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Title:

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

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Title:

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

Abstract

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

Keywords:

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

1. Introduction

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

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

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

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

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

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

2. Materials & Methods

2.1. Biological model, demographic and climatic datasets

2.1.1. Study species

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

2.1.2. Demographic dataset

Data have been collected since June 1994 in the six populations. However, in the first census, the status of non-flowering plants (seedling or rosette) could not be assessed. Thus, matrix population models were based on 22 years of demographic survey (1995-2016), except for one population (Portes, 1996-2016). Data collection is described in details in Fréville et al. (2004). Every 3 months (June, September, December and March), we recorded the presence and the status of each individual within 41 permanent plots and new seedlings were added to the datasets (see Appendix A1). During the flowering period (mid-June), we also surveyed the whole distribution area of the species to count the total number of flowering plants per population (exhaustive count, Table 1 and Appendix A2). A total of 6112 individual life-histories were used to construct population projection models (Table 1 and Appendix A1).

2.1.3. Climatic dataset

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

2.2. Deterministic analyses

2.2.1. Matrix projection models

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

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

From the 22 years of demographic survey, we constructed 21 matrices per population (see appendix B for projection matrices per population). The probabilities of a flowering plant to survive (s_3) and to reproduce the year after (α_3) were very low, in agreement with the monocarpy of the species, and had negligible effects on population dynamics (see appendix B). Using a deterministic MPM (linear, time-invariant), we calculated the asymptotic growth rate λ_a as the dominant eigenvalue of the matrix $\mathbf{A}$ of the corresponding pair-of-years. The model did not include seed bank and migration. Indeed, less than 5% of seeds may remain dormant for one year and seed dispersal among populations is highly limited (Colas et al., 1997; Fréville et al., 2004; Imbert, 2006). The net fecundity fs_0 was estimated as the ratio of the number of seedlings observed in June of a given year over the number of flowering plants observed within permanent plots in June of the previous year. Our three-month survey made it possible to decompose the net fecundity fs_0 into a fecundity term f (number of just-emerged seedlings assessed every three months over number of flowering plants in June $t-1$) and survival of just-emerged seedlings s_0 (number of seedlings observed in June t over total number of just-emerged seedlings observed from June $t-1$ to May t, Colas et al., 2008; Fréville et al., 2004). We obtained four null values in asymptotic growth rates (three for Cruzade and one for Peyral), which corresponded to years with no flowering plant within plots and null values in rosette survival s_2. In such case, the persistence of the plot depended on new rosettes coming from the seedling stage (s_1 never equaled zero), and seed dispersal from the closest flowering plants outside plots. When calculating the geometric mean of asymptotic growth rates over years for each population, we excluded these null values.

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

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

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

where $cov(p_i,p_j)$ 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 λ_a to lower-level vital rates p as:

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

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° > 25°C (corresponding to mean + SD) and the number of freezing days (minimum T° < 0°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 λ_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 selection approach. Starting from the null model, we added at each step the variable having the highest R^2 value in the single-variable models (Appendix E.1). For logistic models, we used R^2_{LR}, the pseudo-coefficient of determination based on the likelihood-ratio test and given by $R^2_{LR} = 1-(L_{null} / L_{full})^{2/n}$ where L_{null} and L_{full} are the likelihoods of the null and the fitted models, respectively (Shinichi Nakagawa et al., 2013). The significance of each added variable in the model was tested using an analysis of deviance (Appendix E.2). From the best model, we reported the estimated coefficient (β) and its significance for each variable in the model after scaling climatic variables. Second, to understand biological processes at a finer scale, we tested for the impact of the seasonal climate on lower-level vital rates by considering only climatic variables that significantly impacted asymptotic growth rates, using the same approach as described above. We included the seasonality effect in GLMs by averaging variables over three-month periods separating two successive censuses (Appendix E.3). GLMs were fitted using R Stats-package (version 3.3.1). The R^2_{LR} was calculated using the R-command 'r.squaredLR' from the MuMIn-package (version 1.15.6).

2.4. Stochastic projections under climate change

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

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

The initial population size N_0 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) from 2010 to 2016, and the scaled eigenvector W from the arithmetic mean matrix over years (2010-2016) when pooling data over populations. N_0 is given by $N_0 = W\frac{Nfr}{w_3}$ where w_3, the third element of the scaled eigenvector, represents the proportion of the number of flowering plants. We simulated population dynamics using 1000 stochastic iterations, each iteration representing a trajectory of population size over 100 years. For a given trajectory we calculated the growth rate λ_j as:

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

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

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

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

Second, following the approach described in Salguero-Gomez et al. (2012), we focused on a particular climate scenario resulting from the Regional Climate Model (RCM) proposed by the Euro-Cordex 2014 project (Jacob et al., 2014). We used the RCP4.5 scenario representing an intermediate scenario of increasing CO_2 concentration until 2060. The regional climate model simulations provided predicted values of daily precipitation and mean temperature. We then extracted these data for the closest geographic location, which is less than 1 km apart from the centroid of the species distribution (43.13710 N, 3.07327 E) and less than 6 km apart from the meteorological station we used to get observed climatic data. Overestimation of precipitation in RCMs is a well-known problem, in particular in areas close to the Mediterranean Sea (Gao et al., 2008; Ruffault et al., 2014). Therefore, to estimate the frequency of extreme years in the future (2020-2099), we used threshold values from the back-projected model values (Salguero-Gomez et al., 2012). Using the back-projected data from the reference period (1971-2005), we defined warm years as those with mean temperature from May t to June t+1 greater than 14.5 + 1.23 (mean + SD) and dry years as those with number of wet days lower than 68.6 - 14.8 (mean - SD). Comparing the observed data and the back-projected data for the overlapping period 1995-2005, we indeed document an overestimation of the number of wet days predicted by the regional model compared to the observed one (paired *t-test* = 4.57, df = 8, $p < 0.002$). In contrast, predicted and observed daily mean temperatures and total precipitation were not significantly different ($p > 0.10$). Simulated data are available on the Drias platform (www.drias-climat.fr).

