

1 **Are endemic species necessarily ecological specialists?**
2 **Functional variability and niche differentiation of two threatened**
3 ***Dianthus* species in the montane steppes of northeastern Iran**

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23 **Abstract**

24 Endemic species are believed to converge on narrow ranges of
25 traits, with rarity reflecting adaptation to specific environmental regimes. We hypothesized that
26 endemism is characterized by limited trait variability and environmental tolerances in two
27 *Dianthus* species (*Dianthus pseudocrinitus* and *Dianthus polylepis*) endemic to the montane
28 steppes of northeastern Iran. We measured leaf functional traits and calculated Grime's
29 competitor / stress-tolerator / ruderal (CSR) adaptive strategies for these and co-occurring
30 species in seventy-five 25-m² quadrats at 15 sites, also measuring a range of edaphic, climatic,
31 and topographic parameters. While plant communities converged on the stress-tolerator strategy,
32 *D. pseudocrinitus* exhibited functional divergence from S- to R-selected (C:S:R = 12.0 : 7.2 :
33 80.8% to 6.8 : 82.3 : 10.9%). Canonical components analysis (CCA), in concert with Pearson's
34 correlation coefficients, suggested strongest associations with elevation, annual temperature,
35 precipitation seasonality, and soil fertility. Indeed, variance (s^2) in R- and S-values for *D.*
36 *pseudocrinitus* at two sites was exceptionally high, refuting the hypothesis of rarity *via*
37 specialization. Rarity, in this case, is probably related to recent speciation by polyploidy
38 (neoendemism) and dispersal limitation. *D. polylepis*, in contrast, converged towards stress-
39 tolerance. 'Endemism' is not synonymous with 'incapable', and polyploid neoendemics promise
40 to be particularly responsive to conservation.

41

42 **Introduction**

43 Endemic species (taxa unique to a defined geographic area) are characteristic elements of local
44 biodiversity. Narrow endemics occupy distinct habitats, often associated with restricted ranges of
45 environmental conditions^{1,2}, or small overall geographic ranges. This association, and that

46 between environmental parameters and traits that affect survival³, suggests that endemics are rare
47 owing to adaptive specialization and selection in favor of limited ranges of trait values and
48 functioning (i.e. evolutionary convergence). In practice, understanding functional variability,
49 survival mechanisms, and associated environmental contexts is necessary to inform conservation
50 actions for such species.

51 Additionally, species coexist in communities, and the relative performance and competition
52 between species is a key aspect of plant survival. Variability in functional trait values for
53 endemic species may differ from that of sympatric (i.e. spatially co-occurring) species, which are
54 often more widespread geographically and may exhibit greater functional diversity. Furthermore,
55 while local environmental conditions may select for species exhibiting a convergent subset of
56 potential trait values, finer-scale divergence within the plant community (i.e. local dissimilarity
57 or variance in trait values) is expected as a result of adaptation to micro-scale environmental
58 regimes (i.e. niche differentiation)⁴. Thus, we expect (1) general functional convergence within
59 the community, but (2) functional divergence between the endemic species and non-endemic
60 sympatric species, and (3) relatively restricted trait variances for the endemics.

61 Functional traits rarely operate in isolation. They usually form part of suites of characters that
62 function together to affect survival. These suites of traits can be described as ‘ecological
63 strategies’ or ‘adaptive strategies’, the nature of which reflects underlying trade-offs in allocation
64 of resources available to the plant toward different functions, such as vegetative growth,
65 regeneration, or maintenance of tissues⁴. Grime’s CSR (competitor, stress-tolerator, ruderal)
66 plant strategy theory⁴⁻⁶ proposes that principal trade-offs faced by plants are between competitive
67 ability (C; rapid investment in large size to allow resource preemption, which is possible only in
68 stable, productive habitats), stress-tolerance (S; maintenance of metabolic function in variable

69 and limiting environments), and ruderalism (R; investment in regeneration and reproduction in
70 productive but disturbed habitats). Indeed, these dimensions are generally the main axes of trait
71 variability in plants worldwide⁷, which can be summarized as conservative to acquisitive
72 resource economics (equivalent to S- to R-selection), and plant size (C-selection). In practice,
73 CSR strategies can be calculated based on the measurement of leaf traits (tissue density and leaf
74 size measurements) that represent the end-points of these gradients of variability and the trade-
75 offs between them^{3,8,9}.

76 For species coexisting within plant communities, quantification and comparison of CSR
77 strategies provide a theoretical framework for understanding functional variability that can
78 expand interpretation beyond the variability evident for single traits⁴. Although co-occurring
79 plant species may exhibit conspicuous convergence in CSR strategies, some studies also
80 demonstrate fine-scale CSR strategy divergence and niche differentiation that may be a key
81 underpinning for coexistence¹⁰. Indeed, when investigated over a wide range of plant
82 communities, CSR strategy convergence (ecological specialization) and limited species richness
83 are evident at extremes of productivity, with high richness associated with divergence in CSR
84 strategies at intermediate productivities¹¹. Endemic species can thus be expected to exhibit CSR
85 strategy divergence with respect to non-endemic sympatric species, but also ecological
86 specialization evident as intraspecific convergence towards extreme strategies.

87 To test these hypotheses, we assessed functional compositions of communities hosting two
88 *Dianthus* species (*Dianthus pseudocrinitus* and *Dianthus polylepis*) endemic to the montane
89 steppes of the Khorassan-Kopet Dagh floristic province (KK) of northeastern Iran (Fig. 1;
90 detailed in Table S1). We selected these taxa because they occur strictly in montane habitats, and
91 can reasonably be expected to have undergone local adaption, leading to some degree of

92 functional convergence with regard to habitat, but divergence with regard to each other. The
93 montane steppes and associated biotas are affected and threatened by human activities, climate
94 change, and topographic barriers¹², and these species are thus important targets for conservation
95 activities.

96 *Dianthus pseudocrinitus* Behrooz. & Joharchi is one of the endemic species in the KK
97 floristic province restricted to a few populations in a narrow distribution. It is critically
98 endangered (CR) according to the International Union for Conservation of Nature (IUCN) Red
99 List categories and criteria¹³. The species is usually found in montane steppes, occurring in the
100 calcareous mountains in northeastern Iran, at elevations of 1600–2300 m. *D. pseudocrinitus*
101 nonetheless produces numerous fertile seeds and is common in disturbed habitats, both
102 suggestive of R-selection¹⁴. *Dianthus polylepis* Bienert ex Boissier, though also endemic, has a
103 broader geographic distribution, throughout the KK floristic province, and includes two nominal
104 subspecies: *D. polylepis* subsp. *polylepis* and *D. polylepis* subsp. *binaludensis* (Rech.f.) Vaezi &
105 Behrooz. with mostly disjunct geographic ranges. These subspecies are morphologically similar
106 and very closely related, probably reflecting local morphological divergence¹⁵. *D. polylepis*
107 subsp. *binaludensis* is restricted to the Binalood Mountains characterized by successions of
108 sedimentary, metamorphic, and igneous rock¹⁶; whereas *D. polylepis* subsp. *polylepis* is
109 distributed broadly in other Khorassan-Kopet Dagh mountains on limestone¹⁷. In terms of
110 conservation status, *D. polylepis* subspecies are considered vulnerable (VU) and least concern
111 (LC), respectively¹³. The subspecies of *D. polylepis* often occur in stressful habitats of rocky
112 slopes, whereas *D. pseudocrinitus* is distributed patchily, in small, scattered populations with
113 high disturbance. These ecological contrasts between closely related species allow comparisons
114 of how different endemics function and survive that may be quite informative.

115 We focused on how functional traits and CSR strategies of these two contrasting endemic
116 *Dianthus* species vary in range and character in their respective habitats and with respect to
117 other, non-endemic, sympatric species. Specifically, we hypothesized that (1) endemic *Dianthus*
118 species exhibit limited ranges of intraspecific functional variability reflecting adaptation to
119 specific environmental conditions, and (2) the plant communities in which the endemics live
120 exhibit functional convergence towards stress-tolerance, but interspecific functional divergence
121 (and niche differentiation) is evident between endemic *Dianthus* species and sympatric species.

122

123 **Results**

124 *Plant functional variability*

125 In total, 78 species occurred (cover \geq 5%) at the different sites, creating the set of species over
126 which CSR strategies were assessed (Fig. 2; Table S2). A clear dominance of relatively stress-
127 tolerant strategies was evident across the sites; indeed, most species showed a proportion of S
128 exceeding 50% (Fig. 2, Supplementary Figs. S1, S2).

