



**HAL**  
open science

# How much do we know and how much do we care about genetic diversity of threatened plants? A case study from the French flora

Juliette Ducrettet, Sandrine Maurice, Eric Imbert

## ► To cite this version:

Juliette Ducrettet, Sandrine Maurice, Eric Imbert. How much do we know and how much do we care about genetic diversity of threatened plants? A case study from the French flora. *Botany Letters*, In press, 170 (1), pp.110-118. 10.1080/23818107.2022.2125902 . hal-03786687

**HAL Id: hal-03786687**

**<https://hal.umontpellier.fr/hal-03786687>**

Submitted on 23 Sep 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

1 **How much do we know and how much do we care about genetic**  
2 **diversity of threatened plants? A case study from the French flora.**

3

4 Juliette Ducrettet, Sandrine Maurice and Eric Imbert\*

5 *ISEM, Univ Montpellier, CNRS, IRD, Montpellier, France*

6 \*Corresponding author: [eric.imbert@umontpellier.fr](mailto:eric.imbert@umontpellier.fr)

7

8

9 Author contributions : SM and EI conceived the ideas. JD, JD, SM and EI designed the methodology; JD  
10 collected and analysed the data and led the writing of the manuscript. All authors contributed critically to  
11 the drafts and gave final approval for publication.

12 **Abstract**

13 Small demographic size and reduced genetic diversity increase the extinction  
14 probability of a population. Genetic diversity within populations for neutral markers is  
15 an heuristic parameter, as it reflects past and ongoing processes acting on populations,  
16 and informs on possible futures. This study presents a synthesis of the knowledge on  
17 neutral genetic diversity for threatened plants in metropolitan France and the use of such  
18 data in management actions. Pairing threatened species with the closest non-threatened  
19 species for which we could find appropriate genetic data, we collected information on  
20 genetic diversity for 25 threatened species and non-threatened controls. We found that  
21 threatened species in France have on average a lower within-population genetic  
22 diversity than non-threatened controls and thus are exposed to risks linked to genetic  
23 erosion. Combining an analysis of recovery plans and a survey addressed to  
24 practitioners, we concluded that genetic diversity is rarely integrated in management  
25 actions. The integration of such information into applied conservation remains a  
26 challenge. We provide some guidelines to collect biological traits impacting within-  
27 population genetic diversity and some specific recommendations for a better  
28 incorporation of population genetics concepts into conservations actions.

29 Keywords: Genetic diversity, conservation, threatened plants, management,  
30 metropolitan France

## 31 **Introduction**

32 Anthropogenic activities such as intensive agricultural practices and urbanization lead to  
33 habitat destruction and fragmentation. For plant species, these environmental changes  
34 affect population dynamics by altering population size, population number and  
35 population isolation (Lande 1988; Camill 2010; Ralls et al. 2018). In particular, small  
36 populations are vulnerable to density-dependent effects (Allee effect) and demographic  
37 stochasticity (Lande 1988; Oostermeijer et al. 2003). The reduction in demographic size  
38 of a population is also accompanied by a reduction in effective population size, i.e an  
39 increase of genetic drift and thus a decrease in within-population genetic diversity  
40 (Ellstrand and Elam 1993). A positive correlation between neutral genetic diversity and  
41 population size is a common observation in natural populations (for a meta-analysis see  
42 Leimu et al. 2006). Furthermore, population fragmentation reduces gene flow among  
43 populations, which also contributes to decrease genetic diversity within populations  
44 (Ellstrand and Elam 1993). The level of both neutral genetic variation and quantitative  
45 genetic variation are expected to be reduced by drift and isolation (Allendorf and  
46 Luikart 2006) and neutral diversity is expected to covary with selected diversity (Kardos  
47 et al. 2021). In addition, in small populations, drift can lead to the fixation of deleterious  
48 alleles, thus increasing genetic load and inbreeding depression (Keller and Waller  
49 2002), and a positive correlation between neutral genetic diversity and fitness is often  
50 observed (Reed and Frankham 2004; Leimu et al 2006). The general framework of  
51 evolutionary rescue has emphasized that population persistence relies partly on  
52 evolutionary potential (Gomulkiewicz and Holt 1995; Gonzalez et al. 2013; Carlson et  
53 al. 2014; Olivieri et al. 2016; Ralls et al. 2018; Thompson 2020), depending both on  
54 population size and standing genetic variation (Frankham et al. 2017).

55 Hence, risks linked to changes in population genetic diversity should also be  
56 included in threat detection (Allendorf and Luikart 2006; Olivieri et al. 2016) and the  
57 decision-making process that leads to management actions should integrate the concept  
58 of evolutionary potential, particularly in the context of global change (Ashley et al.  
59 2003; Smith et al. 2014; Olivieri et al. 2016; Ralls et al. 2018; Thompson 2020).  
60 Evaluations of the integration of genetic issues into management have been carried out  
61 in several countries (Pierson et al. 2016; Taylor et al. 2017; Cook and Sgrò 2018).  
62 Using surveys addressed to people professionally involved in conservation actions,  
63 Taylor et al. (2017) and Cook and Sgrò (2018) showed a low level of integration of key  
64 evolutionary concepts in biodiversity management, in New Zealand and Australia,  
65 respectively. Pierson et al. (2016) used another approach by evaluating how genetic  
66 issues are incorporated into recovery plans. France was included in their analysis but  
67 only through the national action plans (PNA) which are clearly not representative of  
68 conservation actions in France.

69 Our study aims to assess within-population genetic diversity of threatened  
70 Angiosperm species in France and the use of such information in conservation actions.  
71 First, we evaluated the data available for neutral genetic diversity of plants species  
72 considered as threatened in France using the IUCN list and the legal protection status in

73 France. Although it would be best to make congeneric comparisons to control for  
74 confounding effects of phylogeny and life-history traits on genetic diversity  
75 (Gitzendanner and Soltis 2000; Spielman et al. 2004; Hamabata et al. 2019; Hamrick  
76 and Godt 1996; Leimu et al. 2006; Duminil et al. 2007), sometimes genetic data were  
77 not available for a non-threatened congener, in which case we instead compared the  
78 threatened species with its closest relative for which appropriate genetic data were  
79 available. Next, in order to assess the degree of consideration of genetic diversity in  
80 conservation actions in metropolitan France, we analysed available recovery plans and  
81 performed a survey addressed to managers.

