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## The importance of considering the evolutionary history of polyploids when assessing climatic niche evolution

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1 *Niche differentiation following whole-genome duplication? The importance of considering the intricate*  
2 *evolutionary history of polyploids when assessing climatic niche evolution*

3

4 Short running title: *Niche differentiation after polyploidization?*

5

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8

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17

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28

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30

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32

33

34 **Aim**

35 Although whole genome duplication (WGD) is an important speciation force, we still lack a consensus on  
36 the role of niche differentiation in polyploid evolution. In addition, the role of genome doubling *per se* vs.  
37 later divergence on polyploid's niche evolution remains obscure. One reason for this might be that the  
38 intraspecific genetic structure of polyploid complexes and interploidy gene flow is often neglected in  
39 ecological studies. Here, we aim to investigate to which extent these evolutionary processes impact our  
40 inference on niche differentiation of autopolyploids.

41 **Location:** Europe

42 **Taxon:** *Arabidopsis arenosa* (Brassicaceae)

43 **Methods**

44 Leveraging a total of 352 cytotyped populations of diploid-autotetraploid *A. arenosa*, we examined  
45 differences among climatic niches of diploid and tetraploid lineages both globally, and independently for  
46 each tetraploid lineage with respect to the niche of its evolutionary closest relative. Then, we tested if there  
47 was an effect of additional interploidy introgression from other sympatric but more ancestral diploid  
48 lineages of *A. arenosa* on climatic niches of tetraploids.

49 **Results**

50 Ecological niche shift of tetraploids is only detected when the assignment of populations to intraspecific  
51 genetic lineages is considered. We found different patterns of climatic niche evolution (i.e. niche  
52 conservatism, contraction or expansion) in each tetraploid lineage when compared to its evolutionary  
53 closest relatives. We observed an effect of interploidy gene flow in patterns of climatic niche evolution of  
54 tetraploid ruderal plants of *A. arenosa*.

55

56 **Main conclusions**

57 The niche shift of tetraploids in *A. arenosa* is not driven by WGD *per se* but rather reflects dynamic post-  
58 WGD evolution in the species, involving tetraploid migration out of their ancestral area and interploidy  
59 introgression with other diploid lineages. Our study supports that evolutionary processes following WGD  
60 – which usually remain undetected by studies neglecting evolutionary history of polyploids – may play a  
61 key role in the adaptation of polyploids to challenging environments.

62

63 **KEYWORDS**

64 *Arabidopsis arenosa*, climatic niche evolution, ecological niche comparison, genetic structure, interploidy  
65 gene flow, polyploidy  
66

## 67 INTRODUCTION

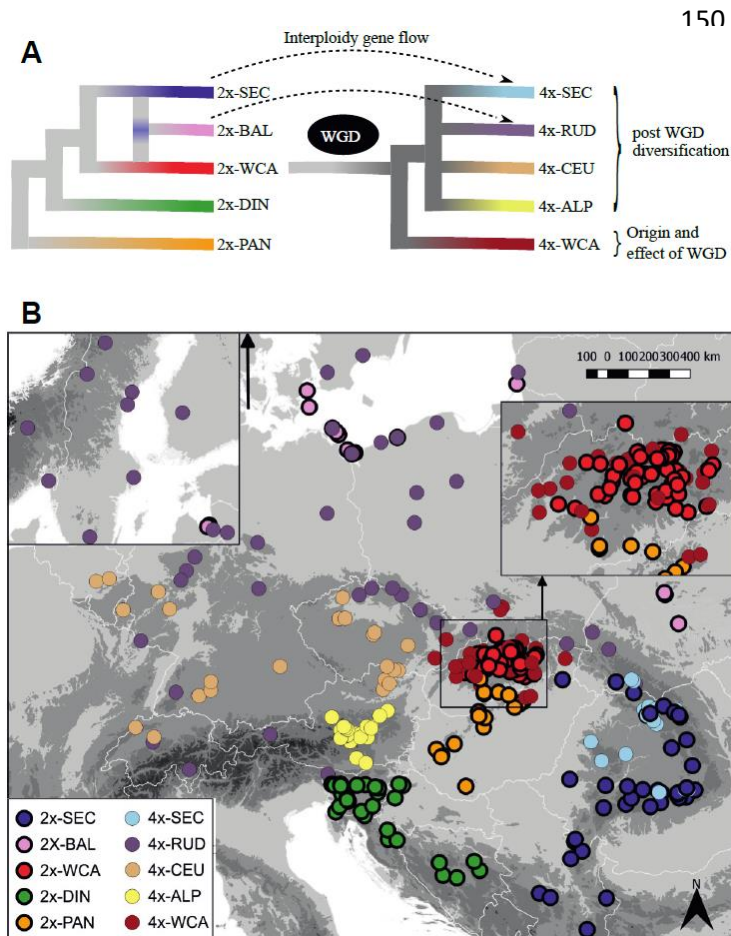
68 Polyploidy is a leading evolutionary force driving speciation and diversification of all plant lineages (Otto  
69 & Whitton, 2000; Wendel, 2000; Soltis, Marchant, Van de Peer & Soltis, 2015). All flowering plants have  
70 experienced one or more episodes of whole-genome duplication (WGD) during their evolutionary history  
71 (Jiao et al., 2011; Wendel, 2015) and it has been estimated that up to 15% of all speciation events in  
72 angiosperms are associated with a ploidy increase (Wood et al., 2009). Polyploid speciation has been  
73 considered a mechanism of sympatric speciation (Coyne & Orr, 2004) given the potential reproductive  
74 isolation that newly formed polyploids can experience due to strong postzygotic barriers among cytotypes  
75 (e.g. differences in the number of sets of chromosomes). However, incomplete postzygotic isolation among  
76 cytotypes is common in plants, thus promoting interploidy reproduction (Sutherland & Galloway, 2017).  
77 Accordingly, polyploid speciation is not an “instantaneous” process and prezygotic reproductive barriers  
78 such as differences in ecological niches between polyploids and closest lower-ploidy progenitors can also  
79 play a key role in assortative mating and thus, polyploid speciation (Levin, 2004; Husband, Baldwin &  
80 Sabara, 2016). Novel phenotypic, physiological and genetic combinations associated with polyploidy  
81 potentially could drive up polyploids to expand to new ecological niches that would have remained  
82 unavailable to their diploid progenitors (Madlung, 2013). In line with this, niche ecological divergence with  
83 respect to progenitors may be more prone to occur in allopolyploids (i.e. formed by genome duplication  
84 after hybridization of two different parental genomes more or less divergent) than autopolyploids (i.e.  
85 formed within the same species or genetic lineage) because a high heterozygosity could allow  
86 allopolyploids to colonize new habitats. Many empirical studies have addressed niche evolution after WGD,  
87 with some of them supporting niche divergence between diploids and polyploids (Theodoridis, Randin,  
88 Broennimann, Patsiou & Conti, 2013; Thompson, Husband & Maherali, 2014; Visger et al., 2016; Muñoz-  
89 Pajares et al., 2018; Decanter, Colling, Elyinger, Heiðmarsson & Matthies, 2020), while others do not  
90 (Godsoe, Larson, Glennon & Segraves, 2013; Glennon, Ritchie & Segraves, 2014; Čertner, Kolář,  
91 Šchönschwetter & Frajman, 2015; Visser & Molofsky, 2015; Castro et al., 2019; 2020a). Yet, there is not a  
92 consistent or universal pattern of the role of niche differentiation in polyploid establishment and evolution.  
93 This incongruence between studies has been explained by methodological issues as an inappropriate  
94 resolution of environmental variables (Kirchheimer et al., 2016), because niche differentiation might be  
95 occurring at a different spatial scale (Čertner, Kúr, Kolář, & Suda, 2019) and/or simply by different  
96 evolutionary histories of polyploid cytotype between studied species – an aspect that has been, however,  
97 often neglected in purely ecological studies. The presence or absence of niche evolution in polyploids  
98 strongly depends on species’ history: e.g. polyploid’s age, multiple origins or the number of ploidy levels,  
99 among others (see Duchoslav et al., 2020). There can also be a phylogenetic signal in environmental traits  
100 (Burns & Strauss, 2011), thus, ecological niches of polyploids can be potentially affected by ancestral

101 niches of progenitors. Consequently, patterns of ecological differentiation could be misunderstood if niches  
102 of the polyploids are not compared to their closest lower-ploidy progenitors. Unfortunately, the intraspecific  
103 genetic structure of polyploid complexes is often unknown due to limitations associated with challenges  
104 surrounding population genetic data analysis of polyploids (Rothfels, 2021; Rojas-Andrés et al., 2020), and  
105 if known, it is rarely taken into account when evaluating polyploid niche evolution (see López-Jurado,  
106 Materos-Naranjo & Balao, 2019 as an exception). Niches of allopolyploids are predicted by the sum of the  
107 niche of their progenitors (Parisod & Broennimann, 2016). This is not the case of strict autopolyploids,  
108 which usually conserve the climatic niche of their unique progenitor species. Nevertheless, hybridization  
109 and interploidy admixture between geographically close diploid and tetraploid populations are common in  
110 many plant species (Aagaard, Săstăd, Greilhuber & Moen, 2005; Stahlberg, 2007; Koutecký, Baďurová,  
111 Štech, Košnar & Karásek, 2011; Monnahan et al., 2019; Šmíd, Douda, Krak & Mandák, 2020). Thus, it  
112 might also occur that autopolyploids come into secondary contact with diploid ancestors that have diverged  
113 before the WGD event. This genetic exchange may result in adaptive introgression that can also influence  
114 patterns of climatic niche evolution (Schmickl & Yant, 2021). Nevertheless, few studies have assessed  
115 whether introgression promotes ecological niche evolution of polyploids, most of them being focused on  
116 strict allopolyploids (Arrigo et al., 2016; Blaine Marchant, Soltis & Soltis, 2016; Manzoor, Griffiths,  
117 Obiakara, Esparza-Estrada & Lukac, 2020). The effect of interploidy introgression in the ecological niche  
118 of autopolyploids remained unexplored.

