Population viability of the narrow endemic Helianthemum juliae (CISTACEAE) in relation to climate variability

Manuel V. Marrero-Gómez*, J. Gerard B. Oostermeijerb, Eduardo Carqué-Álamoa, Ángel Bañares-Baudetac

Abstract

Narrow endemic plants are highly vulnerable to extinction as a result of human disturbance and climate change. We investigated the factors affecting the population viability of Helianthemum juliae, a perennial plant endemic to the Teide National Park on Tenerife, Canary Islands. One population was demographically monitored from 1992 to 2001 and analysed using matrix projection models to determine finite rates of increase and critical stages in the life cycle. Lambda values varied between 0.697 and 1.740, and were highly positively correlated with annual precipitation, but not with temperature. Survival of adults had the highest elasticity, and summed elasticities of the growth and fecundity transitions correlated positively with lambda and precipitation. Most of the mortality in the population seemed drought-related, and no other threats were identified. Deterministic simulations showed population increase, but introducing environmental stochasticity by modelling variation in precipitation from existing data of the past 85 years revealed high extinction probabilities (0.74–0.83 in the next 100 years). This plant is likely to be at risk under scenarios of global warming. Our simulations suggest that augmenting the population would only delay extinction. A more viable option for long-term conservation seems to be the introduction of populations at more humid locations within the Teide caldera.

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1. Introduction

One of the main tasks of the conservation botanist is to protect endangered plant species from extinction. In a way, all plants face the risk of extinction due to various causes, such as habitat destruction, habitat fragmentation, displacement by or hybridization with invasive exotic species, climate change, overharvesting for economic purposes, etc. (Oostermeijer, 2003). Rare plants, however, are particularly sensitive to these threats, because of their restricted distribution and low numbers of populations and individuals (Goodman, 1987; Menges, 1991). Because of this vulnerability, they have always received special attention from conservation organizations. This is certainly true for geographically highly restricted endemic plants, which are exceptional representatives of certain regions. In many cases, the presence of such species has been the motivation for the founding of national parks, such as the Sierra Nevada National Park in Spain (Boletín Oficial del Estado, 1999). It is therefore not surprising that the conservation of endemic plant species often has very high conservation priority in such parks (Marrero et al., 2003a).

Yet, it is not always clear whether endemic species are in need of intensive conservation management (Bañares et al.,
The genus Helianthemum is represented on the Canary Islands by 12 species, of which 7 are endemic to this archipelago (Hansen and Sunding, 1993). They colonize most of the ecosystems existing on these islands; from the xerophytic coastal landscapes to the high mountain shrublands. H. juliae is a small iteroparous shrub that is endemic to the high mountain ecosystem of Tenerife (Canary Islands). Adult plants are up to 30 cm tall and produce between 5 and 40 flower stalks with yellow flowers from their third or fourth year onwards. The average fruit contains 45 seeds. The average life span of individuals is 14 years.

H. juliae is considered critically endangered (CR) (Marrero et al., 2003b). Only three small populations are known from the wall of the Cañadas del Teide caldera (Fig. 1): Cañada de las Pilas (43 adults), Risco Verde (25 adults) and Mesa del Obispo (49 adults). Globally, the species has only 868 individuals (adults and immatures). The Cañada de las Pilas and Mesa del Obispo populations are located on small rocky ledges over an area of 300 m²; the Risco Verde population is found on debris at the base of cliffs covering a surface of 200 m².

At a distance of 800 m from the Cañada de las Pilas population, an experimental introduction (sensu Falk et al., 1996) was established in Cañada de Diego Hernández in 1989–1990. The introduction comprised a total of 350 three-year old plants, planted over an area of 500 m², which were grown ex situ from seeds collected in the Cañada de las Pilas population. In 1992, 122 plants had survived and abundant recruitment by seedlings was observed. In this year, the population was designated for demographic monitoring in order to evaluate the success of the reintroduction and determine the factors that affect population viability in this species.

