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**Title:**

Predicting population viability of the narrow endemic Mediterranean plant *Centaurea corymbosa* under climate change.

**Authors:**

Asma HADJOU BELAID<sup>a</sup>, Sandrine MAURICE<sup>a</sup>, H  l  ne FREVILLE<sup>b</sup>, David CARBONELL<sup>a</sup>, Eric IMBERT<sup>a,\*</sup>

**Address:**

<sup>a</sup> ISEM-Universit   de Montpellier, CNRS, IRD, EPHE-Montpellier, France.

<sup>b</sup> AGAP, Univ Montpellier, CIRAD, INRA, Montpellier SupAgro - Montpellier, France

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

1 **Title:**

2 Predicting population viability of the narrow endemic Mediterranean plant *Centaurea corymbosa*  
3 under climate change.

4  
5 **Abstract**

6 Climate change is a growing threat for global biodiversity, in particular for narrow endemic  
7 species. The Mediterranean region, which harbors an exceptional biodiversity, has been identified  
8 as one of the most sensitive regions to climate change. Based on a 22-year monitoring period, we  
9 analyzed the dynamic and viability of the six extant populations of a narrow endemic plant species  
10 of the Mediterranean area, *Centaurea corymbosa*, to predict their fate under two climatic scenarios.  
11 We constructed matrix projection models to calculate current asymptotic growth rates and to  
12 perform stochastic projections including both demographic and environmental stochasticity. Neither  
13 asymptotic growth rates nor their temporal variance were linked to population size and age at  
14 flowering. Randomization tests showed that asymptotic growth rates were significantly different  
15 among years but not among populations. An increase in temperature and a decrease in the number  
16 of wet days had a negative impact on the whole life-cycle, particularly in the summer period, and  
17 thus reduced asymptotic growth rates. Stochastic projections showed that an increased frequency of  
18 extreme climatic events increased population extinction risk and decreased mean time to extinction.  
19 The warm scenario had a more dramatic impact on population viability than the dry scenario.  
20 Management recommendations are proposed to increase population viability of endangered plant  
21 species such as *C. corymbosa* that face climate change.

22 **Keywords:**

23 *Centaurea corymbosa*; Climate change; Conservation; Extinction risk; Long-term survey; Matrix  
24 projection models; Stochastic projections.

## 25 **1. Introduction**

26 Ongoing climate change is expected to result in increase in drought and warm periods in  
27 several regions due to both an increasing frequency of extreme climatic events and long-term  
28 gradual changes (IPCC, 2007). Compared to some other taxonomic groups, plants are more  
29 vulnerable to climate change since they have relatively low migration capacity (Malcolm et al.,  
30 2006; Thomas et al., 2004). Gradual climate change and extreme events have already caused range  
31 shifts for some plant species (Chen et al., 2011), including range contraction with long-term  
32 population declines and extinctions (Lennartsson and Oostermeijer, 2001; Doak and Morris, 2010;  
33 Selwood et al., 2015, Wiens, 2016), or range expansion (Meer et al., 2016; Williams et al., 2015).  
34 This change is expected to become an even more important driver of global biodiversity loss over  
35 the next century (Heller and Zavaleta, 2009). Thus, population dynamics of many plant species are  
36 expected to be significantly affected by such changes (Breda et al., 2006; Meer et al., 2016; Nicolè  
37 et al., 2011; Ulrey et al. 2016). For conservation purposes, identifying climatic factors that impact  
38 population dynamics and predicting the consequences of climate change on species persistence have  
39 therefore become an important prerequisite to develop effective conservation strategies aimed at  
40 limiting population decline and extinction risk (Cotto et al., 2017; Malcolm et al., 2006; Thomas et  
41 al., 2004).

42 Climate change can either positively or negatively affect population dynamics (Lawson et  
43 al., 2015; Marrero-Gómez et al., 2007). For instance, climate change proved beneficial to  
44 populations of the widespread orchid species (*Orchis purpurea*) and is predicted to induce range  
45 expansion in the near future (Meer et al., 2016; Williams et al., 2015). In contrast, several studies  
46 have documented negative effects of summer temperature on growth rates for other plant species  
47 (Aragón-Gastélum et al., 2017; Riba et al., 2002; Shryock et al., 2014). In some cases, a given  
48 climatic variable has been shown to have diverging effects on separate vital rates within a species  
49 life-history (Csörgő et al., 2017; Jolls et al., 2015; Nicolè et al., 2011; Peñuelas et al., 2004;  
50 Treurnicht et al., 2016). For example, a warm summer increased the flowering probability of  
51 *Dracocephalum austriacum*, whereas it decreased plant survival, leading to reduced effects of  
52 climate on population growth rates (Nicolè et al., 2011). Such opposite effects on population  
53 dynamics and demographic processes make it difficult to predict the net consequences of climate  
54 change on population viability (Meer et al., 2016; Nicolè et al., 2011).

55 The Mediterranean region has been identified as one of the most sensitive regions to  
56 climate change (Ducrocq, 2016). Climate model projections indicate that warming and drying will  
57 likely continue (AllEnvi, 2016). At the end of the century (2080-2099 period), annual mean  
58 temperature is predicted to increase (+3.5°C) with more extreme dry event frequency (+46%) in this  
59 region (Christensen et al., 2007). Moreover, in most areas of the Mediterranean region, precipitation  
60 is predicted to decrease (-12%), particularly in summer (-24%, Christensen et al., 2007). The  
61 Mediterranean region harbors an exceptional biodiversity, including a large number of rare and  
62 endemic plant species. Among them, 36% are narrow endemics, i.e., they grow only in a single area  
63 or have a narrow geographic range (Thompson et al., 2005). Most of these species occur in rocky  
64 habitats, on steep slopes and in open vegetation with low species richness (Lavergne et al., 2004;  
65 Thompson et al., 2005). Such habitats are characterized by their stability both in relation to  
66 vegetation succession and human disturbance (Lavergne et al., 2005). Narrow endemic species are  
67 expected to be particularly sensitive to environmental shifts, as several of these species are  
68 extremely specialized and have evolved low dispersal ability (Isik, 2011; Lavergne et al., 2004,  
69 2005; Thuiller et al., 2005).

70 Projection models that incorporate temporal environmental stochasticity are a powerful tool  
71 for predicting long-term population dynamics under climate change (Andrello et al., 2012; Crone et  
72 al., 2011, 2013; García et al., 2002). An increase in variability in vital rates due to climatic  
73 variations will usually decrease the long-term population growth (Morris et al., 2008). Thus,  
74 temporal variations may amplify population fluctuations and thus increase extinction risk, an effect  
75 being more pronounced for small populations (Isik et al., 2011; Lande et al., 2003; Morris and Doak,  
76 2002). Species life-histories can however buffer the effects of climate variation. For instance, long  
77 duration of the life-cycle has been shown to decrease the impact of environmental stochasticity,  
78 making long-lived species facing climate change less prone to extinction (Morris et al., 2008).  
79 Demographic stochasticity can also be an important driver of population dynamics, whenever  
80 populations are of a small size (Lande et al., 2003). Such processes refer to chance events of  
81 individual survival and reproduction causing random variations in population growth rates (Caswell,  
82 2001; Lande et al., 2003). These variations are expected to be more pronounced in small  
83 populations and thus lead to random fluctuations in population size that increase extinction risks  
84 (Lande et al., 2003; Zeigler, 2013). Including both environmental and demographic stochasticity in  
85 population viability analyses is thus crucial to forecast the fate of populations under climate change  
86 (Crone et al., 2011, 2013; Kaye and Pyke, 2003; Lande et al., 2003).

87 Demographic studies investigating the long-term effect of climate change on narrow  
88 endemic Mediterranean plants remain rare. Such studies have mostly relied on short-term surveys,  
89 thus exploring limited year-to-year climatic variations (Crone et al., 2011) and consider only a  
90 subset of extant populations (e.g. *Centaurea hyssopifolia*; Matesanz et al., 2009, *Brassica insularis*;  
91 Noel et al., 2010, *Ramonda myconi*; Riba et al., 2002), making it difficult to predict species  
92 responses to climate change (Crone et al., 2011; Ehrlén et al., 2016). Long-term demographic  
93 surveys are needed to understand how past climatic variations have affected population dynamics,  
94 and to predict population viability under climate change (Andrello et al., 2012; Franklin et al., 2017;  
95 Hunter et al., 2010; Menges, 2000). Typically, at least 15–20 years of observations are necessary to  
96 predict population growth rate or extinction risk adequately (Zeigler, 2013). This is particularly true  
97 for perennial species, which may have a stage in their life-cycle that allows for species persistence  
98 under unfavorable conditions (Blume-Werry et al., 2016; Huelber et al., 2016; Morris et al., 2008).

99 *Centaurea corymbosa* is a narrow monocarpic short-lived species endemic to the  
100 Mediterranean region. The species grows in the Massif de la Clape in Southern France, on the top  
101 of cliffs and in nearby rocky areas of open vegetation (Colas et al., 1997). Only six populations are  
102 known, which have been surveyed since June 1994 using permanent plots. In this paper, we used  
103 this unique demographic dataset collected during a 22-year period (totaling 6112 individual life-  
104 histories) to predict species dynamics under different climate scenarios. To do so, using matrix  
105 population models, we estimated asymptotic growth rates and vital rates for each population and  
106 each pair-of-years over the 22-year period. First, we tested for spatial and temporal variations in  
107 population dynamics and also tested whether small populations had lower asymptotic growth rate  
108 and showed higher variance in asymptotic growth rate than large populations. In addition, we tested  
109 whether age at flowering could buffer the effects of environmental stochasticity. Next, we assessed  
110 the relationship of climatic variables with demographic parameters over the 22-year period. More  
111 specifically, we tested whether any climatic situation contributing to drought negatively affected  
112 asymptotic growth rates and vital rates, since water availability is essential for the establishment of  
113 newly recruited plants and the survival of vegetative plants. Moreover, because flowering is closely  
114 linked with size and thus with plant growth in monocarpic plants (Meer et al., 2016; Metcalf et al.,  
115 2003; Williams et al., 2015), we tested whether probability of flowering depended on climatic  
116 conditions prevailing only the months before flowering or varied according to a cumulative multi-  
117 year climate effect. Finally, by incorporating both environmental and demographic stochasticity, we  
118 simulated the fate of populations under two climatic scenarios, a warm scenario reflecting an  
119 increase in the frequency of hot years, and a dry scenario corresponding to an increase in the

120 frequency of drought events, and thus tested which of the two scenarios would have the largest  
121 impact on population persistence.

## 122 **2. Materials & Methods**

### 123 *2.1. Biological model, demographic and climatic datasets*

#### 124 *2.1.1. Study species*

125 *Centaurea corymbosa* Pourret (Asteraceae) is a narrow Mediterranean species endemic to  
126 the Massif de la Clape near Narbonne (southern France, 43°13 N, 3°08 E). It is listed in the French  
127 Red Book of endangered species and in the European Habitat Directive list of priority species, thus  
128 precise coordinates of the populations are not given. *C. corymbosa* has been extensively studied  
129 since 1994 and several papers have already reported on its ecological characteristics (Colas et al.,  
130 1996; Imbert, 2006; Imbert et al., 2012; Kirchner et al., 2005), population dynamics (Fréville et al.,  
131 2004; Kirchner et al., 2006) and population genetics (Colas et al., 1997, 2001; Fréville et al., 2001;  
132 Fréville et al., 1998; Hardy et al., 2004; Riba et al., 2005). Here, we only summarize the most  
133 important features and results related to the current study. *C. corymbosa* is restricted to a 3-km<sup>2</sup> area  
134 and is known from only six populations found on different cliffs 0.3-2.3 km apart (mean elevation  
135 132 m, SD = 37.4, n=41 permanent plots, see below). Individuals grow on the top of cliffs and in  
136 rocky areas. These populations are currently not directly threatened by human activities. However,  
137 habitat closure due to the abandonment of grazing contributes to the isolation of open and suitable  
138 habitats, and thus increased fragmentation among patches. The species has a monocarpic perennial  
139 life-cycle. Individuals stay as a rosette for 2 to 13 years before flowering. The flowering period  
140 extends from May to mid-August, and most of the seeds germinate between September and  
141 December. Seeds are dispersed over short distances by wind and ants. Despite suitable habitats in  
142 the vicinity of the six populations, it has been shown that *C. corymbosa* is very unlikely to colonize  
143 new sites (Colas et al., 1997; Olivieri et al., 2016; Riba et al., 2005).