119 *Arabidopsis arenosa* (Brassicaceae) is a diploid-autotetraploid species with a well-described evolutionary  
120 history of its lineages (see Fig. 1), that has recently become an interesting system not only to study polyploid  
121 evolution (Monnahan et al., 2019; Morgan et al., 2021a; 2021b; Bohutínská et al., 2021a), but also  
122 adaptation to extreme conditions (Konečná et al., 2021, Bohutínská et al., 2021b, Knotek et al., 2020, Wos  
123 et al., 2021). Multiple studies have addressed the role of niche differentiation in the autopolyploid evolution  
124 of this system, however, reaching strikingly inconsistent outcomes. Ecological niche modeling was used in  
125 a study conducted by Molina-Henao & Hopkins (2019), which concluded niche expansion but not  
126 divergence of tetraploids of *A. arenosa*. These results contrast with other studies in which an absence of  
127 ecological niche differentiation was described at both the landscape (Kolář et al., 2016b) and intra-  
128 population scales (Wos, Bohutínská, Nosková, Mandáková & Kolář, 2019), and in three contact zones  
129 independently (Morgan et al., 2020). Unfortunately, neither of these studies did cover the whole distribution  
130 range of the species (Wos et al., 2019; Morgan et al., 2020) and they did not integrate the intricate  
131 evolutionary history of this species involving the intraspecific genetic sub-structure of each cytotype and  
132 interploidy gene flow (Kolář et al., 2016b; Molina-Henao & Hopkins 2019). Autotetraploid cytotype of *A.*  
133 *arenosa* originated only once in the Western Carpathians 20,000 to 31,000 generations ago, where it still  
134 coexists with its diploid progenitor until now, but also from where it spread through most of Europe from

135 Romania in the south to Belgium in the west and Scandinavia in the north (Arnold, Kim & Bomblies., 2015;  
136 Monnahan et al., 2019, summarized in Fig. 1). During this expansion, tetraploids also encountered other  
137 earlier diverged diploid lineages of *A. arenosa* and got introgressed by them in at least two contact zones,  
138 in SE Carpathians and the Baltic coast (Monnahan et al., 2019). An intriguing question about to which  
139 extent such intricate evolutionary history has been translated to niche divergence, however, remained  
140 unanswered.

141 In the present study, we aim to examine the impact of the intraspecific genetic structure and interploidy  
142 introgression when testing for autopolyploid niche evolution. More specifically, we test the following  
143 hypothesis: (i) whether niche shift of polyploids is detectable only when polyploid lineages are compared  
144 with their corresponding diploid ancestor(s), not globally; and (ii) whether interploidy introgression events  
145 promote ecological divergence and/or expansion of polyploids. First, we used genome-wide single  
146 nucleotide polymorphism (SNP) genotyping to investigate the genetic structure within *A. arenosa*  
147 tetraploids across the landscape including for the first time samples from the whole geographic distribution  
148 area of the tetraploid cytotype. Second, we compared the environmental niche occupied by diploid and  
149 tetraploid lineages of *A. arenosa*, both globally, and independently for each tetraploid lineage with respect



to the niche of the evolutionary closest diploid lineage, and among them. Third, we investigated the effect of interploidy gene flow in polyploid niche shift by comparing niches of tetraploid Ruderal and SE Carpathian lineages to the niches of its respective sympatric locally-adapted diploid-related lineages.

**Figure 1.** A Summary of evolutionary history of diploid and autotetraploid lineages within *A. arenosa*. Based on our previous knowledge, we examined the impact of the intraspecific genetic structure and the interploidy introgression when testing for autopolyploid climatic niche differentiation. A single whole-genome duplication event occurred within the species is indicated by “WGD”. Interploidy gene flow events are indicated by dashed lines; **B** Geographic distribution of populations from diploid and autotetraploid lineages of *A. arenosa* included in our niche quantification and comparison analyses is shown.

## 173 MATERIAL AND METHODS

### 174 Genomic data

#### 175 **Dataset and library preparation**

176 The cytogeographical patterns in *A. arenosa* have been well documented (Kolář et al., 2016b) and the  
177 genetic structure of diploid populations across their entire distributional range is well known (Kolář et al.,  
178 2016a). However, in the case of tetraploids, the precise identification of genetic lineages still remains  
179 unclear mainly because the whole distribution range of tetraploids of *A. arenosa* has not been fully covered  
180 in previous studies (Arnold et al., 2015), or the number of sampled populations was limited (Monnahan et  
181 al., 2019). In order to identify range-wide tetraploid genetic structure, we generated a dataset of genome-  
182 wide single-nucleotide polymorphisms (SNPs) for a total of 276 tetraploid individuals from 125 populations  
183 (1-4 indiv/pop) using double-digest RADseq (as described in Wos et al., 2019). On top of that, available  
184 published WGS data (Monnahan et al., 2019) from 62 tetraploid populations (155 individuals) were also  
185 integrated to generate a more robust dataset, consisting of a total of 431 individuals from 187 populations.

186

#### 187 **Raw data processing, variant calling and filtration**

188 Raw reads were demultiplexed using FASTX toolkit 0.0.14 and quality trimmed (> 20 Phred quality score)  
189 in Trimmomatic 0.36. Mapping on *Arabidopsis lyrata* reference genome v. 1.0.25 (Hu et al., 2011) was  
190 performed using BWA v. 0.7.3a and the resulting BAM was processed with Picard Tools v. 2.22.1. The  
191 Genome Analysis Toolkit v. 3.8 (GATK, McKenna et al., 2010) was used following the best practice  
192 recommendations (<https://gatk.broadinstitute.org/hc/en-us>). Variant calling was performed for each  
193 individual using the HaplotypeCaller module, setting the ploidy=4 option. Then, we aggregated variants  
194 and performed genotyping across all individuals using GenotypeGVCFs.

195 The coordinates of the identified RAD loci were used to retrieve the corresponding SNPs from a previous  
196 set of genome resequencing data (Monnahan et al., 2019) that was mapped to the same reference genome.  
197 In this way, we extracted the SNP data from the same sites for an additional 155 individuals using GATK.  
198 Both VCF files were merged and the final VCF contained 431 tetraploid individuals from a total of 187  
199 populations. Only biallelic sites that passed the filter parameters indicated by GATK best practices  
200 (<https://gatk.broadinstitute.org/hc/en-us/articles/360035890471-Hard-filtering-germline-short-variants>)  
201 were considered: 'QD < 2.0', 'FS > 60.0', 'MQ < 40.0', 'MQRankSum < -12.5', 'ReadPosRankSum < -8.0',  
202 'SOR > 3.0'. Additionally, for subsequent analyses, only variants that were present in at least 80% of



203 individuals at a minimum sequencing depth of 8x were used, reaching a final dataset of 179,698 SNPs.  
204 Scripts used for processing the data are available at <https://github.com/V-Z/RAD-Seq-scripts>.