129 *Dianthus pseudocrinitus* was the only *Dianthus* species that exhibited general functional
130 divergence, ranging from strong ruderalism at the Rein site (R; C:S:R = 12.0 : 7.2 : 80.8%), an
131 intermediate strategy at Rakhtian and Misino (S/SR; C:S:R = 2.8 : 75.9 : 21.3%; and C:S:R = 7.4
132 : 70.5 : 22.1%, respectively), to strong stress-tolerance at the Biu Pass site (S; C:S:R = 6.8 : 82.3
133 : 10.9%) (Fig. 2). Differences among *D. pseudocrinitus* populations at different sites were
134 apparent for S-selection (ANOVA on arcsine transformed data, predictor variables were sites and
135 response variables were the percentage CSR-scores; $f=34.386$, $df_{\text{numerator}}=3$, $df_{\text{denominator}}=37$,
136 $p=0.000$) and R-selection ($f=43.707$, $df_{\text{numerator}}=3$, $df_{\text{denominator}}=37$, $p=0.000$) but not for C-
137 selection ($f=2.801$, $df_{\text{numerator}}=3$, $df_{\text{denominator}}=37$, $p=0.054$), with a Tukey's post-hoc multiple

138 comparison on data for R-selection (i.e. the highest f-value), suggesting that populations at all
139 sites differed from one another, except for those at Misino and Rakhtian.

140 In terms of interspecific differences, analysis of variance (ANOVA) showed that *D.*
141 *pseudocrinitus* differed significantly from the community mean at the Rein site in terms of R-
142 selection ($f=46.982$, $df_{\text{numerator}}=16$, $df_{\text{denominator}}=146$, $p=0.000$) and S-selection ($f=44.601$,
143 $df_{\text{numerator}}=16$, $df_{\text{denominator}}=146$, $p=0.000$; arcsine transformed data, with species (i.e. taxa present
144 in the plant community) as the predictor variables and percentage CSR-scores as the response
145 variables). Crucially, that *D. pseudocrinitus* exhibited extensive intraspecific variability was
146 evident as extreme values of strategy variance (s^2) compared to the intraspecific variability of
147 sympatric species at the Rakhtian and Rein sites (Table 1). Note that the CSR strategy variability
148 evident for sympatric species is presented in greater detail in Fig. S3.

149 *Dianthus polylepis* subsp. *polylepis* exhibited an extreme stress-tolerant strategy (C:S:R=0.1 :
150 99.1 : 0.8%) across all sites (Fig. S1). Most sympatric species at sites of *D. polylepis* subsp.
151 *polylepis* represented a broadly stress-tolerant strategy (Fig. S1), but interspecific functional
152 variability was evident, including subordinate species (mean cover percentage 5.5–9.0%) with
153 relatively generalist, intermediate strategies (Fig. S1). Intraspecific differences in *Dianthus*
154 *polylepis* subsp. *polylepis* between sites were apparent for C-selection (ANOVA on arcsine
155 transformed data, predictor variables were sites and response variables the percentage CSR-
156 scores; $f=7.599$, $df_{\text{numerator}}=5$, $df_{\text{denominator}}=48$, $p=0.000$) and S-selection ($f=6.686$, $df_{\text{numerator}}=5$,
157 $df_{\text{denominator}}=48$, $p=0.000$) and R-selection ($f=8.099$, $df_{\text{numerator}}=5$, $df_{\text{denominator}}=48$, $p=0.000$), with a
158 Tukey's post-hoc multiple comparison on data for R-selection (i.e. the highest f-value)
159 suggesting that the population at Bezd was distinct from other sites.

160 *D. polylepis* subsp. *binaludensis* exhibited an extremely stress-tolerant strategy (C:S:R = 0.5 :
161 99.5 : 0.0%) at all sites except Zoshk, where it exhibited an intermediate S/SR strategy (Fig. S2).
162 Intraspecific differences in *D. polylepis* subsp. *binaludensis* between sites were apparent for C-
163 selection (ANOVA on arcsine transformed data, predictor variables were sites and response
164 variables the percentage CSR-scores; $f=2.801$, $df_{\text{numerator}}=4$, $df_{\text{denominator}}=46$, $p=0.054$), S-selection
165 ($f=25.796$, $df_{\text{numerator}}=4$, $df_{\text{denominator}}=46$, $p=0.000$) and R-selection ($f=18.476$, $df_{\text{numerator}}=4$,
166 $df_{\text{denominator}}=46$, $p=0.000$), with a Tukey's post-hoc multiple comparison on data for S-selection
167 (i.e. the highest f-value) suggesting that the population at Zoshk was distinct from other sites. At
168 Zoshk, Dahane Jaji and Dizbad, *D. polylepis* subsp. *binaludensis* exhibited significantly lower C-
169 selection ($p \leq 0.05$) with respect to the community mean (*t*-tests within site on arcsine-
170 transformed data).

171

172 ***Site and environmental variables***

173 The CCA (Fig. 3) was constrained by a matrix of soil and topographic data and bioclimatic
174 variables. Seven soil variables (clay, silt, sand, EC, P, CEC and organic carbon) and 15
175 bioclimatic variables were eliminated from the environmental data set owing to high collinearity
176 ($VIF > 10$). Soil organic matter, pH, N, K, lime, elevation, and aspect were the
177 edaphic/topographic variables exhibiting the highest levels of significance ($p < 0.05$; Table 2).
178 Among the 19 bioclimatic variables, annual mean temperature (bio1), temperature seasonality
179 (bio4), annual precipitation (bio12) and precipitation of the wettest quarter (bio16) exhibited the
180 greatest significance. All canonical axes were significant ($p = 0.001$) (Fig. 3; Table 2).

181 Soil and topographic variables showed significant effects on species composition, with
182 eigenvalues for the first four axes of 0.360, 0.284, 0.238 and 0.216, respectively (Fig. 3). The

183 first four axes explained 70.1% of the total variation, with CCA1 accounting for 23.0%. The
184 effect of elevation was greater than that of other factors ($r^2 = 0.578$). For soil factors, organic
185 matter ($r^2 = 0.514$), lime ($r^2 = 0.458$), and total nitrogen ($r^2 = 0.379$) were the strongest
186 explanatory variables, while pH and K showed weaker associations (Table 2). Topographic
187 factors had greater impacts on plant species identity at sites for *D. polylepis* subsp. *binaludensis*,
188 and elevation had the greatest r^2 . However, these factors were negatively associated with some
189 sites of *D. polylepis* subsp. *polylepis* and *D. pseudocrinitus*. Thus, elevation was a major gradient
190 in differentiating the distributions of these species. Of the environmental variables, total N,
191 organic matter, and lime had positive correlations with all sites of *D. pseudocrinitus* and with
192 Balghur and Kardeh Dam sites for *D. polylepis* subsp. *polylepis*. Soil nutrients, particularly total
193 N, were the main environmental factors influencing vegetation properties at these sites.

194 Four bioclimatic variables had significant associations with species composition (Fig. 3B,
195 Table 2). Precipitation of the wettest quarter (bio16) was the strongest bioclimatic variable ($r^2 =$
196 0.824), positively correlated with most sites for *D. polylepis* subsp. *binaludensis* and the Balghur
197 and Khowre-Kalat sites for *D. polylepis* subsp. *polylepis*. Annual precipitation (bio12) and
198 temperature seasonality (bio4; $r^2 = 0.806$ and 0.438, respectively) were also associated with plant
199 community variability; both variables were positively correlated with all *D. pseudocrinitus* sites,
200 but negatively with some sites of *D. polylepis* subsp. *polylepis* and *D. polylepis* subsp.
201 *binaludensis*. The explanatory power of annual mean temperature (bio1) was low ($r^2 = 0.090$). It
202 was positively correlated with the sites of Kardeh Dam and Bezd, for *D. polylepis* subsp.
203 *polylepis*, and the Dizbad and Moghan sites for *D. polylepis* subsp. *binaludensis*, and negatively
204 correlated with sites where *D. pseudocrinitus* occurred. These findings indicate considerable

205 effects of multiple edaphic, topographic, and bioclimatic factors on the vegetation, rather than a
206 single overarching environmental factor.

207

208 *Community CSR scores and environmental factors*

209 These analyses revealed significant correlations between certain soil properties, bioclimatic
210 variables, and CWM strategy scores (Table S3). We noted significant, positive correlations
211 between the degree of C-selection (i.e. CWM-C) and several temperature and precipitation
212 variables, as well as some negative correlations. Indeed, the strongest community-level
213 correlations with environmental factors were between CWM-C and precipitation of driest month
214 (bio14), precipitation seasonality (bio15), precipitation of driest quarter (bio17), and
215 precipitation of warmest quarter (bio18), with the highest correlation coefficient (between
216 CWM-C and temperature annual range, bio7) being 0.4428 ($r^2 = 0.1150$, $p = 0.0029$; Table S3).
217 The degree of stress-tolerance in the community (CWM-S) generally showed the opposite
218 pattern: mostly negative correlations with the same factors, although mean temperature of the
219 wettest quarter (bio8) and precipitation of the driest month (bio14) were not significant. The
220 extent of ruderalism in the community (CWM-R) was not correlated significantly with any
221 climatic factors (Table S3).