#### 144 *2.1.2. Demographic dataset*

145 Data have been collected since June 1994 in the six populations. However, in the first  
146 census, the status of non-flowering plants (seedling or rosette) could not be assessed. Thus, matrix  
147 population models were based on 22 years of demographic survey (1995-2016), except for one  
148 population (Portes, 1996-2016). Data collection is described in details in Fréville et al. (2004).  
149 Every 3 months (June, September, December and March), we recorded the presence and the status

150 of each individual within 41 permanent plots and new seedlings were added to the datasets (see  
151 Appendix A1). During the flowering period (mid-June), we also surveyed the whole distribution  
152 area of the species to count the total number of flowering plants per population (exhaustive count,  
153 Table 1 and Appendix A2). A total of 6112 individual life-histories were used to construct  
154 population projection models (Table 1 and Appendix A1).

### 155 2.1.3. Climatic dataset

156 Climatic data were obtained from the closest meteorological station located at INRA Pech  
157 Rouge (43°1444 N, 3°1338 E, elevation = 40 m) less than 5 km from the populations of *C.*  
158 *corymbosa*. We used daily mean temperature, daily minimum and maximum temperatures and daily  
159 precipitation. Over the 22 years of this study, the Massif de la Clape experienced a classical warm  
160 Mediterranean climate (average mean temperature  $15.1 \pm 0.6$  °C from June  $t$  to May  $t+1$ , Fig. 1)  
161 with a warm summer period. Precipitation regime was also characteristic of the Mediterranean  
162 climate with an average of 540.8 mm per year from June  $t$  to May  $t+1$  with large inter-annual  
163 variation (SD = 175.46, Fig. 1). The number of days with precipitation  $> 1$  mm ranged from 35 days  
164 to 68 days with an average of 48.5 days per pair-of-years (SD = 8.9, Fig. 1).

## 165 2.2. Deterministic analyses

### 166 2.2.1. Matrix projection models

167 As described in Fréville et al. (2004), the life-cycle is based on a prebreeding census  
168 performed before the germination pulse, with a one-year interval from June  $t$  to May  $t+1$ . Three  
169 stages were defined: seedlings (individuals less than 1 year old), rosettes (vegetative plants older  
170 than 1 year), and flowering plants. We estimated lower-level vital rates (survival  $s_i$ , flowering  
171 probability  $\alpha_i$  conditional to survival and fecundity  $f$ ) to construct a stage structured Matrix  
172 Projection Model (MPM). For each population and each pair-of-years, the projection matrix  
173 representing the life-cycle is given by:

$$A = \begin{pmatrix} 0 & 0 & fs_0 \\ s_1(1-\alpha_1) & s_2(1-\alpha_2) & s_3(1-\alpha_3) \\ s_1\alpha_1 & s_2\alpha_2 & s_3\alpha_3 \end{pmatrix}$$

174 From the 22 years of demographic survey, we constructed 21 matrices per population (see  
175 appendix B for projection matrices per population). The probabilities of a flowering plant to survive  
176 ( $s_3$ ) and to reproduce the year after ( $\alpha_3$ ) were very low, in agreement with the monocarpy of the



177 species, and had negligible effects on population dynamics (see appendix B). Using a deterministic  
178 MPM (linear, time-invariant), we calculated the asymptotic growth rate  $\lambda_a$  as the dominant  
179 eigenvalue of the matrix  $\mathbf{A}$  of the corresponding pair-of-years. The model did not include seed bank  
180 and migration. Indeed, less than 5% of seeds may remain dormant for one year and seed dispersal  
181 among populations is highly limited (Colas et al., 1997; Fréville et al., 2004; Imbert, 2006). The net  
182 fecundity  $fs_0$  was estimated as the ratio of the number of seedlings observed in June of a given year  
183 over the number of flowering plants observed within permanent plots in June of the previous year.  
184 Our three-month survey made it possible to decompose the net fecundity  $fs_0$  into a fecundity term  $f$   
185 (number of just-emerged seedlings assessed every three months over number of flowering plants in  
186 June  $t-1$ ) and survival of just-emerged seedlings  $s_0$  (number of seedlings observed in June  $t$  over  
187 total number of just-emerged seedlings observed from June  $t-1$  to May  $t$ , Colas et al., 2008; Fréville  
188 et al., 2004). We obtained four null values in asymptotic growth rates (three for Cruzade and one for  
189 Peyral), which corresponded to years with no flowering plant within plots and null values in rosette  
190 survival  $s_2$ . In such case, the persistence of the plot depended on new rosettes coming from the  
191 seedling stage ( $s_1$  never equaled zero), and seed dispersal from the closest flowering plants outside  
192 plots. When calculating the geometric mean of asymptotic growth rates over years for each  
193 population, we excluded these null values.

#### 194 2.2.2. *Patterns of spatio-temporal variations in asymptotic growth rates*

195 To test for temporal and spatial variation in asymptotic growth rates, we used non-  
196 parametric randomisation tests (Caswell, 2001). Temporal variation was tested by randomly  
197 permuting individual life-histories (status at  $t$  and fate at  $t+1$ ) among pair-of-years when  
198 considering all data as a single population. For spatial variation, we permuted the whole individual  
199 life-history (from germination to death) between populations (see Fréville et al., 2004). Each life-  
200 history appeared exactly once in each randomized dataset, maintaining the original sample sizes.  
201 For each set of permuted data, we calculated asymptotic growth rate for each group (year or  
202 population) and then computed the standard deviation of  $\lambda_a$  between groups. The probability that  
203  $\sigma(\lambda_a) \geq \sigma_{obs}$  under the null hypothesis  $H_0$  (no group effect) was computed based on 2000 random  
204 permutations. We rejected  $H_0$  when this probability was smaller than 0.05 (Caswell, 2001). We used  
205 linear models to test for the effect of population size on asymptotic growth rates and their temporal  
206 variance, using the total number of flowering plants obtained by the exhaustive survey as a proxy of  
207 population size (Table 1). We used also a linear model to test for the effect of mean age at flowering  
208 (Table 1) on the variance in population growth rate.

### 2.2.3. Retrospective and prospective analyses

We performed a life-table response analysis (LTRE) with a random design to assess how lower-level vital rates contributed to the variance in asymptotic growth rates  $\text{var}(\lambda_a)$  observed among years. This analysis was performed on the pooled data over populations, provided that we did not detect significant spatial variation in population growth rates. The decomposition of  $\text{var}(\lambda_a)$  in term of lower-level vital rates  $p$  is expressed as:

$$\text{var}(\lambda_a) \approx \sum_{i,j} \text{cov}(p_i, p_j) \frac{\partial \lambda_a}{\partial p_i} \frac{\partial \lambda_a}{\partial p_j}$$

where  $\text{cov}(p_i, p_j)$  is the covariance of  $p_i$  and  $p_j$  (Caswell, 2001). A prospective analysis was also conducted to assess the population dynamic response to changes in lower-level vital rates. We calculated the elasticity of  $\lambda_a$  to lower-level vital rates  $p$  as:

$$e = \frac{p}{\lambda_a} \frac{\partial \lambda_a}{\partial p}$$

### 2.3. Relationships between demographic parameters and climate

From the raw climatic dataset, we extracted seven relevant variables assumed to have an influence on demographic parameters, given the existing literature (Fréville et al., 2004; Riba et al., 2002) and our knowledge of Mediterranean plant species. We thus calculated the average of daily mean temperature and daily maximum temperature, the number of days with mean  $T^\circ > 25^\circ\text{C}$  (corresponding to mean + SD) and the number of freezing days (minimum  $T^\circ < 0^\circ\text{C}$ ). In addition, we calculated both the average cumulative precipitation and the number of days with precipitation  $> 1$  mm that hereafter will be referred as the number of wet days. We also calculated the number of days with precipitation  $> 20$  mm. This threshold value was equal to mean + SD. We thus considered this variable as reflecting the number of heavy precipitation events in the Massif de la Clape.

We tested for the effect of climate on demographic parameters using generalized linear models with identity link for asymptotic growth rates and fecundity  $f$  (both log-transformed), and logit link for survival and flowering probabilities with the binomial distribution. First, we tested for relationships between annual averages of each climatic variable calculated from June  $t$  to May  $t+1$  and asymptotic growth rates  $\lambda_a$ , and also tested for quadratic effects and multiyear cumulative effect with a time lag of one year of each climatic variable (Appendix E.1). We then tested for the effect of the variables that we found significant in the single-variable GLMs, using a forward stepwise

236 selection approach. Starting from the null model, we added at each step the variable having the  
237 highest  $R^2$  value in the single-variable models (Appendix E.1). For logistic models, we used  $R^2_{LR}$ ,  
238 the pseudo-coefficient of determination based on the likelihood-ratio test and given by  $R^2_{LR} = 1 -$   
239  $(L_{null} / L_{full})^{2/n}$  where  $L_{null}$  and  $L_{full}$  are the likelihoods of the null and the fitted models, respectively  
240 (Shinichi Nakagawa et al., 2013). The significance of each added variable in the model was tested  
241 using an analysis of deviance (Appendix E.2). From the best model, we reported the estimated  
242 coefficient ( $\beta$ ) and its significance for each variable in the model after scaling climatic variables.  
243 Second, to understand biological processes at a finer scale, we tested for the impact of the seasonal  
244 climate on lower-level vital rates by considering only climatic variables that significantly impacted  
245 asymptotic growth rates, using the same approach as described above. We included the seasonality  
246 effect in GLMs by averaging variables over three-month periods separating two successive censuses  
247 (Appendix E.3). GLMs were fitted using R Stats-package (version 3.3.1). The  $R^2_{LR}$  was calculated  
248 using the R-command 'r.squaredLR' from the MuMIn-package (version 1.15.6).

#### 249 *2.4. Stochastic projections under climate change*

250 Based on the IPCC Fourth Assessment Report, the frequency of extreme warm and dry  
251 events is expected to increase (Christensen et al., 2007). We thus built stochastic matrix models to  
252 simulate the fate of *C. corymbosa* populations under two scenarios of climatic variations,  
253 representing an increased frequency of extreme events either for temperature or precipitation  
254 (Bucharovà et al., 2012; Shryock et al., 2014). To simulate the fate of populations, we incorporated  
255 environmental stochasticity by drawing an entire matrix at each time step (sampling with  
256 replacement) among the 21 available matrices (Crone et al., 2011, 2013; Kaye and Pyke, 2003).  
257 Because *C. corymbosa* has small population sizes, we also incorporated demographic stochasticity  
258 in the models. Such stochasticity is due to the independent chance of transition and reproduction  
259 among individuals (Engen et al., 1998; Lande, 1993; Melbourne and Hasting, 2008). From the  
260 existing individuals at year  $t$ , we drew the number of individuals making each transition from stage  
261  $j$  to stage  $i$  including death at each time step in a multinomial distribution characterized by the  $a_{ij}$   
262 transition probabilities of the matrix that we randomly drew (Andrieu et al., 2017; Caswell, 2001;  
263 Melbourne and Hasting, 2008; Morris and Doak, 2002). The number of recruited seedlings was  
264 drawn in a Poisson distribution with mean equal to the  $fs_0$  value of the drawn matrix. In the case of  
265 *C. corymbosa*, demographic stochasticity indeed increased fluctuations in population size over time  
266 and thus increased extinction risk (see Appendix F), in agreement with both theoretical studies (e.g.  
267 Engen et al., 2005; Lande, 1993; Lande, 2003) and empirical ones (e.g. Fujiwara and Caswell, 2001;

268 Melbourne and Hasting, 2008; Jepsom and Forslund, 2012). Therefore, we combined both  
269 demographic and environmental stochasticity to simulate the fate of populations under climate  
270 scenarios.