3. Results

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

Asymptotic growth rates λ_a calculated per population and per pair-of-years showed a decreasing trend over time (β = - 0.01, p = 0.02, Fig. 2A). The slope of the trend for each population separately was significant only for the smallest population (Cruzade: β = -0.04; p = 0.01, Fig. 2D). When pooling populations within each pair-of-years, the geometric mean of asymptotic growth rates over years was 0.880 (Table 1), with λ_a ranging from 0.432 (2006-2007) to 1.815 (2012-2013). Geometric means of λ_a over years per population were all lower than 1 and varied between 0.710 (Peyral) and 0.836 (Enferret1, Table 1). No significant relationship was detected between asymptotic growth rate and population size ($\beta = 0.0003$; $p = 0.46$). Randomization tests showed that the difference in λ_a among years was highly significant ($p < 0.001$, see appendix C). In contrast, asymptotic growth rates λ_a were not significantly different among populations ($p = 0.16$, see appendix C). The variance in λ_a per population was not significantly correlated with mean age at flowering ($\beta = -0.02$; $p = 0.68$) nor with population size ($\beta = 0.0003$; $p = 0.55$).

3.2. Retrospective and prospective analyses

As λ_a did not differ significantly among populations, retrospective and prospective analyses were performed after pooling individuals across populations. The observed variance in asymptotic growth rates among years was equal to 0.083, and was mainly explained by the variation in both the fecundity term (f), the survival of seedlings (s_1) and the survival of rosettes (s_2) having the highest contributions (0.025, 0.023 and 0.021, respectively, Fig. 3), followed by the survival of just-emerged seedling (s_0) and the flowering probability of rosettes (α_2) having a similar contribution (0.008, Fig. 3). Rare events in the life-cycle (flowering probabilities α_1 and α_3, and survival of flowering plants s_3) had negligible contributions (sum to 0.0009, Fig. 3 and appendix D). The largest elasticity of asymptotic growth rate was associated with rosette survival (s_2) followed by the fecundity term f (mean number of just-emerged seedlings per flowering plant), the survival of just-emerged seedling (s_0), seedling survival (s_1) and the flowering probability of rosettes (α_2, Fig. 3). Elasticity of λ_a to the remaining lower-level vital rates representing rare events (s_3, $\alpha_1$and α_3) summed only to 1% (Fig. 3). These latter rates were thus not considered for the GLMs investigating the relationship between lower-level vital rates and climatic variables.

3.3. Relationship between asymptotic growth rates and climate

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

3.4. Relationships between lower-level vital rates and climate

Overall, warming and drought negatively affected vital rates. The mean number of just-emerged seedlings per flowering plants f was negatively impacted by the daily mean temperature during both summer and fall periods (Table 2). The survival of just-emerged seedlings s_0 was positively impacted by the number of wet days during the germination period (both fall and the winter periods), and negatively impacted by the daily mean temperature during both summer and fall periods (Table 2). Seedling survival s_1 was negatively affected by an increase in the daily mean temperature during the summer and fall periods, and positively affected by an increase in the number of wet days during the same periods (Table 2). Rosette survival s_2 decreased with increasing summer daily mean temperature (Table 2). Finally, the flowering probability of rosettes α_2 was negatively impacted by the summer daily mean temperature and positively impacted by the number of wet days during the fall period (Table 2).

3.5. Stochastic projections under climate change

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

To assess the combined effect of environmental and demographic stochasticity on population viability, we compared the fate of the smallest population Cruzade and the largest one Enferret2, using their respective population size at $t = 0$ (see details above and Fig. 4). As we did not detect any significant variation in asymptotic growth rates among populations, we pooled data across population for each pair-of-years to obtain the 21 matrices used to simulate climate change. In the warm scenario, when increasing the frequency of extreme years from q* (4/21 = 0.19) to 0.8, stochastic growth rates decreased from 0.882 to 0.761 for the largest population (Enferret2, Fig. 4A) and from 0.879 to 0.765 for the smallest one (Cruzade, Fig. 4C). Under the RCP4.5 scenario, the predicted frequency of warm year q_{pred} characterized by a daily mean temperature > 15.63 °C for the period 2020-2099 equaled 0.78 and led to the extinction of both populations at 100 years in most simulations (Figs. 4A and 4C, solid black lines). Comparing this scenario with those of no climate change (Figs. 4A and 4C, dashed green lines), extinction probability at 50 years (P_{50}) increased from 0.37 to 0.99 for Enferret2 and from 0.82 to 0.99 for Cruzade, while extinction probabilities at 100 years (P_{100}) were close or equal to 1 for both populations. The mean time to extinction decreased from 57 to 26.4 years for Enferret2, and from 32 to 16 for Cruzade.

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

4. Discussion

4.1 Long term population dynamics of Centaurea corymbosa

Our results demonstrate the need for long-term demographic surveys to better understand the spatio-temporal demographic variability on plants (Blume-Werry et al., 2016; Compagnoni et al., 2016; Crone et al., 2011; Huelber et al., 2016). Indeed, our study based on 22 years of data provided a more accurate picture of the determinants of population dynamics in *C. corymbosa* than the study of Fréville et al. (2004) based on 8 years of data. In Fréville et al. (2004), the standard deviation in asymptotic growth rates $\sigma(\lambda)$ was 0.116 among years and 0.099 among populations, with significant differences among years and populations. In the current study, variation among populations became non-significant and temporal variation in asymptotic growth rates was rather synchronized among populations (Fig. 2). This pattern is not surprising given the narrow distribution of *C. corymbosa* and is largely consistent with studies of other narrowly distributed species (Buckley et al., 2010; Kiviniemi and Löfgren, 2009; Ramula et al., 2008). More importantly, the standard deviation $\sigma(\lambda)$ observed over the 22-year period was much larger (0.230) than the one (0.116) reported in Fréville et al. (2004). In agreement with the results of the permutation tests, we did not find any significant correlation between population dynamics and population size. Indeed, we did not find any evidence that small populations had lower population growth rates. Moreover, the variance in asymptotic growth rates among years did not increase with decreasing population size. In contrast to other demographic studies (Lande et al., 2003; Zeigler, 2013), we thus did not find any evidence of a greater sensitivity of the smallest populations to both environmental and demographic stochasticity in our species. In addition, the variance in asymptotic growth rate was not correlated with mean age at flowering per population. We thus did not find evidence for demographic buffering in populations with greater longevity, in contrast to what has been found at an inter-specific scale in Morris et al. (2008). Population dynamics of *C. corymbosa* is thus mainly affected by environmental factors that vary over time rather than by spatial factors.