## 82 **Materials and Methods**

### 83 *Genetic diversity of threatened plant species in France*

84 The IUCN Red List threatened categorization system (CR, EN, VU) was used to  
85 identify 452 threatened plant species and subspecies occurring in metropolitan France  
86 (<https://uicn.fr/liste-rouge-flore/>, November 2019). In addition, the list of the 387  
87 legally protected Angiosperms species in France was extracted from the institutional  
88 website collecting data on biodiversity in France (<https://inpn.mnhn.fr/>, November  
89 2019). The two lists were merged to define threatened Angiosperm species and  
90 subspecies in metropolitan France. We also added three species (*Arenaria grandiflora*,  
91 *Convolvulus lanuginosus*, *Pinguicula grandiflora*) with a local status of protection that  
92 are known to have been studied for genetic diversity in the area where they are  
93 protected. The final list included 749 plant taxa. We did not check for synonymy at this  
94 stage. It is important to note that genetic diversity is not considered neither in the IUCN  
95 criteria, nor for a legal protection status in France.

96 Using this list, automatic data mining was carried out on NCBI  
97 (<https://www.ncbi.nlm.nih.gov/>), on Google Scholar and on the French registry of Ph-D  
98 theses (<http://theses.fr/>) to find any study on these species. A search on the Web of  
99 Science database was also performed using the list of species (eg TITLE = "SPECIES1"  
100 OR "SPECIES2"...). We obtained 6779 results (20 April 2022), and we refined the  
101 results using the keyword "*genetic*". Among the 625 results, we retained publication  
102 with at least one author from France (Countries/Regions = "France"). For two species  
103 (*Agropyron cristatum* and *Vitis vinifera*) related to largely cultivated plants, a dedicated  
104 search was done.

105 Among all the studies collected, only those with data on within-population  
106 genetic diversity were retained. We used genetic diversity at population scale since it is  
107 the pertinent scale to detect effects of drift, absence of migration and because selection  
108 needs within-population diversity to act. For each species, parameters estimating genetic  
109 diversity within populations were extracted from the studies. We also documented  
110 population size and sampling size, and several life-history traits known to influence  
111 genetic diversity such as mating system, longevity, vegetative reproduction, dispersion  
112 vector and pollination vector (see Appendix 1).

113 As our goal was to compare genetic diversity of threatened species to genetic  
114 diversity of non-threatened species, we searched for studies performed on related non-  
115 threatened species. The collection of data for non-threatened species was performed in  
116 several phases. Ideally, each pair of species should include a threatened and non-  
117 threatened congeneric species (see Lavergne et al. 2004) occurring in the same habitat  
118 and sharing common life-history traits. As we aimed to compare genetic diversity, we  
119 must also have genetic parameters estimated on the same type of genetic markers  
120 although the best comparison would use the same loci for those same markers. We  
121 made a first search on Web of Science using the name of the genus and the types of  
122 genetic markers (e.g. TOPIC= *Anchusa* AND TOPIC= AFLP). In absence of results, we

123 relaxed the congeneric criteria and searched using the family name (e.g. TOPIC=  
124 Caryophyllaceae AND TOPIC= SSR). Species were not considered as a valid control if  
125 they were said to be “rare” or “threatened” by the authors of a study, if they were  
126 cultivated species, or if they were invasive species. When several non-threatened  
127 species were available, we selected the species the most similar to the threatened species  
128 within the pair for life-history traits. For 3 species (*Pinguicula rosea*, *Pinguicula*  
129 *grandiflora* and *Orobanche bartlingii*), we could not find any non-threatened species in  
130 the same family studied with the same markers (AFLP), so we used estimations of  
131 diversity in AFLP from the review on plants by Nybom (2004). For *Eryngium*  
132 *viviparum*, the comparison was made using the only French population and Iberic  
133 populations, since the species is not threatened in Spain (Rasclé et al. 2019). One recent  
134 study on the threatened *Delphinium montanum* documents diversity using SNPs  
135 (Salvado et al. 2022), but we could not find any pertinent study for the non-threatened  
136 control. This species was not included in our comparison.

### 137 *Data analyses*

138 The raw data were the expected heterozygosity within populations, also named Nei’s  
139 gene diversity, extracted from published and unpublished papers (see Appendix 1). We  
140 computed the mean expected heterozygosity per population for each species. Expected  
141 heterozygosity was chosen to estimate genetic diversity because this measure is only  
142 slightly affected by sample size, in contrast to the number of alleles per locus. To test  
143 for the difference in expected heterozygosity between threatened and non-threatened  
144 controls, a non-parametric pairwise comparison test was performed. Because of the  
145 small sample size (see results), we adapted the classical Wilcoxon test for pairwise  
146 comparisons following Manly (1991). First, the V-value was computed using the  
147 *Wilcox.test* function in R (version 4.0.3). Next, the same statistic was computed for  
148 permuted dataset. Species status (threatened vs non threatened) was permuted 1,000  
149 times within pairs, and the original V-value was compared to the distribution of the  
150 permuted values. Finally, the percentage difference in heterozygosity within pairs was  
151 estimated as the signed difference in expected heterozygosity between the threatened  
152 and the non-threatened members of the pair divided by the largest value of expected  
153 heterozygosity in the pair.

### 154 *Considerations of genetic diversity in management actions*

155 First, recovery plans (defined as in Pierson et al. 2016) implemented in France were  
156 downloaded from the website of each of the 10 National Botanic Conservatories acting  
157 in the metropolitan France (Alpin, Bailleul, Bassin Parisien, Brest, Corse, Franche-  
158 Comté, Massif Central, Midi-Pyrénées, Porquerolles, Sud-Atlantique) and from the  
159 website of the French Ministry in charge of biodiversity  
160 (<https://www.ecologie.gouv.fr/>). In each document, we searched for any mention of the  
161 term *genetic* (in French “génétique”), which led us to *population genetics* and *genetic*  
162 *data*. We also documented if any task was assigned to collect data on genetic diversity.

163 We searched for any mention of effective population size (in French “taille efficace”).  
164 We also searched for any reference to habitat and life-history traits such as mating  
165 system, longevity, vegetative reproduction, dispersion vector and pollination vector  
166 (Appendix 2). Finally, management actions directly impacting genetic diversity such as  
167 introduction, reintroduction, reinforcement (sensu Silcok et al. 2019) were also recorded  
168 (Appendix 2). Hereafter, the terms “manipulation of population size” will refer to these  
169 actions.

170         Additionally, as many management actions are not published or are reported in  
171 documents with a very narrow public access, a survey was also conducted using  
172 numerous professional mailing lists (*Conservatoires d’Espaces Naturels*,  
173 *Conservatoires Botaniques Nationaux*, *Parc Nationaux*, *Réseau d’acteurs pour la*  
174 *conservation de la flore méditerranéenne*) and using social networking (Tela Botanica,  
175 Ecodiff) to reach practitioners. The survey was developed using the *Limesurvey*  
176 interface and designed with the purpose of collecting the same types of information as  
177 we gathered from recovery plans (Appendix 3).