271 The initial population size  $N_0$  used to start our simulations was calculated from the stable  
272 stage distribution obtained from the arithmetic mean of the total number of flowering plants  
273 recorded in the population (exhaustive survey) from 2010 to 2016, and the scaled eigenvector  $W$   
274 from the arithmetic mean matrix over years (2010-2016) when pooling data over populations.  $N_0$  is  
275 given by  $N_0 = W \frac{Nfr}{w_3}$  where  $w_3$ , the third element of the scaled eigenvector, represents the  
276 proportion of the number of flowering plants. We simulated population dynamics using 1000  
277 stochastic iterations, each iteration representing a trajectory of population size over 100 years. For a  
278 given trajectory we calculated the growth rate  $\lambda_j$  as:

$$\lambda_j = \exp\left[\frac{\ln(n_j(T)) - \ln(n_j(0))}{T}\right]$$

279 where  $n_j(T)$  and  $n_j(0)$  were the population size of the  $j^{th}$  trajectory at  $t = T$  and  $t = 0$ , respectively,  
280 and  $T$  being the last year at which population size was non-null. The stochastic growth rate  $\lambda_s$  was  
281 obtained as the median of  $\lambda_j$  over 1000 trajectories. Extinction probability at a given time  $t$   
282 corresponds to the number of trajectories for which  $N(t) = 0$  over the total number of trajectories;  
283 we calculated extinction probability at  $t = 50$  years ( $P_{50}$ ),  $t = 100$  years ( $P_{100}$ ) and the mean time to  
284 extinction ( $T_{ext}$ ) based on 100 trajectories over 100 years. We carried out 1000 such simulations,  
285 each of 100 trajectories, to obtain a sampling distribution of  $P_{50}$ ,  $P_{100}$  and  $T_{ext}$ . We calculated mean  
286 value of those parameters over the 1000 simulations and 95% confidence intervals by taking the  
287 2.5<sup>th</sup> and the 97.5<sup>th</sup> percentile of the simulated distribution (Shryock et al., 2014). All stochastic  
288 analyses were implemented using the R popbio-package, version 2.4.3 (Stubben and Milligan,  
289 2007).

290 Climatic scenarios were first simulated by increasing the frequency of drawing matrices  
291 corresponding to extreme warm and extreme dry years (Andrello et al. 2012; Hunter et al., 2010;  
292 Shryock et al., 2014) from the observed frequency over the 22-year period  $q^*$  to  $q = 0.8$ , that  
293 represent, respectively, the warm and the dry scenario. Based on the results of the GLM analyses  
294 testing for the effects of climatic variables on asymptotic growth rates, we used the daily mean  
295 temperature and the number of wet days to characterize warm and dry scenarios, respectively.

296 Following Williams et al. (2015), extreme years corresponded to years with climate values larger  
297 than one standard deviation above the daily mean for temperature and lower than one standard  
298 deviation below the mean for precipitation. In the warm scenario, warm years were represented by  
299 pair-of-years with high daily mean temperature (2006-2007, 2013-2014, 2014-2015 and 2015-2016,  
300 Fig. 1,  $q^*=4/21=0.19$ ). In the dry scenario, dry years were represented by pair-of-years with low  
301 numbers of wet days (2001-2002, 2006-2007 and 2010-2011, Fig. 1,  $q^*=3/21=0.14$ ).

302 Second, following the approach described in Salguero-Gomez et al. (2012), we focused on  
303 a particular climate scenario resulting from the Regional Climate Model (RCM) proposed by the  
304 Euro-Cordex 2014 project (Jacob et al., 2014). We used the RCP4.5 scenario representing an  
305 intermediate scenario of increasing CO<sub>2</sub> concentration until 2060. The regional climate model  
306 simulations provided predicted values of daily precipitation and mean temperature. We then  
307 extracted these data for the closest geographic location, which is less than 1 km apart from the  
308 centroid of the species distribution (43.13710 N, 3.07327 E) and less than 6 km apart from the  
309 meteorological station we used to get observed climatic data. Overestimation of precipitation in  
310 RCMs is a well-known problem, in particular in areas close to the Mediterranean Sea (Gao et al.,  
311 2008; Ruffault et al., 2014). Therefore, to estimate the frequency of extreme years in the future  
312 (2020-2099), we used threshold values from the back-projected model values (Salguero-Gomez et  
313 al., 2012). Using the back-projected data from the reference period (1971-2005), we defined warm  
314 years as those with mean temperature from May  $t$  to June  $t+1$  greater than  $14.5 + 1.23$  (mean + SD)  
315 and dry years as those with number of wet days lower than  $68.6 - 14.8$  (mean - SD). Comparing the  
316 observed data and the back-projected data for the overlapping period 1995-2005, we indeed  
317 document an overestimation of the number of wet days predicted by the regional model compared  
318 to the observed one (paired  $t$ -test = 4.57, df = 8,  $p < 0.002$ ). In contrast, predicted and observed  
319 daily mean temperatures and total precipitation were not significantly different ( $p > 0.10$ ).  
320 Simulated data are available on the Drias platform ([www.drias-climat.fr](http://www.drias-climat.fr)).

### 321 **3. Results**

#### 322 *3.1. Patterns of spatio-temporal variations in asymptotic growth rates*

323 Asymptotic growth rates  $\lambda_a$  calculated per population and per pair-of-years showed a  
324 decreasing trend over time ( $\beta = -0.01$ ,  $p = 0.02$ , Fig. 2A). The slope of the trend for each population  
325 separately was significant only for the smallest population (Cruzade:  $\beta = -0.04$ ;  $p = 0.01$ , Fig. 2D).  
326 When pooling populations within each pair-of-years, the geometric mean of asymptotic growth

327 rates over years was 0.880 (Table 1), with  $\lambda_a$  ranging from 0.432 (2006-2007) to 1.815 (2012-2013).  
328 Geometric means of  $\lambda_a$  over years per population were all lower than 1 and varied between 0.710  
329 (Peyral) and 0.836 (Enferret1, Table 1). No significant relationship was detected between  
330 asymptotic growth rate and population size ( $\beta = 0.0003$ ;  $p = 0.46$ ). Randomization tests showed that  
331 the difference in  $\lambda_a$  among years was highly significant ( $p < 0.001$ , see appendix C). In contrast,  
332 asymptotic growth rates  $\lambda_a$  were not significantly different among populations ( $p = 0.16$ , see  
333 appendix C). The variance in  $\lambda_a$  per population was not significantly correlated with mean age at  
334 flowering ( $\beta = -0.02$ ;  $p = 0.68$ ) nor with population size ( $\beta = 0.0003$ ;  $p = 0.55$ ).

### 335 *3.2. Retrospective and prospective analyses*

336 As  $\lambda_a$  did not differ significantly among populations, retrospective and prospective analyses  
337 were performed after pooling individuals across populations. The observed variance in asymptotic  
338 growth rates among years was equal to 0.083, and was mainly explained by the variation in both the  
339 fecundity term ( $f$ ), the survival of seedlings ( $s_1$ ) and the survival of rosettes ( $s_2$ ) having the highest  
340 contributions (0.025, 0.023 and 0.021, respectively, Fig. 3), followed by the survival of just-  
341 emerged seedling ( $s_0$ ) and the flowering probability of rosettes ( $\alpha_2$ ) having a similar contribution  
342 (0.008, Fig. 3). Rare events in the life-cycle (flowering probabilities  $\alpha_1$  and  $\alpha_3$ , and survival of  
343 flowering plants  $s_3$ ) had negligible contributions (sum to 0.0009, Fig. 3 and appendix D). The  
344 largest elasticity of asymptotic growth rate was associated with rosette survival ( $s_2$ ) followed by the  
345 fecundity term  $f$  (mean number of just-emerged seedlings per flowering plant), the survival of just-  
346 emerged seedling ( $s_0$ ), seedling survival ( $s_1$ ) and the flowering probability of rosettes ( $\alpha_2$ , Fig. 3).  
347 Elasticity of  $\lambda_a$  to the remaining lower-level vital rates representing rare events ( $s_3$ ,  $\alpha_1$  and  $\alpha_3$ )  
348 summed only to 1% (Fig. 3). These latter rates were thus not considered for the GLMs investigating  
349 the relationship between lower-level vital rates and climatic variables.

### 350 *3.3. Relationship between asymptotic growth rates and climate*

351 Asymptotic growth rate, when pooling populations, was best explained by a model  
352 including only two climatic variables ( $R^2 = 0.58$ , Appendix E.2), with a high positive effect of the  
353 annual number of wet days ( $\beta = 0.15$ ,  $p = 0.004$ ) and a negative effect of the annual average daily  
354 mean temperature ( $\beta = -0.11$ ,  $p = 0.03$ ). The number of freezing days, the cumulative precipitation  
355 and the number of days with precipitation  $> 20$  mm proved non-significant ( $p > 0.05$ , Appendix E.1).  
356 No multiyear cumulative effect and no quadratic effect of climatic variables were significant ( $p >$   
357  $0.05$ , Appendices E.1).

358 *3.4. Relationships between lower-level vital rates and climate*

359 Overall, warming and drought negatively affected vital rates. The mean number of just-  
360 emerged seedlings per flowering plants  $f$  was negatively impacted by the daily mean temperature  
361 during both summer and fall periods (Table 2). The survival of just-emerged seedlings  $s_0$  was  
362 positively impacted by the number of wet days during the germination period (both fall and the  
363 winter periods), and negatively impacted by the daily mean temperature during both summer and  
364 fall periods (Table 2). Seedling survival  $s_1$  was negatively affected by an increase in the daily mean  
365 temperature during the summer and fall periods, and positively affected by an increase in the  
366 number of wet days during the same periods (Table 2). Rosette survival  $s_2$  decreased with  
367 increasing summer daily mean temperature (Table 2). Finally, the flowering probability of rosettes  
368  $\alpha_2$  was negatively impacted by the summer daily mean temperature and positively impacted by the  
369 number of wet days during the fall period (Table 2).

370 *3.5. Stochastic projections under climate change*

371 In absence of climate change, when randomly drawing each matrix with equal probability  
372 ( $1/21$ ), stochastic growth rates  $\lambda_s$  were significantly lower than 1 when pooling populations ( $\lambda_s =$   
373  $0.881$ ,  $CI = [0.877, 0.889]$ , Table 1). Stochastic growth rates were also lower than 1 in each  
374 population, ranging from  $0.742$  for the smallest population Cruzade ( $CI = [0.732, 0.770]$ ) to  $0.836$   
375 for the largest one Enferret2 ( $CI = [0.829, 0.851]$ , Table 1).

376 To assess the combined effect of environmental and demographic stochasticity on  
377 population viability, we compared the fate of the smallest population Cruzade and the largest one  
378 Enferret2, using their respective population size at  $t = 0$  (see details above and Fig. 4). As we did  
379 not detect any significant variation in asymptotic growth rates among populations, we pooled data  
380 across population for each pair-of-years to obtain the 21 matrices used to simulate climate change.  
381 In the warm scenario, when increasing the frequency of extreme years from  $q^*$  ( $4/21 = 0.19$ ) to  $0.8$ ,  
382 stochastic growth rates decreased from  $0.882$  to  $0.761$  for the largest population (Enferret2, Fig. 4A)  
383 and from  $0.879$  to  $0.765$  for the smallest one (Cruzade, Fig. 4C). Under the RCP4.5 scenario, the  
384 predicted frequency of warm year  $q_{\text{pred}}$  characterized by a daily mean temperature  $> 15.63$  °C for  
385 the period 2020-2099 equaled  $0.78$  and led to the extinction of both populations at 100 years in  
386 most simulations (Figs. 4A and 4C, solid black lines). Comparing this scenario with those of no  
387 climate change (Figs. 4A and 4C, dashed green lines), extinction probability at 50 years ( $P_{50}$ )  
388 increased from  $0.37$  to  $0.99$  for Enferret2 and from  $0.82$  to  $0.99$  for Cruzade, while extinction

389 probabilities at 100 years ( $P_{100}$ ) were close or equal to 1 for both populations. The mean time to  
390 extinction decreased from 57 to 26.4 years for Enferret2, and from 32 to 16 for Cruzade.