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

In contrast to some studies reporting both negative and positive effects of climate change on vital rates (Meer et al., 2016; Meisner et al., 2014; Nicolè et al., 2011), our study documents a consistent negative effect of increased temperature and drought on lower-level vital rates in *C. corymbosa*. Regarding temperature, the most critical season that impacted lower-level vital rates was the summer period, since increasing summer daily mean temperature negatively affected both fecundity, survival probability and flowering probability. In contrast to our study, flowering probability was found to be positively impacted by high temperature in some temperate plant species (e.g. *Himantoglossum hircinum*, Meer et al., 2016; *Dracocephalum austriacum*, Nicolè et al., 2011). While a negative effect of increasing temperature on flowering probability was also reported in Peñuelas et al. (2004), this pattern was only observed in the southern Mediterranean sites but not in the northern ones. A likely explanation of this negative effect is that warm summers increase evapo-transpiration and decrease soil moisture (Christensen et al., 2004; Peñuelas et al., 2004). This could lead to a decrease in plant biomass as a consequence of rosette shrinking that in turn reduces the amount of resources that a plant can allocate to reproduction (Manders and Smith, 1992). This is particularly true for monocarpic perennial species, where flowering probability has been shown to increase with plant size (Metcalf et al., 2003). Regarding precipitation, the youngest plants were the most impacted by the number of wet days. This factor had a positive effect on both survival of just-emerged seedlings (s_0) during the germination period (fall and winter) and seedling survival (s_1) during the summer and fall periods, which is consistent with several studies showing a positive impact of the frequency of wet days (Riba et al., 2002; Shriver, 2016). Both temperature and precipitation effects may be explained by the fact that recurrent warm and dry days can induce a seasonal water deficit, which may negatively impact the whole life-cycle (Manders and Smith, 1992; Peñuelas et al., 2004; Ruffault et al., 2014). Species growing in rocky habitats, such as *C. corymbosa*, are likely to be the most affected, since these soils have a very low water capacity (Ruiz-Sinoga et al., 2012; Silva et al., 2015). Moreover, herbaceous species such as *C. corymbosa* do not have a deep root system ensuring access to water over dry periods in such rocky habitats.

4.2 Predictions from climate scenarios

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

Stochastic projections predicted population declines ($\lambda_s < 1$) under no climate change. Populations were predicted to decline even faster in the future in response to an increased frequency of extreme years in both the warm and dry scenarios. Such results are consistent with the GLMs showing negative impacts of warming and drought, and several studies investigating population viability in response to climate change (Andrello et al., 2012; Lawson et al., 2015; Marrero-Gómez et al., 2007; Shryock et al., 2014). More importantly, the warm scenario had more severe consequences on population viability than the dry scenario whatever the initial population size. However in our simulations, the initial population size impacted both extinction probability and the mean time to extinction, a pattern consistent with theoretical studies since small populations are more vulnerable to extinction than largest ones (Groom et al., 2005; Lande et al., 2003). Using the RCP4.5 scenario, the change in temperature projected for the period 2071-2099 was of the same order of magnitude than the one predicted by other regional climatic models (Christensen et al., 2007; Ruffault et al., 2014). In contrast, our dry scenario predicted an annual mean number of wet days equal to 66.41 (-3.2%), while other models predicted a much severe decrease (-19.6%, Ruffault et al., 2014). This suggests that uncertainty in climate models should be carefully considered in management plans and when evaluating extinction risk. Such uncertainty is particularly pronounced for the Mediterranean region (Gao et al., 2008; Ruffault et al., 2014).

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

4.3 Management recommendations

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

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

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

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

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Tables

Table 1: Demographic characteristics of each of the six populations of *Centaurea corymbosa*, and the pooled population after pooling data across populations: number of individual life-histories recorded over 22 years (see also Appendix A1), number of surviving plants older than 1 year, mean life-time of individuals that reached the rosette stage, mean age at flowering, geometric mean of asymptotic growth rates (λ_a) over 22 years, minimum and maximum of λ_a, stochastic growth rate (λ_s) when including both demographic and environmental stochasticity (uniform frequency, see text) with the confidence intervals (2.5th and 97.5th percentiles of the simulated distributions) and the rounded mean of total numbers of flowering plants (Nb.FP) 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 λ_a	[$\lambda_a$min, $\lambda_a$max]	λ_s	*CI(λ_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(a), 1.264]	0.804	[0.799, 0.827]	28
Cruzade	456	94	3.4	4.2	0.720	[0.00(a), 1.444]	0.742	[0.732, 0.770]	13

(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.

Table 2: Summary of GLMs explaining the effect of two climatic variables (averaged over three-month periods) on lower-level vital rates. Only climatic variables affecting population growth rate were included in the GLMs. From the best model explaining a given lower-level vital rate, we report the estimated coefficient (β) and its significance (*t-test*) after scaling the climatic variables. 'ns' indicates that the variable tested was not 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 $\boldsymbol{log(f+1)}$	-0.28 **	-0.22 *	ns	ns	ns	ns	ns	ns
Survival of just emerged seedling $\boldsymbol{s_0}$	-0.17 ***	-0.08*	ns	ns	ns	0.24 ***	0.14 ***	ns
Seedling survival $\boldsymbol{s_1}$	-0.28 ***	-0.12$^+$	ns	ns	0.34 ***	0.04 $^+$	ns	ns
Rosette survival $\boldsymbol{s_2}$	-0.45 ***	ns	ns	ns	ns	ns	ns	ns
Flowering probability of rosette $\boldsymbol{\alpha_2}$	-0.23 ***	ns	ns	ns	ns	0.19 *	ns	ns

$^+$P <0.08, *P < 0.05, **P < 0.01, ***P < 0.001.