222 Soil pH and lime content were the only soil variables that showed significant (all negative)
223 correlations with CWM-C. In contrast, silt, pH, K, and lime showed significant positive
224 correlations with CWM-S, and sand and P exhibited significant negative correlations (Table S3).
225 CWM-R exhibited essentially the opposite pattern of correlations to those of CWM-S, but was
226 positively correlated with soil N content, and not related to K and lime.

227

228 Discussion

229 Our analyses revealed general functional convergence towards stress tolerance within the
230 communities of the endemic study species, but the endemic species themselves exhibited
231 differing degrees of functional divergence, in terms of both interspecific divergence from the
232 community and intraspecific divergence between sites. *Dianthus pseudocrinitus* in particular
233 showed a wide range of intraspecific functional divergence over many environmental regimes,
234 suggesting that rarity and endemism, in this case, is not associated with intrinsic functional
235 limitations or a lack of capacity to occupy contrasting niches—in this sense, our Hypothesis 1
236 was not supported. This species was found to exhibit the greatest variance (s^2) in R- and S-
237 selection of any of the co-occurring species at two sites (Table 1), and is thus relatively variable.
238 Indeed, *D. pseudocrinitus* was found in disturbed habitats and anthropogenic sites in which soil
239 properties had changed recently, and is capable of exhibiting strongly ruderal (R) strategies
240 associated with higher soil total N and organic matter. The ecological strategy of *D. polylepis* is
241 evidently different, converging on stress-tolerance (S).

242 If *D. pseudocrinitus* is variable and can be ruderal, why does it occupy a geographically
243 restricted range? Why is it endemic? The genus *Dianthus* is capable of rapid radiation, with rates
244 of 2.2-7.6 species per million years evident in Europe^{18,19} and increased diversification rates
245 coinciding with increasing aridity during the Pleistocene²⁰. *Dianthus pseudocrinitus* appears to
246 be the closest extant relative of *D. polylepis*¹⁴, and thus appears to be a relatively young,
247 “neoendemic” species. Indeed, *D. pseudocrinitus* may be extending its population size, probably
248 via mechanisms such as polyploidy and extensive seed production (it is a tetraploid^{21,22}, with $2n$
249 = 60, whereas *D. polylepis* is diploid¹⁴, $2n = 30$).

250 Polyploidy is both a mechanism by which neoendemics can arise and a potential fitness
251 advantage conferring new trait values and trait plasticities, allowing survival in heterogeneous
252 environments^{23,24} and allowing occupation of new environments and sites. Previous studies have
253 shown extensive unexplained phenotypic variation in some traits of *D. broteri*; high chromosome
254 number variation in this species could be a source of phenotypic instability and variability²⁵.
255 Polyploids may have other fitness advantages over diploids: in a recent experiment, the total
256 output of viable seed in drought and heat-stressed tetraploid plants was over four times higher
257 than in diploids, such that tetraploids constantly produced heavier seeds with longer hygroscopic
258 awns, traits that increase propagule fitness in extreme environments²⁶.

259 Additionally, dispersal traits are likely a significant factor with regard to connectivity among
260 populations in different habitats²⁷. The extent to which dispersal influences a species' geographic
261 distribution at particular spatial scales or in specific environments depends on the mechanism of
262 dispersal and range size²⁸. *Dianthus* species exhibit short-distance seed dispersal^{29,30}. *Dianthus*
263 *pseudocrinitus* is unlikely to be able to disperse effectively to more distant sites and colonize
264 suitable new regions. Indeed, species with limited dispersal occupy smaller geographic ranges
265 because more habitable sites at the range margins remain unoccupied²⁸. *Dianthus pseudocrinitus*
266 produces heavier seeds than *D. polylepis*, due to polyploidy, suggesting that dispersal limitation
267 is particularly important for this species. Therefore, endemic and rare species are not necessarily
268 ecological specialists, and may be restricted more by dispersal limitation and the fact that they
269 have only recently emerged as species.

270 Do plant communities converge on stress-tolerance, with the endemic *Dianthus* species
271 diverging from the rest of the plant community (Hypothesis 2)? A range of strategies was evident
272 in the plant communities, most of which involved some degree of stress tolerance (e.g. Fig. 2;

273 Table S2), which clearly reflects the harsh environments of the study sites. Indeed, all dominant
274 graminoids and some shrub species such as *Lonicera iberica*, *Prunus pseudoprostrata*, and
275 *Rhamnus pallasii*, exhibited strongly stress-tolerant strategies (S and S/SR; Fig. S3). Generally,
276 the endemic *Dianthus* species did not exhibit divergence with respect to the community mean C,
277 S, and R values. However, at the Rein site, *D. pseudocrinitus* exhibited particularly strong
278 variation towards R-selection and divergence from the community was statistically significant.
279 At least, in this case, niche differentiation can be invoked as a possible mechanism for the co-
280 existence of this species alongside other taxa. That is, our Hypothesis 2 was supported at least
281 partially, depending on the site.

282 Which specific environmental factors are associated with plant adaptation in these
283 communities? CCA indicated that both climatic (temperature and precipitation) and edaphic
284 properties were associated with variability in CSR strategies, with greater soil N content
285 associated particularly with ruderalism, and climatic variables particularly associated with
286 variation between C to S selection at the community level. The plant communities at sites of *D.*
287 *polylepis* subsp. *polylepis* and all sites of *D. pseudocrinitus* were influenced mainly by soil
288 factors, whereas plant communities at sites of *D. polylepis* subsp. *binaludensis* were influenced
289 more by topography. More generally, sites hosting each *Dianthus* taxon experience distinct
290 climates (Fig. 1B). In general, factors such as low temperature, strong winds, and high solar
291 radiation are dominant environmental stressors in mountain steppes³¹, in accordance with a
292 general pattern of convergence towards tough, low-specific-leaf-area leaves and S-selection.

293 Despite the majority of the non-endemic species exhibiting convergence towards stress-
294 tolerance, functional divergence was observed among some species adapted to disturbance. Most
295 ruderal species occurred at Balghour and Kardeh Dam, associated with *D. polylepis* subsp.

296 *polylepis*, and at Rein and Rakhtian for habitats of *D. pseudocrinitus*, suggestive of the operation
297 of a disturbance at these sites. Additionally, the CCA results revealed that the distribution of
298 vegetation among these four sites is associated with three soil factors, including N, organic
299 matter, and lime (Fig. 3A). Indeed, although disturbance destroys live biomass, either removing
300 it or redistributing nutrients (e.g. herbivory), or changing its form and altering nutrient cycling
301 (e.g. fire), these effects have a significant influence on total nitrogen availability of soil and rates
302 of net N-mineralization and net nitrification³². Soil changes affect plant growth and species
303 diversity and composition, creating environments conducive to ruderals^{33,34}. Paušič and Čarni³⁵
304 pointed out that traditional land management (e.g. livestock grazing) influences the character of
305 plant strategies, which shifted from broadly S- to broadly CR-selected. Pierce et al.³⁶ also
306 demonstrated that the relative abundance of ruderals increases with disturbance intensity,
307 whereas the dominant stress-tolerating graminoids are suppressed. However, occasional grazing
308 allows coexistence between potential dominants and smaller subordinates and promotes
309 functional and species diversity by sustaining differences in the phenology of leaf growth,
310 photosynthesis, flowering and seed production in grasslands^{37,38}. Our results suggest that
311 increased anthropogenic disturbance is likely to have disproportionately negative impacts on
312 populations of *D. polylepis*, which is a key consideration for the future conservation of the
313 endemic species under study here.

314 These results have wider implications for the conservation of endemic species in general,
315 because they demonstrate that being ‘endemic’ is not synonymous with being ‘incapable’ or
316 ‘over-specialized’. Indeed, conservation of endemic species should assess whether polyploidy,
317 neoendemism and wide variability in functional traits are evident, because species with these
318 characteristics are likely to be capable of responding positively to habitat conservation with little

319 extra intervention (such as supplementary *ex situ* conservation and population reinforcement
320 actions). The fact that not all endemics are born equal, and that some may actually be relatively
321 easy to conserve, is a hopeful message for plant conservationists.