391 The dry scenario had less dramatic consequences on the viability of populations than the  
392 warm scenario (Fig. 4B and 4D). The increase in dry year frequency from  $q^*$  ( $3/21=0.14$ ) to 0.8 led  
393 to a small reduction in  $\lambda_s$  from 0.882 to 0.855 for Enferret2 and from 0.879 to 0.851 for Cruzade  
394 (Figs. 4B and 4D, respectively). The RCP4.5 scenario predicted a frequency of dry years  $q_{\text{pred}}$ ,  
395 corresponding to a number of wet days lower than 53.8 days, equaled to 0.15, a value very close to  
396 the one observed during the 22-year period of our demographic survey. The RCP4.5 scenario did  
397 not result in any significant change in extinction probabilities and mean time to extinction compared  
398 to the scenario of no climate change, whatever the size of populations (Figs. 4B and 4D, solid black  
399 lines).

## 400 **4. Discussion**

### 401 *4.1 Long term population dynamics of *Centaurea corymbosa**

402 Our results demonstrate the need for long-term demographic surveys to better understand  
403 the spatio-temporal demographic variability on plants (Blume-Werry et al., 2016; Compagnoni et  
404 al., 2016; Crone et al., 2011; Huelber et al., 2016). Indeed, our study based on 22 years of data  
405 provided a more accurate picture of the determinants of population dynamics in *C. corymbosa* than  
406 the study of Fréville et al. (2004) based on 8 years of data. In Fréville et al. (2004), the standard  
407 deviation in asymptotic growth rates  $\sigma(\lambda)$  was 0.116 among years and 0.099 among populations,  
408 with significant differences among years and populations. In the current study, variation among  
409 populations became non-significant and temporal variation in asymptotic growth rates was rather  
410 synchronized among populations (Fig. 2). This pattern is not surprising given the narrow  
411 distribution of *C. corymbosa* and is largely consistent with studies of other narrowly distributed  
412 species (Buckley et al., 2010; Kiviniemi and Löfgren, 2009; Ramula et al., 2008). More importantly,  
413 the standard deviation  $\sigma(\lambda)$  observed over the 22-year period was much larger (0.230) than the one  
414 (0.116) reported in Fréville et al. (2004). In agreement with the results of the permutation tests, we  
415 did not find any significant correlation between population dynamics and population size. Indeed,  
416 we did not find any evidence that small populations had lower population growth rates. Moreover,  
417 the variance in asymptotic growth rates among years did not increase with decreasing population  
418 size. In contrast to other demographic studies (Lande et al., 2003; Zeigler, 2013), we thus did not  
419 find any evidence of a greater sensitivity of the smallest populations to both environmental and



420 demographic stochasticity in our species. In addition, the variance in asymptotic growth rate was  
421 not correlated with mean age at flowering per population. We thus did not find evidence for  
422 demographic buffering in populations with greater longevity, in contrast to what has been found at  
423 an inter-specific scale in Morris et al. (2008). Population dynamics of *C. corymbosa* is thus mainly  
424 affected by environmental factors that vary over time rather than by spatial factors.

425 Average and most of the yearly asymptotic growth rates were lower than 1 for each  
426 population and when pooling individuals across populations. Overall, we observed a declining trend  
427 in yearly asymptotic growth rates over the 22-year period (Fig. 2), this trend being significant for  
428 the smallest population and when considering all populations (Figs. 2A and 2D, respectively).  
429 Asymptotic growth rates were negatively impacted by an increase in temperature and positively  
430 impacted by the number of wet days. Consistent with these results, asymptotic growth rates attained  
431 extreme values in years corresponding to extreme climatic events. Indeed, when pooling all  
432 individuals in a single population, the lowest value (0.432, Fig. 2A) was observed in 2006-2007  
433 when the mean temperature was the highest (16.3° C, Fig. 1) and the number of wet days was the  
434 lowest (34 days, Fig. 1). The highest growth rate (1.815, Fig. 2A) corresponded to 2012-2013, when  
435 we observed the second lowest mean temperature (14.2° C, Fig. 1) and the highest number of wet  
436 days (66 days, Fig. 1). Thus, population dynamics of *C. corymbosa* was mainly affected by extreme  
437 climatic events, which are predicted to increase in the future. Climatic variables investigated here  
438 did not show any marked temporal trend over the 22-year period of our demographic survey (Fig.1),  
439 which could explain the weak temporal trend observed in asymptotic growth rates. Overall, our  
440 study confirms that extreme climatic events are an important driver of plant population dynamics as  
441 reported in other studies (Andrello et al., 2012; Davison et al., 2010; McDowell et al., 2008;  
442 Shryock et al., 2014; Ulrey et al., 2016).

443 In contrast to some studies reporting both negative and positive effects of climate change  
444 on vital rates (Meer et al., 2016; Meisner et al., 2014; Nicolè et al., 2011), our study documents a  
445 consistent negative effect of increased temperature and drought on lower-level vital rates in *C.*  
446 *corymbosa*. Regarding temperature, the most critical season that impacted lower-level vital rates  
447 was the summer period, since increasing summer daily mean temperature negatively affected both  
448 fecundity, survival probability and flowering probability. In contrast to our study, flowering  
449 probability was found to be positively impacted by high temperature in some temperate plant  
450 species (e.g. *Himantoglossum hircinum*, Meer et al., 2016; *Dracocephalum austriacum*, Nicolè et  
451 al., 2011). While a negative effect of increasing temperature on flowering probability was also

452 reported in Peñuelas et al. (2004), this pattern was only observed in the southern Mediterranean  
453 sites but not in the northern ones. A likely explanation of this negative effect is that warm summers  
454 increase evapo-transpiration and decrease soil moisture (Christensen et al., 2004; Peñuelas et al.,  
455 2004). This could lead to a decrease in plant biomass as a consequence of rosette shrinking that in  
456 turn reduces the amount of resources that a plant can allocate to reproduction (Manders and Smith,  
457 1992). This is particularly true for monocarpic perennial species, where flowering probability has  
458 been shown to increase with plant size (Metcalf et al., 2003). Regarding precipitation, the youngest  
459 plants were the most impacted by the number of wet days. This factor had a positive effect on both  
460 survival of just-emerged seedlings ( $s_0$ ) during the germination period (fall and winter) and seedling  
461 survival ( $s_1$ ) during the summer and fall periods, which is consistent with several studies showing a  
462 positive impact of the frequency of wet days (Riba et al., 2002; Shriver, 2016). Both temperature  
463 and precipitation effects may be explained by the fact that recurrent warm and dry days can induce  
464 a seasonal water deficit, which may negatively impact the whole life-cycle (Manders and Smith,  
465 1992; Peñuelas et al., 2004; Ruffault et al., 2014). Species growing in rocky habitats, such as *C.*  
466 *corymbosa*, are likely to be the most affected, since these soils have a very low water capacity  
467 (Ruiz-Sinoga et al., 2012; Silva et al., 2015). Moreover, herbaceous species such as *C. corymbosa*  
468 do not have a deep root system ensuring access to water over dry periods in such rocky habitats.

#### 469 *4.2 Predictions from climate scenarios*

470 Both demographic and environmental stochasticity are important factors in determining the  
471 viability of species with small population sizes (Caswell, 2001; Crone et al., 2013; García et al.,  
472 2002). We here showed that climate variation explained a large amount of variation in vital rates  
473 and growth rates in *C. corymbosa*. We thus used stochastic models to predict the fate of *C.*  
474 *corymbosa* populations with both environmental stochasticity arising from climate change and  
475 demographic stochasticity. We did not include density-dependence in our model, which could make  
476 quantitative predictions overly pessimistic (Dahlgren et al., 2016). Population viability analyses are  
477 acknowledged to be relevant tools to quantitatively compare the impact of different scenarios rather  
478 than quantitatively predict the future status of populations (Coulson et al., 2001). We thus used  
479 population viability analyses to compare how the warm and the dry scenarios impacted population  
480 viability of *C. corymbosa* rather than attempting to explicitly predict future population size.

481 Stochastic projections predicted population declines ( $\lambda_s < 1$ ) under no climate change.  
482 Populations were predicted to decline even faster in the future in response to an increased frequency  
483 of extreme years in both the warm and dry scenarios. Such results are consistent with the GLMs

484 showing negative impacts of warming and drought, and several studies investigating population  
485 viability in response to climate change (Andrello et al., 2012; Lawson et al., 2015; Marrero-Gómez  
486 et al., 2007; Shryock et al., 2014). More importantly, the warm scenario had more severe  
487 consequences on population viability than the dry scenario whatever the initial population size.  
488 However in our simulations, the initial population size impacted both extinction probability and the  
489 mean time to extinction, a pattern consistent with theoretical studies since small populations are  
490 more vulnerable to extinction than largest ones (Groom et al., 2005; Lande et al., 2003). Using the  
491 RCP4.5 scenario, the change in temperature projected for the period 2071-2099 was of the same  
492 order of magnitude than the one predicted by other regional climatic models (Christensen et al.,  
493 2007; Ruffault et al., 2014). In contrast, our dry scenario predicted an annual mean number of wet  
494 days equal to 66.41 (-3.2%), while other models predicted a much severe decrease (-19.6%,  
495 Ruffault et al., 2014). This suggests that uncertainty in climate models should be carefully  
496 considered in management plans and when evaluating extinction risk. Such uncertainty is  
497 particularly pronounced for the Mediterranean region (Gao et al., 2008; Ruffault et al., 2014).

498 Faced with climate change, populations can either migrate or adapt by microevolution or  
499 phenotypic plasticity to avoid extinction (Groom et al., 2005; Lande et al., 2003). In the  
500 Mediterranean region, many narrow endemic species are characterized by a low ability to colonize  
501 existing suitable habitats due to several biological traits such as low dispersal ability (Colas et al.  
502 1997; Lavergne et al., 2004; Thompson et al. 2005). In *C. corymbosa*, self-incompatibility and  
503 monogamy make successful colonization even less likely (Colas et al., 1997). Thus, for such species,  
504 persistence mainly depends upon their ability to respond plastically to climate change or to become  
505 locally adapted to new environmental conditions (Cotto et al., 2017; Knight et al. 2008; Menges,  
506 2000). Theoretical work suggests that perennial species should display slower evolutionary  
507 responses than annual plants, since higher adult survival limits the adaptive capacity of local  
508 populations (Cotto et al., 2017). Moreover, small populations have a lower evolutionary potential,  
509 since they become genetically impoverished due to the impact of genetic drift. Using a shorter  
510 survey (1995-2001), Fréville et al. (2001) showed that demographic rates were not correlated with  
511 intra-population genetic diversity in *Centaurea corymbosa* (Fréville et al., 2001). Using the same  
512 genetic data (Table 1 in Fréville et al., 2001), we likewise confirmed that genetic diversity was  
513 correlated with neither  $\lambda_s$  (Spearman correlation  $\rho = 0.26$ ,  $p = 0.61$ ) nor the slope of regression in  
514 asymptotic growth rates over years ( $\rho = 0.09$ ,  $p = 0.89$ ). Thus, our results do not support evidence  
515 for accumulation of deleterious mutations (Lynch et al., 1995), nor a loss of standing variation due  
516 to genetic drift in small populations of *C. corymbosa*.

518 Persistence of narrow endemic species in the Mediterranean region may have been favored  
519 by the capacity of those species to grow in rocky habitats (Thompson et al., 2005), since these  
520 remote habitats do not face direct threats due to human activities. Demographic studies of cliff-  
521 dwelling species have shown unusual demographic stability and resilience of these plants (García,  
522 2003; Lavergne et al., 2005; Picó and Riba, 2002; Thompson et al., 2005), likely arising from much  
523 higher importance of rosette survival than recruitment for the maintenance of populations (Cotto et  
524 al., 2017; Larson et al., 2000; Silva et al., 2015). In a scenario of no climate change, rosette survival  
525 (that had the highest elasticity on growth rates) should be increased from 0.71 to 0.92 to ensure the  
526 persistence of *C. corymbosa* in a deterministic model (Appendix G). However, management actions  
527 aimed at increasing specific vital rates, such as watering plants are not feasible in such rocky  
528 habitats. Implementing management actions that reduce the negative effects of demographic,  
529 genetic and environmental stochasticity by manipulating population size and population number  
530 appear much more promising.