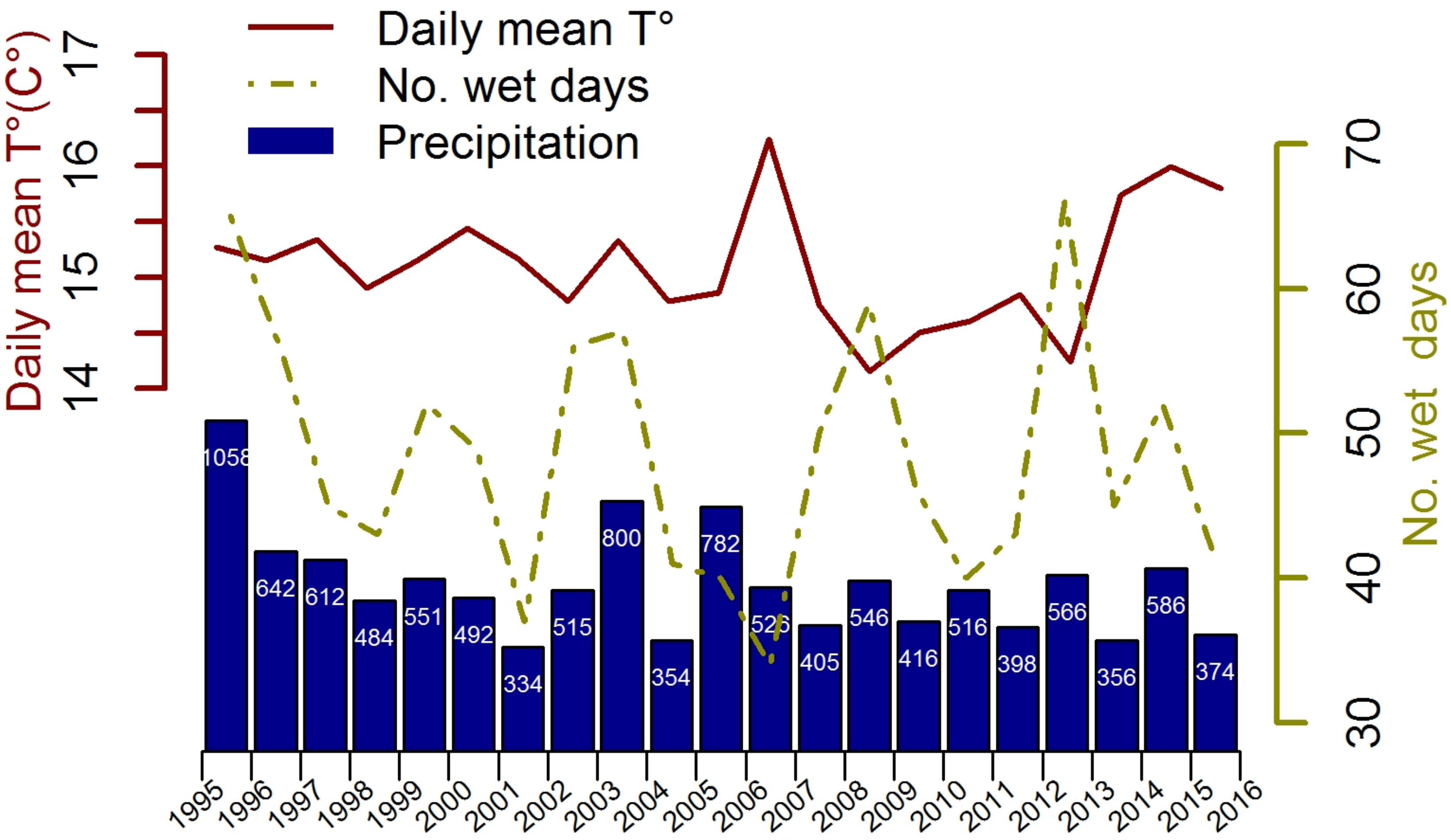
Figure legends

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

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

Figure 3: Contribution of lower-level vital rates to the variance of λ_a observed among years, and elasticity of growth rates to these vital rates calculated on the arithmetic mean matrix calculated over 21 pair-of-years matrices.

