two
962 levels of spatial extent: (a)–(d) local and (e) regional. Alternating black/grey dots
963 mark detected SNPs within each of eight chromosomes (numbers); red lines
964 represent the false discovery rate (FDR, 10%). Values of genetic differentiation F_{ST} as
965 a function of the log(q value) can be found in Table S7.

966
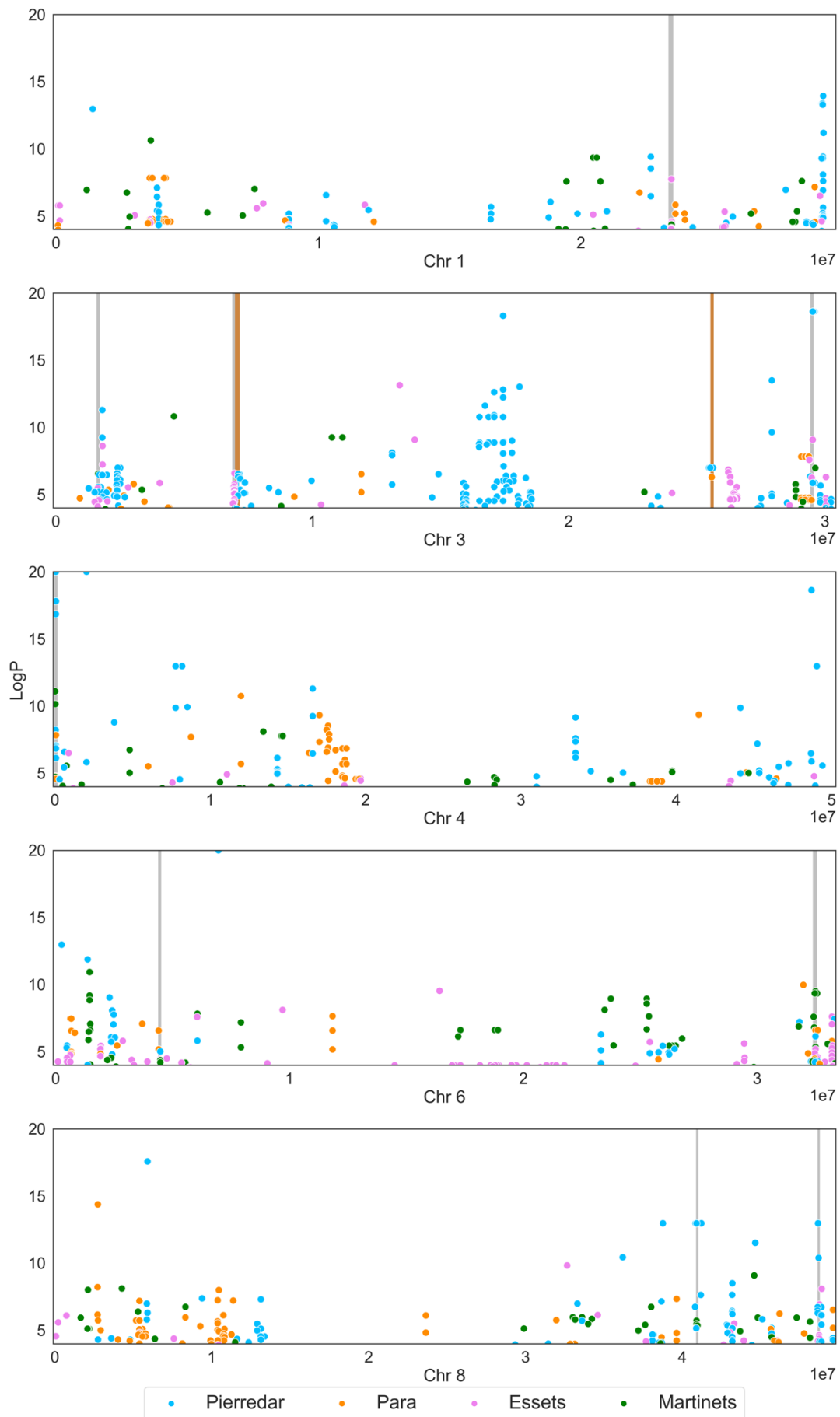
967 FIGURE 5 Genomic regions indicating signatures of adaptation. Significant high-
968 impact single-nucleotide polymorphisms (SNPs) in *Arabis alpina*, identified in
969 genotype–environment association (GEA) analyses, with common chromosomal
970 blocks. Panels show the log *p*-value of all high-impact SNPs identified per local
971 population (denoted with different colours) for each of the five (out of eight)
972 chromosomes (CHR) of *A. alpina* for which common blocks could be found. Blocks
973 are denoted if detected in at least two populations, with vertical lines in grey for GEA
974 analyses and in brown for outlier analyses. Numbers in x-axis denote length of
975 chromosome in Mbp.