178         We thus used two sources of information to study the consideration of genetic  
179 diversity in management actions: the synthesis of management plans available on-line,  
180 hereafter “recovery plans”, and the answer of managers to the survey, hereafter  
181 “surveys”.



## 182 Results

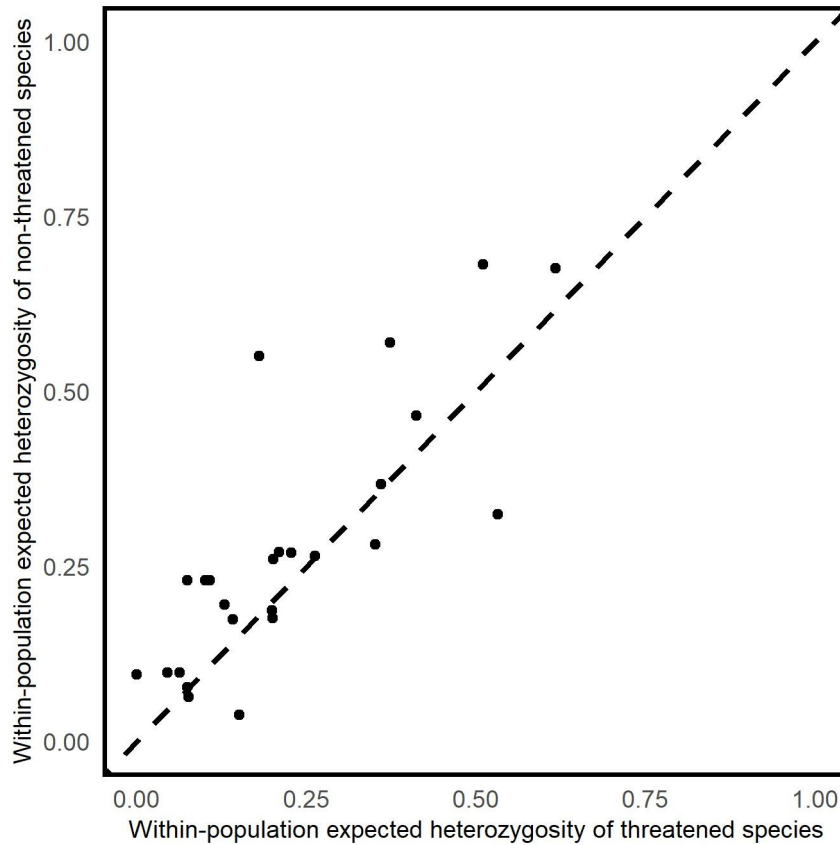
### 183 Genetic diversity of threatened plant species in France

184 From the initial list containing more than 700 plant threatened species, within-  
185 population expected heterozygosity at neutral nuclear loci was gathered only for 25  
186 threatened species (Appendix 1). Only 12 species are considered as threatened species  
187 under IUCN criteria on the French redlist, and two species (*Aster pyrenaeus* and  
188 *Biscutella neustriaca*) are considered as threatened at a global scale. All the 25  
189 threatened species have a French legal protection status either at the national scale (17  
190 species) or at the local scale (8 species). Twenty-two non-threatened species filled the  
191 require conditions to build the pairs, 13 in same genus and 9 in the same family than a  
192 threatened species. For the 3 other pairs, we used data from Nybom (2004, see Materials  
193 and Methods section, Appendix 1). AFLPs (N=20, He=0.20 SD 0.08) and  
194 microsatellites (N=16, He=0.43 SD 0.21) were the most frequently used marker types.  
195 ISSR (N=10, He= 0.14 SD 0.07) and allozymes (N=4, He=0.08 SD 0.05) are the least  
196 frequent and the least diverse markers.

197 All the threatened species in the dataset are perennials except *Ranunculus*  
198 *nodiflorus* and *R. lateriflorus* which are annuals (Appendix 1, Table S1). Threatened  
199 species are mainly polycarpic (76%) and their pollination is mostly entomophilous  
200 (76%). Agents of seed dispersal varied: anemochory (24%), barochory (28%),  
201 hydrochory (8%), and zoochory (8%) (missing data for 8 species). Mating system is  
202 generally considered as allogamous (36%) or mixed (20%). There are 44% of  
203 threatened species able to reproduce asexually. For most pairs, threatened species share  
204 the same life-history traits as their non threatened relatives (Appendix 1, Table S1). In  
205 contrast to life history-traits, demographic parameters of threatened species were highly  
206 variable. For threatened species, mean population sizes ranged from 56 (*Arenaria*  
207 *grandiflora*) to 50150 (*Narcissus triandrus* ssp. *capax*). Some species occur in a single  
208 locality (*Eryngium viviparum*) or few nearby localities (3 islets for *N. triandrus* ssp.  
209 *capax*, 6 populations for *Centaurea corymbosa*) while other species have a widespread  
210 distribution beyond the French territory (e.g. *Brassica insularis*, *Cypripedium*  
211 *calceolus*).

212 Over all pairs, the average of the signed differences on within-population  
213 expected heterozygosity between threatened and non-threatened plants is -18.5%. For 6  
214 pairs, the threatened species (*Anchusa crispa*, *Convolvulus lanuginosus*, *Cypripedium*  
215 *calceolus*, *Eryngium alpinum*, *Liparis loselii*, *Ranunculus lateriflorus*) showed a greater  
216 heterozygosity than the non-threatened species. Over the 19 pairs out of 25 showing a  
217 reduction of heterozygosity in the threatened species, the average difference is -33.2%.  
218 On the whole, threatened species had a lower expected heterozygosity than their non-  
219 threatened controls (Figure 1, P-value= 0.0065). When removing the three threatened  
220 species for which the within-population heterozygosity was compared to the average  
221 value from Nybom (2004), the result remains significant (p=0.0337 for N=22 pairs).

222  
223  
224  
225  
226  
227  
228  
229  
230  
231  
232  
233  
234  
235  
236  
237  
238  
239  
240  
241



**Figure 1:** Within-population heterozygosity ( $H_e$ ) of threatened plant species in France and non-threatened species. The dashed line represents the  $X=Y$  line, *i.e.* a point on this line would indicate that threatened and non-threatened species have the same level of heterozygosity.

