

1 **Patterns of genetic diversity in rare and common orchids focusing on the Korean**
2 **Peninsula: implications for conservation**

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20 **Abstract** To provide basic information for orchid conservation, we surveyed the plant
21 allozyme literature to summarize genetic diversity and structure data for (i) rare orchids
22 native to the Korean Peninsula, and (ii) their congeners irrespective of being common and
23 rare or Korean or not. A total of 68 taxa (32 taxa in Korea and 37 outside Korea; *Goodyera*
24 *repens* being included in both datasets) were considered in this study. Overall, rare Korean
25 orchid species had significantly lower levels of genetic diversity than their common
26 congeners and common orchids in general at both population and species levels. However,
27 mean values of G_{ST} (or F_{ST}) for rare and common orchids (Korean or not) did not differ
28 significantly from each other. We found patterns of both low and high genetic diversity in
29 rare Korean orchids. Many rare orchids harbored a complete lack of allozyme variation or
30 extremely low within-population variation, perhaps due to rarity associated with random
31 genetic drift and/or, for the case of warm-temperate orchids, to founder effects during post-
32 glacial re-colonization. In contrast, high levels of genetic variation were found for a few
33 orchids that have become recently rare (due to over-collection during the past several
34 decades), probably because there have not been sufficient generations for the initial diversity
35 to be substantially eroded. In addition, several orchids occurring in the main mountain system
36 of the Korean Peninsula (the Baekdudaegan), that served as a glacial refugium, maintained
37 moderate to high levels of within-population genetic diversity. Based on our genetic data,
38 conservation priority should be given to rare orchid species. Particularly, urgent measures
39 should be implemented on Jeju Island, a popular vacation spot, because it also a hotspot for
40 threatened orchids with low levels of genetic diversity.

41

42 **Keywords** Allozymes · Conservation · Genetic diversity · Orchidaceae · Korean Peninsula

43

44 **Introduction**

45

46 It is generally agreed that a complex network of factors shapes genetic diversity in plant
47 populations and species, and these can be classified into two large categories (Gray, 1996): (i)
48 ‘intrinsic’ biological properties of the species (mainly the life-history traits such as mode of
49 pollination, breeding system, seed dispersal mechanism, habit, or life-form) and (ii)
50 ‘extrinsic’ dynamic processes that affect species’ distributions, existence or persistence
51 (mainly historical factors that include occurrence of bottlenecks, divergence events, or
52 Quaternary expansions/retreats). Other traits that may influence genetic diversity patterns are
53 the biogeographical affinities (boreal, temperate, etc.), the historical and/or contemporary
54 geographic range. Geographic range is known to be one of the major factors determining the
55 levels of genetic variation of plant species on the basis of a series of meta-analyses. Perhaps
56 the best known example is the compilation of Hamrick & Godt (1989), who gathered
57 allozyme data from 653 studies (449 species representing 165 genera) at the global level and
58 found that species with widespread ranges had significantly higher levels of genetic diversity
59 than range-restricted ones. A further compilation of species studied by means of another
60 codominant marker (microsatellites) yielded similar results (95 species; Nybom, 2004); in
61 addition, a recent compilation carried out in the western Mediterranean Basin also reported
62 significantly higher levels of allozyme diversity in widespread species compared to endemic
63 ones (33 species; López-Pujol et al., 2009).

64 These heterospecific (mixed species) compilations, despite having the advantage of
65 including a large number of species, have been criticized for the absence of a congruent
66 statistical approach. Given that life-history traits often show strong phylogenetic inertia (i.e.,
67 a tendency of close-related species to share them; Morales, 2000; Losos, 2008), analyzing the
68 species independently (as is done in the abovementioned compilations) may lead to statistical

69 pseudo-replication (Silvertown & Dodd, 1996; Aguinagalde et al., 2005). Although not as
70 effective as using phylogenetically independent contrasts (Felsenstein, 1985), limiting
71 comparisons to congeneric pairs would be a reliable alternative, as we can be quite confident
72 that these share a more recent common ancestor than species in other genera (Silvertown &
73 Dodd, 1996). Congeneric comparisons have been employed by Karron (1987), who compared
74 11 pairs of rare and widespread congeneric plants (48 species) in relation to their genetic
75 diversity; in 10 pairs, rare species had lower genetic diversity than their widespread
76 congeners. Later, Gitzendanner & Soltis (2000) performed a similar study with 36 congeneric
77 pairs (107 taxa), generally obtaining lower diversity for rare species. More recently, Cole
78 (2003) extended this approach to a total of 247 plant species representing 57 genera, whose
79 results were close to those reported by Gitzendanner & Soltis (2000).

80 Although they are not strictly comparisons between widespread and range-restricted
81 species, those comparisons between threatened and non-threatened taxa can be regarded as a
82 relatively accurate surrogate, given the well-known correlation between extent of species'
83 range and extinction risk (e.g., Purvis et al., 2000; Payne & Finnegan, 2007; Cardillo et al.,
84 2008). Indeed, geographic range plays a key role in listing the species on the IUCN Red List,
85 and for most of the cases it is the only criterion used to classify a given species as threatened
86 (Gaston & Fuller, 2009). Spielman et al. (2004) compared the heterozygosity in 170
87 threatened/non-threatened pairs of taxa (taxonomically related but not necessarily
88 congeneric), from which 36 were plant species. The authors found that in 27 pairs the
89 threatened taxa had lower heterozygosity than the non-threatened species.

90 Orchidaceae are one of the largest families of flowering plants (ca. 26,000 species;
91 Chase et al., 2015). Considerable variation in life forms is known in the family, with
92 approximately 30% of the species being terrestrial and the majority of the remainder growing
93 as epiphytes or lithophytes (Gravendeel et al., 2004). Orchids are also among the most

94 endangered plant taxa (Pillon & Chase, 2007; Swarts & Dixon, 2009; Vogt-Schilb et al., 2015;
95 Zhang et al., 2015); clearly, more attention is needed to preserve the biodiversity of wild
96 orchids for several reasons. Many orchid species rely on a complex set of interactions with
97 other organisms (e.g., the need of host trees for epiphytes and mycorrhizal fungi for
98 terrestrial orchids, or the existence of intricate pollination syndromes) for their survival
99 (Bronstein et al., 2014). These requirements make them extremely sensitive to environmental
100 changes (Swarts & Dixon, 2009). Environmental human-mediated changes (e.g.,
101 deforestation, overharvesting, urbanization, changes in agricultural practices, trampling,
102 pollution, soil disturbance, etc.) have been reported as the most important drivers for orchid
103 decline (Swarts & Dixon, 2009, Liu et al., 2014; Fay et al., 2015; Vogt-Schilb et al., 2015;
104 but see Catling & Kostiuk, 2011 who found that trail disturbance benefited some wild
105 orchids); in fact, orchids are often the first biological indicators of ecosystem decay (Roberts
106 & Dixon, 2008). Direct impacts on orchids, such as mass collections by orchid hunters
107 (because of their high commercial value), are of serious concern (Swarts & Dixon, 2009).
108 The uses of orchids as ornamental, medicinal (especially in traditional Chinese medicine),
109 and even alimentary plants (such as the *salep* in Iran) have brought many species to the brink
110 of extinction in the wild (Ghorbani et al., 2014; Liu et al., 2015). In addition, orchids are
111 typically characterized by small, spatially isolated populations (e.g., Vásquez et al., 2003;
112 Tremblay et al., 2005; Phillips et al., 2011), mainly a consequence of ecological
113 specialization and low reproductive success (Roberts & Dixon, 2008); thus, orchid
114 populations often have small effective population size, which makes them particularly
115 susceptible to the effects of random genetic drift (Chung et al., 2004a; Roberts & Dixon,
116 2008).

117 On the Korean Peninsula, 97 orchid species [103 taxa (species plus subspecies and
118 varieties) in 42 genera] are known (Lee et al., 2007; Lee, 2011). Thirty five and 48 species

119 are listed as threatened by the Ministry of Environment (MOE, 2012, 2014) and Korea
120 National Arboretum (KNA, 2012), respectively, which highlights the critical status of wild
121 orchids in the Peninsula (Lee & Choi, 2006). As a part of a larger project on conservation
122 biology on the Korean orchids, we have conducted allozyme studies in the Orchidaceae from
123 South Korea since the mid-1990s; at present, genetic data on 32 taxa (31 species plus one
124 variety; ca. one third of the Korean orchid flora) in 21 genera which are broadly
125 representative of the Korean orchid flora (covering 11 out of 14 tribes in the four subfamilies)
126 are available. In this study, we summarize current information on allozyme-based genetic
127 diversity in South Korean orchids. We also summarize the available genetic information on
128 congeners (of the studied Korean orchids) from other parts of the world, in order to get
129 additional insights into the patterns of genetic diversity of Korean orchids and to provide
130 insights into associations between rarity and genetic diversity in plants. Specific aims of the
131 present study are the following: (i) to describe the patterns of genetic variability (within and
132 among populations) of Korean orchids; (ii) to determine whether rare Korean orchids differ
133 in the patterns of genetic diversity from common ones; (iii) to see whether the empirical
134 observation of lower genetic diversity for rare species compared to their widespread
135 congeners is also applicable to our species' dataset, and (iv) to provide recommendations for
136 the conservation of Korean orchids.