## 205 **Identification of genetic lineages**

206 Population genetic structure was inferred using Bayesian clustering analyses in STRUCTURE v. 2.3.2  
207 (Pritchard, Stephens & Donnelly, 2000), which allowed us to take into consideration autotetraploid  
208 genotypes. Before running STRUCTURE, the dataset was pruned to avoid linkage among SNPs. Taking  
209 into account the average length of RADseq fragments (350 bp), we randomly selected one SNP per each  
210 1000-bp window to avoid linkage disequilibrium. We discarded those SNPs showing a lower minor allele  
211 frequency of 0.05 and a higher minor frequency of 0.95 to remove uninformative singletons and errors in  
212 the dataset. Python scripts used for pruning and formatting the input data for STRUCTURE are available  
213 at [https://github.com/MarekSlenker/vcf\\_prune](https://github.com/MarekSlenker/vcf_prune). In STRUCTURE, we run ten replicates per each value of  $K$   
214 between 1 and 10 applying a burn-in of  $10^4$  iterations followed by  $10^5$  MCMC iterations. Convergence  
215 among different replicates per each  $K$  value was evaluated in R using a script  
216 (<https://github.com/MarekSlenker/structureSum>) that ran modified functions previously coded by Ehrich  
217 (2006). The results for every value of  $K$  were visualized using CLUMPAK (Kopelman, Mayzel, Jakobsson,  
218 Rosenberg & Mayrose, 2015). The optimal value of groups in our dataset was identified according to several  
219 criteria (i.e.  $K = 5$  is the highest value of  $K$  showing a positive of the results among the ten replicates; Fig.  
220 S1). Each population was assigned to the cluster for which the highest proportion of membership was  
221 observed. We further investigated the population structure inferred by STRUCTURE running principal  
222 component analysis (PCA). Based on putatively neutral four-fold degenerate (4dg) SNPs and using  
223 ADEGENET package in R (Jombart, 2008) we summarized the neutral genetic variability among the  
224 identified lineages within our tetraploid samples. Additionally, we calculated pairwise Nei's genetic  
225 distances (Nei, 1972) among the same lineages to quantify the genetic differentiation between them using  
226 StAMPP R package (Pembleton, Cogan & Forster, 2013).

227

## 228 Niche comparison analyses

### 229 **Occurrence data and climatic variables**

230 For the climatic niche comparison analyses, we used both diploid and tetraploid occurrences of *A. arenosa*  
231 with known affiliations to the genetic lineages (Supplementary Table 1). We collected leaf material from  
232 diploid and tetraploid populations of *A. arenosa* in 2011–2020 across their entire European distribution  
233 range and we checked the ploidy level of each individual using flow cytometry as described in Kolář et al.

234 (2015). Geographical coordinates were obtained from GPS during field surveys. The lineage assignment to  
235 tetraploid populations was done according to the Bayesian clustering of the SNP data obtained in this study  
236 (see details above and Supplementary Table 2). To avoid potential bias caused by admixture between  
237 different tetraploid lineages, we excluded equivocal populations showing less than 50% membership to one  
238 single cluster from the niche comparison analyses (in total 21 populations, see Supplementary Table 2). In  
239 case of diploids, the assignment was based on previous Bayesian clustering of a set of populations covering  
240 the entire range of the diploid cytotype (Kolář et al., 2016a) and the geographical location of additionally  
241 sampled populations. A total of 352 localities including 2x and 4x cytotypes of *A. arenosa* assigned to  
242 intraspecific genetic lineages were analyzed (see Supplementary Table 1). In order to avoid unequal  
243 representation caused by biased sampling in different areas, the obtained sampling points were filtered and  
244 those that were closer than 10-km distance were removed. The number of occurrences per cytotype and  
245 lineage is indicated in Supplementary Table 3. Environmental data related to temperature (BIO1-BIO11  
246 variables) and precipitation (BIO12-BIO19 variables) were extracted for all occurrence points from  
247 WorldClim at 30-s (ca. 1 km) resolution (Hijmans, Cameron, Parra, Jones & Jarvis, 2005).

#### 248 **Niche quantification and comparison**

249 Several climatic niche comparisons were performed: i) between diploids and tetraploids of *A. arenosa*  
250 globally, without considering the assignment to intraspecific genetic lineages; ii) independently between  
251 each tetraploid lineage and its evolutionary closest diploid relative; iii) among tetraploid lineages that  
252 diverged after the WGD event; and iv) between tetraploid and locally sympatric diploid lineages. Then, we  
253 tested if there was an effect of other sympatric but more ancestral diploid lineages of *A. arenosa* on climatic  
254 niches of tetraploids. Quantification and comparison of climatic niches were performed using a statistical  
255 framework developed by Broennimann et al. (2012). It applies a kernel density function to calculate the  
256 smoothed density of occurrences and environmental values along the first two axes of a multivariate  
257 analysis (PCA-env). This method ensures that the niche overlap is independent of the resolution of the grid.  
258 We considered the first two axes of the PCA calibrated on the environmental space of the study area, which  
259 was divided into a grid of 100 x 100 cells with each cell corresponding to a unique set of environmental  
260 conditions. The environmental space was produced by extracting the same climatic values for 10,000  
261 occurrence points randomly sampled from 100-km buffer zones around the occurrences of diploid and  
262 tetraploid *A. arenosa* records. This common environmental space, which theoretically corresponds to the  
263 potential habitat of the species, was used for all pairs of comparisons. Occurrence density grids had a  
264 resolution of 100 and a species density threshold of zero. Niche overlap, equivalence and similarity tests  
265 implemented in the R package “ecospat” (Di Cola et al., 2017) were performed to compare the divergence  
266 between lineages. Niche overlap calculation is based on Schoener’s *D* metric (Schoener, 1968) that ranges

267 from 0 (no overlap) to 1 (complete overlap). To evaluate the significance of niche overlap ( $\alpha = 0.05$ ), we  
268 performed an equivalency test (Warren, Glor & Turelli, 2008), which uses random bootstrap resampling of  
269 presence occurrence points of both lineages to calculate if a null distribution of  $D$  and the observed  $D$  are  
270 significantly different ( $p < 0.05$ ; niches are not statistically equivalent) or not (niches are equivalent). The  
271 significance of niche overlap was also evaluated by similarity tests, which use bootstrap resampling to  
272 assess whether the niche of one lineage predicts the other better than would be expected by chance ( $\alpha =$   
273  $0.05$ ). If observed  $D$  is greater than the null distribution, niches are more similar than expected. Values  
274 lower than the null distribution indicate that niches are not similar and non-significant values mean a lack  
275 of power of the test to detect differences or similarities. However, simply testing if niches of diploid and  
276 tetraploid cytotypes are equivalent or different does neither fully account for dynamics of niche evolution,  
277 nor reflects complex reticulated evolutionary history of the species. In order to understand alternative  
278 processes driving niche evolution in *A. arenosa* we have quantified niche dynamics per each genetic  
279 lineage, using niche unfilling (U), stability (S) and expansion (E) indices (Guisan, Petitpierre, Broennimann,  
280 Daehler & Kueffer, 2014) and calculating niche optimum and breadth along the axes of temperature and  
281 precipitation variation. Niche optimum and breadth of each lineage was calculated following the procedure  
282 described in Theodoridis et al. (2013) and Kirchheimer et al. (2016). We randomly sampled 100 cells of  
283 the gridded space of each lineage with the probability of selection weighted by the density of the species  
284 occurrences. We calculated the niche optimum and breadth, calculating the median and the standard  
285 deviation of the scores along the two PCA axes, respectively. This re-sampling was repeated 1000 times  
286 and differences in the distribution of optimum and breadth values were compared using Welch's t-tests in  
287 R. The results were visualized using boxplots for each PCA axis. In order to test for an effect of the studied  
288 lineages on the niches' optimum and breadth for each PCA axis, we first performed an ANOVA test, and  
289 then we performed a Tukey HSD test to perform all the possible pairs-comparisons.

290

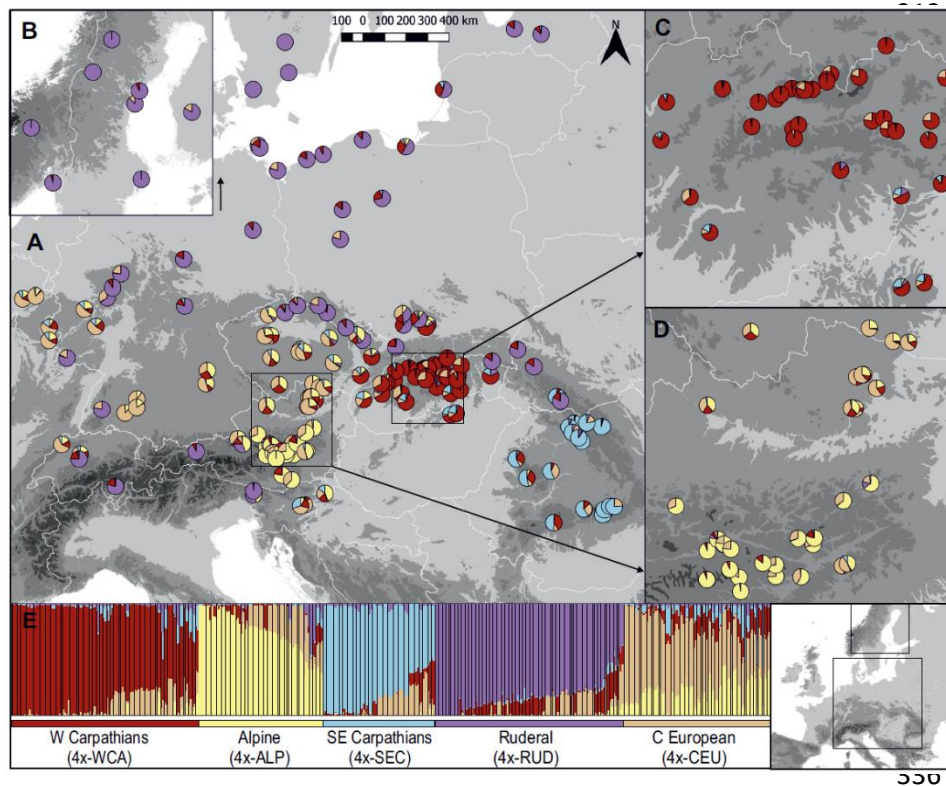
## 291 RESULTS

### 292 Genetic structure within *A. arenosa* tetraploids

293 We have obtained a total of 179,698 filtered SNPs for the 431 tetraploid individuals of *A. arenosa* included  
294 in our study. The average depth is  $11\times$  and our dataset comprises 13.1% of missing data over populations  
295 and sites. Bayesian clustering analyses support the existence of five distinct genetic clusters among  
296 tetraploids of *A. arenosa*. These clusters are geographically separated (Fig. 2). Two of them (dark red and  
297 light blue) are restricted to populations located in W and SE Carpathians, respectively. The majority of  
298 populations from the Western part of Central Europe (further referred to as C Europe) are included in a