#### 242 *Considerations of genetic diversity in management actions*

243 Sixty-two recovery plans concerning 59 protected species were found on-line. Two  
244 species (*Centranthus trinervis* and *Liparis loeselii*) were studied in more than one plan.  
245 From the on-line survey, we collected data for 21 species, six species were mentioned  
246 both in recovery plans and in the survey. Overall, we collected information for 74  
247 species. Among them, 20 are considered as threatened on the IUCN national list, 26  
248 species are protected at the national level and the others are locally protected either at  
249 the department or regional level which justifies management actions. Habitat  
250 management, with 46 citations out of 74, is the most frequent action recommended for  
251 *in situ* management. Legal protection for habitat was recommended for 45 species.  
252 Manipulation of population size was recommended for 21 species with introduction for  
253 11 species, reinforcement for 15 species, and reintroduction for 5 species. Among  
254 species in this dataset, six species (*Anchusa crispera*, *Aster pyrenaicus*, *Biscutella*  
255 *neustriaca*, *Eryngium viviparum*, *Liparis loeselii*, *Ranunculus nodiflorus*) were in the  
256 previous analysis on genetic diversity.

257 Life-history traits are unequally represented in recovery plans. While habitat and  
258 species longevity are well characterized (100%, 96.8% respectively Table 1), the  
259 ecology of dispersal and pollination are often not considered (29%, 22.6% respectively  
260 Table 1). Important information such as the mating system is even more rarely given in  
261 recovery plans (13 occurrences, Table 1), and tests for self-compatibility have also  
262 seldom been carried out (Table 1). When manipulations of population size are  
263 implemented, information on mating system and self-incompatibility are more often

264 considered (Table 1). Population size is often known (92%) but no reference to *effective*  
265 *population size* could be found in any conservation plan. Mention of “genetic” occurred  
266 in more than 79% of plans (Table 1). Mention of “genetic” is often associated with the  
267 preservation of diversified *ex situ* material (80%) and rarely with threats such as genetic  
268 erosion (32%) or population persistence (14%). Only 10 recovery plans used already  
269 existing genetic data (Table 1) and 8 of these 10, plus 4 others called for the collections  
270 of genetic data (Table 1). Overall only 14 documents out of 62 referred in some way to  
271 the use of genetic data.

272         The 21 surveys collected also confirm that reproductive system is less reported  
273 than other life-history traits (Table 2). Habitats, longevity, seed dispersal and pollination  
274 vectors are known for all species addressed in the survey (Table 2). In contrast, mating  
275 system and self-incompatibility tests were reported by only 57% and 19% of  
276 respondents respectively (Table 2). In particular, self-incompatibility tests were carried  
277 out for only four species. Seven respondents (out of 21) indicated the use of genetic  
278 data. Twelve management actions including manipulation of population size were  
279 documented (Table 2) and nine of them used only a single population source. For two  
280 manipulations of population size, *Saxifraga hirculus* and *Acis nicaeensis*, two  
281 populations were used as seed source. For one of the manipulation of population size  
282 (*Orchis purpurea*), the number of populations source was not documented. Genetic data  
283 were available for five of the twelve species concerned by manipulation of population  
284 size (Table 2).

**Table 1 :** Information available in recovery plans about life-history traits of the species concerned and other topics related to genetics. In the second column, are given the number (percentage) of recovery plans in which the topics is fill in for the species considered. In the last column, are given the same informations for recovery plans including manipulation of population size. « Mention of genetic » means that the topic is discussed but not that genetic data is provided.

285

Topics	Overall ( %)	Recovery plans including manipulation of population size ( %)
Habitat	62 (100)	12 (100)
Longevity	60 (96.8)	11 (91.7)
Vegetative reproduction	14 (22.6)	6 (50.0)
Dispersion vector	18 (29.0)	10 (83.3)
Pollination vector	14 (22.6)	5 (41.7)
Mating system	13 (20.9)	5 (41.7)
Self-incompatibility test	7 (11.3)	3 (25.0)
Mention of genetic	49 (79.0)	10 (83.3)
Genetic data	10 (16.1)	4 (33.3)
Task to collect genetic data	12 (19.3)	4 (33.3)

286

287 **Table 2**: Information available in surveys about life-history traits of the species  
 288 concerned and other topics related to genetics. In the second column, are given the  
 289 number (percentage) of surveys in which the topics is fill in for the species considered.  
 290 In the last column, are given the same informations for actions including manipulation  
 291 of population size.  
 292

Topics	Overall (%)	Actions including manipulation of population size (%)
Species habitat	21 (100)	12 (100)
Species longevity	20 (95.2)	12 (100)
Vegetative reproduction	20 (95.2)	12 (100)
Dispersion vector	21 (100)	12 (100)
Pollination vector	21 (100)	12 (100)
Mating system	12 (57.1)	8 (66.7)
Self-incompatibility test	4 (19.0)	4 (33.3)
Genetic data	7 (33.3)	5 (41.7)

293

## 294 Discussion

295 Our review of the studies performed on the French flora showed that genetic diversity is  
296 known for a low number of threatened species. When documented, within-population  
297 expected heterozygosity is usually lower in threatened species than in non-threatened  
298 controls. Threatened plants having lower genetic diversity is consistent with other  
299 studies of plants such as the one performed on 21 species considered to be threatened on  
300 the world IUCN redlist (Spielman et al. 2004). As the threatened species included in our  
301 study share common life-history traits (Table S1) with their widespread relatives, this  
302 low genetic diversity is likely to result from a reduced population size or geographic  
303 isolation. The relative contribution of these two factors need information on genetic  
304 structure to be quantified (Ellstrand and Elam 1993). For instance, the French  
305 population of *Eryngium viviparum* is highly isolated from the Iberian populations of the  
306 same species and showed much lower diversity than the Iberian populations indicating  
307 that the low genetic diversity is probably linked to geographical isolation (Rasclé et al.  
308 2019). Gitzendanner and Soltis (2000) have also found that overall rare species have  
309 lower genetic diversity than their common congeners, with some exceptions as we  
310 observed for 6 species. Some studies have reported that a narrow distribution or a  
311 threatened status does not necessarily result in low neutral genetic diversity (Jiménez-  
312 Mejías et al. 2015; Médail and Baumel 2018; Teixeira and Huber 2021), in particular  
313 because a lag is expected between population reduction and loss of genetic variation  
314 (Kardos et al. 2021).