137

138 **Materials and Methods**

139

140 **Data Collection**

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142 We gathered all published (and several unpublished) allozyme analyses of orchids in the
143 Korean Peninsula. A total of 32 taxa (that are indicated by "S. Korea" after taxa names in

144 Table 1) from Korea (plus *Cymbidium goeringii* in Japan) have been analyzed at the same
145 laboratory by MY Chung & MG Chung since the mid-1990s. In addition, studies of 37
146 congeneric taxa of the Korean orchids sampled from outside Korea (i.e., 37 taxa outside
147 Korea), that were conducted at different laboratories, were included in this study to make
148 comparisons between rare and common taxa (with a total of 46 entries; Table 1). Given that
149 *Goodyera repens* was included in both datasets ('in' and 'outside' Korea; Table 1), a total of
150 68 taxa were considered in this study. For those studies from which allozyme data were
151 reused for subsequent papers by the same authors, and for studies examining conspecific
152 populations occurring on close locations, we only included data from a single study that
153 involved the largest number of populations to avoid data duplication (Karron, 1987). On the
154 contrary, all genetic data for widespread taxa examined on more than one occasion (e.g.,
155 *Epipactis helleborine*, *G. repens*) were included when these studies involved geographically
156 very separated populations (i.e., from different countries).

157 In this work we followed plant names according to "The Plant List (2013)" except for
158 *Neolindleya* (= *Gymnadenia*) *camtschatica* and *Amitostigma gracile* for which we used the
159 names *Galearis camtschatica* and *Hemipilia gracile* provided by Jin et al. (2014) and Tang et
160 al. (2015) based on molecular systematics studies, respectively (Table 1).

161

162 **Designations of Rare vs. Common Orchids**

163

164 Although there is no widely accepted threshold or a definition by which a taxon is termed
165 "rare" or "common", for Korean orchids we considered that a given taxon was rare if it was
166 included in either *Rare plants in Korea* (KNA, 2012) or *Korean Red List of Threatened*
167 *Species* (MOE, 2014) except for two species. The two newly recorded terrestrial orchids
168 *Habenaria dentata* in Hapcheon County, Gyeongsangnam Province (Lee et al., 2013a) and

169 *Liparis pterosepala* on Jeju Island (Lee et al., 2010) were not listed in KNA (2012) and MOE
170 (2014), but they are extremely rare in South Korea. For other orchids outside the Korean
171 Peninsula, we have mostly relied on authors' descriptions about abundance, population sizes
172 or geographic ranges when included within papers. For example, in North America, as
173 *Cypripedium parviflorum* is more ecologically diverse and shows a wider geographical
174 distribution (although in many cases, local US populations are quite scattered and limited,
175 and many populations have undergone dramatic declines) than its congeners *C. arietinum*, *C.*
176 *candidum*, *C. fasciculatum*, *C. kentuckiense*, and *C. reginae*, we considered the former as
177 "common" whereas the latter species were regarded as "rare" (Case, 1994; Aagaard et al.,
178 1999; Kennedy & Walker, 2007). Although *C. acaule* is not as widely distributed as *C.*
179 *parviflorum*, it is common in parts of the eastern US and Canada, and most populations
180 remain stable in size and distribution
181 (<http://explorer.natureserve.org/servlet/NatureServe?searchName=Cypripedium+acaule>).
182 When the information was not provided in the gathered studies, we referred to various
183 sources of information (e.g., <http://www.efloras.org>, <http://www.iucnredlist.org>,
184 <http://plants.usda.gov>, or <http://www.orchidspecies.com>). It should be noted that, for the case
185 of widespread species, they can be "common" in some parts of their distribution area but
186 "rare" in others. This occurs in two cases: *Cymbidium goeringii* and *Goodyera repens*. As
187 mentioned above, the former is relatively common in South Korea, but it is a rare orchid in
188 Japan. In Japan *C. goeringii* was listed as critically endangered species in the 1997 list (EAJ,
189 2000), but later it was delisted in the 2012 list (EAJ, 2015). As in Japan it is a relatively rare
190 species compared to southern Korea (mainly due to over-collection; M.Y. Chung & M. G.
191 Chung, pers. obs.; T. Yahara, pers. comm.), we still consider it a rare orchid in the former
192 country. In contrast, *G. repens* is extremely rare in South Korea (KNA, 2012), but it is

193 common in NE Poland, where conifer forest communities suitable for this species are
194 abundant (Brzosko et al., 2013; Table 1).

195

196 **Data Analysis**

197

198 As done by Hamrick & Godt (1989, 1996) and Godt & Hamrick (2001), standard parameters
199 that describe genetic diversity and structure were extracted from these studies; these
200 parameters include percent polymorphic loci ($%P$), mean number of alleles per locus (A), and
201 gene or genetic diversity (i.e., Hardy–Weinberg expected heterozygosity, H_e). We used the
202 subscripts “P” or “S” to denote population means or species’ (or pooled samples) values,
203 respectively. Since these values were not reported in all orchid studies, we calculated some of
204 the measures (in particular measures at the species level) from allele frequency data provided
205 in the papers. Following Hamrick & Godt (1989, 1996), we also compiled data on population
206 structuring (G_{ST} or F_{ST}).

207 We compared levels of genetic diversity between rare orchids in Korea and their
208 common congeners if available. To do this, we averaged all entries for those taxa examined
209 by different authors (e.g., *Cephalanthera rubra*, *Cypripedium parviflorum* var. *pubescens* and
210 *Epipactis helleborine*) to obtain a single estimate per taxon. We thus obtained average values
211 from rare taxa in South Korea and from their congeners (where more than one was available;
212 e.g., *Cypripedium*); in total, comparisons were possible for nine congeneric pairs (39 taxa;
213 see the numbers 2, 4, 6, 7, 8, 10, 13, 15, and 19; Table 1) for this dataset.

214 Following Karron (1987) and Gitzendanner & Soltis (2000), we plotted each measure
215 of diversity in rare taxa against that of the widespread congener. We further conducted
216 Wilcoxon signed-rank tests between rare and common congeners for each genetic parameter
217 to determine whether differences between two groups were statistically significant. We also

218 performed a Spearman's rank correlation analysis between rare and common congeners for
219 each measure; the higher correlation between the rare and common species for each genetic
220 measure, the smaller the differences in the measurements between two groups.

221 As heterospecific comparisons, we compared rare Korean orchids (24 taxa or entries)
222 with common ones (32 entries) provided in Table 1. To do this, we used a single entry per
223 taxon by averaging all entries of the same taxa with the exception of *Cymbidium goeringii*
224 and *Goodyera repens*. For the former, South Korean and Japanese ranges were treated as a
225 common taxon and a rare one, respectively; for the latter South Korean and NE Polish ranges
226 were treated as a rare taxon and a common one, respectively (Table 1). Similarly, we
227 compared rare orchids (38 entries) with common ones (32 entries) provided in Table 1. We
228 used a Wilcoxon rank-sum test (or Mann-Whitney *U*-test) to assess the significance of
229 differences in all measured parameters of diversity between rare and common taxa.

230

231 **Results**

232

233 **Congeneric Comparisons**

234

235 A different relationship for the levels of genetic diversity was observed between rare and
236 common congeners (Fig. 1). The majority of the nine points on the graphs are away from the
237 lines of equality (e.g., eight points for %*P_P*, Fig. 1A), indicating different levels of diversity
238 in rare and common congeners. A very similar pattern was observed at the species level (data
239 not shown). These visual interpretations were supported by the correlation analyses that
240 showed that for all measures of genetic diversity, at both population and species levels, there
241 was neither high nor significant correlation between rare species and their common congeners
242 (Table 2). Indeed, for both population and species level estimates, Wilcoxon signed-rank tests

243 revealed that rare species had significantly lower levels of genetic diversity than their
244 common congeners (Table 2). We did not conduct statistical analysis for G_{ST} or F_{ST} values
245 for the two groups because only data for three pairs were available (Table 1).