299 third cluster (light orange). Only populations from the Eastern Alps form a separate fourth cluster (light  
300 yellow). Finally, some populations sampled in human-made ruderal stands (mainly railways tracks and  
301 roadsides) in the Alps, Germany and the Czech Republic are clustered together with all populations located  
302 in Northern Europe and the Baltic Sea coast (purple).

303 Principal Component Analysis based on genetic data confirms the genetic differentiation of *A. arenosa*  
304 tetraploids into the five lineages and further indicates the level of differentiation among them. Ruderal  
305 populations (4x-RUD) are separated from the others along the first axis, while populations located in SE  
306 Carpathians (4x-SEC) are differentiated from the rest along the second axis (Supplementary Figure 2a).  
307 Alpine (4x-ALP), W Carpathians (4x-WCA) and C European (4x-CEU) populations cluster together in  
308 the PCA of the complete dataset but get clearly distinct in a separate analysis excluding the populations  
309 identified within the 4x-RUD and 4x-SEC lineages (Supplementary Figure 2b). Nei's genetic distances  
310 calculated among lineages reflect the fact that the genetic divergence among them is generally low  
311 (Supplementary Figure 2c).



**Figure 2.** Rangewide genetic differentiation of tetraploid *A. arenosa*. **A** Geographic distribution of populations used in the genomic analyses (color pie charts reflecting the proportional assignment to particular clusters identified by STRUCTURE and representing tetraploid lineages within *A. arenosa*: W Carpathians (dark red), Alpine (light yellow), SE Carpathians (light blue), Ruderal (purple), C European (light orange); **B** Detail of Scandinavia; **C** Detail of the Western Carpathian region; **D** Detail of the Austrian region; **E** Individual assignment into each of the five genetic clusters revealed by STRUCTURE.

### 337 Niche quantification and comparison between diploids and tetraploids globally

338 The variation explained by the two first axes of the PCA-env is 41.5% and 30.4% respectively, which means  
 339 a 71.9% of the total variance. Environmental variables related to precipitation (BIO12-BIO19) are highly  
 340 correlated to PC1, while temperature-related variables (BIO1-BIO11) are mainly correlated to PC2 (Fig.  
 341 3a). The contribution of each variable to the two first axes of the PCA is summarized in Supplementary  
 342 Table 4. Annual precipitation (BIO12), precipitation of the driest quarter and month (BIO17 and BIO14)  
 343 together with precipitation of the coldest quarter (BIO19) show the highest percentage of correlation to  
 344 PC1. Mean temperature of the coldest quarter (BIO11) and minimum temperature of the coldest month  
 345 (BIO6) are the most correlated variables to PC2.

346 When the niche of diploids and tetraploids of *A. arenosa* is compared globally, i.e. ignoring the assignment  
 347 to intraspecific genetic lineages, the niche equivalency test does not have enough power to detect niche  
 348 differentiation, while the similarity test indicates that niches are more similar than expected by chance  
 349 independent of the direction of the test (Table 1). These results indicate niche conservatism between  
 350 diploids and tetraploids when they are globally compared (Fig. 3b). Accordingly, tetraploids show a relative  
 351 high niche overlap with diploids (50.2 %), very high stability index value ( $S = 0.947$ ) and almost zero  
 352 expansion and niche unfilling ( $E = 0.053$  and  $U = 0.079$ , respectively).

353 **Table 1.** Niche overlap percentage values, results for equivalency and similarity tests and niche dynamic indices (expansion,  
 354 stability and unfilling) are shown for pairwise comparisons (lineage 1 vs. lineage 2).

| <i>Arabidopsis arenosa</i> |        | % Niche overlap | Niche equivalency | Niche similarity |                | Indices of niche change |               |               |
|----------------------------|--------|-----------------|-------------------|------------------|----------------|-------------------------|---------------|---------------|
| 1                          | 2      |                 |                   | 1 → 2            | 2 → 1          | Expansion (E)           | Stability (S) | Unfilling (U) |
| 2x-ALL                     | 4x-ALL | 50.2            | ns (EQUIVALENT)   | More similar *   | More similar * | 0.053                   | 0.947         | 0.079         |
| 2x-WCA                     | 4x-ALL | 62.8            | ns (EQUIVALENT)   | More similar *   | More similar * | 0.252                   | 0.748         | 0.006         |
| 2x-WCA                     | 4x-WCA | 64.9            | ns (EQUIVALENT)   | More similar *   | More similar * | 0.017                   | 0.983         | 0.127         |
| 2x-WCA                     | 4x-ALP | 52.1            | ns (EQUIVALENT)   | ns               | ns             | 0.215                   | 0.785         | 0.350         |
| 2x-WCA                     | 4x-SEC | 24.6            | ns (EQUIVALENT)   | ns               | ns             | 0.097                   | 0.903         | 0.400         |
| 2x-WCA                     | 4x-RUD | 28.1            | ns (EQUIVALENT)   | ns               | ns             | 0.336                   | 0.664         | 0.207         |
| 2x-WCA                     | 4x-CEU | 7.7             | ns (EQUIVALENT)   | ns               | ns             | 0.479                   | 0.521         | 0.607         |
| 4x-WCA                     | 4x-ALP | 46.8            | ns (EQUIVALENT)   | ns               | ns             | 0.329                   | 0.672         | 0.347         |
| 4x-WCA                     | 4x-CEU | 14.4            | ns (EQUIVALENT)   | ns               | ns             | 0.447                   | 0.553         | 0.438         |
| 4x-WCA                     | 4x-RUD | 32.4            | ns (EQUIVALENT)   | ns               | ns             | 0.364                   | 0.636         | 0.098         |
| 4x-WCA                     | 4x-SEC | 21.6            | ns (EQUIVALENT)   | ns               | ns             | 0.258                   | 0.742         | 0.390         |

355  
 356 \* The ecological niches are significantly ( $P < 0.05$ ) more similar than expected