The local microhabitat differences are minimal among the native and the reintroduced populations, especially in relation with the factors that might affect soil water availability. The differences in altitude among the sites are less than 100 m (2141–2236 m a.s.l.), they all have a West-exposition (Azimuth 268–276°), the slope is similar (36–42°) and the substrate has identical characteristics: weakly developed soils (Orthents) over salic geological materials.

2. Materials and methods

2.1. Species and study area

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2.2. Data collection and analysis

2.2.1. Life stages

Demographic censuses were made during 10 years. We installed a 10 x 10 m² monitoring plot protected with a 1.75 m high aluminium fence with the aim to exclude rabbit grazing. All individuals were labelled with aluminium identification tags and were classified at each census in one of the following four categories: Juveniles (small, vegetative individuals with a height <15 cm and no signs of previous flower stalks); Vegetative adults (individuals >15 cm with evidence of previous flower stalks but vegetative at the moment of censusing), young reproductive adults (plants <20 cm tall with flower stalks) and mature reproductive adults (>20 cm tall with flower stalks). In the beginning, the plot enclosed 22 mature reproductive adults, seven young reproductive adults, 10 vegetative and seven juvenile individuals.

We devised this stage classification to characterize the population using a biological approach (Lefkovitch, 1965; Werner, 1975), which relies on field observations of developmental stages. First, individual plants were classified in the basic stages, i.e. juveniles, vegetative and reproductive individuals. Later, the reproductive individuals were divided into two categories based on the intensity of flowering. The first class (young reproductive adults) comprises the adults in their first or second year of flowering. They have a small size (<20 cm) and produce less than 50 flowers. The second class (mature reproductive adults) includes the larger plants (>20 cm tall) with more than 50 flowers. This subdivision was based on field observations of growth and survival rates of reproductive adults. We did not consider a seed stage because seeds germinated directly after dispersal, so we assumed a short-lived seed bank. Hence, introducing seeds into the life cycle model would introduce a time-lag (Caswell, 2001). We recorded the numbers of seedlings in the autumn and spring cohorts during additional censuses in December and March. We mapped
the position of all recent seedlings, and tagged them with small plastic sticks.

Each year, at the end of the summer, just before the first autumnal rains, new individuals emerging in the plot were tagged and the life stage and size (number of stalks, flowers and fruits) for new and old the plants were recorded. The transitions between the four different life stages observed in the study population are shown in the life-cycle diagram (Fig. 2).

The collection of demographic data is sometimes considered a threat to small populations that grow in restricted areas. Trampling of seedlings and small individuals may occur, and researchers may cause soil compaction. We avoided these negative effects on the natural populations by working in the experimentally introduced population, which we assumed experienced highly similar environmental conditions.

2.2.2. Analysis of demographic data

Transition probabilities were obtained by calculating the proportion of individuals in each category experiencing each specific fate from one year to the next. Fecundity was calculated as follows. First, we annually counted the total number of capsules produced by each plant, and removed two capsules from each plant to count the seeds, obtaining the average number of seeds per capsule and, by multiplying this value with the total number of capsules, the total seeds per individual. Secondly, we estimated the proportional contribution of each reproductive life stage to the total number of seeds produced in the plot. Thirdly, the total number of juveniles counted in the following year was allocated to the two reproductive life stages according to their proportional contribution to the total reproductive effort. Finally, the number of recruits per reproductive life stage was divided by the total number of plants in each stage to obtain fecundity.

We first used Lefkovitch matrices based on the classification of individuals into life stages (Caswell, 2001). The basic matrix model is given by: $n_{t+1} = An_t$; where $n_t$ and $n_{t+1}$ are vectors whose elements, $a_{ij}$ are the number of individuals that belong to the $i$th category at time $t$ and $t + 1$, respectively, and $A$ is a non negative square matrix, whose elements, $a_{ij}$ represent the transitions or contributions from individuals in the $j$th category to the $i$th category after one time step (Caswell, 2001).