315 A second major conclusion from our study is that population genetics was not  
316 considered in most recovery plans or by practitioners. Although some references to  
317 genetics can be found in recovery plans, collection of genetic data is only included or  
318 recommended in 14 plans out of 62 (23%). While Pierson et al. (2016) also found a low  
319 proportion of plans that included genetics, they noted that in France recovery plans  
320 propose the collection of genetic data at a relatively high rate (80%) in comparison to  
321 other European countries (e.g. Netherlands 35 %, UK 30 %). However, their study only  
322 included five *Plan National d'Actions (PNA)*, which are the most complete but not the  
323 most common kind of conservation plans in France. In our study, we included other  
324 kinds of recovery plans and found 19.3% of them recommended the collection of  
325 genetic data. In Australia, the positive perception of genetics by practitioners is not  
326 always translated in an actual use of genetics (Cook and Sgrò 2018). In New Zealand,  
327 the actual use of genetic techniques varies according to conservation issues (Taylor et  
328 al. 2017). International and national policies usually insist on the importance of genetic  
329 diversity (Cook and Sgrò 2017; Hoban et al. 2021), in particular for long-term  
330 persistence. However practical recommendation fail to incorporate genetic factors into  
331 conservation plans (Cook and Sgrò 2017; Hoban et al. 2021), as we found here for  
332 France. Furthermore, specific concepts linked to genetic diversity, such as inbreeding  
333 depression, gene flow or mating system, are rarely mentioned in conservation plans, in  
334 contrast to the conservation scientific literature (Cook and Sgrò 2017). Hence,  
335 insufficient integration of genetic diversity and related concepts into conservation plans

336 seems to be the rule in several countries including France. An international standard for  
337 species recovery plans explicitly including genetic aspects should be developed (Pierson  
338 et al. 2016).

339         Several recommendations can be made to improve the integration of population  
340 genetic diversity in conservation actions. A better spread of the concept of effective  
341 population size ( $N_e$ ) would be one of the recommendations since it is directly related to  
342 genetic threats and population extinction (Allendorf and Luikart 2006; Hoban et al.  
343 2022). Effective population size is often smaller than the demographic population size  
344 (eg. Allendorf and Luikart 2006; Hoban et al. 2020 but see Vitalis et al. 2004). So far,  
345 methods to estimate  $N_e$  are clearly too difficult to be applied in most natural populations  
346 because of the quality and quantity of genetic or demographic data necessary and  
347 because of the complexity of the statistical tools involved. However, collection of data  
348 on life-history traits particularly affecting genetic diversity and  $N_e$  can be recommended  
349 (Hoban et al. 2020), yet we have found that most conservation plans are conducted with  
350 only moderate knowledge on such ecological and biological traits. Acquisition of data  
351 about the mating system of the species is a minimum requirement since it directly  
352 affects  $N_e$  and the structure of genetic diversity (Duminil et al. 2007; Hoban et al.  
353 2020). Nevertheless, there is much less information about mating systems than others  
354 traits in conservation plans in Australia (Cook and Sgrò 2018) and in France (this  
355 study). Life-history traits are also important for other aspects of management, for  
356 example, the longevity of a species decreases the probability to reach reproduction stage  
357 per seed, therefore, increases the number of seeds to use in an introduction (Machinsky  
358 and Haskin 2012). The absence of information about basic biological characteristics of  
359 plant species probably helps to explain some of the failures of reintroduction actions  
360 (Godefroid et al. 2011).

361         We also reported that the majority (nine out twelve) of manipulations of  
362 population size are performed with one source population and two others used only two  
363 populations as sources. Increasing population size reduces the demographic risk and  
364 future genetic erosion whatever the origin of the introduced individuals. However to  
365 address genetic issues linked to past genetic erosion, genetic mixing is required, thus  
366 individuals should originate from a different population, provided outbreeding and local  
367 adaptation issues are addressed before mixing populations (Hoffmann et al. 2021;  
368 Teixeira and Huber 2021). This would make conservation actions more effective, as  
369 would supplementing information on neutral genetic diversity with information on  
370 functional genetic diversity (Teixeira and Huber 2021). This highlights the importance  
371 of improving knowledge on evolutionary theory in the training of conservation  
372 management staff.

373         Several factors, including social, political and economic considerations, explain  
374 the absence of integration of evolutionary theory into conservation plans, but the  
375 training of practitioners is likely to be one of the most important causes (Taylor et al.  
376 2017; Cook and Sgrò 2018; Sandstrom et al. 2019). Furthermore, despite the  
377 recommendation to use open-access research, results from research in conservation  
378 biology do not percolate to practitioners (Taylor et al. 2017). While scientific  
379 publications is an important source for general interpretations, several constraints were

380 pointed out by practitioners, essentially the lack of time and language constraints for  
381 some non-native English speakers (Fabian et al. 2019). Another possible explanation to  
382 the conservation-genetic gap is that genetic is not directly considered in IUCN criteria  
383 to evaluate species status (Willi et al. 2022). Finally, because population genetic studies  
384 are costly and time-consuming, the lack of financial resources is also a problem (Taylor  
385 et al. 2017; Cook and Sgrò 2019). However, as we pointed out above, some biological  
386 traits, such as the mating system, can be collected in natural populations without  
387 technical requirements or costly technology. Another element to consider is that  
388 management strategies tend to focus on short-term responses and perceptible threats  
389 rather than imperceptible and dynamic processes (Mace and Purvis 2008). As a result,  
390 habitat management and the census of population size (i.e. number of flowering plants)  
391 are the most frequent actions.

392 A general recommendation concerns the importance of communication between  
393 researchers and practitioner (Taylor et al. 2017; Fabian et al 2019; Holderegger et al.  
394 2019; Taft et al. 2020; Hohenlohe et al. 2021). Regular networking events between  
395 practitioners and conservation geneticists, such as Annual Meetings in Conservation  
396 Genetics (Holderegger et al. 2019), or conservation geneticist hub bringing together  
397 genetic researchers to provide one platform of expertise visible to managers (Taylor et  
398 al. 2017) should be more widespread. It also would be beneficial to increase the number of  
399 collaborative partnerships between genetic researchers and conservation managers to  
400 support management strategies of specific wild populations (Taft et al. 2020; Hohenlohe  
401 et al. 2021).

#### 402 Acknowledgements

403 We thank the practitioners that participated in the on-line surveys, and the RESEDA-  
404 FLORE consortium. Khalid Belkihr contributed significantly to the scripts used for the  
405 data mining. We are also indebted to John Thompson for comment on a previous  
406 version of this paper. JD is funded by the OFB and Labex Cemeb RENPOP project.