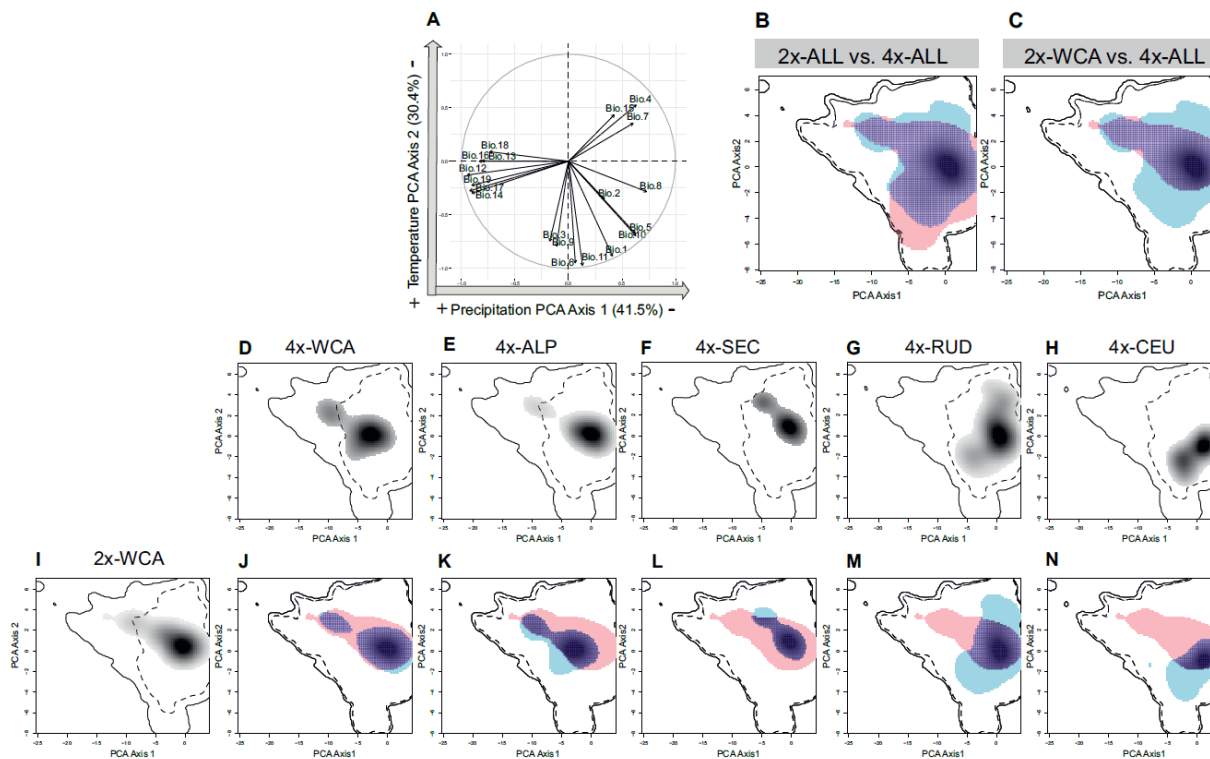
357

### 358 Niche quantification and comparison between related diploid and tetraploid intraspecific lineages

359 To integrate niche data with evolutionary history (Fig. 1), we firstly reconstructed niche evolution reflecting  
 360 the single evolutionary origin of all *A. arenosa* tetraploid lineages from the ancestral diploid lineage (2x-

361 WCA). Niche conservatism is observed when comparing all *A. arenosa* tetraploid lineages to the 2x-WCA  
362 lineage, but excluding other diploid lineages from the analysis that did not contribute to the origin of  
363 autotetraploids (Fig. 3c). In this case, the proportion of niche overlap of tetraploids with the 2x-WCA  
364 diploid lineage is 62.8% (Table 1). The stability index value is high ( $S = 0.748$ ) while the expansion and  
365 unfilling values are  $E = 0.252$  and  $U = 0.006$ . Interestingly, when each tetraploid lineage was compared  
366 independently to the ancestral 2x-WCA lineage, the resulting patterns are very different from the previous  
367 global comparison and from each other (Fig. 3). Specifically in the W Carpathians, niches of diploids and  
368 tetraploids are more similar than expected by chance, independent of the direction of the test (Table 1).  
369 Furthermore, a high niche overlap is observed between 2x and 4x W Carpathians lineages (64.9%) with  
370 high stability and very low values for expansion and niche unfilling indices ( $S = 0.983$ ,  $E = 0.017$  and  $U =$   
371  $0.127$ ). These results together suggest that in the W Carpathians, diploid and tetraploid lineages show  
372 similar ecological niches. In contrast, similarity tests were non-significant (Table 1) when comparing other  
373 tetraploid lineages to the ancestral diploid (2x-WCA). A high overlap was found between niches  
374 corresponding to 4x-ALP and 2x-WCA (52.1%), also showing a high stability value ( $S = 0.785$ ) and  
375 intermediate values of niche expansion ( $E = 0.215$ ) and unfilling ( $U = 0.350$ ). In the case of 4x-SEC lineage,  
376 niche contraction compared to the 2x-WCA lineage is indicated by an intermediate value of unfilling index  
377 ( $U = 0.400$ ) and a high stability index ( $S = 0.903$ ) but almost zero expansion ( $E = 0.097$ ). In this case, the  
378 percentage of niche overlap is 24.6% (Table 1). The 4x-RUD lineage has experienced niche expansion  
379 compared to the 2x-WCA lineage ( $S = 0.664$  and  $E = 0.336$ ), whose niche was partially filled by the Ruderal  
380 one ( $U = 0.207$ ). These results indicate that niche expansion of the 4x-RUD has occurred towards areas of  
381 more extreme temperatures while it has not filled the “high-alpine” niche portion occupied by its 2x-WCA  
382 ancestor lineage, which is characterized by high precipitation values. The niche occupied by the 4x-CEU  
383 lineage has also significantly expanded ( $S = 0.521$  and  $E = 0.479$ ), but in this case tetraploids almost did  
384 not fill the niche occupied by the 2x-WCA lineage ( $U = 0.607$ ).

385 Niche optimum (calculated as the median of the scores along each axis of PCA-env) reflects a higher  
386 optimal precipitation value (PC1) for 2x-WCA when compared to all tetraploid lineages, with the exception  
387 of the 4x-ALP (Fig. 4). Optimal temperature values (PC2) are higher for tetraploids than for 2x-WCA  
388 except for the 4x-SEC lineage. Niche breadth in terms of precipitation (PC1) is lower for all tetraploid  
389 lineages compared to the 2x-WCA lineage (Fig. 4). In terms of temperature (PC2), niche breadth is not  
390 significantly different among 2x-WCA, 4x-WCA and 4x-CEU lineages. Temperature breadth is higher for  
391 2x-WCA than for the 4x-ALP and 4x-SEC lineages but lower than for the 4x-RUD one.



392

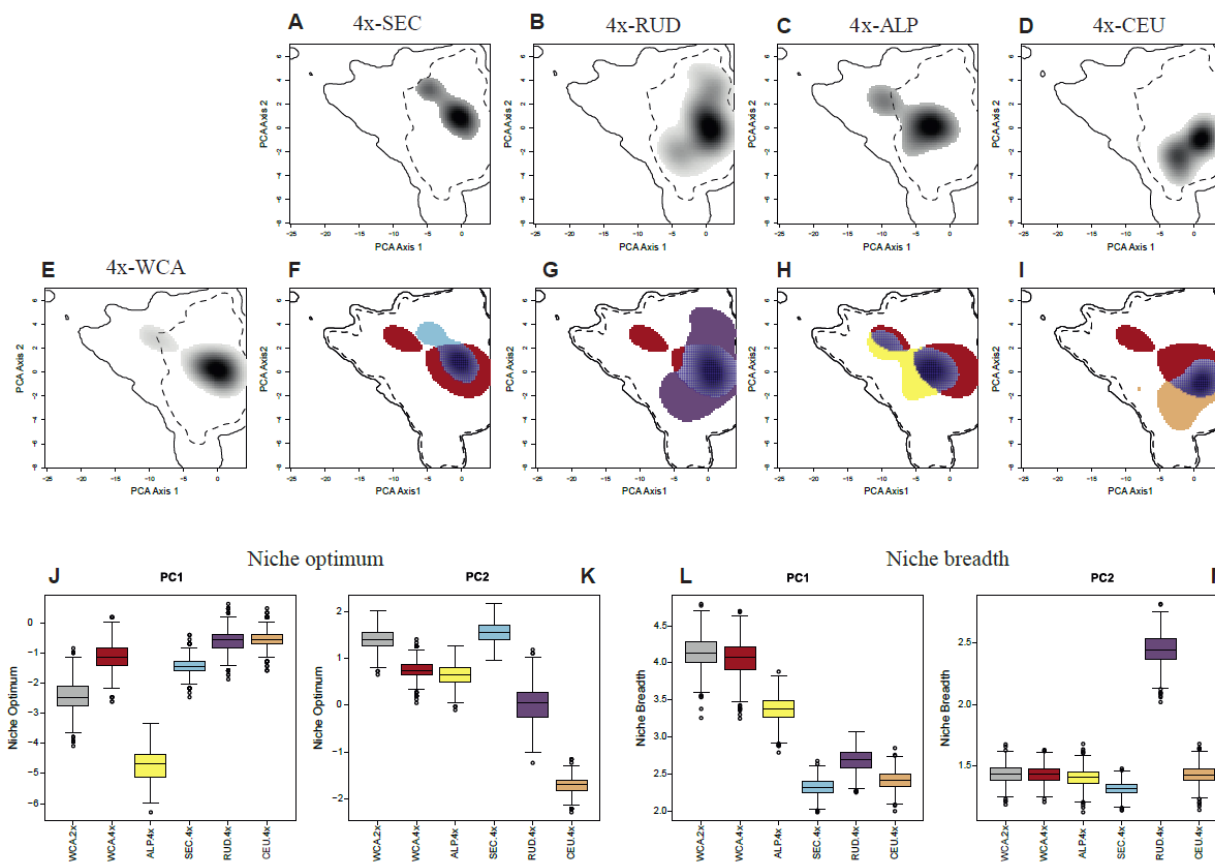
393 **Figure 3.** Climatic niche dynamics of diploid and tetraploid *A. arenosa* lineages. The fraction of the diploid niche that remains  
 394 unfilled by tetraploids represents tetraploid niche contraction (pink), whereas climatic space occupied by the tetraploid and not by  
 395 the diploids indicates niche expansion (blue). The fraction of the tetraploid climatic niche that overlaps with diploids indicates  
 396 niche stability (dark blue). **A** Correlation circle of 19 environmental variables along the first two axes of PCA-env. The percentage  
 397 of variation and the main environmental gradient explained by each axis is indicated; **B** Niche of all *A. arenosa* diploids compared  
 398 to the niche of all *A. arenosa* tetraploids without considering their assignment to different lineages; **C** Niche of ancestral diploid  
 399 lineage (2x-WCA) compared to the niche of all *A. arenosa* tetraploids; **D-I** Climatic niche reconstruction of each *A. arenosa*  
 400 tetraploid lineage and the ancestral diploid W Carpathian lineage. Occurrence density grids are represented by a black-to-white  
 401 downward gradient along the two first axes of PCA-env; **J-N** Comparisons of climatic niches of each tetraploid lineage to their  
 402 ancestral diploid lineage.