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


Daily mean T°
No. wet days
Precipitation
Daily mean T°(C°)
14
15
16
17
No. wet days
30
40
50
60
70
1058
642
612
484
551
492
334
515
800
354
782
526
405
546
416
516
398
566
356
586
374
1995
1996
1997
1998
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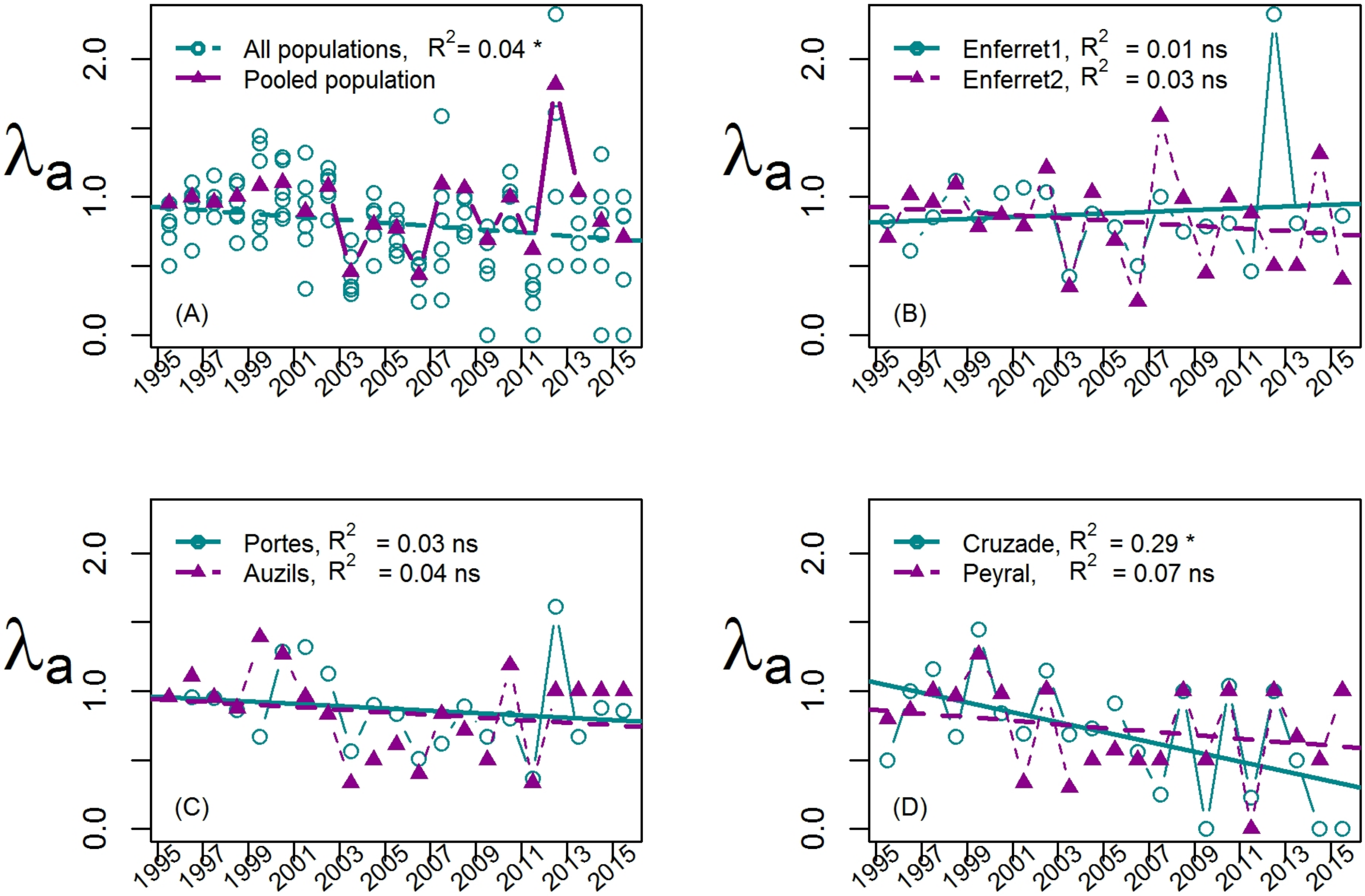
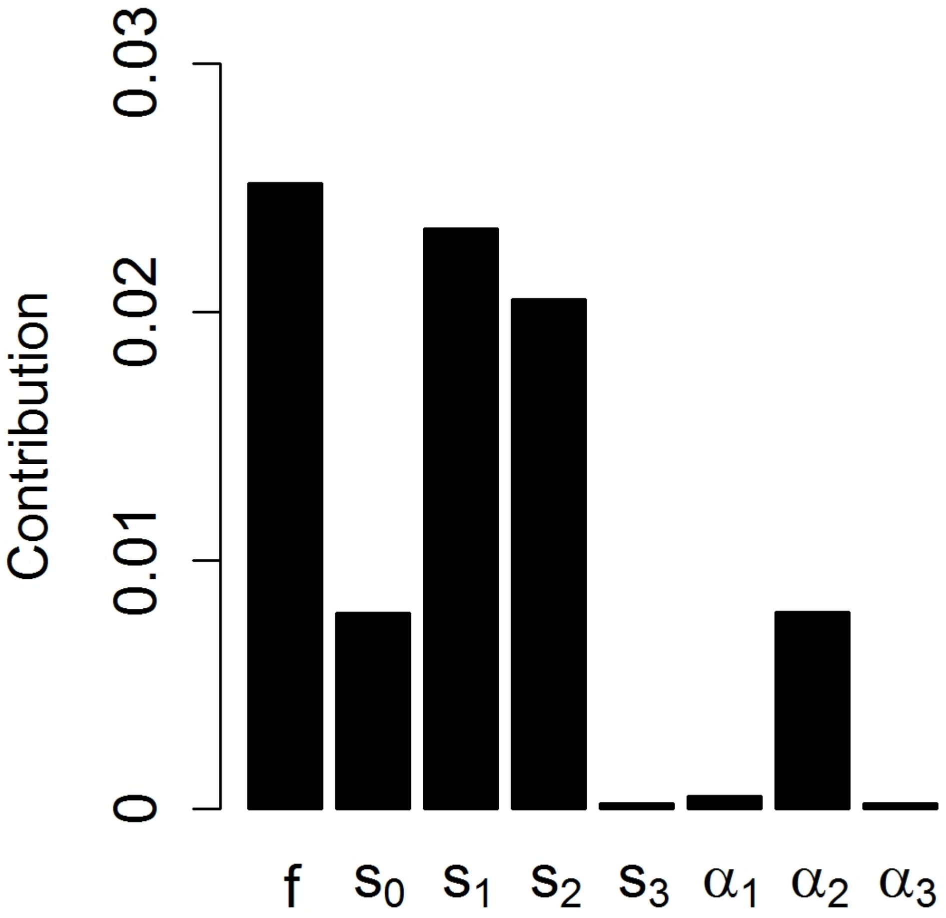
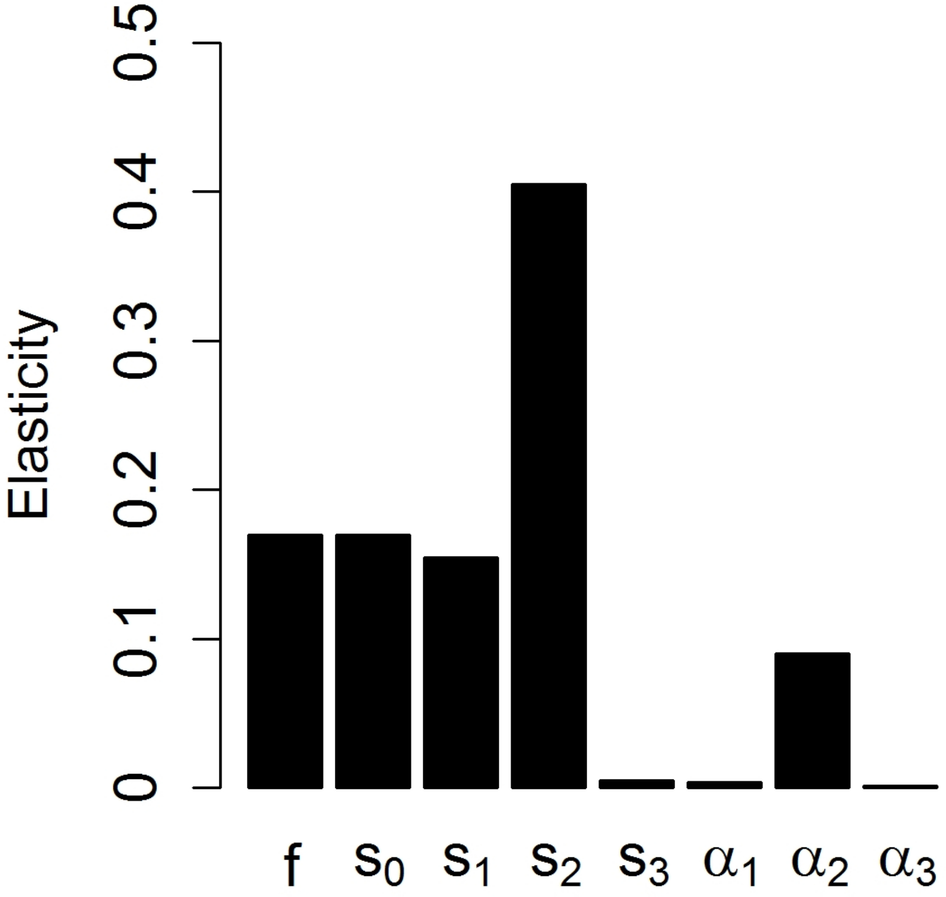
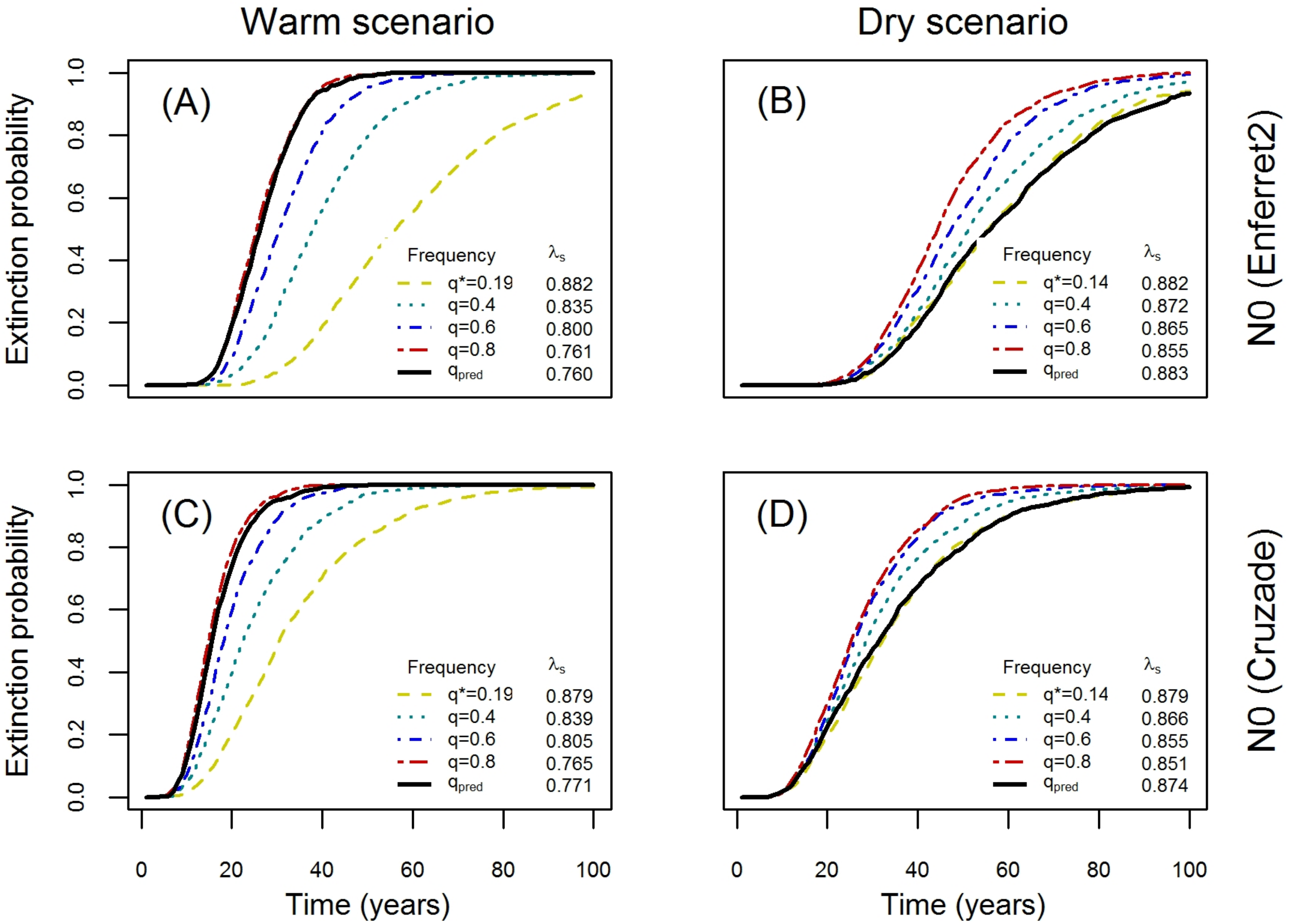
2011
2012
2013
2014
2015
2016