We used the Pop-Tools 2.4 spreadsheet for Excel (Hood, 2002) to calculate the main demographic parameters from the projection matrices: the finite rate of increase ($\lambda$) of the population, the stage-specific reproductive values and the stable-stage distribution, and the elasticity matrices. The latter were used to study the relative importance of different phases of the life cycle for the population growth rate (de Kroon et al., 1986). The bootstrap method (Caswell, 2001; Kalisz and McPeek, 1992) was used to establish 95% confidence intervals for $\lambda$. We used an R-script that randomly resampled
each annual matrix with replacement 5000 times. The log-
likelihood ratio, $G$ (Sokal and Rohlf, 1981; Zar, 1984) was used
to determine significant differences in transition probabilities
between data sets.

In order to test for possible relationships between $k$ and
climatic variables, we conducted two regression analysis
using $k$ as dependent variable and annual total precipitation
and annual average temperature as independent variables.
At the same time we used the climatic data of the last 85
years to detect historical trends that could be used for predic-
tive models. For an analysis of precipitation at a short term
we used the data of the Diego Hernández meteorological sta-
tion, situated very close to the monitoring plot. Analysis of
long-term trends in temperature and precipitation was based
on climatic data of Izaña meteorological station (at 6 km dis-
stance), with records since 1916; and Diego Hernández meteo-
rological station (at 500 m distance) with data from 1990.
Using the data available from these two stations, we estab-
lished a correlation between the two stations for the last 10
years and obtained an equation that could be used to calcu-
late for the last century the amount of precipitation in the
area where the species grows. The obtained equation was:

$$P_{DH} = 0.664P_I + 48.8 \quad (r^2 = 0.821),$$

where $P_{DH}$ is the annual precipitation at the Diego Hernández
station, and $P_I$ is the annual precipitation observed at Izaña station.

2.2.3. Stochastic simulations of population dynamics

To simulate environmental stochasticity we constructed a
demographic model using the software package Stella (High
Performance Systems, 1998). The mathematical basis of this
model was identical to the matrix model described above.
Stella software allows a greater deal of flexibility in relating
transitions to other variables than software designed purely
for the analysis of matrix models. With the aim to avoid col-
linearity problems, we chose to introduce stochasticity by
randomly drawing an entire matrix (from the nine available
matrices) for each simulated time-step. All simulations pro-
jected population dynamics over 100 time-steps (years) and
each simulation was iterated 100 times.

To calculate the stochastic growth rate, the numeric values
for the population size ($n_t$) generated for each year of a simu-
lation were used. It was obtained from the average growth rate
over a long simulation (Dennis et al., 1991; Caswell, 2001; García
and Iriondo, 2002) as follows: $\log \lambda_s = (\log n_t - \log n_0)/t$; where $n_t$
and $n_0$ are the population size at the end and at the begin-
ing of the simulation, respectively, and ‘$t$’ is the total duration of
the simulation (100 years). Stochastic growth rate is presented as
$\log k_s$ (Caswell, 2001) and $\lambda_s$ (Tuljapurkar et al., 2003). Addition-
ally, the probabilities of quasi-extinction were calculated using
an approximation of the matrix model to a diffusion model
(Tuljapurkar and Orzack, 1980), where we considered two dif-
f erent quasi-extinction scenarios: $n_0 = 5 (n_q = 5)$ and $n_0 = 10$
($n_q = 10$). So we can define a quasi-extinction threshold ($\theta$) as
$n_0/n_0$ and the probability of eventual quasi-extinction ($P_q$) as
the probability that $n_t/n_0$ ever falls below ($\theta$); this is 1 if $\log \lambda_s \leq 0$,
and $\exp((2\log \lambda_s \log \theta)/\sigma^2)$ if $\log \lambda_s > 0$ (Caswell, 2001). In this
model the quasi-extinction time ($T_q$) is defined as the first time
that $n_t$ reaches $n_q$ and its distribution responds to a inverse

![Life cycle graph for Helianthemum juliae and the corresponding transition matrix. Circles indicate life stages, arrows represent the possible transitions among them, and letters show the connection between each transition and its matrix entry (F, fecundity; G, growth; S, survival).](image-url)
Gaussian distribution (Folks and Chhikara, 1978) with mean $E(T_0)$ and variance $V(T_0)$ as follows: $E(T_0) = -\log(\lambda)/\log(\lambda_i)$; $V(T_0) = -\sigma^2\log(\lambda)/\log(\lambda)^3$.