322

323 **Conclusions**

324 One endemic species, *D. pseudocrinitus*, exhibited a range of CSR strategies (R, S/SR, and S)
325 over a range of environmental parameters, indicating that endemism, in this case, is not likely to
326 be related to functional or ecological specialization. Rather, additional phenomena including
327 neoendemism and dispersal limitation can be significant factors associated with rarity. Findings
328 differed for the closely related species, *D. polylepis*. As such, each species must be evaluated on
329 a case-by-case basis, even amongst congeneric species. These findings further suggest that
330 endemism is not inevitably associated with vulnerability.

331

332 **Materials and Methods**

333 *Study Area*

334 Fieldwork was undertaken in different habitats across the ranges of *D. pseudocrinitus* and *D.*
335 *polylepis* during three successive years (2016-2018), in the mountain steppes of northeastern
336 Iran, between 34°20' and 39°13' N and 55°05' and 61°20' E. The area belongs to the Khorassan-
337 Kopet Dagh floristic province (KK) in the Irano-Turanian region. The Kopet Dagh range is
338 located in the northernmost part of the area, including the high peaks of Allaho-Akbar and
339 Hezar-Masjed mountains. Northern ranges of Khorassan comprise the mountains of Ghorkhod,
340 Aladagh, Salook, Shah-Jahan, and Binalood. The Sabzevar and Kashmar-Torbat ranges are

341 oriented mainly east-west at the southern border of the KK floristic region, where Kuh-e Gar and
342 Bezq are the highest peaks¹² (Fig. 1A-B).

343 The climate is continental and the mean annual precipitation is 175–300 mm on the plains and
344 foothills and 300–380 mm in montane regions. Precipitation falls unevenly, predominantly in
345 late autumn, winter, and early spring (October to May), often with summer drought (June to
346 September)¹². The mean annual temperature varies 12–19°C, depending on elevation³⁹. The
347 highest mean monthly air temperatures occur from June to August, with the maximum
348 temperature rarely exceeding 45°C. The lowest mean monthly temperatures, from December to
349 February, can reach -25°C in the high mountains⁴⁰. Most of the KK region is characterized by a
350 Mediterranean or Irano-Turanian xeric-continental bioclimate, except for high montane areas in
351 the central KK, where a Mediterranean or Irano-Turanian pluvi-seasonal continental bioclimate
352 is evident, with shorter summer drought and higher annual precipitation^{40,41}.

353

354 *Quadrat survey and sampling*

355 Based on geographic distances and contrasting ecological conditions, we selected 15 sites where
356 the endemic *Dianthus* species occur (Table S1; Fig. 1B-C). Five 5×5 m quadrats were
357 established at each site, and longitude, latitude, and elevation recorded by GPS. In each quadrat,
358 canopy cover was estimated visually as a percentage of ground area. In total, 75 quadrats were
359 sampled in the study area, covering much of the geographic ranges of the two endemic *Dianthus*
360 taxa. The vascular plant species occurring within all quadrats were collected and identified,
361 following Rechinger⁴⁴ and Assadi et al.⁴⁵. Accessions were deposited in the herbarium of the
362 Ferdowsi University of Mashhad (FUMH; herbarium numbers 11011–11386).

363

364 ***Functional traits and CSR classification***

365 We determined leaf area (LA), leaf dry-matter content (LDMC), and specific leaf area (SLA) for
366 all species of each quadrat with a cover $\geq 5\%$, following the leaf area and weight measurement
367 methodologies of Pérez-Harguindeguy et al.⁴⁶. The material was collected from April to early
368 July, 2016-2018, when leaves were fully expanded and mature. We selected only the most
369 prevalent species ($\geq 5\%$ cover) in light of their greater influence on ecosystem processes^{47,48} and
370 because performing a fully replicated functional analysis of all transitory and infrequent species
371 with sufficient sample sizes was not feasible.

372 Leaf material was collected from 10 individuals of each species, packed in moist paper bags,
373 sealed in plastic bags and stored in a thermal box until storage at 4°C for 12-24 h. Depending on
374 the size of leaves, 2-10 undamaged, fully expanded young leaves (including the petiole) were
375 measured per individual (replication thus involved a mean value for each individual and 10
376 individual replicate plants, from which species' means were calculated for each site). We
377 determined the leaf area using a digital scanner and Leaf Area Measurement v1.3 software
378 (Andrew Askew, University of Sheffield, UK). Turgid leaf fresh weight (LFW) was obtained
379 from saturated leaves, and leaf dry weight was determined after drying for 72 h in an oven at
380 70°C.

381 For CSR strategy analysis, values of LA, SLA, and LDMC were inserted into the 'StrateFy'
382 spreadsheet³ to calculate C, S, and R percentages for each species. CSR coordinates were plotted
383 in ternary plots using SigmaPlot version 10 (Systat Software Inc., San Jose, California, USA).
384 Community-weighted mean (CWM) values for C, S, and R scores were calculated for each site
385 using species' mean CSR score values weighted by their relative cover^{10,49}, using R 3.5.0 with
386 the *FD* package^{49,50}. Correlations between CWM-CSR and environmental variables were tested

387 using Pearson correlation coefficients. Simple linear regressions of each of the three scores on
388 each of the 33 environmental variables were calculated to test significance, in R.

389

390 *Environmental factors*

391 Environmental data encompassing soil type, topography, and climate were recorded for each
392 quadrat. Soil samples (~500 g) were taken at a depth of 15-25 cm, placed in a polyethylene bag,
393 labeled, and transported to the laboratory. The following properties were measured: pH,
394 electrical conductivity (EC), cation-exchange capacity (CEC), organic carbon, organic matter,
395 total nitrogen, K, P, lime, silt, sand, and clay percentage.

396 Bioclimatic variables were extracted from the WorldClim global climate database, with a 30"
397 spatial resolution⁵¹. The latitude and longitude of each quadrat were recorded in the software
398 ArcGIS 10.3.1., and corresponding values of the bioclimatic variables were extracted for each
399 quadrat site (Table S4).

400

401 *Statistical analysis*

402 Canonical correspondence analysis (CCA)⁵² was used to explore relationships between sites and
403 environmental factors. Variance inflation factors (VIF) of variables were used to quantify how
404 much a regression coefficient is inflated by the presence of other explanatory variables. Collinear
405 environmental variables with high variance inflation factors (>10) were eliminated from further
406 analyses. Finally, we used a permutation test (999 permutations, $P < 0.05$) to test significance of
407 the R^2 for each environmental variable with respect to the canonical axes of CCA. All of these
408 analyses were conducted using R 3.5.0 software⁵³ with the *vegan* package⁵⁴.

409

410 **Data Availability**

411 Data used in conducting this study are available for researchers upon request to the
412 corresponding author for reasonable use in research.

413

414 **Additional Information**

415 **Supplementary information**

416 **Fig. S1.** CSR classification of six sites related to *Dianthus polylepis* subsp. *polylepis*.

417 **Fig. S2.** CSR classification of five sites related to *Dianthus polylepis* subsp. *binaludensis*.

418 **Fig. S3.** CSR classification (individual variation) of the most dominant species at the sites of the
419 three endemic *Dianthus* taxa.

420 **Table S1.** Location details of the 15 sites in the study area for three endemic *Dianthus* taxa.

421 **Table S2.** List of the dominant plant species and their tertiary CSR categories, collected from the
422 15 study sites associated with the three endemic *Dianthus* taxa.

423 **Table S3.** Relationships between CWM-CSR and environmental variables from a Pearson's
424 correlation coefficient and significance test using linear regressions.

425 **Table S4.** Environmental variables used in the study. Climate data were obtained from
426 WorldClim (www.worldclim.org).