531 Previous studies have shown the importance of biological features such as self-  
532 incompatibility and low dispersal ability on the population persistence of *C. corymbosa* (Colas et al.  
533 1997). Two new populations were introduced in 1994 on the top of unoccupied cliffs thus  
534 confirming the existence of suitable but empty habitats nearby existing natural populations (Colas et  
535 al., 2008; Kirchner et al., 2006). Introduced populations exhibited on average higher plant survival  
536 than natural populations, mainly because seeds had been introduced manually in a priori suitable  
537 microsites (Colas et al. 2008). However, fecundity in introduced populations was lower than in  
538 natural ones, likely as a consequence of low local density of flowering plants, leading to strong  
539 pollen limitation (Colas et al. 2008). One introduced population has been extinct for 5 years, while  
540 the other population only harbored 35 plants in the last census performed in December 2017. In the  
541 future, protocols should be carefully designed to ensure successful introductions. For instance,  
542 introducing a large number of seeds (>1000) distributed over a few sites and at yearly intervals  
543 should allow population persistence on the short term (Colas et al., 2008; Kirchner et al., 2006).

544 Faced with accelerated climate change, conservation policies for endangered species, such  
545 as *C. corymbosa*, should be reconsidered. As our study demonstrated the importance of climate on  
546 the fate of populations, introductions in distant habitats should be considered, although such  
547 assisted colonization event requires suitable and available habitats at a larger scale. At present,  
548 prioritization actions of conservation rely on the climatic niche of the species (Jones et al., 2016;

549 Oliver et al., 2016), and depend on our ability to define new protected areas in Northern localities  
550 (Araújo et al., 2011; Bellard et al., 2012) or microrefugia (i.e. location with a low impact of climate  
551 change, Jones et al., 2016; Ulrey et al. 2016). Recently, an increasing amount of empirical evidence  
552 has been gathered to document that organisms, including plants, can show microevolutionary  
553 responses in natural populations (Franks et al., 2014; Thomann et al., 2013), suggesting plants can  
554 adapt to new environmental conditions (Thompson et al., 2005). Therefore, reinforcement, which  
555 allows increasing population size and thus reducing extinction risk arising mainly from  
556 demographic and genetic stochasticity, is also potentially an efficient and reasonable management  
557 strategy for species facing climate change.

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571 **Tables**

572 **Table 1:** Demographic characteristics of each of the six populations of *Centaurea corymbosa*, and the pooled population after pooling data across  
 573 populations: number of individual life-histories recorded over 22 years (see also Appendix A1), number of surviving plants older than 1 year, mean  
 574 life-time of individuals that reached the rosette stage, mean age at flowering, geometric mean of asymptotic growth rates ( $\lambda_a$ ) over 22 years, minimum  
 575 and maximum of  $\lambda_a$ , stochastic growth rate ( $\lambda_s$ ) when including both demographic and environmental stochasticity (uniform frequency, see text) with  
 576 the confidence intervals (2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of the simulated distributions) and the rounded mean of total numbers of flowering plants (Nb.FP)  
 577 recorded by the exhaustive count over the 22 years (see appendix A2). Populations are ranked by decreasing order of total number of flowering plants.

Population	Nb. individuals	Nb. one year plants	Mean longevity of the rosettes (years)	Mean age at flowering (years)	Mean $\lambda_a$	$[\lambda_a \text{min}, \lambda_a \text{max}]$	$\lambda_s$	$CI(\lambda_s)$	Nb.FP
Pooled pop.	6112	1579	3.5	5.0	0.880	[0.432, 1.815]	0.881	[0.877, 0.889]	478
Enferret2	1712	286	3.3	4.5	0.749	[0.240, 1.585]	0.836	[0.829, 0.851]	173
Enferret1	1165	324	3.6	5.1	0.836	[0.425, 2.325]	0.824	[0.819, 0.837]	147
Auzils	1175	415	3.5	5.7	0.783	[0.331, 1.391]	0.792	[0.786, 0.807]	81
Portes	1064	268	3.7	6.2	0.819	[0.364, 1.610]	0.824	[0.818, 0.842]	34
Peyral	540	192	3.2	4.7	0.710	[0.00 <sup>(a)</sup> , 1.264]	0.804	[0.799, 0.827]	28
Cruzade	456	94	3.4	4.2	0.720	[0.00 <sup>(a)</sup> , 1.444]	0.742	[0.732, 0.770]	13

578 (a) The null values of asymptotic growth rates corresponded to pair-of-years with no flowering plant within plots and null values for rosette survival  $s_2$ .



580 **Table 2:** Summary of GLMs explaining the effect of two climatic variables (averaged over three-month periods) on lower-level vital rates. Only  
581 climatic variables affecting population growth rate were included in the GLMs. From the best model explaining a given lower-level vital rate, we  
582 report the estimated coefficient ( $\beta$ ) and its significance (*t-test*) after scaling the climatic variables. ‘ns’ indicates that the variable tested was not  
583 significant in the model, based on a forward stepwise selection approach (see text and appendix E.3 for details).

	Daily mean temperature				No. wet days			
	Summer [Jun-Aug]	Fall [Sep-Nov]	Winter [Dec-Fev]	Spring [Mar-May]	Summer [Jun-Aug]	Fall [Sep-Nov]	Winter [Dec-Fev]	Spring [Mar-May]
Fecundity term $\log(f+1)$	-0.28 **	-0.22 *	ns	ns	ns	ns	ns	ns
Survival of just emerged seedling $s_0$	-0.17 ***	-0.08*	ns	ns	ns	0.24 ***	0.14 ***	ns
Seedling survival $s_1$	-0.28 ***	-0.12 <sup>+</sup>	ns	ns	0.34 ***	0.04 <sup>+</sup>	ns	ns
Rosette survival $s_2$	-0.45 ***	ns	ns	ns	ns	ns	ns	ns
Flowering probability of rosette $\alpha_2$	-0.23 ***	ns	ns	ns	ns	0.19 *	ns	ns

584 <sup>+</sup>P < 0.08, \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001.