#### 407 Data availability statement

408 The data that support the findings of this study are available from supplementary  
409 materials.

410 Table S1: Description of 6 life-history traits within pairs of species according to the  
411 status of the species, Appendix 1: Dataset on genetic diversity of threatened plant  
412 species in France, Appendix 2: Information that has been searched in recovery plans,  
413 Appendix 3: Survey addressed to practitioners, Appendix 4: Dataset on considerations  
414 of genetic diversity in management actions



415

416

417

418

## 419 Literature cited

- Allendorf F, Luikart G. 2006. Conservation and genetics of populations. Malden (MA). Blackwell Publ. ISBN-13: 978-1-4051-2145-3
- Ashley MV, Willson MF, Pergams ORW, O'Dowd DJ, Gende SM, Brown JS. 2003. Evolutionary enlightened management. *Biol Conserv.* 111: 115–123. [https://doi.org/10.1016/S0006-3207\(02\)00279-3](https://doi.org/10.1016/S0006-3207(02)00279-3)
- Camill, P. 2010. Global Change. *Nature Education Knowledge* 3: 49
- Carlson SM, Cunningham CJ, Westley PAH. 2014. Evolutionary rescue in a changing world. *Trends Ecol Evol.* 29: 521–530. <https://doi.org/10.1016/j.tree.2014.06.005>
- Cook CN, Sgrò CM. 2017. Aligning science and policy to achieve evolutionarily enlightened conservation. *Conserv Biol.* 31: 501–512. <https://doi.org/10.1111/cobi.12863>
- Cook CN, Sgrò CM. 2018. Understanding managers' and scientists' perspectives on opportunities to achieve more evolutionarily enlightened management in conservation. *Evol Appl.* 11: 1371–1388. <https://doi.org/10.1111/eva.12631>
- Cook CN, Sgrò CM. 2019. Conservation practitioners' understanding of how to manage evolutionary processes. *Conserv Biol.* 33: 993–1001. <https://doi.org/10.1111/cobi.13306>
- Conservatoire botanique national alpin. 2020. [accessed Mar 2020]. <http://www.cbn-alpin.fr/>.
- Conservatoire botanique national de Bailleul. 2020. [accessed Mar 2020]. <https://www.cbnbl.org/>.
- Conservatoire botanique national du bassin parisien. 2020. [accessed Mar 2020]. <https://cbnbp.mnhn.fr/cbnbp/>.
- Conservatoire botanique national de Brest. 2020. [accessed Mar 2020]. <http://www.cbnbrest.fr/>.
- Conservatoire botanique national de Corse. 2020. [accessed Mar 2020]. <http://cbnc.oec.fr/>.
- Conservatoire botanique national Franche-Comté. 2020. [accessed Mar2020]. <http://cbnfc-ori.org/>.
- Conservatoire botanique national Massif Central. 2020. [accessed Mar 2020]. <https://www.cbnmc.fr/>.
- Conservatoire botanique national Midi-Pyrénées. 2020. [accessed Mar 2020]. <http://cbnmpm.blogspot.com/>.
- Conservatoire botanique national Méditerranéen de Porquerolles. 2020. [accessed Mar 2020]. <http://www.cbnmed.fr/src/prez.php>.
- Conservatoire botanique national Sud Atlantique. 2020. [accessed Mar 2020]. <http://www.cbnsa.fr/>.
- Duminil J, Fineschi S, Hampe A, Jordano P, Salvini D, Vendramin GG, Petit RJ. 2007. Can Population Genetic Structure Be Predicted from Life-History Traits?. *Am. Nat.* 169: 662–672. <https://doi.org/10.1086/513490>

- Ellstrand NC, Elam DR. 1993. Population Genetic Consequences of Small Population Size: Implications for Plant Conservation. *Annu Rev Ecol Syst.* 24: 217–242. <https://doi.org/10.1146/annurev.es.24.110193.001245>
- Fabian Y, Bollmann K, Brang P, Heiri C, Olschewski R, Rigling A, Stofer S, Holderegger R. 2019. How to close the science-practice gap in nature conservation? Information sources used by practitioners. *Biol Conserv.* 235: 93–101. <https://doi.org/10.1016/j.biocon.2019.04.011>
- Frankham R, Ballou J, Ralls K, Eldridge M, Dudash M, Fenster C, Lacy R, Sunnucks P. 2017. *Genetic Management of Fragmented Animal and Plant Populations*. Oxford: Oxford University Press. <https://doi.org/10.1093/oso/9780198783411.001.0001>
- Garner BA, Hoban S, Luikart G. 2020. IUCN Red List and the value of integrating genetics. *Conserv Genet.* 21: 795–801. <https://doi.org/10.1007/s10592-020-01301-6>
- Gitzendanner MA, Soltis PS. 2000. Patterns of genetic variation in rare and widespread plant congeners. *Am J Bot.* 87: 783–792.
- Godefroid S, Piazza C, Rossi G, Buord S, Stevens A-D, Agurauja R, Cowell C, Weekley CW, Vogg G, Iriondo JM, et al. 2011. How successful are plant species reintroductions? *Biol Conserv.* 144: 672–682. <https://doi.org/10.1016/j.biocon.2010.10.003>
- Gomulkiewicz R, Holt RD. 1995. When does evolution by natural selection prevent extinction? *Evolution.* 49: 201–207. <https://doi.org/10.2307/2410305>
- Gonzalez A, Ronce O, Ferriere R, Hochberg ME. 2013. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. *Philos Trans R Soc B Biol Sci.* 368: 20120404. <https://doi.org/10.1098/rstb.2012.0404>
- Hadjou Belaid A, Maurice S, Fréville H, Carbonell D, Imbert E. 2018. Predicting population viability of the narrow endemic Mediterranean plant *Centaurea corymbosa* under climate change. *Biol Conserv.* 223: 19–33. <https://doi.org/10.1016/j.biocon.2018.04.019>
- Hamabata T, Kinoshita G, Kurita K, Cao P-L, Ito M, Murata J, Komaki Y, Isagi Y, Makino T. 2019. Endangered island endemic plants have vulnerable genomes. *Commun Biol.* 2: 1–10. <https://doi.org/10.1038/s42003-019-0490-7>
- Hamrick JL, Blanton HM, Hamrick KJ. 1989. Genetic structure of geographically marginal populations of Ponderosa pine. *Am J Bot.* 76: 1559–1568. <https://www.jstor.org/stable/pdf/2444394.pdf>
- Hardion L, Verlaque R, Rosato M, Rosselló JA, Vila B. 2015. Impact of polyploidy on fertility variation of Mediterranean *Arundo L.* (Poaceae). *C R Biol.* 338: 298–306. <https://doi.org/10.1016/j.crv.2015.03.013>
- Hoban S, Bruford M, D’Urban Jackson J, Lopes-Fernandes M, Heuertz M, Hohenlohe PA, Paz-Vinas I, Sjögren-Gulve P, Segelbacher G, Vernesi C, et al. 2020. Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. *Biol Conserv.* 248: e108654. <https://doi.org/10.1016/j.biocon.2020.108654>
- Hoban S, Campbell CD, da Silva JM, Ekblom R, Funk WC, Garner BA, Godoy JA, Kershaw F, MacDonald AJ, Mergeay J, et al. 2021. Genetic diversity is considered important but interpreted narrowly in country reports to the Convention on Biological