246

247 **Heterospecific Comparisons**

248

249 We expanded our analyses to mixed species (heterospecific) comparisons between rare ($N =$
250 24 in Korea and $N = 38$ in Korea plus other countries) and common orchids ($N = 32$)
251 compiled in Table 1. For both population and species level values, Wilcoxon rank-sum tests
252 showed that rare Korean orchids had significantly lower levels of genetic diversity than
253 common orchids (all cases $P < 0.0001$; Table 3). A very similar result was found between
254 rare orchids ($N = 38$) and common orchids ($N = 32$) (again all cases $P < 0.0001$; Table 3).
255 Finally, mean values of G_{ST} (or F_{ST}) for rare orchids and common congeners did not differ
256 significantly from each other [rare orchids in Korea ($N = 13$) vs. common orchids ($N = 25$),
257 mean $G_{ST} = 0.169$ vs. 0.194 , $P = 0.176$; rare orchids ($N = 22$) vs. common orchids ($N = 25$),
258 mean $G_{ST} = 0.189$ vs. 0.194 , $P = 0.412$; Table 3].

259

260 **Discussion**

261

262 **Congeneric Comparisons**

263

264 For both population and species level estimates, rare Korean orchid species have significantly
265 lower levels of genetic diversity than their common congeners (Table 2), as expected (Karron,
266 1987; Gitzendanner & Soltis, 2000; Cole, 2003; see also Spielman et al., 2004). The only
267 exception is the pair *Cymbidium goeringii*/*C. kanran*, a common and a rare species studied

268 from Korea (Table 1). It is noteworthy that there is no allozyme-based genetic variation
269 within and among populations in up to six Korean native rare species from our congeneric
270 pairs dataset (*Cephalanthera subaphylla*, *Cypripedium japonicum*, *Epipactis papillosa*,
271 *Goodyera repens*, *Liparis pterosepala*, and *Oreorchis coreana*) (Table 1), which significantly
272 contributes to the observed differences for the pairwise comparisons. In addition,
273 *Bulbophyllum drymoglossum* and *Platanthera hologlottis* show very low estimates of H_{ep}
274 (Table 1). As Chung et al. (2009) suggested, rare species with small population sizes
275 (probably due to historical stochastic events) are susceptible to random genetic drift (RGD),
276 leading to allelic fixation at many neutral loci within populations. Population genetic theory
277 predicts that populations of species that have suffered RGD should exhibit low H_{ep} and high
278 G_{ST} due to the fixation of alternative alleles (e.g., Barrett & Kohn, 1991; Ellstrand & Elam,
279 1993). Although allozyme-based G_{ST} estimates are not available in the six abovementioned
280 species (as these are monomorphic), the other two species showing low levels of H_{ep}
281 (*Bulbophyllum drymoglossum* and *Platanthera hologlottis*) have moderate G_{ST} (0.253 and
282 0.328, respectively; Table 1). In addition, low levels of microsatellite-based within-
283 population genetic variation ($\%P_P = 35$; $A_P = 1.53$; $H_{ep} = 0.109$ based on 10 polymorphic loci)
284 but a much higher among-population divergence ($\Phi_{ST} = 0.81$ including one Japanese
285 population) have been detected in South Korean populations of *Cypripedium japonicum* (Son
286 & Son, 2016). The low H_{ep} values and the high Φ_{ST} values support the role played by RGD in
287 shaping the patterns of genetic diversity of some rare Korean orchids.

288 One of the best examples where rarity reflects the lack of allozyme diversity is
289 probably that of *Goodyera repens* in South Korea. This species is widely distributed in Asia,
290 Europe, and North America (Chen et al., 2001) and may represent a relictual descendant of an
291 alpine community that was more widespread during the late Pleistocene (Kallunki, 1976).
292 Unlike Korean populations (that are monomorphic in three populations; Table 1), 11

293 populations from NE Poland maintain high levels allozyme diversity ($%P_P = 50$; $A_P = 1.68$;
294 $H_{ep} = 0.197$; Table 1; Brzosko et al., 2013); the authors attributed its common occurrence
295 under pine and spruce forests as the main factor shaping levels of genetic diversity of Polish
296 populations. Thus, lack of allozyme diversity of *G. repens* in three alpine Korean populations
297 might be attributable to its rarity in the country [it is a species listed as “vulnerable” by MOE
298 (2012, 2014) and “critically endangered” by KNA (2012) with only 10 populations occurring
299 throughout Korea].

300 *Oreorchis coreana* is another example of a very rare species in Korea, as it is found in
301 a small area on Jeju Island and has only five low-density populations (MOE, 2014). It shows
302 no genetic variation, in contrast to its close congener *O. patens*, a common orchid in East
303 Asia that in Korea has high levels of genetic diversity (Chung et al., 2012 and Table 1).
304 *Oreorchis coreana* was considered in the past endemic to Jeju Island, but it also occurs in
305 Nasushiobara City, Tochigi Prefecture, Honshu (Japan) (Takashima et al., 2016). Unlike on
306 Jeju Island, only ca. 10 individuals in a single population are known in Honshu. Although the
307 levels of genetic diversity for the Nasushiobara population have not been surveyed, one
308 would expect a lack of allozyme diversity in this population because there is no sequence
309 divergence in the ITS regions between Jeju and Nasushiobara populations. This finding also
310 suggests that the Japanese population is probably the result of recent long-distance dispersal
311 from Jeju Island rather than an old relict population separated via vicariance (Takashima et
312 al., 2016).

313 Finally, it should be also taken into account that a formerly common species could
314 have become recently rare (e.g., due to over-collection by orchid hunters), a situation that has
315 often been reported for orchids (Swarts & Dixon, 2009; Vogt-Schilb et al., 2015; Zhang et al.,
316 2015). However, when population reduction has taken place recently (e.g., several decades
317 ago), little alteration in the levels of genetic diversity occurs because there have not been

318 sufficient generations for the initial diversity to be substantially eroded by RGD (Chung et al.,
319 2004a). Moreover, if population size reduction has been at random regarding individual
320 genotypes, the loss of genetic variation should be even more limited (Chung & Chung, 1999).
321 Thus, rare species that were formerly common but with most of their populations recently
322 decimated [and, hence, that were treated as “rare” by KNA (2012) and/or MOE (2012, 2014)]
323 might exhibit comparable levels of genetic diversity to common ones [e.g., *Cymbidium*
324 *goeringii* in Japan (Chung & Chung, 2000); *C. kanran* on Jeju Island (MY Chung et al.,
325 unpubl. data); *Cypripedium macranthos* in South Korea (Chung et al., 2009); Table 1].

326

327 **Heterospecific comparisons**

328

329 Regarding heterospecific (mixed species of orchids) comparisons, the rare orchids—
330 regardless of being Korean or not—have significantly lower levels of genetic diversity than
331 the common orchids at both population and species levels, with the exception of a few cases
332 (Tables 1 and 3). Such results agree with former compilations and meta-analyses of
333 heterospecific data (e.g., Hamrick & Godt, 1989, 1996; Godt & Hamrick, 2001; Nybom,
334 2004; López-Pujol et al., 2009) and also with our congeneric comparisons.

335 It should be noted that a total lack of allozyme diversity is found in 10 (ca. 42%) of 24
336 rare orchid species in South Korea [similarly, 14 (ca. 37%) out of 38 rare orchids provided in
337 Table 1]. This observation may result from rarity associated with RGD. As seen in the two
338 rare orchids *Bulbophyllum drymoglossum* and *Platanthera hologlottis*, *Pelatantheria*
339 *scolopendrifolius* and *Pogonia minor* exhibit low H_{eP} and moderate to high G_{ST} values,
340 suggesting that populations of these species were historically rare; this pattern of genetic
341 diversity would be the natural result of continued RGD (Barrett & Kohn, 1991). Another
342 scenario, which is not mutually exclusive with the former, is more related to historical events.

343 Quaternary climatic cycles can often leave a distinctive signature on levels of genetic
344 diversity found within populations or species (Hewitt, 1996, 2000; Soltis et al., 2006; Qiu et
345 al., 2011). Warm-temperate plant elements on the Korean Peninsula, currently limited to
346 southern coastal areas, shifted southwards during the Last Glacial Maximum (LGM, ca.
347 21,000 yrs before present) towards glacial refugia putatively located in southern portions of
348 Jeju Island, southern Japan, and/or southern China (Chung et al., 2013a; Lee et al., 2013b,
349 2014; Chung et al., 2017). The low H_{EP} found in the five warm-temperate orchid species
350 (*Bletilla striata*, *Habenaria dentata*, *Pecteilis radiata*, *Peristylus densus*, and *Tipularia*
351 *japonica*; Table 1) might be due to founder effects during post-glacial re-colonization from a
352 single source population (Chung et al., 2013b); a pattern of continued small size over time of
353 founding populations would enhance the loss of genetic diversity by processes of RGD
354 (Frankham et al., 2002; Templeton, 2006).