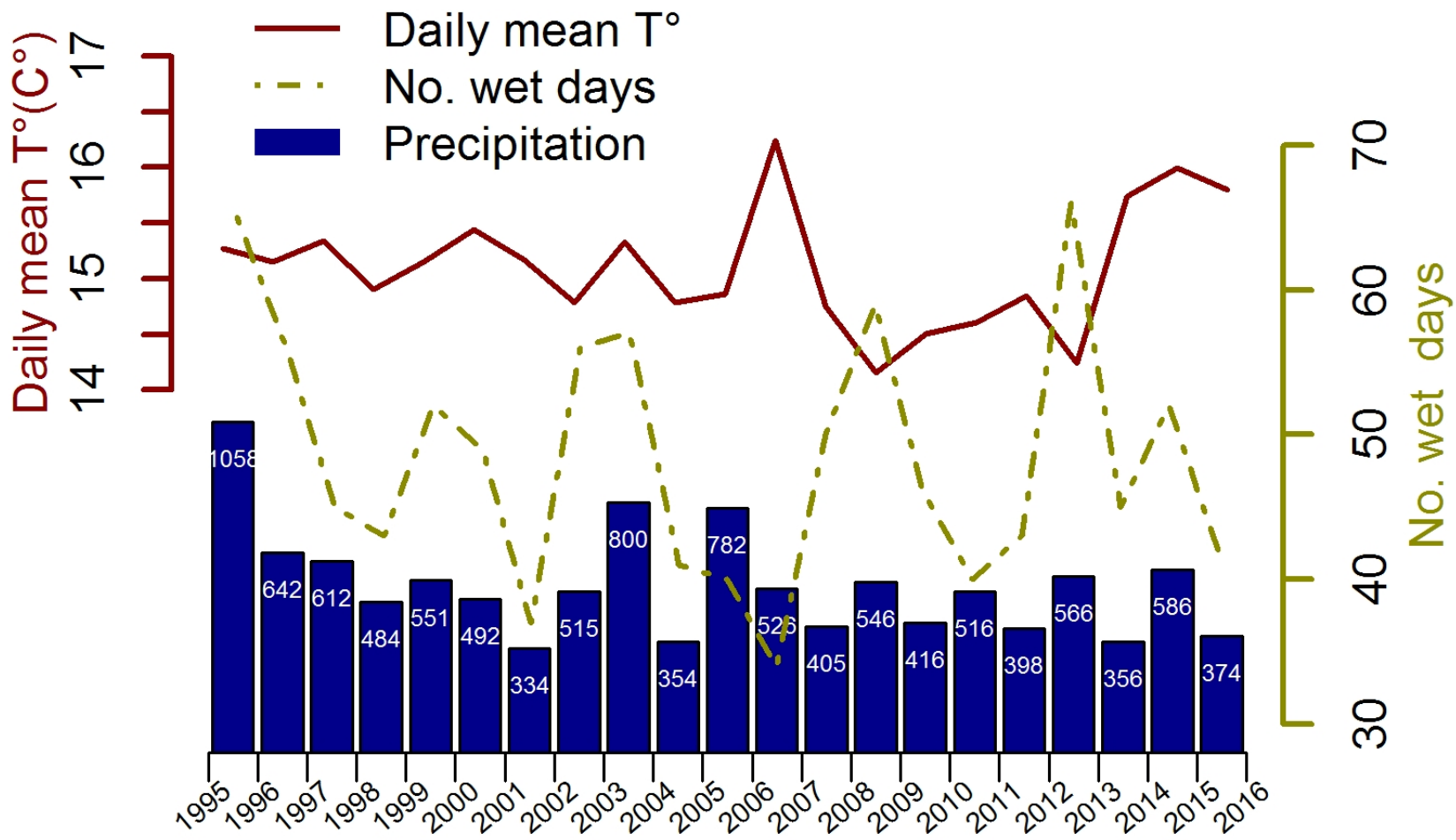
585 **Figure legends**

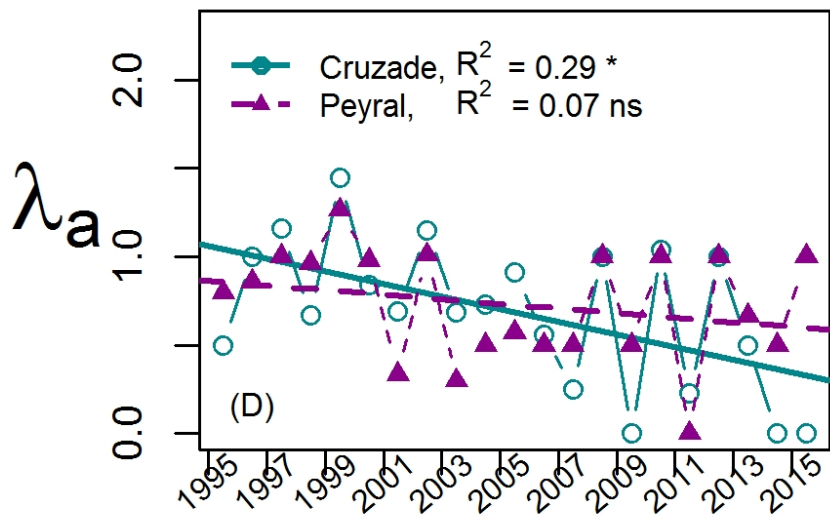
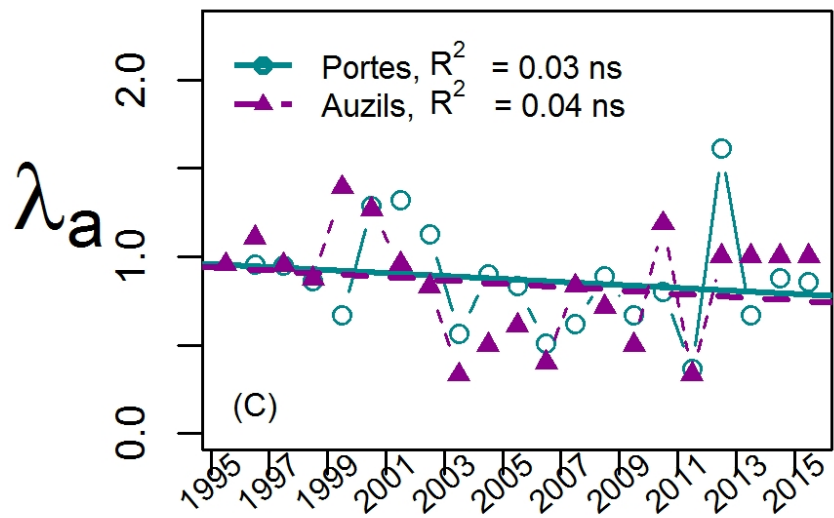
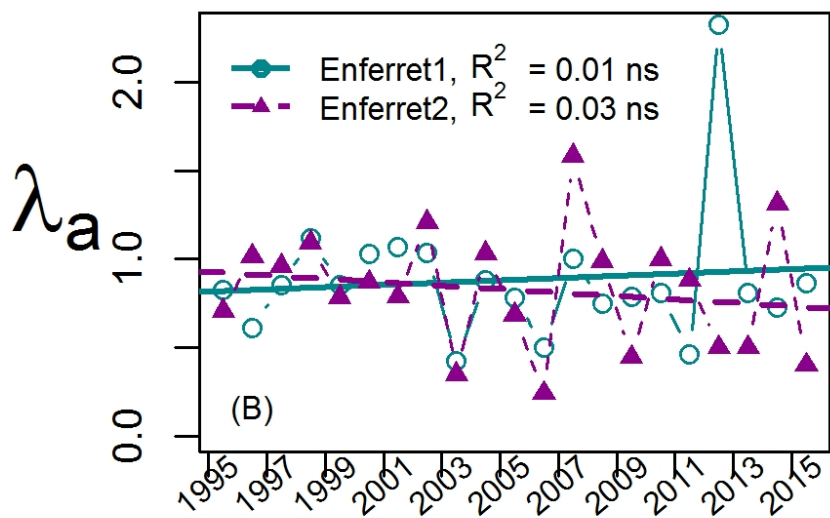
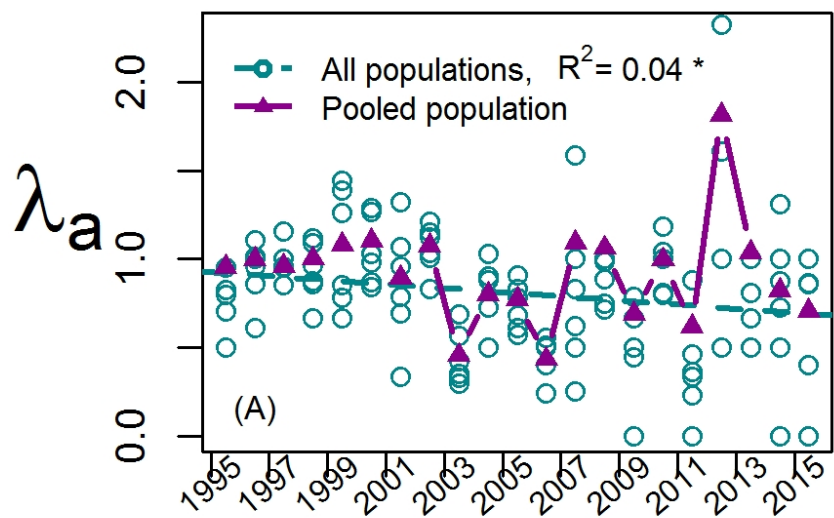
586 **Figure 1:** Climatic variation observed in the Massif de la Clape between 1995 and 2016. Climatic  
587 variables were calculated per pair-of-years from June( $t$ ) to May( $t+1$ ). The solid line represents the  
588 average daily mean temperature ( $C^\circ$ ), and the dashed line represents the number of wet days.  
589 Values in the vertical bars indicate the cumulative precipitation per pair-of-years. Year on the x-axis  
590 corresponds to June( $t$ ). Data were obtained from INRA Pech Rouge.

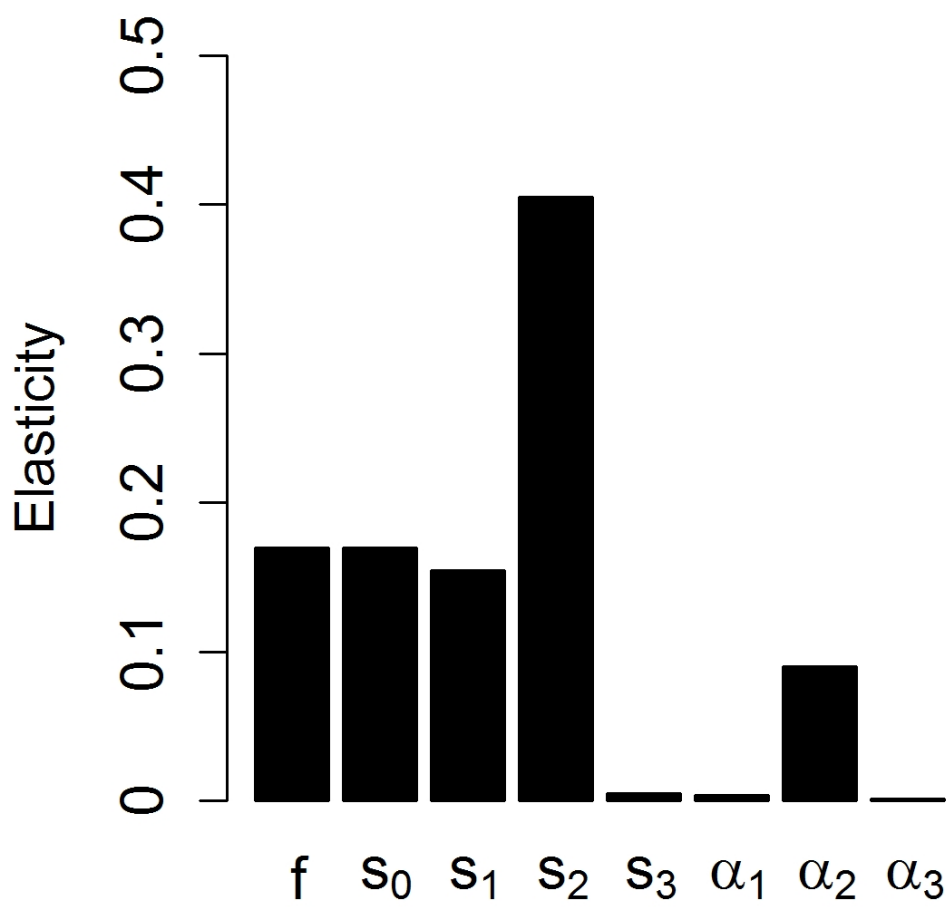
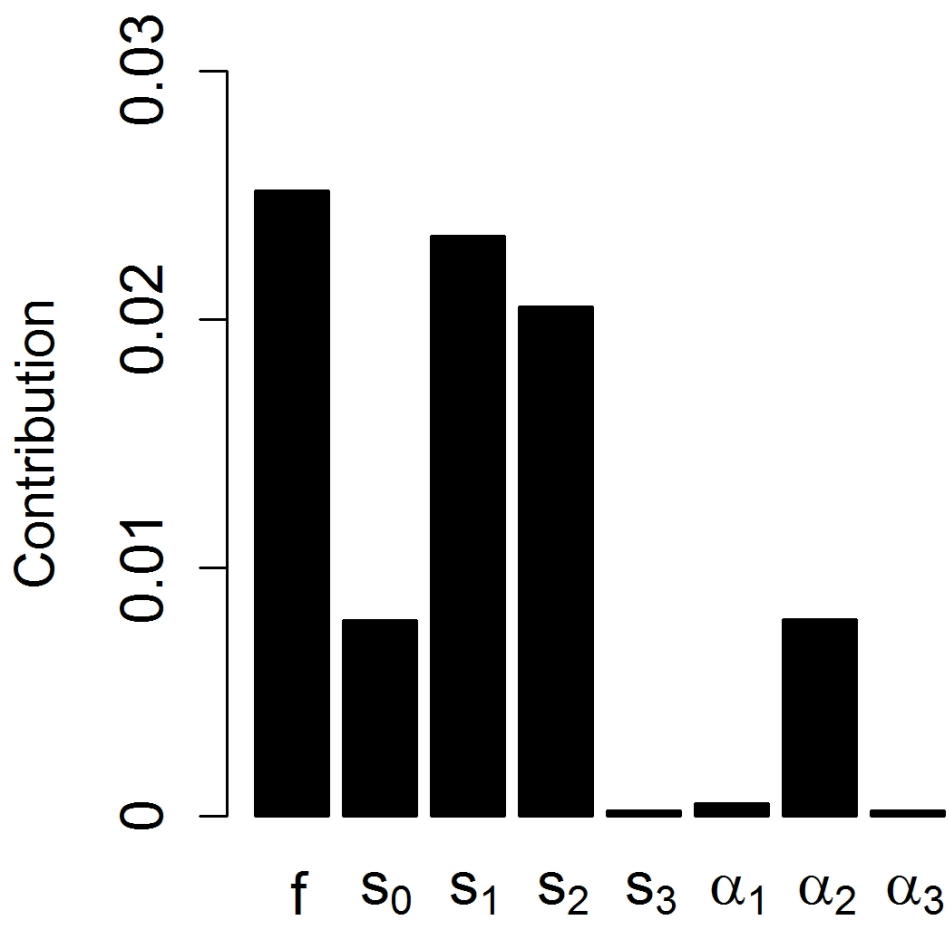
591 **Figure 2:** Asymptotic growth rates ( $\lambda_a$ ) per pair-of-years. Panel A represents yearly  $\lambda_a$  values  
592 (circles) with their trend over years (dashed line) calculated from 125 matrices. The solid line  
593 represents the values of  $\lambda_a$  (triangles) pooling individuals in a single population. Panels B, C and D  
594 represent the trend in  $\lambda_a$  over years for the largest populations (E2 and E1), the medium size  
595 populations (Au and Po) and the smallest ones (Pe and Cr).  $R^2$  corresponds to the r-squared value  
596 obtained from the linear regression and “ns” indicates that the slope was not significantly different  
597 from 0. Year on the x-axis corresponds to June ( $t$ ).

598 **Figure 3:** Contribution of lower-level vital rates to the variance of  $\lambda_a$  observed among years, and  
599 elasticity of growth rates to these vital rates calculated on the arithmetic mean matrix calculated  
600 over 21 pair-of-years matrices.