Diversity: Current actions and indicators are insufficient. *Biol Conserv.* 261: 109233. <https://doi.org/10.1016/j.biocon.2021.109233>

Hoban S, Archer FI, Bertola LD, Bragg JG, Breed MF, Bruford MW, Coleman MA, Ekblom R, Funk WC, Grueber CE, Hand BK, Jaffé R, Jensen E, Johnson JS, Kershaw F, Liggins L, MacDonald AJ, Mergeay J, Miller JM, Muller-Karger F, O'Brien D, Paz-Vinas I, Potter KM, Razgour O, Vernesi C, Hunter M.E. 2022. Global genetic diversity status and trends: towards a suite of Essential Biodiversity Variables (EBVs) for genetic composition. *Biol Rev.* e12852 <https://doi-org.inee.bib.cnrs.fr/10.1111/brv.12852>

Hoffmann AA, Miller AD, Weeks AR. 2021. Genetic mixing for population management: From genetic rescue to provenancing. *Evol Appl.* 14: 634–652. <https://doi.org/10.1111/eva.13154>

Holderegger R, Balkenhol N, Bolliger J, Engler JO, Gugerli F, Hochkirch A, Nowak C, Segelbacher G, Widmer A, Zachos FE. 2019. Conservation genetics: Linking science with practice. *Mol Ecol.* 28: 3848–3856. <https://doi.org/10.1111/mec.15202>

Hohenlohe PA, Funk WC, Rajora OP. 2021. Population genomics for wildlife conservation and management. *Mol Ecol.* 30: 62–82. <https://doi.org/10.1111/mec.15720>

Inventaire National du Patrimoine Naturel. 2019. [accessed Nov 2019]. <https://inpn.mnhn.fr/accueil/index>

IUCN/SSC. 2013. Guidelines for Reintroductions and Other Conservation Translocations. Gland, Switzerland: IUCN Species Survival Commission. Version 1.0.

Jiménez-Mejías P, Fernández-Mazuecos M, Amat ME, Vargas P. 2015. Narrow endemics in European mountains: high genetic diversity within the monospecific genus *Pseudomisopates* (Plantaginaceae) despite isolation since the late Pleistocene. *J Biogeogr.* 42: 1455–1468. <https://doi.org/10.1111/jbi.12507>

Kardos M, Armstrong EE, Fitzpatrick SW, Hauser S, Hedrick PW, Miller JM, Tallmon DA, Funk WC. 2021. The crucial role of genome-wide genetic variation in conservation. *Proc Natl Acad Sci.* 118: e2104642118. <https://doi.org/10.1073/pnas.2104642118>

Keller LF, Waller DM. 2002. Inbreeding effects in wild populations. *Trends Ecol Evol.* 17: 230–241. [https://doi.org/10.1016/S0169-5347\(02\)02489-8](https://doi.org/10.1016/S0169-5347(02)02489-8)

Lande R. 1988. Genetics and demography in biological conservation. *Science.* 241: 1455–1460. <https://doi.org/10.1126/science.3420403>

Lavergne S, Debussche M, Thompson JD. 2005. Limitations on reproductive success in endemic *Aquilegia viscosa* (Ranunculaceae) relative to its widespread congener *Aquilegia vulgaris*: the interplay of herbivory and pollination. *Oecologia.* 142: 212–220. <https://doi.org/10.1007/s00442-004-1721-1>

Lavergne S, Thompson JD, Garnier E, Debussche M. 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos.* 107: 505–518. <https://doi.org/10.1111/j.0030-1299.2004.13423.x>

Leimu R, Mutikainen P, Koricheva J, Fischer M. 2006. How general are positive relationships between plant population size, fitness and genetic variation? *J Ecol.* 94: 942–952. <https://doi.org/10.1111/j.1365-2745.2006.01150.x>

Mace GM, Purvis A. 2008. Evolutionary biology and practical conservation: bridging a widening gap. *Mol Ecol.* 17: 9–19. <https://doi.org/10.1111/j.1365-294X.2007.03455.x>

Maschinski, J, Haskins K.E. 2012. *Plant Reintroduction in a Changing Climate: Promises and Perils*. Washington: Island Press. <https://doi.org/10.5822/978-1-61091-183-2>.

Manly BFJ. 1991. *Randomization and Monte Carlo methods in biology*. London: Chapman and Hall. ISBN 0-412-72130-9

Médail F, Baumel A. 2018. Using phylogeography to define conservation priorities: The case of narrow endemic plants in the Mediterranean Basin hotspot. *Biol Conserv.* 224: 258–266. <https://doi.org/10.1016/j.biocon.2018.05.028>

Ministère de la Transition écologique. 2020. [accessed 2020 March ]. <https://www.ecologie.gouv.fr/>.

National Center for Biotechnology Information. 2019. [accessed Nov 2019]. <https://www.ncbi.nlm.nih.gov/>

Nybom H. 2004. Comparison of different nuclear DNA markers for estimating intraspecific genetic diversity in plants: DNA-markers and plant genetic diversity. *Mol Ecol.* 13: 1143–1155. <https://doi.org/10.1111/j.1365-294X.2004.02141.x>

Olivieri I, Tonnabel J, Ronce O, Mignot A. 2016. Why evolution matters for species conservation: perspectives from three case studies of plant metapopulations. *Evol Appl.* 9: 196–211. <https://doi.org/10.1111/eva.12336>

Oostermeijer JGB, Luijten SH, den Nijs JCM. 2003. Integrating demographic and genetic approaches in plant conservation. *Biol Conserv.* 113: 389–398. [https://doi.org/10.1016/S0006-3207\(03\)00127-7](https://doi.org/10.1016/S0006-3207(03)00127-7)

Pierson JC, Coates DJ, Oostermeijer JGB, Beissinger SR, Bragg JG, Sunnucks P, Schumaker NH, Young AG. 2016. Genetic factors in threatened species recovery plans on three continents. *Front Ecol Environ.* 14: 433–440. <https://doi.org/10.1002/fee.1323>

Quilichini A, Debussche M, Thompson JD. 2004. Geographic differentiation of morphological traits and isozymes in the Mediterranean island endemic *Anchusa crispa*: implications for the conservation of a protected species. *Biol Conserv.* 118: 651–660. <https://doi.org/10.1016/j.biocon.2003.10.014>