355 The Baekdudaegan (BDDG, the main mountain system of the Korean Peninsula)
356 served as a glacial refugium for a large assemblage of boreal and temperate plants during the
357 LGM (Chung et al., 2017). In many cases (with the exception of *Goodyera repens*), plants
358 from the BDDG maintain moderate to high levels of within-population genetic diversity
359 (Table 3; Table 1 in Chung et al., 2017) because these mountains might provide relatively
360 stable habitats, ensuring relatively large population sizes. Species belonging to this scenario
361 might include *Cypripedium macranthos*, *Galearis cyclochila*, *Liparis makinoana*, and
362 *Oreorchis patens* in South Korea (Chung et al., 2005a, 2005b, 2009, 2012; Chung, 2009a).
363 *Neottianthe cucullata*, in spite of being located in the BDDG, has low levels of within-
364 population allozyme variation, which might be due to a relatively small scale of sampling
365 (four populations were collected within a 1.2–km linear distance; Chung, 2009a). A total lack
366 of allozyme diversity was also found in the autogamous *Liparis kumokiri* in South Korea, a
367 common orchid that occurs on lowlands (K. Suetsugu, pers. comm.). In contrast, the self-

368 incompatible and genetically-diverse congener *L. makinoana* mostly occurs in the BDDG and
369 its vicinity (Oh et al., 2001), which illustrates the role of these mountains in preserving the
370 genetic diversity of plant species.

371 There are five rare taxa in South Korea (*Calanthe discolor*, *C. reflexa*, *C. sieboldii*,
372 *Cremastra appendiculata* var. *variabilis*, and *Galearis cyclochila*) and *Cypripedium*
373 *macranthos* var. *rebunense* (endemic to Rebun Island, Japan) that, unexpectedly, exhibit
374 moderate to high levels of genetic variation within populations (Table 1). Like *Cymbidium*
375 *kanran* on Jeju Island, the three *Calanthe* species have been the target of orchid collectors
376 during the past several decades (Chung et al., 2013c). As explained above, recent negative
377 effects (i.e., human-mediated disturbance) could not have altered levels of genetic diversity in
378 remnant populations. Even though their distributions are relatively narrow, locally common
379 populations could maintain moderate levels of genetic variation. All these species, in addition
380 to *Cypripedium macranthos* in South Korea and *Cymbidium goeringii* in Japan, appear to
381 belong to this category.

382 As heterospecific comparisons, our mean estimates ($N = 68$) of genetic diversity for
383 orchids are similar to those ($N = 32$ and 16 , respectively) compiled by Case (2002) and
384 Hamrick & Godt (1996) (Table 3), which are also comparable to the average values for all
385 plants ($N = 725$; Hamrick & Godt, 1989), narrowly distributed plants ($N = 101$; Hamrick &
386 Godt, 1989), short-lived herbaceous plants ($N = 152$; Hamrick & Godt, 1989), plants with
387 outcrossing-animal breeding system ($N = 172$, Hamrick & Godt, 1989), rare plants in the
388 southeastern US ($N = 52$; Godt & Hamrick, 2001), and plants from NW Mediterranean Basin
389 ($N = 36$; López-Pujol et al., 2009), but somewhat higher than endemic plants ($N = 81$,
390 Hamrick & Godt, 1989) (Table 3).

391 The degree of genetic differentiation among populations of orchids was once
392 controversial (Forrest et al., 2004), due to the low mean value reported in one of the few

393 meta-analyses available at that time ($G_{ST} = 0.087$, $N = 16$; Hamrick & Godt, 1996). Our mean
394 ($G_{ST} = 0.190$, $N = 68$) is comparable, nevertheless, to those averaged by most of the previous
395 studies ($G_{ST} = 0.146$, 0.161 , and 0.163 ; Phillips et al., 2012; Forrest et al., 2004; Case, 2002,
396 respectively) (Table 3). The slightly higher G_{ST} value estimated in this study is partly due to
397 the inclusion of *Pelatantheria scolopendrifolius* ($G_{ST} = 0.899$; Chung et al., 2007a) and
398 *Hemipilia gracile* ($G_{ST} = 0.781$; Chung, 2009a), two orchids with disproportionate levels of
399 genetic differentiation. The lack of significant differences in the mean G_{ST} values between
400 rare and common orchids from our datasets are in agreement with the study of Hamrick &
401 Godt (1989) for plants in general. However, Phillips et al. (2012) found that rare terrestrial
402 orchid species had significantly higher population genetic differentiation than common ones
403 (mean rare $F_{ST} = 0.279$, $N = 13$; mean common $F_{ST} = 0.092$, $N = 22$; Mann–Whitney U -test,
404 $P = < 0.001$). These differences among studies might be due to different criteria for choosing
405 papers for the meta-analyses and perhaps also different criteria for classifying species into
406 rare and common (Phillips et al., 2012). We further test whether our results would change
407 when six rare species of our dataset (that were formerly common but with most of their
408 populations recently decreased) were considered, instead, as common ones (e.g., three
409 *Calanthe* species, *Cremastra appendiculata* var. *variabilis*, *Cymbidium goeringii* in Japan,
410 and *Cypripedium macranthos*); again, we did not detect significant differences between the
411 groups regarding G_{ST} (data not shown).

412

413 **Conservation implications for rare orchids in Korea**

414

415 There are two main “hotspots” of orchids on the Korean Peninsula regarding species richness;
416 the BDDG (that stretches ca. 1625 km), in which 40 taxa (38.8% of total orchids) occur, and
417 Jeju Island (1848 km², also a tourist hotspot), where 60 taxa (58.3%) can be found (Lee,

418 2011). Jeju Island is, however, much more significant as a hotspot for threatened species; for
419 example, of the 48 orchid species designated by Korea National Arboretum (KNA) in 2012
420 as rare/threatened plants (KNA, 2012), 37 occur on Jeju, whereas only seven are found in the
421 main ridge (or in the immediate vicinity) of the BDDG. A similar trend is found in the
422 *Korean Red List of Threatened Species* (MOE, 2014); out of 35 threatened orchid species,
423 only five occur on the main ridge of the BDDG or its vicinity, whereas 29 grow on Jeju.

424 The BDDG has a high floristic richness of over 1500 taxa just in South Korea (Lim,
425 2003). It is mainly covered by temperate deciduous forests (with *Quercus mongolica* and
426 *Pinus densiflora* as dominant species) in its southern and central sections, whereas mixed
427 forests (*Abies*, *Betula*, *Pinus*, *Tilia*, *Ulmus*) are common in its northern section (Yi, 2011).
428 Under relatively stable habitats along the BDDG, many plant species might have persisted
429 with large population sizes and consequently maintained moderate to high levels of genetic
430 diversity (Chung & Chung, 2014; Chung et al., 2017). This may partly account for why in the
431 BDDG there are relatively few threatened orchid species. The floristic richness of the BDDG
432 as well as its role as a Pleistocene glacial refugium has stressed the need to ensure effective
433 and integral conservation of this mountain range. Although these mountains remain relatively
434 well preserved, some conservation measures have been already undertaken, whereas others
435 have been suggested in detail in Chung et al. (2016, 2017), including enlarging the current
436 network of protected areas, stopping of deforestation activities (especially worrisome in
437 North Korea), and increasing cooperation between the two Koreas.