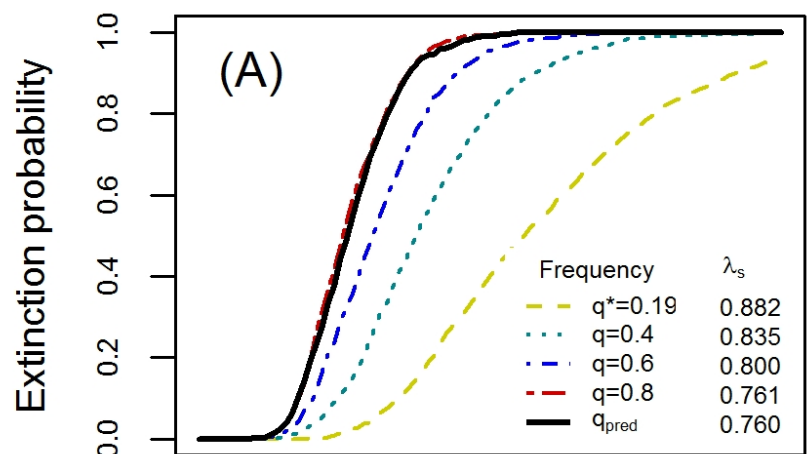
601 **Figure 4:** Predicted consequences of the warm and dry scenarios on the viability of populations  
602 using two different initial population sizes representing the largest (Enferret2) and the smallest  
603 (Cruzade) populations when incorporating both demographic and environmental stochasticity (see  
604 text for details). Panels (A) and (C) represent the warm scenario for the largest population size ( $N_0 =$   
605  $\{685\ 796\ 118\}$ , Enferret2), and the smallest one ( $N_0 = \{41\ 47\ 7\}$ , Cruzade). Panels (B) and (D)  
606 represent the dry scenario for Enferret2 and Cruzade, respectively. The warm scenario consisted of  
607 an increase in the frequency of years with extremely high temperatures (4 extreme years out of 21:  
608 2006-2007, 2013-2014, 2014-2015), and the dry scenario an increase in the frequency of years with  
609 an extremely low number of wet days (3 extreme years out of 21: 2001-2002, 2006-2007 and 2010-  
610 2011). ‘q’ indicates the frequency of extreme years with  $q^*$  the observed frequency over the 22-year  
611 of our demographic survey and  $q_{\text{pred}}$  the frequency predicted by the RCP4.5 climatic model for the  
612 warm and dry scenarios ( $q_{\text{pred}}$  are 0.78 and 0.15, respectively, see text). The initial population size  
613 was estimated as the stable stage distribution predicted by the mean matrix over years after pooling  
614 data across populations, using the mean total number of flowering plants recorded from 2010 to  
615 2016 in Enferret2 and Cruzade, respectively.



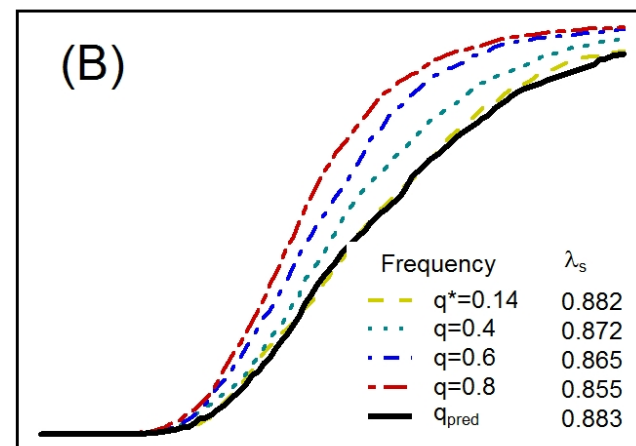




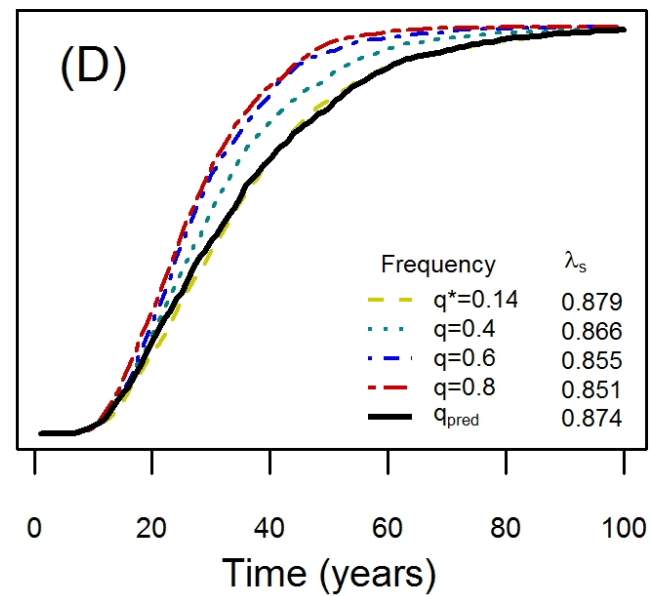
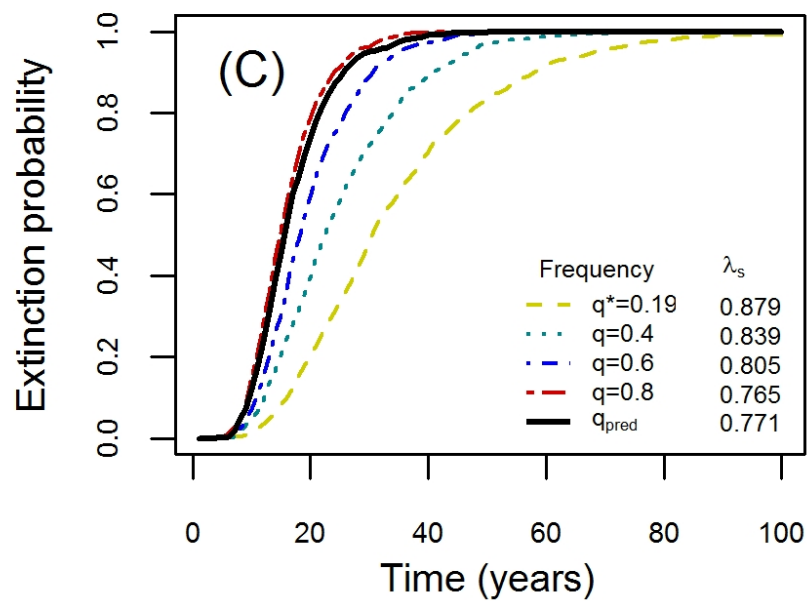
Warm scenario



Dry scenario



NO (Enferret2)



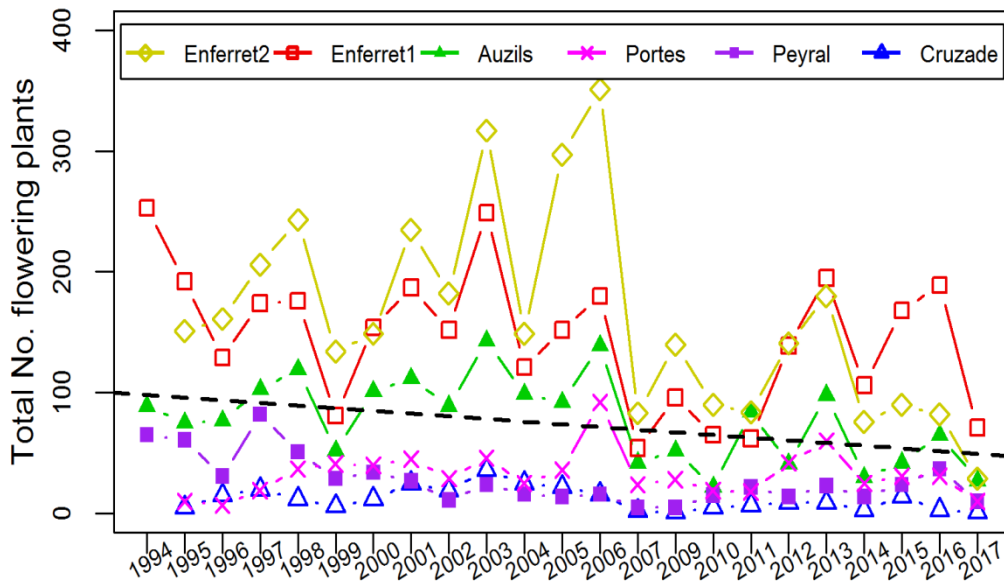
NO (Cruzade)

## Appendices:

**Appendix A1:** Number of individuals recorded within the 41 permanent plots over the 22-year period. Number of new seedlings represents all new plants recorded in the permanent plots every 3 months during year  $t$  to  $t+1$ , out of which some did not survive until June  $t+1$  with a probability  $1-s_0$ , and thus did not reach the seedling stage. The number of individuals recorded in June ( $t$ ) in each life-stage of the life-cycle used to construct population projection models, is given for: Seedling, the one-year plants that survive until June ( $t$ ), Rosette, vegetative plants older than one year, and Flowering plants that represent reproductive plants. The total number of individuals per year did not include the new seedlings. The total individual life-histories (6112) corresponds to the sum of number of new seedlings (5779) and number of rosettes and flowering plants at the first census (315+18).

Year	New seedlings	Seedling stage	Rosette stage	Flowering plant stage	Total
1994	NA	NA	315	18	333
1995	467	234	161	35	430
1996	258	145	184	48	377
1997	608	181	160	48	389
1998	427	165	195	28	388
1999	349	204	178	37	419
2000	284	164	218	41	423
2001	1097	475	204	30	709
2002	466	356	250	17	623
2003	167	115	357	30	502
2004	299	197	144	12	353
2005	73	45	137	17	199
2006	262	30	97	22	149
2007	72	42	40	9	91
2008	182	47	45	9	101
2009	368	102	43	6	151
2010	67	29	36	3	68
2011	29	15	44	3	62
2012	50	8	20	6	34
2013	116	93	19	7	119
2014	89	45	41	4	90
2015	31	10	48	5	63
2016	18	9	35	2	46
Total	5779	2711	2971	437	

**Appendix A2:** Total number of flowering plants per year recorded by the exhaustive count per population. The dashed line corresponds to the trend of the number of flowering plants over time ( $\beta = -2.21$ ,  $p = 0.02$ ). The growth rate calculated from the number of flowering plants was equal to 0.92.

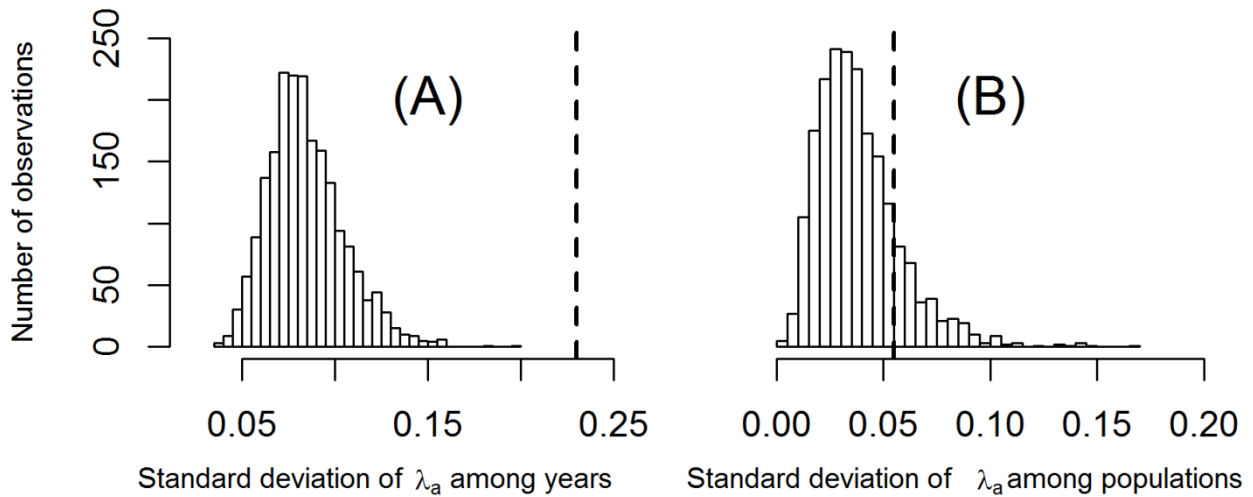


**Appendix B:** Projections matrices per population. The fecundity term  $fs_0$  was estimated as the geometric mean of  $fs_0$  obtained per pair-of-years, other parameters are obtained by pooling data over years.

Population	$a_{13}$ $fs_0$	$a_{21}$ $s_1 (1-\alpha_1)$	$a_{22}$ $s_2 (1-\alpha_2)$	$a_{23}$ $s_3 (1-\alpha_3)$	$a_{31}$ $s_1 \alpha_1$	$a_{32}$ $s_2 \alpha_2$	$a_{33}$ $s_3 \alpha_3$
Pooled pop.	5.104	0.351	0.586	0.024	0.011	0.120	0.038
Enferret2	4.267	0.345	0.509	0.029	0.029	0.165	0.029
Enferret1	3.834	0.347	0.595	0.000	0.009	0.119	0.035
Auzils	4.549	0.379	0.598	0.026	0.000	0.094	0.026
Portes	4.283	0.294	0.640	0.017	0.011	0.113	0.017
Peyral	3.601	0.404	0.573	0.067	0.000	0.108	0.067
Cruzade	2.819	0.361	0.593	0.020	0.016	0.174	0.082



**Appendix C:** Distribution of the standard deviation of asymptotic growth rates under the null hypothesis of: (A) no difference among years and (B) no difference among populations. The x-axis represents the standard deviation of  $\lambda_a$  calculated (A) over the 21 year values, (B) over the 6 population values. The y-axis represents the number of observations. The dashed vertical lines indicate the observed value. Randomization tests were based on 2000 permutations.