A process of restricted random selection to simulate the climatic variables was introduced in the Stella model. From the analysis of the climatic and demographic data we established ‘good years’ in which the annual precipitation was higher than 350 mm, because we found that in these years $\lambda$ was larger than 1. Consequently, ‘bad years’ were imposed when annual precipitation was lower than 350 mm and $\lambda < 1$. From the climatic data of the last 85 years, we calculated the percentage probability of good years ($p_g$) that was used to introduce a Montecarlo function in the model. If the Montecarlo function selected a good year, a second random function picked a matrix from the set of the five matrices that had $\lambda > 1$. For cases in which the Montecarlo function selected a bad year, a random selection occurred from the set of the four observed matrices with $\lambda < 1$.

Finally, we used an additional model of climate-related stochasticity, in which $\lambda$ was first calculated directly from the randomly selected precipitation value using the equation that relates $\lambda$ to precipitation in Izaña and Diego Hernández (see Section 2.2.2), and then subsequently used to calculate the new population size.

2.2.4. Extrapolation to the natural populations
In order to translate the observations from our experimental study population to the natural situation, we used a set of parameters that was easily measurable without disturbing the populations. In 2000, we determined population structure, seedling mortality and fruit production of the natural and planted populations. To determine fruit production, the number of capsules per individual was counted in each population. To assess seedling mortality, 100 recent seedlings were labelled in December. Survivors were counted in November of the next year. We tested differences between the planted and the natural population of Cañada de las Pilas with a G-test. We selected only this population for three reasons: (1) to minimize the disturbance of the other natural sites introduced by our visits; (2) our field observations indicated that only this population had a sufficient number of seedlings; and (3) the population of Mesa del Obispo had not been discovered yet.

2.2.5. Retrospective analysis
Using the correlation between the precipitation record of the Izaña and Diego Hernández stations, we calculated the theoretical annual precipitation in the last century for the area where the species grows. Then, these data were used to calculate a theoretical value of $\lambda$ for each year. With these $\lambda$ values and the average population size (268 individuals), we calculated the hypothetical population size at the beginning of the 20th century.

3. Results

3.1. Deterministic transition matrix analysis
The $\lambda$ value of the average matrix was 1.247. However, the $\lambda$ values were quite variable among the nine transition matrices (Table 1). Higher values (>1) were obtained from 1993 to 1998. In the most recent years, $\lambda$’s were <1. We observed an increase in $\lambda$ during the first four years of monitoring, reaching a maximum of 1.740 in 1995–1996. From that year on, $\lambda$ decreased to 0.697 in 2001.

The stable stage structure obtained from the average matrix differed significantly from the observed initial distribution ($G = 51.936; P < 0.010$) for all stages, and shows lower values for juveniles (0.152) and young reproductive adults (0.152), and higher values for mature reproductive adults (0.478) and vegetatives (0.217). As expected, the highest reproductive value corresponded to the reproductive adult stages and the lowest to the juvenile and vegetative adult stages (Table 1).

The highest elasticities (Table 1) were associated with the survival of mature reproductive adults and the transitions from juvenile to small reproductive adult.

A diagram of the relative contribution of Growth ($G$), Survival ($L$) and Fecundity ($F$) to the lambda of each matrix (Silvertown et al., 1993) shows that all matrices are concentrated towards the bottom right-hand of the triangle (Fig. 5). This pattern corresponds to high elasticities for survival ($L$), and low for fecundity ($F$) elements. Higher $\lambda$’s corresponded to years with higher elasticities for fecundity and growth, and smaller $\lambda$’s were associated with years with higher elasticities for survival. Likewise, years with a precipitation >350 mm corresponded with high fecundity and growth elasticities, and years with precipitations <350 mm corresponded with high elasticities for survival.