438 Jeju Island was on the “crossroads” of several post-glacial colonization routes,
439 consequently harboring different floristic elements including subtropical, temperate, boreal,
440 and arctic-alpine species (Kong & Watts, 1993; Dolezal et al., 2012; Chung et al., 2013a).
441 Currently, Jeju harbors 1990 taxa of vascular plants (Kim, 2009), with about 13% of native
442 Korean orchid species exclusively occurring here (Lee, 2011). Some of the reasons why Jeju

443 has many rare orchids might be due to the island's relatively small area (less than 2000 km²)
444 and/or recent plant immigration (colonization) by a single or few dispersal events from
445 adjacent regions (perhaps, from southern Japan; Eum et al., 2011). Fortunately, Hallasan
446 National Park (1950 m at peak) has been designated as an UNESCO Biosphere Reserve
447 (covering 830.94 km²; Chung & Hwang, 2015) in 2002, and a World Heritage Site in 2007,
448 for its pristine environments, unique altitudinal zonation of vegetation and high endemism
449 (Kong & Watts, 1993; Dolezal et al., 2012). In addition, five wetlands have been included on
450 the list of Ramsar Wetlands (<http://www.ramsar.org/wetland/republic-of-korea>), and the
451 whole island was recognized as an UNESCO Global Geopark in 2010 (Chung & Hwang,
452 2015). Although the biosphere reserve—that represents ca. 45% of the total land area of
453 Jeju—is well preserved, large destruction is taking place in the low peripheral areas of
454 *Gotjawal*, a forest often called the “lung” of Jeju (Kang et al., 2013), while several
455 development projects (including the construction of a new airport, resorts and residential
456 complexes; Bridger, 2016) have been planned. To protect and conserve plants and animals,
457 further expansion of the biosphere reserve to the whole island has been suggested (Chung &
458 Hwang, 2015).

459 To our best knowledge, this study is the first to summarize levels of genetic diversity
460 focusing on the Korean orchids, although it also includes data from several orchid species
461 outside the Korean Peninsula. As Godt & Hamrick (2001) stressed, empirical genetic studies
462 of rare plants can provide insights that may guide conservation and management plans. We
463 found that 24 rare Korean orchids maintain significantly lower within-population genetic
464 variation than their common congeners and common orchid species at the global level. Of
465 particular concern, we found that ten species exhibit a total lack of allozyme genetic diversity
466 (*Cephalanthera subaphylla*, *Cypripedium japonicum*, *Epipactis papillosa*, *Goodyera repens*,
467 *Habenaria dentata*, *Liparis pterosepala*, *Oreorchis coreana*, *Pecteilis radiata*, *Peristylus*

468 *densus*, and *Tipularia japonica*; Table 1). In addition, other six species (*Bletilla striata*,
469 *Galearis cyclochila*, *Neottianthe cucullata*, *Pelatantheria scolopendrifolius*, *Platanthera*
470 *hologlottis*, and *Pogonia minor*; Table 1) also harbor extremely low levels of within-
471 population genetic variation.

472 Based on the genetic data presented here, conservation priority should be given to rare
473 orchid species on the Korean Peninsula. Particularly, special attention should be paid to Jeju,
474 as a large part of the orchids that exhibit low levels of genetic diversity occur on this island
475 (*Cephalanthera subaphylla*, *Goodyera repens*, *Liparis pterosepala*, *Oreorchis coreana*,
476 *Pelatantheria scolopendrifolius*, *Peristylus densus*, *Platanthera hologlottis*, *Pogonia minor*,
477 and *Tipularia japonica*). One of these species is endemic to Jeju (*Liparis pterosepala*),
478 another is quasi-endemic (*Oreorchis coreana*), and a third species' Korean occurrences are
479 restricted to Jeju (*Peristylus densus*). In addition, the rare terrestrial orchid *Nervilia nipponica*
480 (formerly known as an endemic orchid to southern Japan) was newly recorded on Jeju (Kim
481 et al., 2009), exhibiting extremely low levels of nrDNA genetic diversity (Eum et al., 2011).
482 We recommend periodic monitoring of the rare orchid species on Jeju to detect any declining
483 trend in their populations.

484 Another take-home message from this study is that the results of genetic analyses of
485 seven orchid species (three *Calanthe* species, *Cymbidium kanran*, *Cypripedium macranthos*,
486 *Galearis cyclochila*, and *Liparis kumokiri*) could not have been predicted based on
487 generalizations from the allozyme literature or on analyses of congeneric species with similar
488 life history traits, again stressing the importance of empirical genetic studies (Godt &
489 Hamrick, 2001). Such genetic studies would also be important to elucidate the evolutionary
490 trajectories of rare and endangered orchids on the Korean Peninsula (including Jeju),
491 especially if conspecific populations from adjacent countries are included. In addition, these
492 studies are essential to design tailored conservation measures. For example, in the specific

493 case of warm-temperate orchids, individuals from their colonization sources (e.g., the former
494 LGM refugial areas in southeastern Japan) could be used as source populations for their *in*
495 *situ* (reinforcement and reintroduction) or *ex situ* conservation, if genetic analyses
496 demonstrate that they are genetically similar to the Korean populations (combining two
497 genetically-divergent populations may result in outbreeding depression; Fenster & Dudash,
498 1994).

499

500 **Future perspectives**

501

502 In future studies, some issues on how natural and/or artificial habitat (population)
503 fragmentation and gene flow (or lack of) impact the genetic diversity and demography of rare
504 orchid species and also how global warming may impact some of these species must be
505 studied in depth (Liu et al., 2010; Chung et al., 2014). In fact, recent studies have shown that
506 many orchids are extremely susceptible to habitat destruction or disturbance compared to
507 other plants because they have “above” and “below” ground limitations (i.e., pollinator
508 specialization, limited recruitments, and mycorrhizal specificity; Cozzolino & Widmer, 2005;
509 Wateman et al., 2011; McCormick & Jacquemyn, 2014). Thus, in parallel to genetic and
510 phylogeographic surveys, long-term ecological studies (e.g., minimum viable population size
511 and demographic dynamics, extent of seed dispersal, pollination biology and ecology, seed
512 germination ecology, association of mycorrhizal fungi, processes of colonization and
513 population growth) are also necessary before effective conservation strategies can be
514 designed and implemented. Unfortunately, this suggestion is critical because only a few such
515 works focused on Korean orchids are available to date.

516

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- 894

895 **Table 1** Comparisons of allozyme-based genetic diversity and genetic differentiation for
 896 orchids in South Korea (**bold faced**) and their available congeners. The number in the
 897 column represents an alphabetic order of 21 genera^a

	Species (country sampled) (R/C) ^b	Ecol. affinity ^c / Range ^d (R/C) ^c	GF ^f	NP ^g	Genetic parameter ^h						Ref ⁱ	
					%P _S	%P _P	A _S	A _P	H _{CS}	H _{CP}		G _{ST}
1.	<i>Bletilla striata</i> (S. Korea) (R)	WT/CSC, MY, SJ, SK (R)	T	16	15.0	12.8	1.15	1.13	0.060	0.049	0.130	1
2.	<i>Bulbophyllum drymoglossum</i> (S. Korea) (R)	WT/SC, SJ, SK, TW (R)	E, L	2	4.8	2.4	1.05	1.03	0.016	0.011	0.253	2
	<i>B. adiantinum</i> (Brazil) (C)	TR/ BR (C)	E, R	2	100.0	92.9	na	2.95	na	0.439	0.018	3
	<i>B. bidentatum</i> (Brazil) (C)	TR/ BR (C)	R	1	100.0	100.0	3.80	3.80	0.612	0.612	na	3
	<i>B. epiphytum</i> (Brazil) (C)	TR/ BR (C)	E	2	100.0	92.7	na	3.20	na	0.466	0.166	3
	<i>B. exaltatum</i> (Brazil) (C)	TR/ BR, GU, VE (C)	E, R	20	100.0	66.1	4.11	2.07	0.338	0.266	0.230	4
	<i>B. insectiferum</i> (Brazil) (C)	TR/ BR (C)	R	1	92.9	92.9	2.60	2.60	0.439	0.439	na	3
	<i>B. involutum</i> (Brazil) (C)	TR/ BR (C)	R	7	100.0	69.9	3.33	2.00	0.333	0.267	0.232	4
	<i>B. plumosum</i> (Brazil) (C)	TR/ BR (C)	E	4	100.0	92.9	na	2.95	na	0.439	0.008	3
	<i>B. regnellii</i> (Brazil) (C)	TR/ BR (C)	E	1	92.9	92.9	3.40	3.40	0.481	0.481	na	3
	<i>B. rupicola</i> (Brazil) (C)	TR/ BR (C)	R	1	100.0	100.0	3.40	3.40	0.490	0.490	na	3
	<i>B. sanderianum</i> (Brazil) (C)	TR/ BR (C)	R	2	66.7	38.9	1.89	1.60	0.179	0.160	0.145	4
	<i>B. weddellii</i> (Brazil) (C)	TR/ BR (C)	R	4	77.8	47.2	2.56	1.68	0.238	0.183	0.269	4
3.	<i>Calanthe discolor</i> (S. Korea) (R)	WT/CSC, SJ, SK (C)	T	9	88.2	68.6	2.59	2.01	0.244	0.227	0.068	5
	<i>C. reflexa</i> (Jeju Is. in S. Korea) (R)	WT/CSC, JJ, MY, SJ, TW (C)	T	2	47.1	47.1	1.53	1.50	0.186	0.185	0.006	5
	<i>C. sieboldii</i> (S. Korea) (R)	WT/HU, RY, SK, TW (C)	T	3	76.5	66.7	2.35	1.96	0.293	0.280	0.072	5
4.	<i>Cephalanthera longibracteata</i> (S. Korea) (C)	T/K, J, NEC (C)	T	3	30.0	18.0	1.45	1.27	0.097	0.036	0.247	6
	<i>C. subaphylla</i> (S. Korea) (R)	B, T/BH, EH, K, J, NEC, RFE (R)	T	2	0.0	0.0	1.00	1.00	0.000	0.000	na	7
	<i>C. damasonium</i> (C. Italy) (C)	T, WT/BH, EU, IN, MY, NWY, SWA (C)	T	13	0.0	0.0	1.00	1.00	0.000	0.000	na	8
	<i>C. longifolia</i> (C. Italy) (C)	B, T/BH, CC, EU, IN, KAS, MY, NAF, NE, PA, SWA, SWC (C)	T	3	55.6	48.1	1.67	1.59	0.188	0.168	0.104	8
	<i>C. rubra</i> (C. Italy) (C)	T/EU to CEA (C)	T	7	66.7	33.3	1.67	1.33	0.180	0.127	0.247	8
	<i>C. rubra</i> (NE Poland) (C)		T	9	53.9	13.9	1.54	1.14	0.125	0.059	0.267	9
5.	<i>Cremastra appendiculata</i> var. <i>variabilis</i> (S. Korea) (R)	T, WT/CSC, J, SK, NV, TH (C)	T	12	50.0	48.1	1.77	1.70	0.231	0.215	0.066	10