427

428 **Competing Interests**

429 The authors declare no competing interests.

430

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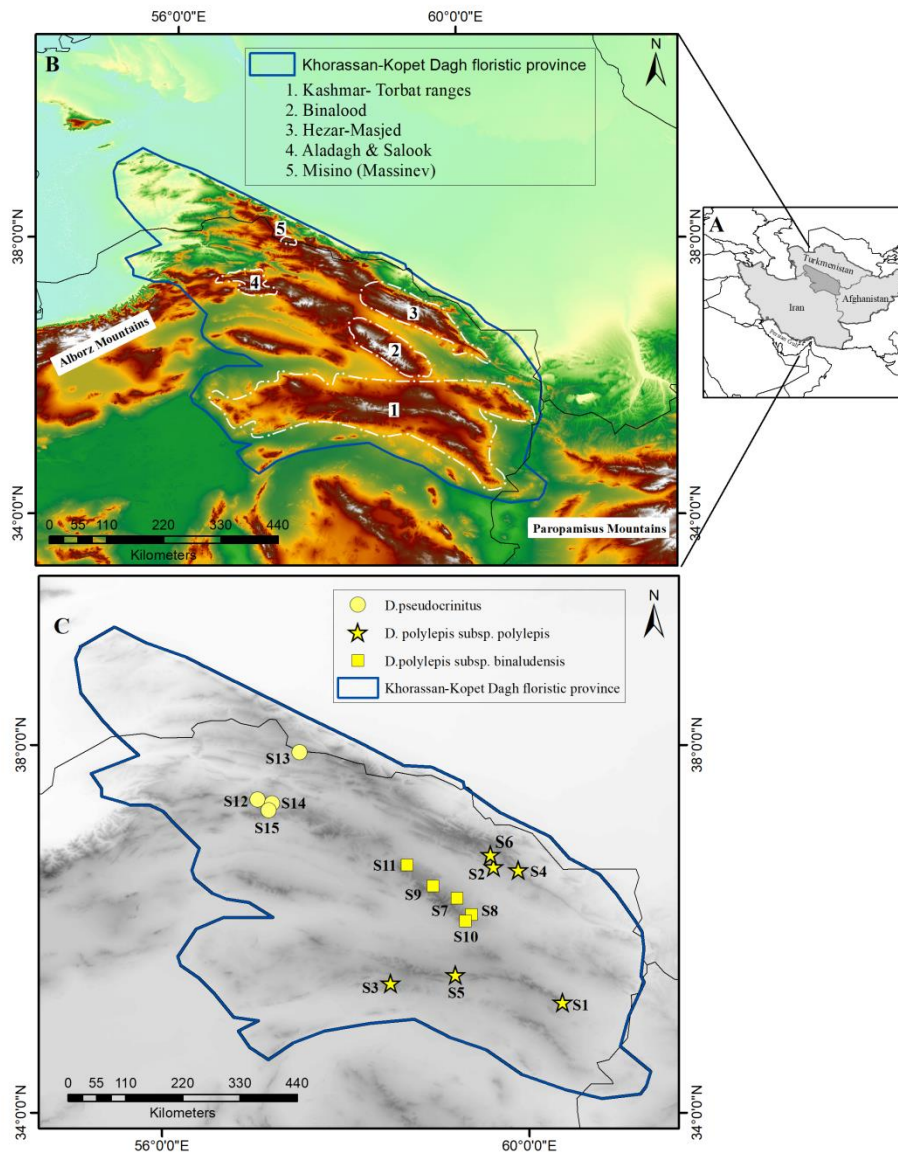
570 fieldwork, data collection, and species determination. Thanks to Daniel Negreiros for help with
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573

574 **Author contributions**

575 M.B., H.E., F.M. and M. M. conceived and designed the study; M.B collected and analyzed the
576 data, and wrote the first draft, S. P., H. E, F. M. and M. M helped with revising drafts of the
577 paper. All authors read and approved the final draft.

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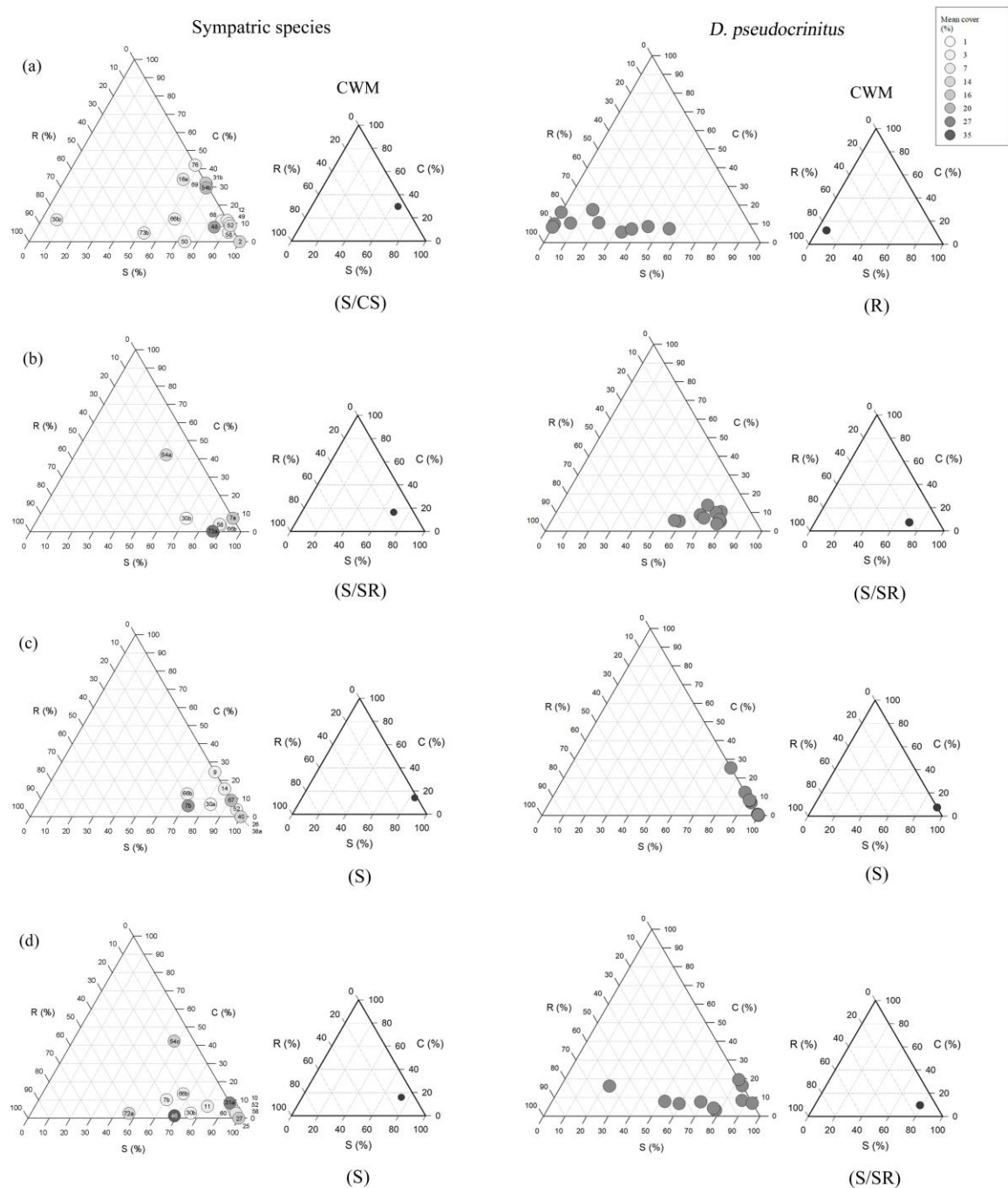


579

580 **Fig. 1.** The maps of the study area and sampling sites; **A:** Geographic position of Khorassan-Kopet Dagh
 581 floristic province (KK) in northeastern Iran and southern Turkmenistan. **B:** Locations of the mountain
 582 systems in KK where samplings were carried out; **C:** Sampling sites: Stars (*Dianthus polylepis* subsp.
 583 *polylepis* sites): S1. Bezd, S2. Kardeh Dam, S3. Kuhsorkh, S4. Khowr, S5. Khomari Pass, S6. Balghur.
 584 Squares (*D. polylepis* subsp. *binaludensis* sites): S7. Zoshk, S8. Moghan, S9. Dahane Jaji, S10. Dizbad,
 585 S11. Baharkish. Circles (*Dianthus pseudocrinitus* sites): S12. Rein, S13. Misino, S14. Biu Pass, S15.
 586 Rakhtian. Prepared by ArcGIS 10.3 software (www.esri.com)

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590 **Fig. 2.** CSR classification of four sites related to *Dianthus pseudocrinitus* (a-d) showing the relative
 591 importance of the C, S and R axes for sympatric (non-*Dianthus*) species within the plant community (left
 592 side) and the individuals of *D. pseudocrinitus* (right side) in each site (a. Rein; b. Misino; c. Biu Pass; d.
 593 Rakhtian). The species are represented in gray scale according to their mean cover (%). The numbering
 594 indicated in the circles corresponds to Table S2. The small triangles show the community weighted mean
 595 (CWM) strategies at each site for the sympatric species and the individuals of *D. pseudocrinitus*.