3.2. Stochastic simulation model
When environmental stochasticity was introduced by randomly drawing (Fig. 4) from the nine transition matrices, the stochastic growth rate of the population ($\log(\lambda)$) was 0.12 ($\lambda_s = 1.13$), indicating a very low extinction risk. The initial population size used in the simulations was that observed in 2001 ($N = 313$ individuals). The quasi-extinction probabilities are practically zero: $P(q5) = 1.33 \times 10^{-21}$, $P(q10) = 1.02 \times 10^{-17}$. However, these results did not correspond with the field observations, where the populations apparently did not increase. This is probably due to the fact that even though we studied the population for 10 years, we encountered a relatively high proportion (55%) of good years (i.e. years with precipitation >350 mm and $\lambda > 1$) in comparison to the frequency of years with high precipitation observed during the past 85 years in the extrapolated data for Diego Hernández (30%).

Population growth rate increased with annual precipitation during the study period ($r^2 = 0.934, P = 0.0001$). However, temperature was not significantly correlated with $\lambda$ ($r^2 = 0.002, P = 0.856$). We observed that when the annual precipitation fell below 350 mm, $\lambda$ values were <1, and vice versa. Accordingly we used the 350 mm threshold as the limit between good and bad years. The frequency of years with >350 mm precipitation during the last 85 years was 30%. The probability of a sequence of three consecutive good years in these data was 10%, which is considerably lower than the probability of randomly drawing three
consecutive good matrices during the simulations, which turned out to be c. 35%.

Introducing in the model a random selection of matrices (Fig. 4) with a Montecarlo function restricted to drawing good years maximally 30% of the time (reflecting the data of the Diego Hernández station inferred from the Izaña station), the results of the simulations are dramatically different. The population fluctuates severely, with maximum population sizes of 1,500 individuals. Under these conditions, 83% of the iterations resulted in a population size below one individual within 100 years. \( \lambda = -0.032 \) (\( \bar{\varphi} = 0.967 \)) and the

\[
\log_{10} \lambda = -0.050 \quad (\varphi = 0.950)
\]

the quasi-extinction probabilities for \( N_q = 5 \) and \( N_q = 10 \) were both 1, with mean times of extinction \( T_q(5) = 81 \), and \( T_q(10) = 68 \).