403

#### 404 Niche quantification and comparison among tetraploid lineages

405 Furthermore, we inferred niche evolution during tetraploid expansion. To do so, we compared the niche of  
 406 each tetraploid lineage to the niche of tetraploids from the W Carpathians (4x-WCA) which occupy the  
 407 presumed area of origin of tetraploid *A. arenosa* cytotype and are thus closest to the “ancestral polyploid”  
 408 niche (Fig. 1). Similarity tests were not significant for any pair-wise comparison (Table 1). Percentages of  
 409 niche overlap varied from 14.4 % (4x-CEU) to 46.76 % (4x-ALP). All tetraploid lineages showed some  
 410 degree of niche expansion relative to the 4x-WCA lineage occupying the ancestral area (Fig. 4), with values  
 411 of E indices ranging between 0.258 (4x-SEC) and 0.447 (4x-CEU). The 4x-RUD lineage almost entirely  
 412 filled the niche of 4x-WCA ( $U = 0.098$ ) while other lineages show values of unfilling indices that vary  
 413 between 0.347 (4x-ALP) and 0.438 (4x-CEU). The optimal value of precipitation (PC1) is shown to be

414 highest for 4x-ALP and lowest for 4x-RUD and 4x-CEU lineages, while in terms of temperature (PC2) is  
 415 the 4x-SEC which showed the coldest optimal value. Specifically, 4x-RUD and 4x-CEU lineages show the  
 416 highest optimal values of temperature (Fig. 4). Niche breadth indicates that 4x-WCA occupies the broadest  
 417 gradient of precipitation compared to all other tetraploid lineages, while the temperature breadth is much  
 418 higher for the 4x-RUD lineage than from other tetraploid lineages (Fig. 4).



419  
 420 **Figure 4.** A-E Climatic niche reconstruction for each tetraploid lineage of *A. arenosa*. Occurrence density grids are represented by  
 421 a black-to-white downward gradient along the two first axes of PCA-env. F-I Niche comparisons between each tetraploid lineage  
 422 and the ancestral W Carpathian tetraploid. The fraction of the W Carpathian tetraploid niche that remains unfilled is represented in  
 423 dark red, whereas niche expansion of each tetraploid lineage is colored according to Fig. 2. The niche overlap is indicated in dark  
 424 blue. J-M Niche optimum and breadth for W Carpathian diploid and each of the tetraploid *A. arenosa* lineages along the PC1 and  
 425 PC2 axes.

426  
 427 **Niche quantification and comparison between tetraploid and locally sympatric diploid lineages**

428 Last, we investigated niche evolution when taking into account the influence of strong inter-ploidy  
 429 introgression from more divergent diploid lineages of *A. arenosa* which co-occur with particular tetraploid  
 430 lineages within two contact zones (Fig. 1): SE Carpathians (4x-SEC lineage introgressed by 2x-SEC) and

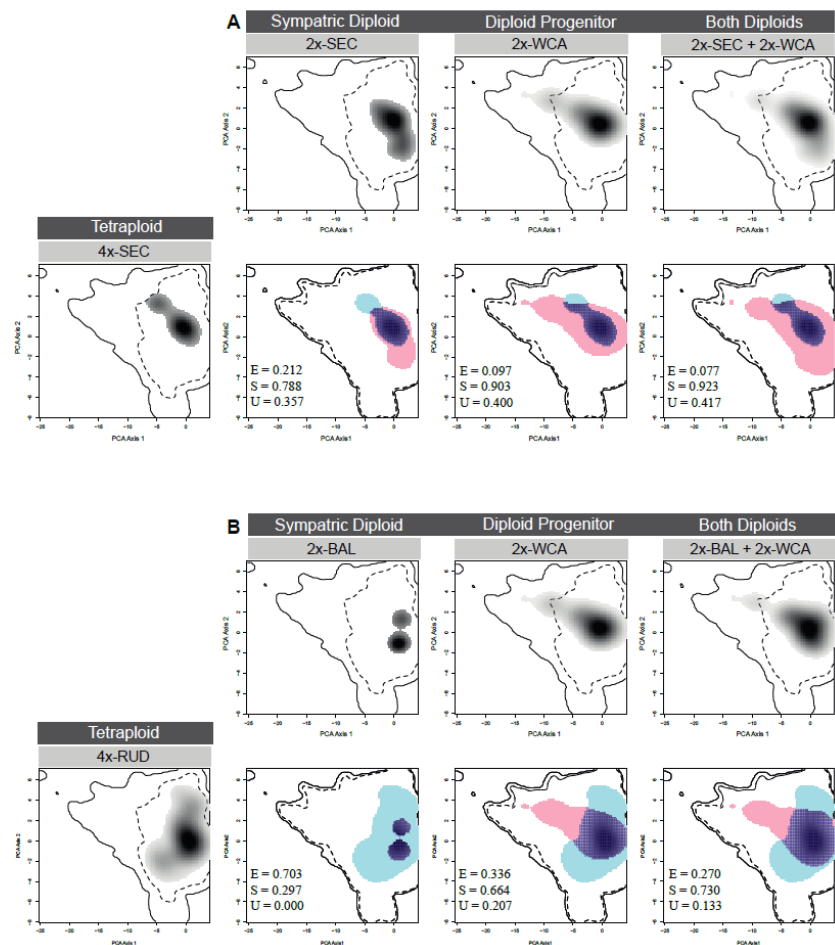


431 Baltic coast (4x-RUD lineage introgressed by 2x-BAL). When we compared the observed niche of the 4x-  
 432 SEC lineage to the combined niche of both diploid lineages that served as source gene pools (2x-WCA and  
 433 2x-SEC), we do not observe substantive changes in niche dynamics index values with respect to the  
 434 previous comparison including 4x-SEC lineage and only the ancestral diploid 2x-WCA lineage (Fig. 3l,  
 435 Fig. 5a). It is shown that tetraploids have barely expanded their niche ( $S = 0.923$  and  $E = 0.077$ ) and that a  
 436 considerable proportion of the niche of the diploid lineages has not been filled by 4x-SEC ( $U = 0.417$ ).  
 437 Thus, niche contraction with respect to both diploid lineages has occurred in the 4x-SEC lineage towards  
 438 warmer and more humid areas.

439 Comparing the observed niche of 4x-RUD to those predicted by the combination of niches of both diploid  
 440 lineages that contributed to its genetic make-up (2x-WCA and 2x-BAL), we observe differences with  
 441 respect to the previous comparison including just the ancestral diploid 2x-WCA lineage (Fig. 3m, Fig. 5b).  
 442 We observe a lower niche expansion of 4x-RUD lineage with respect to both diploid lineages ( $E = 0.270$ ).  
 443 A lower unfilling index value ( $U = 0.133$ ) and a higher stability ( $S = 0.730$ ) are also shown (Fig. 5B).

444 **Figure 5.** Climatic niche comparison of  
 445 observed and expected niches for SE  
 446 Carpathians tetraploid (A) and Ruderal  
 447 tetraploid (B) lineages. Occurrence  
 448 density grid for each diploid and  
 449 tetraploid lineage is represented in the  
 450 climatic space along the first two  
 451 principal components (black & white  
 452 plots). The observed niche of each  
 453 tetraploid lineage is compared to the  
 454 observed niche of their respective  
 455 putative diploid ancestors and to their  
 456 expected niches, which are calculated as  
 457 the combined niche spaces of diploid  
 458 ancestors. The fraction of the tetraploid  
 459 climatic niche that overlaps with diploid  
 460 ancestors indicates niche stability (S,  
 461 dark blue), whereas the fraction that  
 462 remains unfilled represents tetraploid  
 463 niche contraction (U, pink). Climatic  
 464 space occupied by the tetraploid lineages  
 465 while not predicted by the combination  
 466 of diploid progenitors indicates niche  
 467 expansion (E, blue).