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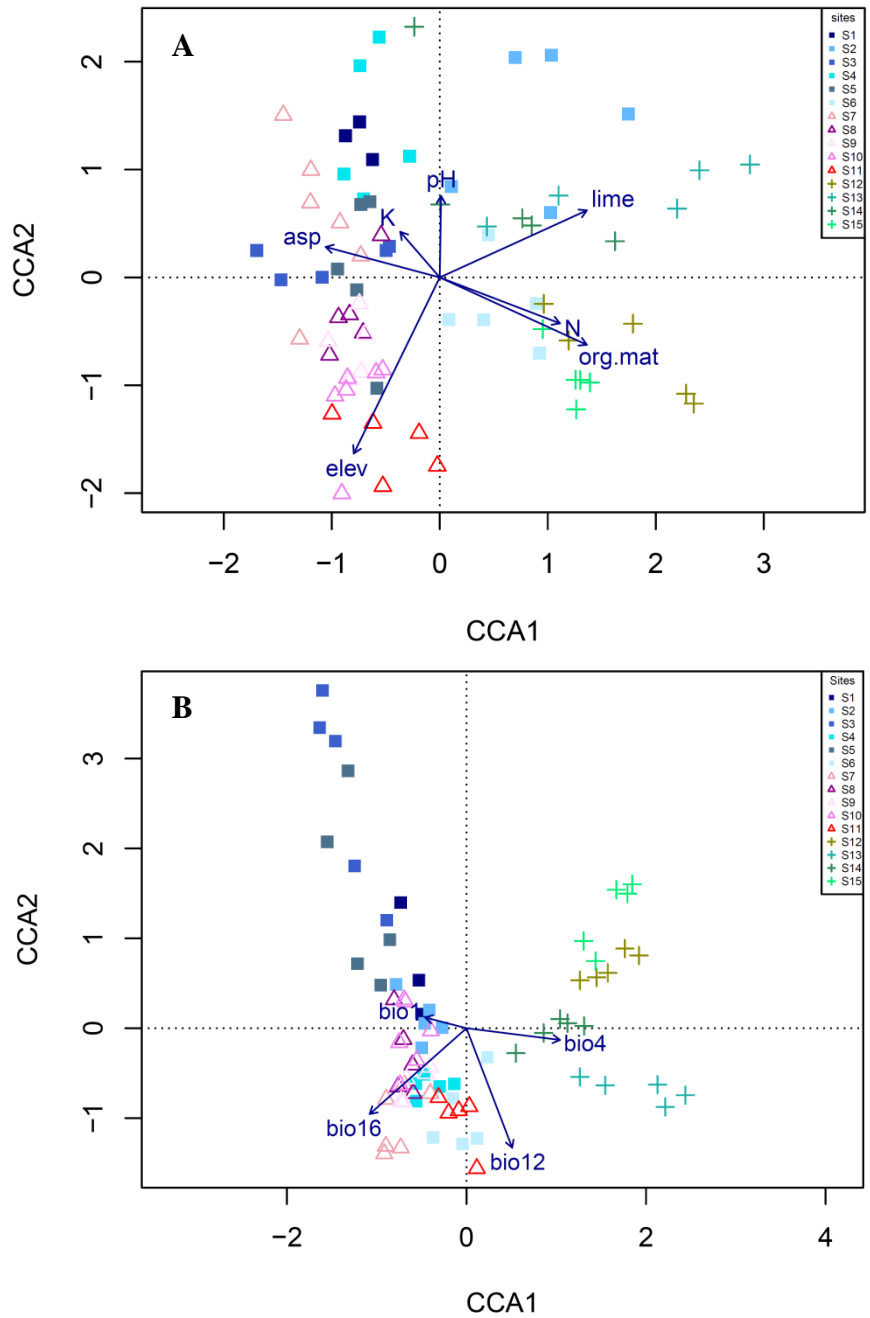


Fig. 3. CCA ordination of the first two axes showing the distribution of the 75 plots for the 15 study sites. A: soil variables (K: potassium; N: total nitrogen; org. mat: organic matter; lime: calcium carbonate) and topography (elev: elevation; asp: aspect); B: bioclimatic variables (bio1: annual mean temperature; bio4: temperature seasonality; bio12: annual precipitation; bio16: precipitation of wettest quarter).

626 **Table 1.** Variance (s^2) in C-, S-, and R-selection values (%) for *D. pseudocrinitus* and other species at the
 627 (a). Rein and (b). Rakhrian sites, with species ordered according to decreasing variance in R-selection
 628 (n=10). Species authorities are reported in Table S2.

629

Species	Variance (s^2)		
	C-selection	S-selection	R-selection
(a). Rein site			
<i>Dianthus pseudocrinitus</i>	15.1	400.8	333.3
<i>Thymus trautvetteri</i>	148.4	103.2	229.4
<i>Tanacetum polycephalum</i>	101.8	150.3	195.3
<i>Centaurea virgata</i>	185.3	393.8	157.1
<i>Minuartia hamata</i>	0.0	128.1	128.1
<i>Stachys turcomanica</i>	8.0	143.8	109.3
<i>Melica persica</i>	24.4	47.3	84.4
<i>Bromus danthoniae</i>	27.0	140.3	62.9
<i>Lonicera iberica</i>	2.7	37.6	35.1
<i>Taeniatherum caput-medusae</i>	8.5	31.0	19.8
<i>Onobrychis cornuta</i>	4.5	17.5	16.3
<i>Cerasus pseudoprostrata</i>	2.7	26.9	15.8
<i>Phlomis cancellata</i>	14.4	20.4	4.3
<i>Acantholimon bodeanum</i>	0.8	1.7	0.0
<i>Elymus hispidus</i>	54.0	43.2	0.0
<i>Verbascum cheiranthifolium</i>	77.6	77.6	0.0
(b). Rakhrian site			
<i>Dianthus pseudocrinitus</i>	31.1	436.3	419.0
<i>Klasea leptoclada</i>	1.1	324.3	309.4
<i>Thymus transcaspicus</i>	1.2	188.2	192.8
<i>Artemisia kopetdaghensis</i>	17.0	186.6	160.4
<i>Stachys turcomanica</i>	9.7	203.6	152.5
<i>Dianthus orientalis subsp. stenocalyx</i>	1.3	117.9	100.6
<i>Boissiera squarrosa</i>	3.6	93.8	96.1
<i>Phlomis cancellata</i>	34.6	124.7	63.3

<i>Cerasus pseudoprostrata</i>	2.7	24.4	21.9
<i>Rhamnus pallasii</i>	1.0	1.4	2.3
<i>Astragalus verus</i>	6.5	6.5	0.0
<i>Crucianella gilanica</i>	0.0	0.0	0.0
<i>Elymus hispidus</i>	3.4	3.4	0.0
<i>Onobrychis cornuta</i>	1.7	1.7	0.0

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633 **Table 2.** Correlations between environmental variables and the canonical correspondence analysis (CCA)
634 ordination (see Fig. 3).

Variables	CCA1	CCA2	R²	Pr(>r)
Soil factors				
pH	0.19433	0.98094	0.1433	0.007**
N	0.79419	-0.60767	0.361	0.001***
K	-0.38333	0.92361	0.1411	0.004**
lime	0.99797	0.06363	0.453	0.001***
org.mat	0.77712	-0.62935	0.5312	0.001***
elev	-0.63087	-0.77589	0.589	0.001***
asp	-0.91272	-0.40858	0.2559	0.001***
Bioclimatic factors				
bio1	-0.96793	0.25122	0.0901	0.046*
bio4	0.99227	-0.12407	0.4389	0.001***
bio12	0.35779	-0.9338	0.8067	0.001***
bio16	-0.74837	-0.66328	0.8248	0.001***

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638 **Table S1.** Location details of the 15 sites in the study area for three endemic *Dianthus* taxa.

Species	Site name	Site name	Elevation range (m)	Latitude	Longitude
<i>D. polylepis</i> subsp. <i>polylepis</i>	S1	Bezhd	1505-1525	35° 11' 48.1"	60° 21' 33.8"
	S2	Kardeh Dam	1475-1491	36° 40' 19.9"	59° 36' 43.9"
	S3	Kuhsorkh	1493-1520	35° 24' 19.1"	58° 29' 25.1"
	S4	Khowre- Kalat	1776-1799	36° 38' 20.0"	59° 52' 45.1"
	S5	Khomari Pass	1855-1893	35° 29' 47.4"	59° 11' 36.2"
	S6	Balghour	1794-1803	36° 48' 18.7"	59° 34' 29.6"
<i>D. polylepis</i> subsp. <i>binaludensis</i>	S7	Zoshk	1793-1822	36° 19' 54.1"	59° 12' 38.2"
	S8	Moghan	1964-1974	36° 09' 11.2"	59° 22' 06.6"
	S9	Dahane Jaji	1796-1970	36° 28' 45.8"	58° 57' 22.0"
	S10	Dizbad	2007-2048	36° 05' 01.0"	59° 18' 00.7"
	S11	Baharkish	2179-2245	36° 41' 31.2"	58° 40' 03.7"
<i>D. pseudocrinitus</i>	S12	Rein	1871-1899	37° 24' 06.8"	57° 02' 27.6"
	S13	Misino	1647-1695	37° 54' 53.3"	57° 29' 44.9"
	S14	Biu Pass	1664-1674	37° 21' 31.7"	57° 11' 56.4"
	S15	Rakhtian	1880-1923	37° 17' 11.0"	57° 08' 59.3"

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642 **Table S2.** List of the dominant plant species and their tertiary CSR categories, collected from the 15
643 study sites associated with *Dianthus* species. Repetition of species with different letters (a, b, c, d)
644 represents measurements from more than one site.