All populations, R^2= 0.04 *
Pooled population
Enferret1, R^2 = 0.01 ns
Enferret2, R^2 = 0.03 ns
Portes, R^2 = 0.03 ns
Auzils, R^2 = 0.04 ns
Cruzade, R^2 = 0.29 *
Peyral, R^2 = 0.07 ns
(A)
(B)
(C)
(D)
λ_a
0.0
1.0
2.0
1995
1997
1999
2001
2003
2005
2007
2009
2011
2013
2015


Contribution
0.03
0.02
0.01
0
f
s_0
s_1
s_2
s_3
α_1
α_2
α_3


Elasticity
0.5
0.4
0.3
0.2
0.1
0
f
s_0
s_1
s_2
s_3
α_1
α_2
α_3

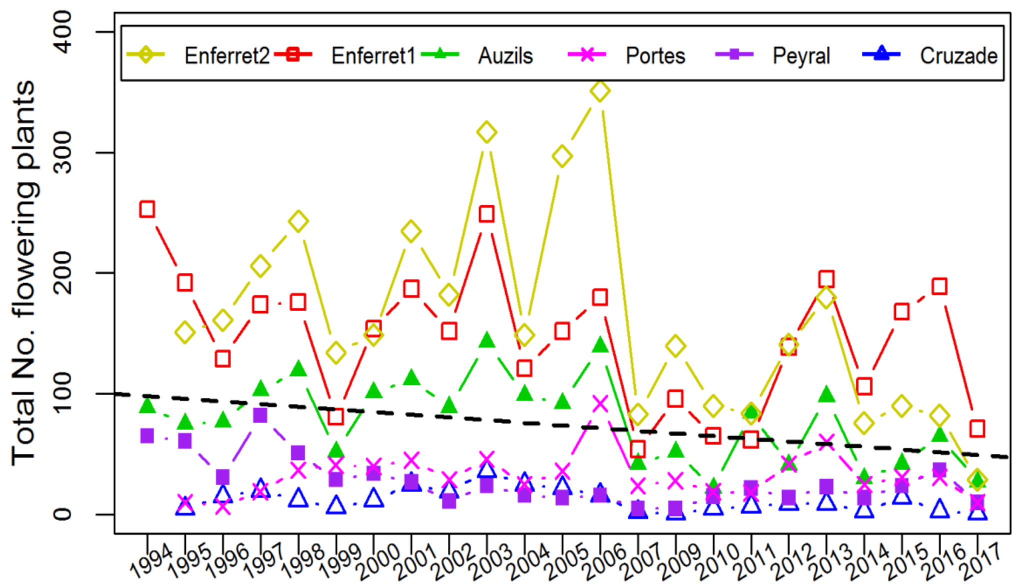

Warm scenario
Dry scenario
Extinction probability
Extinction probability
N0 (Enferret2)
N0 (Cruzade)
(A)
(B)
(C)
(D)
Time (years)
Time (years)
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
Frequency
λ_s
q*=0.19 0.882
q=0.4 0.835
q=0.6 0.800
q=0.8 0.761
q_{pred} 0.760
Frequency
λ_s
q*=0.14 0.882
q=0.4 0.872
q=0.6 0.865
q=0.8 0.855
q_{pred} 0.883
Frequency
λ_s
q*=0.19 0.879
q=0.4 0.839
q=0.6 0.805
q=0.8 0.765
q_{pred} 0.771
Frequency
λ_s
q*=0.14 0.879
q=0.4 0.866
q=0.6 0.855
q=0.8 0.851
q_{pred} 0.874

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	

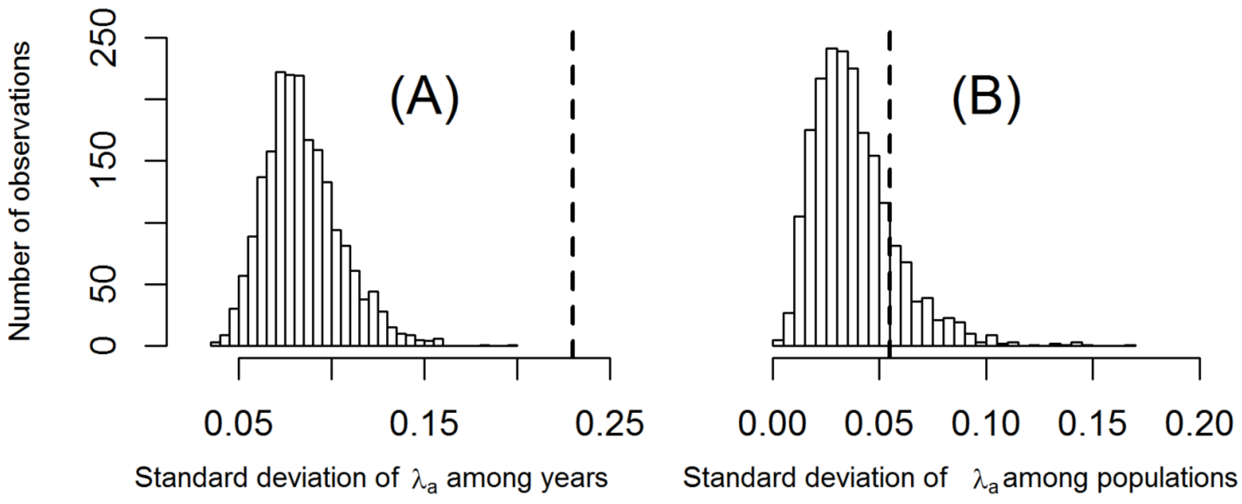
Appendix A2: Total number of flowering plants per year recorded by the exhaustive count per population. The dashed line corresponds to the trend of the number of flowering plants over time (β = -2.21, p = 0.02). The growth rate calculated from the number of flowering plants was equal to 0.92.