468



469 DISCUSSION

470 *1. Varying extent of niche differentiation and expansion across tetraploid intraspecific lineages*

471 It is usually assumed that polyploids have a different ecological niche than diploids, reflecting a WGD-  
472 driven shift in important functional traits, which in turn strengthens prezygotic isolation between ploidies  
473 and contributes to polyploid speciation (Levin, 2004; Husband et al., 2016). However, the existence and  
474 potentially the extent of ploidy-related niche differentiation differ between individual species and  
475 sometimes even among case studies (Glennon et al., 2014, Visger et al., 2016, Muñoz-Pajares et al., 2018,  
476 Castro et al., 2019). One explanation for this controversy is that niche evolution of polyploids might be  
477 detectable only when polyploid lineages are compared with their corresponding diploid ancestors but,  
478 unfortunately, the intraspecific genetic structure of polyploid complexes is often ignored when testing  
479 climatic niche evolution of polyploids. To test for this effect, we compared niches of ploidy cytotypes of  
480 *A. arenosa* – a species surrounded with controversy regarding the level of niche differentiation of its diploid  
481 and autotetraploid cytotype (Molina Henao & Hopkins, 2019, Morgan et al., 2020) – using the largest  
482 population sampling to date coupled with genotyping of each population. We assigned each autotetraploid  
483 population to one of the five major genetic lineages based on our genomic analyses (Fig. 2), which  
484 corresponded with previous genetic structuring results based on smaller sampling (Arnold et al., 2015;  
485 Monnahan et al., 2019) and put our results in the context of polyploid origin and interploidy gene flow by  
486 integrating with previous population genomic investigations involving both ploidies (Monnahan et al.,  
487 2019; Fig. 1).

488 In our study, niche shift was not supported when we compared diploid and tetraploid cytotypes globally,  
489 i.e. ignoring the intraspecific genetic structure (Fig. 3b, Table 1). However, we identified highly variable  
490 patterns of niche differentiation when the climatic niche of each tetraploid lineage was compared  
491 independently to the niche of the ancestral diploid lineage (2x-WCA). Niche conservatism between diploids  
492 and tetraploids was only found within the zone of primary coexistence (W Carpathians), where tetraploids  
493 of *A. arenosa* originated. This result corresponds with previous studies that found neither regional climatic  
494 nor local habitat differences between diploid and tetraploid populations of *A. arenosa* in this contact zone  
495 (Wos et al., 2019; Morgan et al., 2020). The fact that diploids and tetraploids do not show niche  
496 differentiation indicates that tetraploids can coexist in the same niche as their diploid progenitors. These  
497 results confirm growing body of empirical works showing that polyploids and diploids living in similar  
498 ecological niches tend to be common in autopolyploids (Godsoe et al., 2013; Glennon et al., 2014;  
499 Kirchheimer et al., 2016; Castro et al., 2019). Some such autopolyploids can escape or reduce competition  
500 with diploid progenitors by other changes in phenology, pollinators or parasite interactions (Thompson et  
501 al., 2014; Segraves & Thompson, 1999), or by post-pollination prezygotic barriers involving pollen

502 competition and altered pollen-stigma interactions (Husband, 2016; Castro, Loureiro, Husband & Castro,  
503 2020b). In the autotetraploid *A. arenosa*, other processes than niche differentiation might promote  
504 reproductive isolation between cytotypes, which in turn allowed tetraploids to get established in sympatry  
505 with their diploid progenitors. On the other hand, we cannot rule out the possibility of ongoing interploidy  
506 gene flow in this zone, which might mitigate niche differences between diploids and tetraploids. After the  
507 postulated single origin ~20–30 thousands of generations ago (Monnahan et al., 2019), tetraploids of *A.*  
508 *arenosa* spread across Europe and diversified into four additional lineages (Fig. 1). When niches of these  
509 allopatric tetraploid lineages are compared to the ancestral diploid lineage (2x-WCA), the results largely  
510 vary among lineages (Fig. 3). While tetraploids from SE Carpathians (4x-SEC) exhibited a considerable  
511 niche contraction, the Alpine, Ruderal and C European tetraploid lineages have significantly expanded their  
512 niche with respect to the ancestral diploids (Table 1, Fig. 3). Furthermore, when we compared the climatic  
513 niches of these diverged tetraploid lineages to the tetraploid lineage that still occupies the ancestral area  
514 (4x-WCA) we also observed significant differentiation, suggesting notable post-WGD evolution of  
515 tetraploid niches (Table 1, Fig. 4). Most of them have experienced some niche expansion with respect to  
516 the ancestral 4x-WCA (Table 1, Fig. 4), and they have colonized very different climatic conditions either  
517 towards drier and warmer (4x-RUD and 4x-CEU), colder (4x-SEC), or more humid environments (4x-  
518 ALP).

519 Overall, our study confirms that niche evolution of polyploids is detectable only when polyploid lineages  
520 are compared with their corresponding diploid ancestor lineage, not globally. While niche similarity is  
521 observed when comparing the niches of cytotypes coexisting in the ancestral area of the tetraploid cytotype,  
522 niche expansion is mainly driven by post-WGD diversification into several lineages, primarily those that  
523 colonized warmer and drier anthropogenic habitats. These results demonstrate that niche shift is likely not  
524 driven by WGD *per se* in *A. arenosa* but rather reflects dynamic post-WGD evolution in the species,  
525 involving tetraploid migration and potential further interactions of tetraploids with other diploid lineages  
526 as is discussed in the next section.

527

## 528 2. Contribution of interploidy introgression to tetraploid niche expansion

529 Previous analyses demonstrated that genetic distinctness of particular lineages (4x-SEC, 4x-RUD) reflects  
530 strong interploidy gene flow after secondary contact with distantly related diploid lineages that have  
531 diverged before the WGD event (Monnahan et al., 2019). Such interploidy gene flow could have increased  
532 phenotypic and genetic variation which may allow tetraploids to colonize new ecological niches, in a way  
533 that is somewhat analogous to expectations stemming from hybrid origin of allopolyploids (e.g. Parisod &  
534 Broennimann, 2016; Huynh, Broennimann, Guisan, Felber & Parisod, 2020). Accordingly, the effect of  
535 introgression can be tested using an ecological niche comparison approach by looking at changes in terms

536 of niche dynamic components such as unfilling and expansion. Here we leveraged the exceptionally well-  
537 described evolutionary history of *A. arenosa* involving localized post-WGD introgression from divergent  
538 diploids into two distinct tetraploid lineages (4x-SEC and 4x-RUD, Fig. 1; Monnahan et al., 2019) to assess  
539 if considering a niche of such additional diploid “donor” in addition to the 2x-WCA ancestor help to explain  
540 inter-ploidy niche divergence. Although notable effects have been observed in both cases, the results, once  
541 again, differed for each lineage. In the case of the 4x-SEC lineage, adding niche requirements of the  
542 sympatric 2x-SEC lineage do not explain tetraploid expansion but rather indicate tetraploid’s contraction  
543 in terms of temperature. These results show that interploidy gene flow between the 4x-SEC and the  
544 sympatric but evolutionary distant 2x-SEC has not led to a broader niche of the 4x-SEC lineage (Fig. 5a).  
545 On the other hand, introgression of the Baltic diploid lineage (2x-BAL) into the 4x-RUD lineage has slightly  
546 increased the ecological range of tetraploids towards colder conditions (Fig. 5b). This partly explains the  
547 massive expansion of the tetraploid Ruderal lineage towards more northerly habitats that are characteristic  
548 for the Baltic lineage. Indeed, previous studies have demonstrated that introgression of alleles involved in  
549 flowering time regulation from 2x-BAL to 4x-RUD has played a role in the early flowering of tetraploid  
550 ruderal *A. arenosa* plants (Baduel, Hunter, Yeola & Bomblies, 2018). Our results suggest a potential effect  
551 of interploidy gene flow in patterns of climatic niche evolution of tetraploid ruderal plants of *A. arenosa*.  
552 Thus, our study is one of the few examples supporting that interploidy introgression may be an important  
553 process for ecological adaptation of wild plants to challenging environments.

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562 **Author contributions:** NPG, GŠ, FK and KM conceived the ideas; GŠ, EZ, ML, FK and KM collected  
563 most of the plants; GŠ performed the lab work; VZ proceed the raw genomic data; MŠ wrote the script  
564 for pruning the input data for STRUCTURE and updated the script for detecting the convergence among  
565 replicates; JC wrote the script for calculating niche optimum and breadth; NPG analysed the data; NPG  
566 led the writing.