645

No.	Species name	CSR	Chorotype	No.	Species name	CSR	Chorotype
1	<i>Acantholimon avenaceum</i> Bunge	S	KK Omni *	40	<i>Hedysarum longipedunculatum</i> Ranjbar & Karamian	SC	IT [*] KK-Alborz ^{**}
2	<i>Acantholimon bodeanum</i> Bunge	S	IT ^{KK} - Alborz ^{**}	41	<i>Hymenocrater elegans</i> Bunge	R/CR	IT [*] KK-Alborz [*]
3	<i>Acantholimon erinaceum</i> (Jaub. & Spach) Lincz.	S	IT ^{C&E}	42	<i>Hymenocrater oxyodontus</i> Rech.f.	S/SR	IT ^C *
4	<i>Acantholimon spinicalyx</i> Koeie & Rech.f.	S	KK ^{E-S} **	43	<i>Hymenocrater platystegius</i> Rech.f.	S/SR	IT ^{KK} **
5	<i>Acanthophyllum glandulosum</i> Buhse ex Boiss.	S	IT ^{C&E}	44	<i>Jurinea sintenesii</i> Bornm.	S	IT ^{KK} *
6	<i>Agropyron cristatum</i> (L.) Gaertn.	S	PL	45a	<i>Klasea latifolia</i> (Boiss.) L.Martins	CS	IT ^C
7a	<i>Artemisia kopetdaghensis</i> Krasch. Popov & Lincz. ex Poljakov	S	KK ^{Omni} (exc. NW)*	45b	<i>Klasea latifolia</i> (Boiss.) L.Martins	C/CS	IT ^C
7b	<i>Artemisia kopetdaghensis</i> Krasch. Popov & Lincz. ex Poljakov	S/SR	KK ^{Omni} (exc. NW)*	46	<i>Klasea leptoclada</i> (Bornm. & Sint.) L.Martins	S/SR	KK ^{W-C} *
8	<i>Astragalus floccosus</i> Boiss.	S		47	<i>Lactuca orientalis</i> (Boiss.) Boiss.	CR	IT
9	<i>Astragalus pendulinus</i> Popov. & B.Fedtsch	S/SC	KK ^{Omni} (exc. S) *	48	<i>Lonicera iberica</i> M.Bieb.	S	IT ^{Cauc} -Turk.
10	<i>Astragalus verus</i> Olivier	S	IT ^C	49	<i>Melica persica</i> Kunth	S	IT
11	<i>Boissiera squarrosa</i> (Banks & Sol.) Nevski	S	IT-M	50	<i>Minuartia hamate</i> (Hauskn.) Mattf.	S/SR	IT-M
12	<i>Bromus danthoniae</i> Trin.	S	PL	51	<i>Noccaea trinervia</i> Steud.	SR	IT
13	<i>Bromus tectrom</i> L.	S/SR	PL	52	<i>Obobrychis cornuta</i> (L.) Desv.	S	IT ^{KK-E}
14	<i>Bupleurum falcatum</i> L. subsp. <i>cernuum</i> (Ten.) Arcang.	S	IT ^{Omni}	53a	<i>Obobrychis verae</i> Sirj.	S	IT ^{KK-Afgh.} *
15	<i>Carex stenophylla</i> Wahlenb.	S/SR	PL	53b	<i>Obobrychis verae</i> Sirj.	S/CS	IT ^{KK-Afgh.} *
16a	<i>Centaurea virgata</i> subsp. <i>squarrosa</i> (Willd.) Gugler	SC	IT	54a	<i>Phlomis cancellata</i> Bunge	SC/CSR	IT ^{KK-Afgh.} *
16b	<i>Centaurea virgata</i> subsp. <i>squarrosa</i> (Willd.) Gugler	S/SC	IT	54b	<i>Phlomis cancellata</i> Bunge	S/CS	IT ^{KK-Afgh.} *
16c	<i>Centaurea virgata</i> subsp. <i>squarrosa</i> (Willd.) Gugler	S	IT	54c	<i>Phlomis cancellata</i> Bunge	SC	IT ^{KK-Afgh.} *
16d	<i>Centaurea virgata</i> subsp. <i>squarrosa</i> (Willd.) Gugler	SR/CSR	IT	55a	<i>Poa bulbosa</i> L.	S	IT-ES-M
17	<i>Cirsium congestum</i> Fisch. & C.A. Mey. ex DC.	SC		55b	<i>Poa bulbosa</i> L.	S/SR	IT-ES-M
18	<i>Cotoneaster nummularius</i> Fisch. & C.A.Mey.	S	IT	56	<i>Poa versicolor</i> Besser subsp. <i>araratica</i> (Trautv.) Tzvelev	S	IT
19a	<i>Cousinia chaetocephala</i> Kult.	CS	KK ^{C-E} **	57	<i>Polygonum paronychioides</i> C.A.Mey.	S/SR	IT
19b	<i>Cousinia chaetocephala</i> Kult.	CS/CSR	KK ^{C-E} **	58	<i>Prunus pseudoprostrata</i> (Pojar.) Rech.f.	S	IT ^{KK-Alborz}
20a	<i>Cousinia discolor</i> Bunge	S/CS	KK ^E *	59	<i>Prunus turcomanica</i> (Pojar.) Gilli	S	KK ^{Omni} *
20b	<i>Cousinia discolor</i> Bunge	CS	KK ^E *	60	<i>Rhamnus pallasii</i> Fisch. & C.A.Mey.	S	IT-ES
21	<i>Cousinia elata</i> Boiss. & Buhse	S/CS	IT ^{KK-Alborz}	61	<i>Rosa persica</i> Michx. ex Juss.	S	IT ^{C&E}
22	<i>Cousinia eryngioides</i> Boiss.	C/CS	IT ^C *	62	<i>Salvia abrotanoides</i> (Kar.) Sytsma	S/CS	IT ^{C&E}
23a	<i>Cousinia freynii</i> Bornm.	CS	KK ^{W-C-E} *	63	<i>Sanguisorba minor</i> Scop.	CS/CSR	IT-ES-M
23b	<i>Cousinia freynii</i> Bornm.	C/CS	KK ^{W-C-E*}	64	<i>Silene swertifolia</i> Boiss.	R/CR	IT
24	<i>Cousinia platyraphis</i> Kult.	S/CS	KK ^{C-S} **	65a	<i>Stachys lavandulifolia</i> Vahl	S/CSR	IT ^C
25	<i>Crucianella gilanic</i> subsp. <i>transcaspica</i> (Ehrend.) Ehrend. & Schönb. -Tem	S	IT	65b	<i>Stachys lavandulifolia</i> Vahl	S	IT ^C
26	<i>Crucianella sintenisii</i> Bornm.	S	KK ^{NW-W-C} **	66a	<i>Stachys turcomanica</i> Trautv.	S	IT ^{KK-Alborz}
27	<i>Dianthus orientalis</i> subsp. <i>stenocalyx</i> (Boiss.) Rech.f.	S	IT ^C **	66b	<i>Stachys turcomanica</i> Trautv.	S/SR	IT ^{KK-Alborz}
28	<i>Dianthus polylepis</i> subsp. <i>binaludensis</i> (Rech.f.) Vaezi & Behrooz.	S	KK ^{C-E**}	67	<i>Stipa arabica</i> Trin. & Rupr.	S	IT
29	<i>Dianthus polylepis</i> subsp. <i>polylepis</i>	S	KK ^{C-E-S*}	68	<i>Taeniattherum caput-medusae</i> (L.) Nevski	S	IT-ES-M
30a	<i>Dianthus pseudocrinitus</i> Behrooz. & Joharchi	S	KK ^{W**}	69	<i>Tanacetum polycephalum</i> Sch. -Bip.	S/CS	IT ^{W&C}