**Appendix D:** Arithmetic mean and coefficient of variation of lower-level vital rates over years after pooling data over populations, sensitivity and elasticity of growth rates to these vital rates calculated at the arithmetic mean matrix over 21 matrices, and contributions of lower-level vital rates to the variation of growth rates among years.

	$f$	$s_0$	$s_1$	$s_2$	$s_3$	$\alpha_1$	$\alpha_2$	$\alpha_3$
Mean	13.235	0.484	0.363	0.732	0.059	0.016	0.181	0.217
CV	0.644	0.395	0.505	0.184	1.046	2.598	0.386	1.352
Sensitivity	0.017	0.457	0.55	0.721	0.117	0.31	0.648	0.008
Elasticity	0.170	0.170	0.155	0.405	0.005	0.004	0.090	0.001
Contribution	0.025	0.008	0.023	0.021	<0.001	<0.001	0.008	<0.001

**Appendix E.1:** Single-variable log-linear models showing the relationship between asymptotic growth rates and each climatic variable.  $R^2$  corresponds to the coefficient of determination for the tested model.

Climatic variable in year $t$	$R^2$	Estimate	p-value
Daily mean $T^\circ$	0.31	-0.320	<b>0.011</b>
Daily maximal $T^\circ$	0.30	-0.250	<b>0.009</b>
Precipitation	0.01	-0.001	0.672
No. days with $T^\circ > 25$	0.18	-0.013	0.052
No. freezing days	0.03	0.008	0.451
No. wet days	0.46	0.021	<b>0.001</b>
No. days with precip. > 20mm	0.04	-0.021	0.381
<b>Climatic variables in year <math>t-1</math></b>			
Daily mean $T^\circ$	0.003	0.031	0.251
Daily maximal $T^\circ$	0.006	0.032	0.233
Precipitation	0.058	-0.001	0.452
No. days with $T^\circ > 25$	0.005	-0.002	0.253
No. freezing days	0.001	0.001	0.360
No. wet days	0.012	-0.004	0.250
No. days with precip. > 20mm	0.010	-0.009	0.141
<b>Quadratic effect</b>			
Daily mean $T^\circ$	0.30	-0.011	<b>0.010</b>
Daily maximal $T^\circ$	0.30	-0.006	<b>0.009</b>
Precipitation	0.01	0.000	0.631
No. days with $T^\circ > 25$	0.18	-0.001	0.052
No. freezing days	0.02	0.000	0.540
No. wet days	0.43	0.003	<b>0.002</b>
No. days with precip. > 20mm	0.04	-0.001	0.411

**Appendix E.2:** Selection models for assessing the relevance of climatic variables to explain variations in asymptotic growth rates based on a forward stepwise selection approach. The significance of each added variable in the model was tested using an analysis of deviance. The null model included only the intercept.

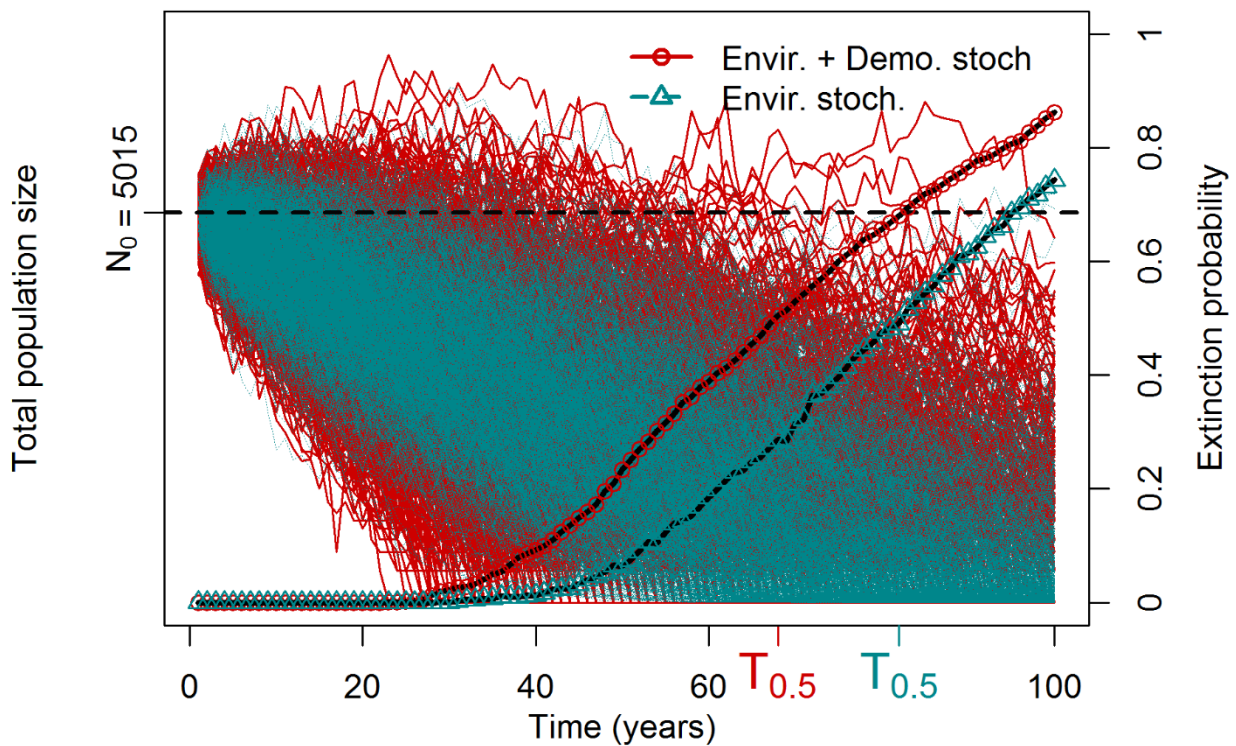
<b>Model</b>	<b>Compared models</b>	<b>p-value</b>
M0: Null model		
M1: No. wet days	M0, M1	<b>0.001</b>
M2: No. wet days + (No. wet days) <sup>2</sup>	M1, M2	0.311
M3: No. wet days + Daily mean T°	M1, M3	<b>0.031</b>
M4: No. wet days + Daily mean T° + (Daily mean T°) <sup>2</sup>	M3, M4	0.292
M5: No. wet days + Daily mean T° + Daily maximal T°	M3, M5	0.890
M6: No. wet days + Daily mean T° + (Daily maximal T°) <sup>2</sup>	M3, M6	0.843

**Appendix E.3:** Selection models for assessing the relevance of climatic variables to explain variations in lower-level vital rates based on a forward stepwise selection approach. P-values correspond to the F-test for the log-linear models and to Chi-test for the generalized linear models with binomial error. The null model included only the intercept. We denoted the number of days with Precipitation > 1mm by “P” and the mean daily temperature by “T”. The seasons are denoted by **1, 2, 3 and 4** to indicate **summer, fall, winter and spring**, respectively (see the main text and Table 2)

Lower-level vital rate	Model	Compared models	p-value
$\log(f+1)$	M0: Null model		
	M1: T1	M0, M1	<b>0.012</b>
	M2: T1+T2	M1, M2	<b>0.031</b>
	M3: T1+T2+T3	M2, M3	0.165
	M4: T1+T2+T4	M2, M4	0.583
	M5: T1+T2+P1	M2, M5	0.794
	M6: T1+T2+P2	M2, M6	0.222
	M7: T1+T2+P3	M2, M7	0.806
	M8: T1+T2+P4	M2, M8	0.236
	Selected model: $\log(f+1) \sim T1+T2$		
$S_0$	M0: Null model		
	M1: P2	M0, M1	<b>&lt;0.001</b>
	M2: P2+P3	M1, M2	<b>&lt;0.001</b>
	M3: P2+P3+T2	M2, M3	<b>0.006</b>
	M4: P2+P3+T2+T1	M3, M4	<b>&lt;0.001</b>
	M5: P2+P3+T2+T1+P1	M4, M5	0.082
	M6: P2+P3+T2+T1+T3	M4, M6	0.087
	M7: P2+P3+T2+T1 +T4	M4, M7	0.120
	M8: P2+P3+T2+T1 +P4	M4, M8	0.091
Selected model: $S_0 \sim T1+T2+ P2+P3$			
$S_I$	M0: Null model		
	M1: T1	M0, M1	<b>&lt;0.001</b>
	M2: T1+P1	M1, M2	<b>&lt;0.001</b>
	M3: T1+P1+P2	M2, M3	<b>0.002</b>
	M4: T1+P1+P2+T4	M3, M4	0.974

	M5: T1+P1+P2+P3	M3, M5	0.352
	M6: T1+P1+P2+P4	M3, M6	0.072
	M7: T1+P1+P2+T3	M3, M7	0.316
	M8: T1+P1+P2+T2	M3, M8	<b>0.030</b>
	Selected model: $S_I \sim T1 + T2 + P1 + P2$		
$S_2$	M0: Null model		
	M1: T1	M0, M1	<b>&lt;0.001</b>
	M2: T1 + P1	M1, M2	0.692
	M3: T1+P2	M1, M3	0.115
	M4: T1+P3	M1, M4	0.174
	M5: T1+ P4	M1, M5	0.092
	M6: T1+ T2	M1, M6	0.163
	M7: T1+T3	M1, M7	0.662
	M8: T1+T4	M1, M8	0.365
	Selected model: $S_2 \sim T1$		
$\alpha_2$	M0: Null model		
	M1: T1	M0, M1	<b>0.005</b>
	M2: T1+ T4	M1, M2	0.122
	M3: T1+P1	M1, M3	0.251
	M4: T1+P4	M1, M4	0.071
	M5: T1+P2	M1, M5	<b>0.020</b>
	M6: T1+P2+P3	M5, M6	0.415
	M7: T1+P2+T2	M5, M7	0.868
	M8: T1+P2+T3	M5, M8	0.976
	Selected model: $\alpha_2 \sim T1 + P2$		

**Appendix F:** Relative effect of demographic stochasticity and environmental stochasticity on the viability of *C. corymbosa* populations. Simulations were performed either by incorporating only environmental stochasticity through whole matrix selection (see text), or both environmental stochasticity and demographic stochasticity introduced through multinomial sampling of the stable stage distribution (see text). Projections were simulated using 1000 stochastic iterations, each iteration representing a trajectory of population size over 100 years. The initial population size,  $N_0 = \{2148, 2497, 370\}$ , used to start our simulations was calculated from the stable stage distribution obtained from the arithmetic mean of the total number of flowering plants recorded in the population (exhaustive survey, Appendix A2) from 2010 to 2016, and the scaled eigenvector  $W$  from the arithmetic mean matrix over years (2010-2016) when pooling data over populations (see text for details). Extinction probability at a given time  $t$  corresponds to the number of trajectories for which  $N(t) < I$  over the total number of trajectories.  $T_{0.5}$  represents the time corresponding to an extinction probability equal to  $P = 0.5$ .



**Appendix G:** Required values of lower-level vital rates for achieving population persistence in a deterministic model ( $\lambda_a=1$ ), using two different methods: lower-level vital rates values were either predicted from the elasticity values, or directly from the global mean matrix after pooling individuals over populations and years to obtain a single population. For both methods, we varied only one vital rate at a time, while keeping others at their observed value in the mean matrix.

Vital rates	Observed value	Required value	
		Elasticity prediction	Prediction from the global matrix
Survival of just-emerged seedling $s_0$	0.477	0.811	0.790
Rosette survival $s_2$	0.707	0.918	0.937
Fecundity term $f$	11.16	18.98	18.50