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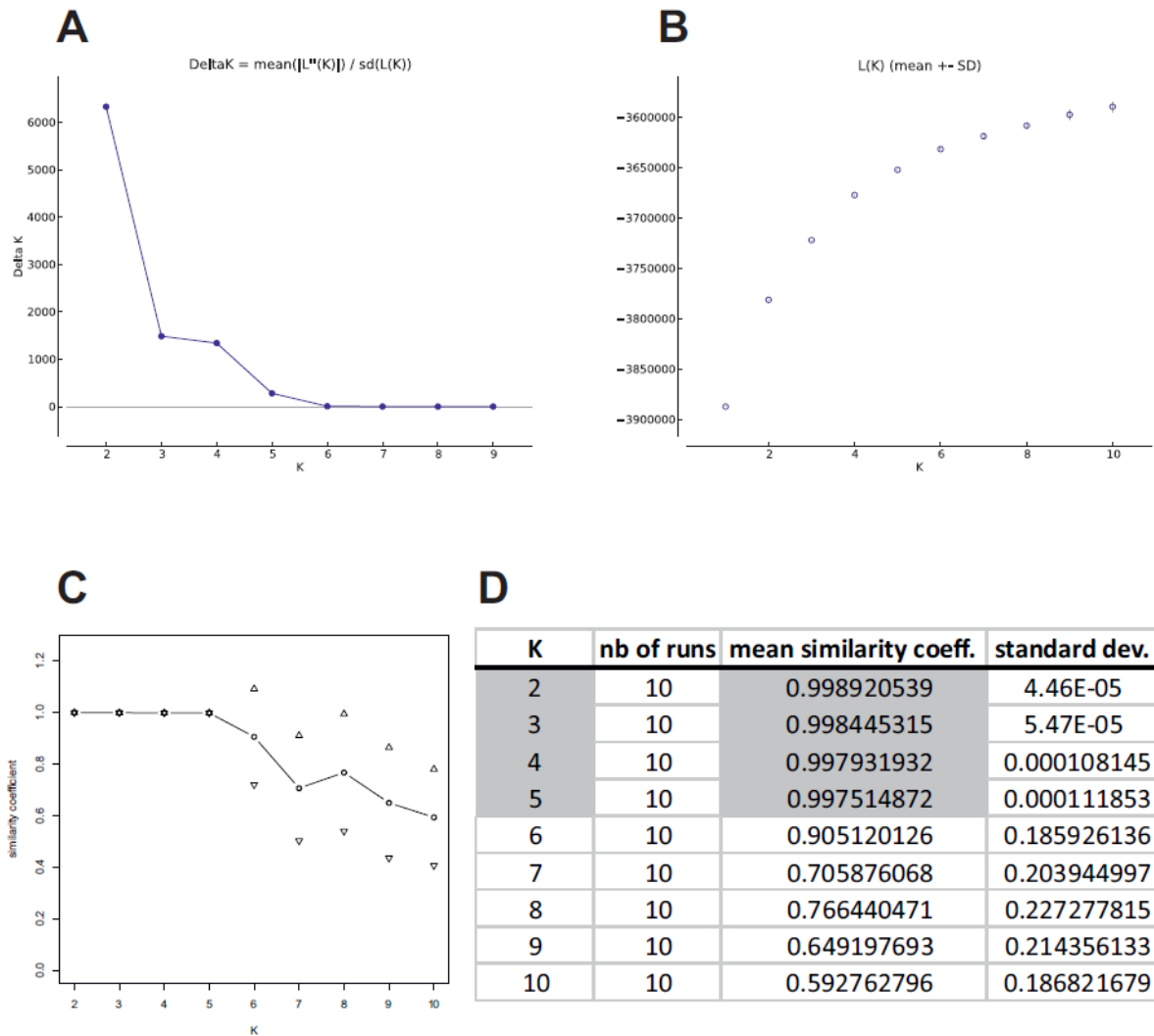
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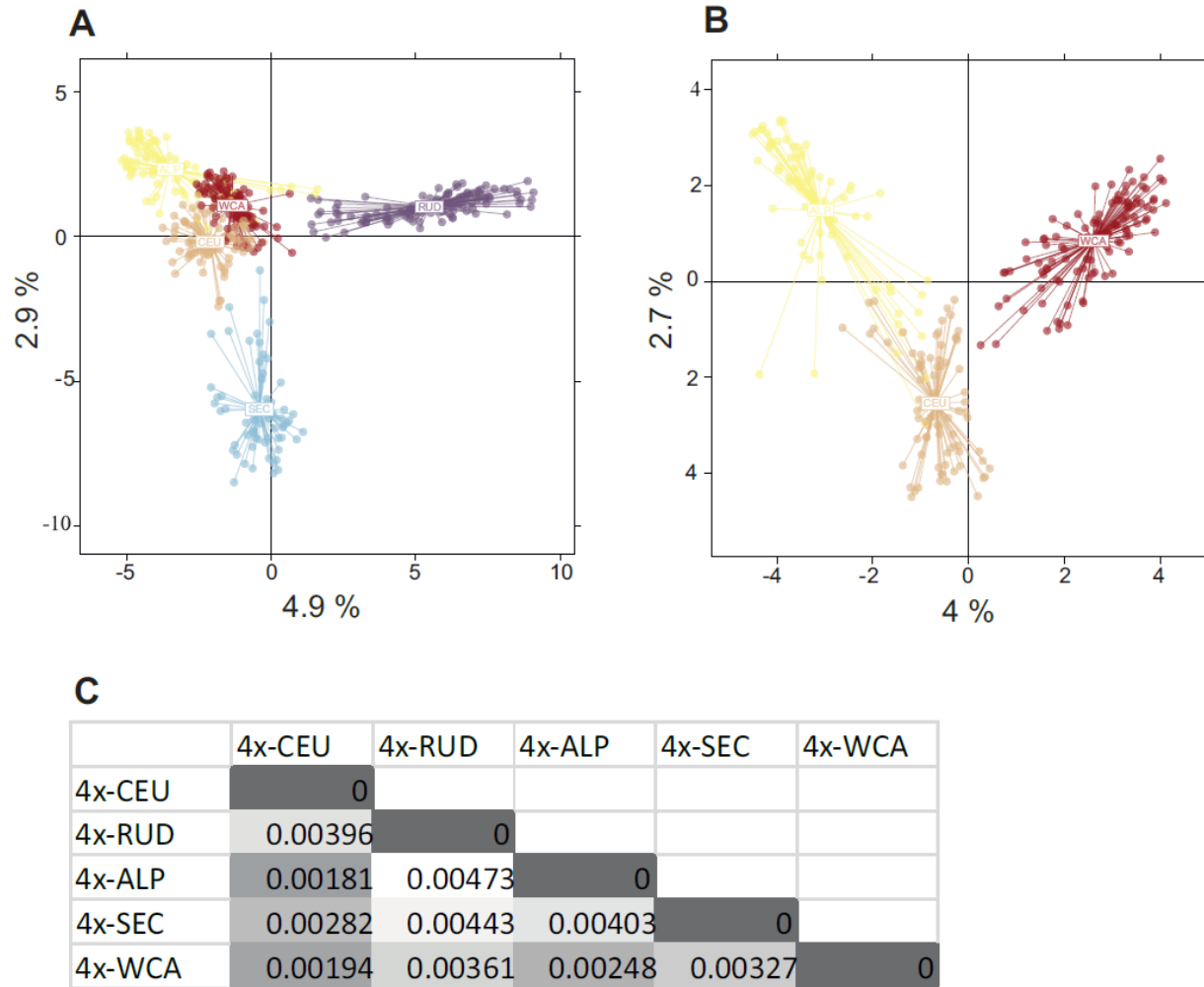
753 SUPPLEMENTARY INFORMATION



754

755 **Figure S1.** Summary of delta  $K$ , likelihood and convergence values of STRUCTURE replicates of  
 756 tetraploid *A. arenosa* SNP dataset; **A, B** Mean delta  $K$  and likelihood values respectively, both calculated  
 757 based on the Evanno method (Evanno, Regnaut & Goudet 2005), **C, D** Plot and values of mean similarity  
 758 coefficients and standard deviation considering 10 replicates for each value of  $K$ .

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760

761 **Figure S2. A** Principal Components Analysis (PCA) of all tetraploid *A. arenosa* lineages identified in this

762 study. Axis 1 and axis 2 explains 4.9% and 2.9% of the variation, respectively, **B** PCA including W

763 Carpathians, C European and Alpine tetraploid lineages of *A. arenosa*. Two first axes explain 4% and 2.7%

764 of the total variance, respectively. **C** Nei's genetic distances among the identified lineages.

765 **Table S1.** Details of the *Arabidopsis arenosa* populations included in this study. Ploidy, lineage  
766 assignment, population code, number of individuals used for genomic analyses ( $N_{ga}$ ), populations used for  
767 niche comparison analyses ( $N_{nc}$ ) and locality details for each population are shown.

768 **Table S2.** Details on tetraploid *Arabidopsis arenosa* populations analyzed in this study. Population code,  
769 number of genotyped samples per population (sample size), ploidy level, methodological approach used to  
770 generate the data, lineage assignment and admixture proportions obtained by STRUCTURE are shown.

771 **Table S3.** Number of occurrences per cytotype and per lineage included in the niche quantification analyses  
772 before and after the filtering (closer than 10-km distance were removed).

773 **Table S4.** Description of environmental variables extracted from WorldClim and their contribution to the  
774 two first axes of the PCA-env.