30b	<i>Dianthus pseudocrinitus</i> Behrooz. & Joharchi	S/SR	KK ^{W**}	70	<i>Thalictrum isopyroides</i> C.A.Mey.	S/CSR	IT ^{Omi}
30c	<i>Dianthus pseudocrinitus</i> Behrooz. & Joharchi	R	KK ^{W**}	71a	<i>Thalictrum sultanabadense</i> Stapf	CSR	IT ^C
31a	<i>Elymus hispidus</i> (Opiz) Melderis	S	IT-ES-M	71b	<i>Thalictrum sultanabadense</i> Stapf	SR/CSR	IT ^C
31b	<i>Elymus hispidus</i> (Opiz) Melderis	S/SR	IT-ES-M	72a	<i>Thymus transcaspicus</i> Klokov.	SR	KK ^{W-C-E*}
32	<i>Eremurus spectabilis</i> M.Bieb.	S/CS	IT	72b	<i>Thymus transcaspicus</i> Klokov.	S/SR	KK ^{W-C-E*}
33	<i>Eryngium billardieri</i> F.Delaroche	S/CS	IT ^C	73a	<i>Thymus trautvetteri</i> Klokov. & Desj. –Shost.	S	IT ^{Cauc.-Turk.}
34	<i>Eryngium bungei</i> Boiss.	C/CR	IT ^C	73b	<i>Thymus trautvetteri</i> Klokov. & Desj. –Shost.	SR	IT ^{Cauc.-Turk.}
35a	<i>Euphorbia microsciadia</i> Boiss.	S/SR	IT ^C	74	<i>Trigonella subenervis</i> Rech.f.	SR/CSR	KK ^{C-E-S**}
35b	<i>Euphorbia microsciadia</i> Boiss.	SR	IT ^C	75	<i>Varthemia persica</i> D.C.	S/SR	IT ^C
36	<i>Ferula flobelliloba</i> Rech.f. & Aellen	CS	KK ^{C-E**}	76	<i>Verbascum cheiranthifolium</i> Boiss.	CS	IT ^{W&C}
37	<i>Ferula ovina</i> (Boiss.) Boiss.	C	IT ^{C&E}	77	<i>Verbascum speciosum</i> Schrad.	CS	IT-M
38a	<i>Festuca valesiaca</i> Gaudin	S	IT-ES	78	<i>Vicia subvillosa</i> (Ledeb.) Boiss.	SR/CSR	IT
38b	<i>Festuca valesiaca</i> Gaudin	S/SR	IT-ES				
39	<i>Gundelia tournefortii</i> L.	CS	IT				

646 PL: Pluri-regional; ES: Euro-Siberian; M: Mediterranean; IT: Irano-Turanian; KK: the Khorassan-Kopet Dagh floristic province (of the Irano-Turanian region).

648 *Regional endemic species.

649 **Iranian endemic species.

650 **Table S3.** Relationships between CWM-CSR and environmental variables from a Pearson's correlation
 651 coefficient and significance test using linear regressions.

Variables	CWM-C			CWM-S			CWM-R		
	Pearson's correlation	R ²	Pr(>r)	Pearson's correlation	R ²	Pr(>r)	Pearson's correlation	R ²	Pr(>r)
clay	0.0668	0.0045	0.5687	0.0246	0.0006	0.8341	-0.1270	0.0161	0.277
silt	-0.0484	0.0023	0.6799	0.1954	0.0382	0.0929	-0.2629	0.0691	0.0227*
sand	0.1165	0.0135	0.3195	-0.2329	0.0542	0.0443*	0.2376	0.0565	0.0401*
pH	-0.332	0.1103	0.0036**	0.3270	0.1070	0.0042**	-0.1167	0.0136	0.3188
EC	-0.0378	0.0014	0.7476	0.0527	0.0028	0.6529	-0.0390	0.0015	0.7397
N	-0.0883	0.0078	0.4513	0.0792	0.0063	0.4994	0.10179	0.0429	0.0745
P	0.1214	0.0147	0.2994	-0.2367	0.0561	0.0406*	0.2380	0.0566	0.0397*
K	-0.1256	0.0157	0.2830	0.2016	0.0406	0.0828	-0.1741	0.0303	0.1351
org.car	-0.1323	0.0175	0.2578	0.0848	0.0072	0.4693	0.0291	0.0008	0.8044
org.mat	-0.1193	0.0142	0.3079	0.0677	0.0045	0.5640	0.0409	0.0017	0.7273
lime	-0.2548	0.0649	0.0274*	0.2947	0.0868	0.0103*	-0.1621	0.0263	0.1648
CEC	-0.0647	0.0042	0.5813	0.0638	0.0041	0.5866	-0.0229	0.0005	0.8455
alt	-0.0187	0.0003	0.8736	0.0778	0.0060	0.5070	-0.1057	0.0112	0.3668
aspect	0.0302	0.0009	0.7973	-0.053	0.0028	0.6512	0.0492	0.0024	0.6748
bio1	0.1124	0.0126	0.3370	-0.0937	0.0088	0.4239	0.0112	0.00012	0.9240
bio2	0.0705	0.0812	0.0132*	-0.0622	0.0492	0.0557	0.0127	5.95e-06	0.9834
bio3	0.1249	0.0639	0.0286*	-0.0928	0.0384	0.0919	-0.0065	2.234e-07	0.9968
bio4	-0.3049	0.01875	0.2414	0.2064	0.0072	0.4680	0.0493	0.0012	0.7664
bio5	-0.0183	0.0003	0.8764	-0.0465	0.0360	0.1030	-0.0535	0.0024	0.6760
bio6	-0.4245	0.0027	0.6538	0.2782	8.328e-05	0.9381	0.0838	0.0027	0.6547
bio7	0.4428	0.1150	0.0029**	-0.2795	0.0696	0.0222*	-0.1054	6.126e-06	0.9832
bio8	0.1579	0.0643	0.0282*	-0.0899	0.0213	0.2112	-0.0536	0.0070	0.4752
bio9	-0.4192	0.0173	0.2599	0.2697	0.0109	0.3720	0.0910	1.866e-05	0.9707
bio10	-0.4306	0.0049	0.5476	0.2785	0.0038	0.5961	0.0911	0.0001	0.9141
bio11	0.3007	0.0156	0.2857	-0.1993	0.0086	0.4285	-0.0557	4.201e-05	0.9560
bio12	0.2849	0.0929	0.0078**	-0.2219	0.0426	0.0755	0.0024	0.0024	0.6742
bio13	0.2529	0.0104	0.3849	-0.1960	0.0022	0.6917	0.0005	0.0028	0.6486
bio14	-0.1369	0.1802	0.0001***	0.0851	0.0774	0.0157	0.0348	0.0070	0.4746
bio15	0.2072	0.1961	6.9e-05***	-0.1897	0.0781	0.0152*	0.0490	0.0111	0.3681
bio16	-0.0526	0.0249	0.1759	0.0091	0.0081	0.4427	0.0525	0.0029	0.6477
bio17	0.3391	0.1757	0.0002***	-0.2638	0.0728	0.0192*	0.0025	0.0083	0.4373
bio18	-0.2536	0.1854	0.0001***	0.14605	0.0776	0.0155*	0.0837	0.0083	0.4370
bio19	0.1317	0.0904	0.0087**	-0.1045	0.0397	0.0864	0.0043	0.0031	0.6351

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654 **Table S4.** Environmental variables used in the study. Climate data were obtained from WorldClim
 655 (www.worldclim.org).

Variable	Abbreviation	Data source
Annual mean temperature	bio1	Worldclim
Mean diurnal range	bio2	Worldclim
Isothermality	bio3	Worldclim
Temperature seasonality	bio4	Worldclim
Max temperature of warmest month	bio5	Worldclim
Min temperature of coldest month	bio6	Worldclim
Temperature annual range	bio7	Worldclim
Mean temperature of wettest quarter	bio8	Worldclim
Mean temperature of driest quarter	bio9	Worldclim
Mean temperature of warmest quarter	bio10	Worldclim
Mean temperature of coldest quarter	bio11	Worldclim
Annual precipitation	bio12	Worldclim
Precipitation of wettest month	bio13	Worldclim
Precipitation of driest month	bio14	Worldclim
Precipitation seasonality	bio15	Worldclim
Precipitation of wettest quarter	bio16	Worldclim
Precipitation of driest quarter	bio17	Worldclim
Precipitation of warmest quarter	bio18	Worldclim
Precipitation of coldest quarter	bio19	Worldclim
Clay content	clay	calculated
Silt content	silt	calculated
Sand content	sand	calculated
Soil pH	pH	calculated
Electrical conductivity of soil ($\mu\text{s}/\text{m}$)	EC	calculated
Soil total nitrogen (%)	N	calculated
Soil phosphorus (%)	P	calculated
Soil potassium (%)	K	calculated
Soil organic carbon content	org.car	calculated
Soil organic matter content	org.mat	calculated
Calcium carbonate (%)	lime	calculated
Cation exchange capacity of soil (meq /100 g)	CEC	calculated
Elevation (m)	alt	—
Aspect (°)	aspect	—

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