Ralls K, Ballou JD, Dudash MR, Eldridge MDB, Fenster CB, Lacy RC, Sunnucks P, Frankham R. 2018. Call for a Paradigm Shift in the Genetic Management of Fragmented Populations. *Conserv Lett.* 11: e12412. <https://doi.org/10.1111/conl.12412>

Rasclé P, Flaven E, Bioret F, Magnanon S, Glemarec E, Gallet S, Imbert E. 2019. Genetic consequences of long-term isolation for the last French population of *Eryngium viviparum* (Apiaceae). *Bot J Linn Soc.* 191: 285–298. <https://doi.org/10.1093/botlinnean/boz035>

Reed DH, Frankham R. 2003. Correlation between Fitness and Genetic Diversity. *Conserv Biol.* 17: 230–237. <https://doi.org/10.1046/j.1523-1739.2003.01236.x>

Rodger YS, Pavlova A, Sinclair S, Pickup M, Sunnucks P. 2021. Evolutionary history and genetic connectivity across highly fragmented populations of an endangered daisy. *Heredity.* 126: 846–858. <https://doi.org/10.1038/s41437-021-00413-0>

Salvado P, Aymerich Boixader P, Parera J, Vila Bonfill A, Martin M, Quélenec C, Lewin J-M, Delorme-Hinoux V, Bertrand JAM. 2022. Little hope for the polyploid

endemic Pyrenean Larkspur (*Delphinium montanum*): Evidences from population genomics and Ecological Niche Modeling. *Ecol Evol.* 12: e8711. <https://doi.org/10.1002/ece3.8711>

Sandström A, Lundmark C, Andersson K, Johannesson K, Laikre L. 2019. Understanding and bridging the conservation-genetics gap in marine conservation. *Conserv Biol.* 33: 725–728. <https://doi.org/10.1111/cobi.13272>

Sarrazin F, Lecomte J. 2016. Evolution in the Anthropocene. *Science.* 351: 922–923. <https://doi.org/10.1126/science.aad6756>

Silcock JL, Simmons CL, Monks L, Dillon R, Reiter N, Jusaitis M, Vesk PA, Byrne M, Coates DJ 2019. *Biological Conservation* 236: 211-222.

Smith TB, Kinnison MT, Strauss SY, Fuller TL, Carroll SP. 2014. Prescriptive Evolution to Conserve and Manage Biodiversity. *Annu Rev Ecol Evol Syst.* 45: 1–22. <https://doi.org/10.1146/annurev-ecolsys-120213-091747>

Spielman D, Brook BW, Frankham R. 2004. Most species are not driven to extinction before genetic factors impact them. *Proc Natl Acad Sci.* 101: 15261–15264. <https://doi.org/10.1073/pnas.0403809101>

Taft HR, McCoskey DN, Miller JM, Pearson SK, Coleman MA, Fletcher NK, Mittan CS, Meek MH, Barbosa S. 2020. Research–management partnerships: An opportunity to integrate genetics in conservation actions. *Conserv Sci Pract.* 2: e218. <https://doi.org/10.1111/csp2.218>

Taylor RH, Dussex N, van Heezik Y. 2017. Bridging the conservation genetics gap by identifying barriers to implementation for conservation practitioners. *Glob Ecol Conserv.* 10: 231–242. <https://doi.org/10.1016/j.gecco.2017.04.001>

Teixeira JC, Huber CD. 2021. The inflated significance of neutral genetic diversity in conservation genetics. *Proc Natl Acad Sci.* 118: e2015096118. <https://doi.org/10.1073/pnas.2015096118>

Thompson JD. 2020. *Plant Evolution in the Mediterranean: Insights for conservation.* 2nd ed. Oxford: Oxford University Press. <https://doi.org/10.1093/oso/9780198835141.001.0001>

UICN comité français. 2019. [accessed Nov 2019]. <https://uicn.fr/liste-rouge-flore/>.

Vitalis R, Glémin S, Olivieri I. 2004. When Genes Go to Sleep: The Population Genetic Consequences of Seed Dormancy and Monocarpic Perenniality. *Am Nat.* 163: 295–311. <https://doi.org/10.1086/381041>

Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NJ, Miller KA, Byrne M, Coates DJ, Eldridge MDB, Sunnucks P, et al. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evol Appl.* 4: 709–725. <https://doi.org/10.1111/j.1752-4571.2011.00192.x>

Willi Y, Kristensen TN, Sgrò CM, Weeks AR, Ørsted M, Hoffmann AA. 2022. Conservation genetics as a management tool: The five best-supported paradigms to assist the management of threatened species. *Proc Natl Acad Sci.* 119: e2105076119. <https://doi.org/10.1073/pnas.2105076119>

421 **Table S1.** Description of 6 life-history traits within pairs of species according to the  
 422 status of the species (threatened and not threatened NT, see text for details). Life-  
 423 history traits are considered only for the 47 species in the dataset. Details are given in  
 424 Appendix 1.  
 425  
 426

Longevity of NT species		Longevity of threatened species			Total		
		Perennial	Annual				
Perennial		20	2	22			
Missing data		3	0	3			
Total		23	2				
Reproduction event of NT species		Reproduction event of threatened species			Total		
		Monocarpic	Polycarpic				
Monocarpic		2	0	2			
Polycarpic		3	17	20			
Missing data		1	2	3			
Total		6	19				
Vegetative reproduction of NT species		Vegetative reproduction of threatened species			Total		
		Absent	Present	Missing data			
Absent		2	1	0	3		
Present		2	6	3	11		
Missing data		3	4	4	11		
Total		7	11	7			
Pollination vector of NT species		Pollination vector of threatened species				Total	
		Anemophily	Entomophily	Hydrophily	Missing data		
Anemophily		1	1	0	0	2	
Entomophily		0	17	1	0	18	
Hydrophily		0	0	0	0	0	
Missing data		0	1	0	4	5	
Total		1	19	1	4		
Dispersion vector of NT species		Dispersion vector of threatened species				Total	
		Anemochory	Barochory	Hydrochory	Zoochory	Missing data	
Anemochory		3	2	0	0	0	5
Barochory		2	2	0	1	0	5

Hydrochory	0	1	2	0	1	4
Zoochory	0	1	0	1	0	2
Missing data	1	1	0	0	7	9
Total	6	7	2	2	8	

427

428

429 Table 1 (follow)

430

Mating system of NT species	Mating system of threatened species				Total
	Autogamy	Mixed	Allogamy	Missing data	
Autogamy	2	1	0	0	3
Mixed	0	2	1	1	4
Allogamy	1	1	7	1	10
Missing data	3	1	1	3	8
Total	6	5	9	5	

431