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904 **Table 1 Continued.**

Species (country sampled) (R/C) ^b	Ecol. affinity ^c / Range ^d (R/C) ^e	GF ^f	NP ^g	Genetic parameter ^h						Ref ⁱ	
				%P _s	%P _p	A _s	A _p	H _{es}	H _{ep}		G _{ST}
6. <i>Cymbidium goeringii</i> (S. Korea) (C)	WT/BH, CSC, J, SK, TW, NWI (C)	T	16	71.0	63.0	2.71	2.08	0.251	0.240	0.098	11
<i>C. goeringii</i> (Japan) (R)		T	7	71.4	62.2	2.21	1.95	0.240	0.230	0.027	12
<i>C. kanran</i> (Jeju Is. in S. Korea) (R)	WT/SC, SJ, TW (R)	T	1	66.7	66.7	2.83	2.83	0.173	0.173	na	7
7. <i>Cypripedium japonicum</i> (S. Korea) (R)	T/CSC, J, K (R)	T	6	0.0	0.0	1.00	1.00	0.000	0.000	na	13
<i>C. macranthos</i> (S. Korea) (R)	B/J, K, NEC, R, TW (C)	T	4	50.0	46.7	1.50	1.47	0.200	0.185	0.059	13
<i>C. macranthos</i> var. <i>rebunense</i> (Rebun Is. in Japan) (R)	B/RI (R)	T	5	62.0	60.4	1.85	1.69	0.187	0.183	0.085	14
<i>C. acaule</i> (Michigan, USA) (C)	B, T/CEC, EUS (C)	T	4	46.2	34.7	1.77	1.44	0.095	0.080	0.164	15
<i>C. arietinum</i> (Michigan, USA) (R)	B, T/CEC, GL, NEUS (R)	T	4	0.0	0.0	1.00	1.00	0.000	0.000	na	15
<i>C. calceolus</i> (Poland) (C)	B, T/EU, J, NEC, NK, R (C)	T	32	54.6	36.4	2.36	1.58	0.228	0.151	0.137	16
<i>C. candidum</i> (Michigan, USA) (R)	B, T/MWUS (R)	T	5	66.7	38.3	2.00	1.43	0.054	0.050	0.069	15
<i>C. fasciculatum</i> (Washington, USA) (R)	T/WUS (R)	T	3	25.0	19.5	na	1.20	0.040	0.030	0.040	17
<i>C. kentuckiense</i> (Arkansa, Oklahoma, Texas, Virginia in USA) (R)	T/SUS (R)	T	8	25.0	12.5	1.33	1.15	0.050	0.042	0.182	18
<i>C. parviflorum</i> var. <i>makasin</i> (Indiana, Michigan in USA) (C)	B, T/NECA, NUS, SUNA (C)	T	8	81.8	69.3	2.40	1.80	0.290	0.230	0.199	19
<i>C. parviflorum</i> (Georgia, Missouri, Oklahoma, Virgia in USA) (C)	T/SEUS (C)	T	8	54.5	35.2	1.90	1.40	0.130	0.130	0.149	19
<i>C. parviflorum</i> var. <i>pubescens</i> (northern form) (Illinois, Indiana, Michigan, Ohio in USA) (C)	B, T/CAN, EUS, SUNA (C)	T	12	81.8	65.2	2.50	1.70	0.220	0.200	0.137	19
<i>C. parviflorum</i> var. <i>pubescens</i> (southern form) (SE USA, Ohio in USA) (C)	T/SEUS (C)	T	12	81.8	50.8	2.50	1.60	0.190	0.160	0.209	19
<i>C. reginae</i> (Michigan, USA) (R)	B, T/CEC, EUS (R)	T	3	18.2	15.2	1.27	1.15	0.037	0.024	0.349	15
<i>C. reginae</i> (SE USA, Ohio in USA) (R)		T	9	10.0	7.8	1.20	1.11	0.051	0.038	0.212	20
8. <i>Epipactis thunbergii</i> (S. Korea) (C)	T, WT/EZ, J, SK (C)	T	8	4.3	3.8	1.04	1.04	0.020	0.013	0.388	21
<i>E. papillosa</i> (S. Korea) (R)	T/J, K, SLF (R)	T	8	0.0	0.0	1.00	1.00	0.000	0.000	na	22
<i>E. atrorubens</i> (NE Poland) (R)	B, T/EU, ES, CEA (C)	T	4	9.1	9.1	1.14	1.12	0.042	0.034	0.265	23
<i>E. helleborine</i> (NE Poland) (C)	T/EUA, CEA to J (C)	T	5	40.9	32.7	1.68	1.51	0.141	0.115	0.220	24
<i>E. helleborine</i> (Scotland, England) (C)		T	13	na	33.2	na	1.46	na	0.145	0.240	25
<i>E. helleborine</i> (Belgium, Denmark, England, France, Germany, Scotland, Switzerland) (C)		T	35	na	55.0	na	1.77	na	0.230	0.200	26
<i>E. helleborine</i> (Canada, naturalized) (C)		T	12	na	58.0	na	1.90	na	0.232	0.090	26
<i>E. helleborine</i> (C. Italy) (C)		T	4	62.5	59.0	2.00	1.82	0.238	0.233	0.033	27
<i>E. helleborine</i> (Denmark) (C)		T	13	88.9	73.6	2.78	2.63	0.302	0.274	0.087	28

907 **Table 1** Continued.