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 λ_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**	**α_1**	**α_2**	**α_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°	0.31	-0.320	**0.011**
Daily maximal T°	0.30	-0.250	**0.009**
Precipitation	0.01	-0.001	0.672
No. days with T°>25	0.18	-0.013	0.052
No. freezing days	0.03	0.008	0.451
No. wet days	0.46	0.021	**0.001**
No. days with precip.>20mm	0.04	-0.021	0.381
Climatic variables in year *t-1*			
Daily mean T°	0.003	0.031	0.251
Daily maximal T°	0.006	0.032	0.233
Precipitation	0.058	-0.001	0.452
No. days with T°>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
Quadratic effect			
Daily mean T°	0.30	-0.011	**0.010**
Daily maximal T°	0.30	-0.006	**0.009**
Precipitation	0.01	0.000	0.631
No. days with T°>25	0.18	-0.001	0.052
No. freezing days	0.02	0.000	0.540
No. wet days	0.43	0.003	**0.002**
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.

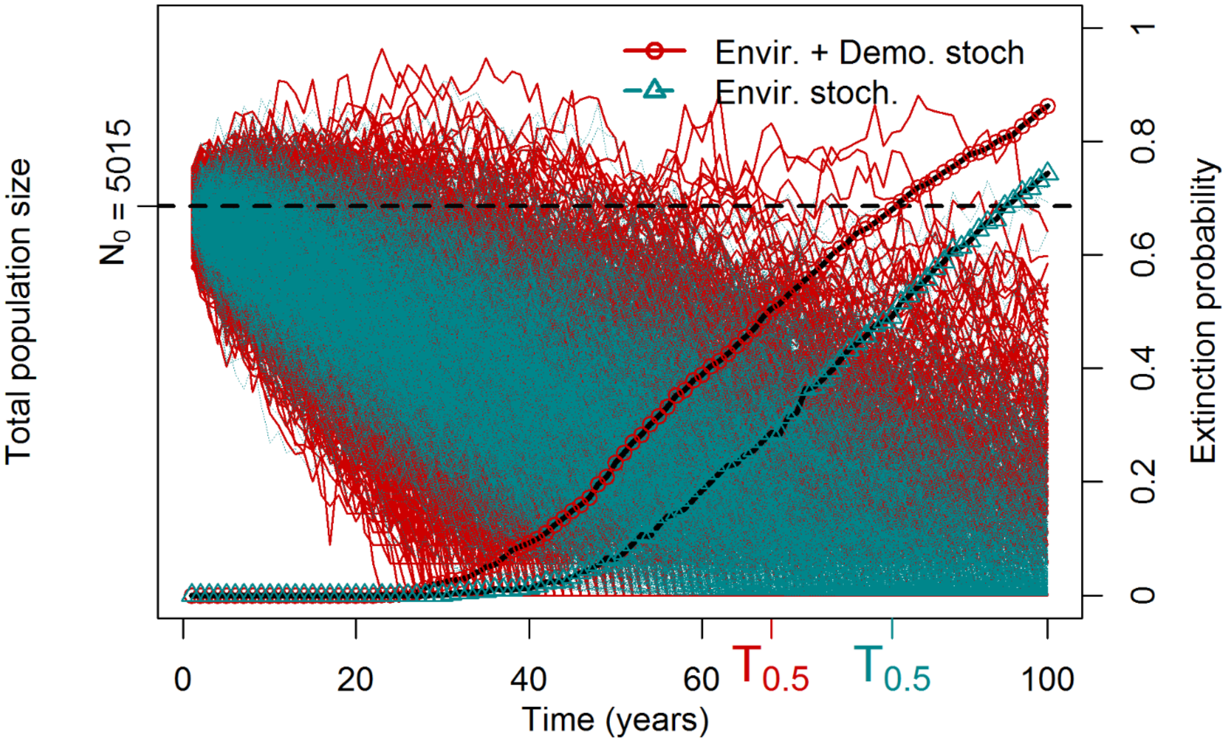
Model	Compared models	p-value
M0: Null model		
M1: No. wet days	M0, M1	**0.001**
M2: No. wet days + (No. wet days)^2	M1, M2	0.311
M3: No. wet days + Daily mean T°	M1, M3	**0.031**
M4: No. wet days + Daily mean T°+ (Daily mean T°)^2	M3, M4	0.292
M5: No. wet days + Daily mean T°+ Daily maximal T°	M3, M5	0.890
M6: No. wet days + Daily mean T°+ (Daily maximal T°)^2	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	**0.012**
	M2: T1+T2	M1, M2	**0.031**
	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*) ~ T1+T2		
S_0	M0: Null model		
	M1: P2	M0, M1	**<0.001**
	M2: P2+P3	M1, M2	**<0.001**
	M3: P2+P3+T2	M2, M3	**0.006**
	M4: P2+P3+T2+T1	M3, M4	**<0.001**
	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 ~ T1+T2+ P2+P3		
S_1	M0: Null model		
	M1: T1	M0, M1	**<0.001**
	M2: T1+P1	M1, M2	**<0.001**
	M3: T1+P1+P2	M2, M3	**0.002**
	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	**0.030**
	Selected model: S_1 ~ T1 +T2+ P1+ P2		
S_2	M0: Null model		
	M1: T1	M0, M1	**<0.001**
	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 ~ T1		
α_2	M0: Null model		
	M1: T1	M0, M1	**0.005**
	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	**0.020**
	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: α_2 ~ 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 $N(t) < 1$ 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 (λ_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