Supporting Information

976 **Supporting Information**

977 Supportin information is available for this paper currently as a zip archive, except for

978 Figure S2 shared via a link to Google Doc (see below).

979

980 Table S1 Geographical coordinates and values of the 13 environmental factors for

981 each sampled individual of *Arabis alpina* in the four local populations.

982

983 Table 2 Definitions of the 13 environmental factors.

984

985 Table S3 The genomic inflation factor λ, calculated using latent factor mixed models

986 (LFMMs), for single-nucleotide polymorphisms (SNPs) and polymorphic transposable

987 elements (TEs) in *Arabis alpina*.

988

989 Table S4 Spearman's ρ between pairs of 13 environmental factors, measured in the

990 four local populations of *Arabis alpina*.

991

992 Table S5 Summary results of the latent factor mixed models (LFMMs) for the single-

993 nucleotide polymorphisms (SNPs) and the polymorphic transposable elements (TEs)

994 in *Arabis alpina*.

995

996 Table S6 Associated single-nucleotide polymorphisms (SNPs) and polymorphic

997 transposable elements (TEs) in *Arabis alpina*, based on the latent factor mixed

998 models (LFMMs). (a) SNPs regional, (b) TEs regional, (c) SNPs local and (d) TEs local.

999

1000 Table S7 Results of the outlier detection analyses, using BayeScan, based on single-

1001 nucleotide polymorphisms (SNPs) in *Arabis alpina* at the regional and local levels.

1002

1003 Table S8 Annotated single-nucleotide polymorphisms (SNPs) in *Arabis alpina* at the

1004 regional and local levels, based on the results of latent factor mixed models

1005 (LFMMs).

1006

1007   Table S9 Results of the gene ontology (GO) enrichment analysis for latent factor

1008   mixed models (LFMMs) with single-nucleotide polymorphisms (SNPs) and

1009   polymorphic transposable elements (TEs) in *Arabis alpina* at the regional and local

1010   levels.

1011

1012   Table S10 Annotated associated polymorphic transposable elements (TEs) in *Arabis*

1013   *alpina* at the regional and local levels, based on the latent factor mixed models

1014   (LFMMs).

1015

1016   Table S11 Annotated single-nucleotide polymorphisms (SNPs) in *Arabis alpina* at the

1017   regional and local levels, based on outlier detection analyses using BayeScan.

1018

1019   Table S12 Gene ontology (GO) terms in *Arabis alpina* at the regional and local levels,

1020   based on the results of outlier detection analyses of single-nucleotide

1021   polymorphisms (SNPs) using BayeScan.

1022

1023

1024   Figure S1 Principal component analysis (PCA) including the 304 individuals of *Arabis*

1025   *alpina* from the four local populations, based on the twelve retained environmental

1026   factors.

1027

1028   Figure S2 Manhattan plots of the latent factor mixed model (LFMM) analyses for

1029   *Arabis alpina*.

1030   https://drive.google.com/file/d/1_VbJxP9xHOdYLqtuMdzN3rcrosPwjqeg/view?usp=s

1031   hare_link

1032

1033   Figure S3 Shared genes and gene ontology terms between levels of spatial extent in

1034   *Arabis alpina*.

1035

1036   Figure S4 Plots of the results of the outlier detection analyses (using BayeScan),

1037   based on the genome scan of single-nucleotide polymorphisms (SNPs) in *Arabis*

1038 *alpina*: (a) regional analysis and (b)–(e) local analyses. (b) Essets, (c) Martinets, (d)

1039 Para and (e) Pierredar.

1040

1041 Figure S5 Manhattan plots of the results of the outlier detection analysis (using

1042 BayeScan), based on the genome scan of polymorphic transposable elements (TEs) in

1043 *Arabis alpina*.