Species (country sampled) (R/C) ^b	Ecol. affinity ^c / Range ^d (R/C) ^e	GF ^f	NP ^g	Genetic parameter ^h						Ref ⁱ	
				%P _s	%P _p	A _s	A _p	H _{es}	H _{ep}		G _{ST}
<i>E. leptochila</i> (Scotland, England) (C)	T/WEU (C)	T	2	57.1	26.5	1.71	1.36	0.152	0.117	na	29
<i>E. microphylla</i> (C. Italy) (R)	T/EUA (R)	T	2	0.0	0.0	1.00	1.00	0.000	0.000	na	27
<i>E. palustris</i> (C. Italy) (R)	B/CIB (R)	T	1	29.0	29.0	1.29	1.29	0.085	0.085	na	27
<i>E. phyllanthus</i> (Denmark) (R)	T/WEU (R)	T	6	0.0	0.0	1.00	1.00	0.000	0.000	na	28
<i>E. phyllanthus</i> (Scotland, England) (R)		T	2	7.1	7.1	1.07	1.07	0.028	0.028	na	29
<i>E. purpurata</i> (Denmark) (R)	T/WEU (R)	T	5	0.0	0.0	1.00	1.00	0.000	0.000	na	28
9. <i>Galearis (Orchis) cyclochila</i> (S. Korea) (R)	B/J, K, NEC, NEQ, R (C)	T	2	50.0	46.4	1.71	1.68	0.216	0.210	0.030	30
<i>G. (Gymnadenia) camtschatica</i> (Ulleung Is. in S. Korea) (R)	B/J, K, NEC, RFE (C)	T	4	18.2	18.2	1.18	1.18	0.066	0.067	0.000	31
10. <i>Goodyera rosulacea</i> (S. Korea) (C)	T/SK (C)	T	7	31.6	27.8	1.37	1.31	0.100	0.126	0.150	32
<i>G. repens</i> (S. Korea) (R)	B/BH, C, EU, IN, J, K, KAS, MY, NA, NE, R, TW (C)	T	3	0.0	0.0	1.00	1.00	0.000	0.000	na	7
<i>G. repens</i> (NE Poland) (C)		T	11	50.0	50.0	1.90	1.68	0.210	0.197	0.060	33
<i>G. procera</i> (Hong Kong) (C)	TR, WT/BA, BH, CA, HA, IN, IND, LA, MY, NE, PH, RY, SC, SR, TH, TW, VI, YT (C)	T	15	33.3	21.8	1.33	1.22	na	0.073	0.523	34
11. <i>Habenaria dentata</i> (S. Korea) (R)	T, WT, TR/CA, IN, LA, MY, NE, SC, SJ, SK, TH, TW, VI (C)	T	1	0.0	0.0	1.00	1.00	0.000	0.000	na	7
12. <i>Hemipilia (Amitostigma) gracile</i> (S. Korea) (C)	T/CSC, J, K, TW (R)	L	17	5.3	2.5	1.11	1.03	0.026	0.009	0.781	31
13. <i>Liparis kumokiri</i> (S. Korea) (C)	B, T/J, K, RFE (C)	T	17	0.0	0.0	1.00	1.00	0.000	0.000	na	35, 36
<i>L. makinoana</i> (S. Korea) (C)	B, T/J, K, RFE (C)	T	4	73.3	70.0	2.27	2.07	0.346	0.317	0.107	35, 36
<i>L. pterosepala</i> (Jeju Is., S. Korea) (R)	WT/JJ (R)	T	2	0.0	0.0	1.00	1.00	0.000	0.000	na	7
14. <i>Neottianthe (Gymnadenia) cucullata</i> (S. Korea) (R)	B, T, WT/BH, C, EEU, J, K, MO, NE, R (C)	T	4	27.3	12.5	1.27	1.13	0.039	0.036	0.081	31
15. <i>Oreorchis patens</i> (S. Korea) (C)	B/C, J, K, RFE, TW (C)	T	12	76.5	62.8	2.53	1.96	0.258	0.237	0.075	37
<i>O. coreana</i> (Jeju Is. in S. Korea) (R)	WT/JJ, SJT (R)	T	4	0.0	0.0	1.00	1.00	0.000	0.000	na	37
16. <i>Pecteilis (Habenaria) radiata</i> (S. Korea) (R)	T, WT/SK, J, WH (R)	T	1	0.0	0.0	1.00	1.00	0.000	0.000	na	7
17. <i>Pelatantheria (Sarcanthus) scolopendrifolius</i> (S. Korea) (R)	WT/CC, SJ, SK (R)	E, L	3	4.8	1.6	1.10	1.02	0.015	0.002	0.899	2

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910

911 **Table 1** *Continued.*

	Species (country sampled) (R/C) ^b	Ecol. affinity/ Range ^d (R/C) ^c	GF ^f	NP ^g	Genetic parameter ^h						Ref ⁱ	
					%P _s	%P _p	A _s	A _p	H _{es}	H _{ep}		G _{ST}
18.	<i>Peristylus densus</i> (Jeju Is.) (R) (= <i>Habenaria flagellifera</i>)	WT/JJ, SJ (R)	T	1	0.0	0.0	1.00	1.00	0.000	0.000	na	7
19.	<i>Platanthera hologlottis</i> (S. Korea) (R)	B/C, J, K, RFE (C)	T	3	10.0	6.7	1.10	1.07	0.047	0.031	0.328	7
	<i>P. leucophaea</i> (NE USA) (R)	T/NEUS (R)	T	7	25.0	11.9	1.67	1.18	0.103	0.033	0.754	38
	<i>P. chlorantha</i> (NE Poland) (R)	B, T/C, J, K, R, WA, EU (C)	T	6	33.3	25.6	1.60	1.36	0.102	0.078	0.251	9
	<i>P. bifolia</i> (NE Poland) (C)	B, T/EUA (C)	T	14	33.3	22.3	na	1.48	na	0.093	0.048	39
20.	<i>Pogonia minor</i> (S. Korea) (R)	T, TR, WT/J, SK, ST (C)	T	11	14.3	2.7	1.14	1.04	0.010	0.008	0.211	31
21.	<i>Tipularia japonica</i> (S. Korea) (R)	WT/SK, SJ (R)	T	8	0.0	0.0	1.00	1.00	0.000	0.000	na	22

912 ^a *Abbreviations:* %P, the percent polymorphic loci; A, mean number of alleles per locus, H_e,
 913 Hardy–Weinberg expected heterozygosity or genetic diversity; G_{ST} or F_{ST}, measures of
 914 among-population differentiation; na, not available; the subscripts “P” or “S” denote
 915 population means or species’ (or pooled samples) values, respectively.

916 ^b R/C, rare or common in area, regions, country or countries that sampled for allozyme studies.

917 ^c Ecological affinity: B, boreal; T, temperate; TR, tropical; WT, warm temperate (or subtropical).

918 ^d Range: BA, Bangladesh; BH, Bhutan; BR, Brazil; C, China; CA, Cambodia; CAN, Canada; CC,
 919 central China; CEA, central Asia; CEC, central and eastern Canada; CIB, circumboreal regions; CSC,
 920 central and southern China; CUS, central United States of America; EC, eastern Canada; EH, eastern
 921 Himalayas; EEU, eastern Europe; ES, eastern Siberia; EU, Europe; EUA, Eurasia; EUS, eastern US;
 922 EZ, eastern Zhejiang, South China; GL, States around the Great Lakes in US; GU, Guyana; HA,
 923 Hainan Island, South China; HU, Hunan, southern China; IN, India; IND, Indonesia; J, Japan; JJ, Jeju
 924 Island, South Korea; K, Korea; KAS, Kashmir; LA, Laos; MO, Mongolia; MWUS, Midwest US; MY,
 925 Myanmar; NA, North America; NAF, northern Africa; NCUS, North Central US; NE, Nepal; NEC,
 926 northeastern China; NECA, northeastern California, US; NEQ, northeastern Qinghai, western China;
 927 NEUS, North Eastern US; NI, northern India; NK, northern Korea; NUS, northern US; NV, North
 928 Vietnam; NWI, Northwest India; NWY, northwestern Yunnan, South China; PA, Pakistan; PH,
 929 Philippines; R, Russia; RFE, Russian Far East; RI, Rebun Island, Japan; RY, Ryukyu Islands,

930 southern Japan; SA, Sakhalin; SC, South China; SCUS, South Central US; SEUS, southeastern US;
931 SJ, southern Japan; SJT, Tochigi Prefecture in southern Japan; SK, southern Korea; SLF, Fengcheng
932 in southern Liaoning, northeastern China; SR, Sri Lanka; ST, southern Taiwan; SUNA, subarctic
933 North America; SUS, South US; SWA, South Western Asia; SWC, South Western China; TH,
934 Thailand; TW, Taiwan; TX, Texas, USA; VE, Venezuela; VI, Vietnam; WA, Western Asia; WEU,
935 Western Europe; WH, Western Henan, South China; WUS, West US; WCUS, West Central US; YT,
936 Yakushima and Tanekashima Islands, southern Japan.

937 ^e R/C, rare or common at regional or global levels (at the species level). See more explanations in
938 Materials and Methods section.

939 ^f Growth form: E, epiphytic; L, lithophytic, R, rupicolous (inhabiting the rock areas or in rock
940 crevices); T, terrestrial.

941 ^g NP, number of populations examined.

942 ^h %P, percentage of polymorphic loci; *A*, mean number of allele per locus; *H_e*, genetic diversity.
943 Allozyme-based genetic diversity parameters are well described in Berg & Hamrick (1997).The
944 subscript “S” denotes species’ (or pooled samples) values, while the subscript “P” indicates
945 population means. *G_{ST}* (*F_{ST}*), measures of among-population differentiation.

946 ⁱ Source references: 1, Chung et al. (2013b); 2, Chung et al. (2007a); 3, Azevedo et al. (2007); 4,
947 Ribeiro et al. (2008); 5, Chung et al. (2013c); 6, Chung et al. (2004b); 7, M.Y. Chung & M. G. Chung
948 (unpubl. data); 8, Scacchi et al. (1991); 9, Brzosko & Wróblewska (2013); 10, Chung et al. (2013d);
949 11, Chung & Chung (1999); 12, Chung & Chung (2000); 13, Chung et al. (2009); 14, Izawa et al.
950 (2007); 15, Case (1994); 16, Brzosko et al. (2011); 17, Aagaard et al. (1999); 18, Case et al. (1998);
951 19, Wallace & Case (2000); 20, Kennedy & Walker (2007); 21, Chung & Chung (2007); 22, Chung
952 (2009b); 23, Brzosko et al. (2006); 24, Brzosko et al. (2004); 25, Hollingsworth & Dickson (1997); 26,
953 Squirrell et al. (2001); 27, Scacchi et al. (1987); 28, Ehlers & Pedersen (2000); 29, Harris & Abbott
954 (1997); 30, Chung et al. (2005a); 31, Chung (2009a); 32, Chung & Chung (2010); 33, Brzosko et al.

955 (2013); 34, Wong & Sun (1999); 35, Chung et al. (2005b); 36, Chung et al. (2007b); 37, Chung et al.
956 (2012); 38, Wallace (2002); 39, Brzosko et al. (2009).

957 **Table 2** Summary statistics of the genetic diversity for rare orchids in Korea and their
958 common congeners at the global scale (nine pairs)^a

Parameter	Mean values (SE)		Wilcoxon signed-rank test		Rare vs. common orchid correlation	
	Rare	Common	Z	P	Corr. coef. (r_s)	P
%P _P	11.04 (7.41)	45.00 (6.68)	-2.547	0.006	0.347	0.359
A _P	1.24 (0.20)	1.74 (0.15)	-1.836	0.038	0.402	0.291
H _{eP}	0.031 (0.019)	0.181 (0.032)	-2.666	0.005	0.237	0.552
%P _S	12.43 (7.39)	54.88 (7.33)	-2.666	0.005	0.237	0.552
A _S	1.28 (0.21)	2.11 (0.21)	-2.380	0.010	0.682	0.069
H _{eS}	0.033 (0.021)	0.209 (0.029)	-2.520	0.007	0.546	0.171

959 ^a Wilcoxon signed-rank tests were conducted for comparing both population (subscript “P”)

960 and species (subscript “S”) level values for each measure.

961

962 **Table 3** Summary of allozyme-based genetic parameters for rare, common orchids, plants
 963 having similar life history-traits, and species from two areas largely recognized as harboring
 964 glacial refugia [i.e., the Baekdudaegan (BDDG, the main mountain system of the Korean
 965 Peninsula), the southeastern US, northwestern Mediterranean Basin]^a

Category	%P _S	%P _P	A _S	A _P	H _{CS}	H _{EP}	G _{ST}	Ref ^b
Rare orchids in Korea (<i>N</i> = 24)	21.8	18.6	1.34	1.22	0.075	0.070	0.169 (<i>N</i> = 12)	1
Rare orchids in Table 1 (<i>N</i> = 38)	23.3	19.2	1.37	1.27	0.073	0.066	0.189 (<i>N</i> = 21)	1
Common orchids in Table 1 (<i>N</i> = 32)	62.3	50.4	2.17	1.90	0.225	0.217	0.194 (<i>N</i> = 25)	1
Means for orchids (<i>N_S</i> = 68; <i>N_P</i> = 68)	41.0	33.2	1.71	1.55	0.135	0.134	0.190 (<i>N</i> = 68)	1
Means for orchids (<i>N_S</i> = 32; <i>N_P</i> = 36)	46.2	33.7	1.83	1.46	0.119	0.107	0.163 (<i>N</i> = 32)	2
Means for orchids (<i>N_S</i> = 16)	44.8	na	na	na	0.137	na	0.087 (<i>N</i> = 16)	3
Means for orchids (<i>N_S</i> = 71)	na	na	na	na	na	na	0.161 (<i>N</i> = 71)	4
Means for orchids (<i>N_S</i> = 52)	na	na	na	na	na	na	0.146 (<i>N</i> = 52)	5
All plants (<i>N_S</i> = 725; <i>N_P</i> = 725)	52.2	35.1	1.99	1.53	0.153	0.116	0.225 (<i>N</i> = 830)	6
Endemic plants (<i>N_S</i> = 81; <i>N_P</i> = 100)	40.0	26.3	1.80	1.39	0.096	0.063	0.248 (<i>N</i> = 52)	6
Plants narrowly-distributed (<i>N_S</i> = 101; <i>N_P</i> = 115)	45.1	30.6	1.83	1.45	0.137	0.105	0.242 (<i>N</i> = 82)	6
Short-lived herbaceous perennials (<i>N_S</i> = 152; <i>N_P</i> = 159)	41.3	28.0	1.70	1.40	0.116	0.096	0.233 (<i>N</i> = 119)	6
Plants with outcrossing-animal breeding system (<i>N_S</i> = 172; <i>N_P</i> = 164)	51.1	35.9	1.99	1.54	0.167	0.124	0.197 (<i>N</i> = 124)	6
Plants occurring mainly in the BDDG in Korea ^c (<i>N_S</i> = 16, <i>N_P</i> = 16)	64.3	46.0	2.20	1.72	0.193	0.159	0.175 (<i>N</i> = 16)	7
Rare plants in the southeastern US (<i>N_S</i> = 52; <i>N_P</i> = 52)	46.7	33.3	1.87	1.53	0.123	0.100	0.187 (<i>N</i> = 52)	8
Plants from NW Mediterranean Basin (<i>N_P</i> = 36)	na	34.2	na	1.53	na	0.113	0.248 (<i>N</i> = 36)	9

966 ^a Na, not available.

967 ^b Source references: 1, present study; 2, Case (2002); 3, Hamrick & Godt (1996); 4,
 968 Forrest et al. (2004); 5, Phillips et al. (2012); 6, Hamrick & Godt (1989); 7, Chung et al.
 969 (2017); 8, Godt & Hamrick (2001); 9, López-Pujol et al. (2009).

970 ^c Only species with most of their populations in Korea (more than half) occurring on main
 971 ridge or on immediate vicinity of the BDDG.

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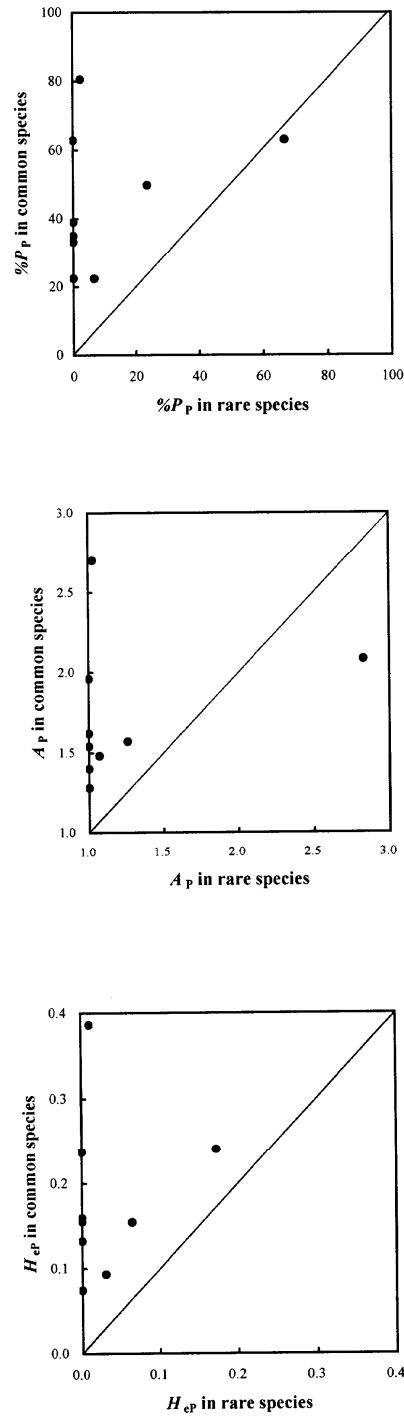
974 **Figure legends**

975

976 **Fig. 1** Plots of genetic variation in rare Korean orchid species vs. their common
977 congeners (nine pairs) at the population level. The line in each graph represents the
978 portion of the graph where rare and common congeners have the same levels of genetic
979 parameters. (A), $\%P_P$; (B), A_P ; (C), H_{eP}

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Fig. 1