<table>
<thead>
<tr>
<th>( \lambda )</th>
<th>CI</th>
<th>Demographic matrix</th>
<th>Stable-stage distribution</th>
<th>Reproductive value</th>
<th>Elasticity matrix</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.931</td>
<td>0.818–1.021</td>
<td>1992–1993</td>
<td>J 0.286 Y 0.429 M 0.000 V 0.000</td>
<td>0.060 0.174 0.010 0.000</td>
<td>J 0.000 Y 0.000 M 0.022 V 0.000</td>
</tr>
<tr>
<td>1.358</td>
<td>1.000–1.471</td>
<td>1993–1994</td>
<td>J 0.667 Y 0.333 M 0.000 V 0.000</td>
<td>0.518 0.119 0.129 0.000</td>
<td>J 0.129 Y 0.000 M 0.134 V 0.000</td>
</tr>
<tr>
<td>1.146</td>
<td>0.925–1.242</td>
<td>1994–1995</td>
<td>J 0.656 Y 0.188 M 0.000 V 0.000</td>
<td>0.377 0.076 0.124 0.000</td>
<td>J 0.000 Y 0.000 M 0.092 V 0.000</td>
</tr>
<tr>
<td>1.740</td>
<td>1.605–1.819</td>
<td>1995–1996</td>
<td>J 0.596 Y 0.404 M 0.000 V 0.000</td>
<td>0.647 0.115 0.131 0.000</td>
<td>J 0.112 Y 0.000 M 0.152 V 0.000</td>
</tr>
<tr>
<td>1.545</td>
<td>1.315–1.616</td>
<td>1996–1997</td>
<td>J 0.320 Y 0.336 M 0.000 V 0.000</td>
<td>0.663 0.068 0.067 0.000</td>
<td>J 0.000 Y 0.000 M 0.118 V 0.000</td>
</tr>
<tr>
<td>1.375</td>
<td>1.317–1.422</td>
<td>1997–1998</td>
<td>J 0.539 Y 0.362 M 0.000 V 0.000</td>
<td>0.552 0.099 0.096 0.000</td>
<td>J 0.145 Y 0.000 M 0.387 V 0.000</td>
</tr>
<tr>
<td>0.898</td>
<td>0.813–0.966</td>
<td>1998–1999</td>
<td>J 0.577 Y 0.291 M 0.000 V 0.000</td>
<td>0.025 0.143 0.000 0.000</td>
<td>J 0.016 Y 0.000 M 0.000 V 0.000</td>
</tr>
<tr>
<td>0.916</td>
<td>0.859–0.974</td>
<td>1999–2000</td>
<td>J 0.500 Y 0.331 M 0.000 V 0.000</td>
<td>0.024 0.234 0.000 0.000</td>
<td>J 0.000 Y 0.000 M 0.000 V 0.000</td>
</tr>
<tr>
<td>0.697</td>
<td>0.595–0.786</td>
<td>2000–2001</td>
<td>J 0.520 Y 0.110 M 0.000 V 0.000</td>
<td>0.222 0.000 0.000 0.000</td>
<td>J 0.000 Y 0.000 M 0.000 V 0.000</td>
</tr>
<tr>
<td>1.247</td>
<td></td>
<td>Average matrix</td>
<td>J 0.516 Y 0.309 M 0.000 V 0.000</td>
<td>0.540 0.111 0.114 0.011</td>
<td>J 0.116 Y 0.000 M 0.000 V 0.000</td>
</tr>
</tbody>
</table>

The alternative model of climate-related stochasticity where \( k \) was first calculated directly from randomly selected precipitation values, the results were similar, but less dramatic. Population size below one within 100 years occurred in 74% of the iterations; log\( \lambda_s = -0.032 \) (\( \bar{\varphi} = 0.967 \)) and the
quasi-extinction probabilities for $N_q = 5$ and $N_q = 10$ were both 1, with mean times of extinction above 100 years: $T_{q(5)} = 115$, and $T_{q(10)} = 105$.

3.3. Comparisons between natural and planted populations

No differences between the demographic structure of planted and natural populations were observed ($G = 4.996$, $P = 0.172$). In addition, there were no significant differences in fruit production ($G = 0.238$, $P = 0.625$) and seedling mortality ($G = 2.028$, $P = 0.154$). These results suggest that the dynamics of the natural populations was quite similar to that of the newly founded population.

3.4. The species in the past

The retrospective simulations indicated that the species probably experienced better, but also worse, moments in the past. In the first decades of the 20th century, $H. juliae$ most likely had stable populations with a relatively high number of individuals (near 1500). However, between 1935 and 1945, several consecutive years with low precipitation probably nearly drove the species to extinction. After 1955, a slow recovery to the current situation must have occurred when good and bad years alternated (Fig. 3).

4. Discussion

Population Viability Analysis examines the risk of extinction of populations in response to a variety of factors. Simulating the population dynamics under a set of relevant environmental factors can provide insights into the potential for species persistence. The results indicate that $H. juliae$ has experienced significant fluctuations in population size, with periods of stability and decline. Understanding the factors that contribute to these changes is crucial for developing effective conservation strategies.
conditions and/or experimental treatments allows managers to evaluate the efficacy of specific management actions and to project what will happen if a certain management strategy is implemented (Song, 1996). However PVA models must be used with caution, because they are just models, or “caricatures of reality” (Beissinger and Westphal, 1998). Accordingly, one must be aware of the limitations of the models, especially when the results are to be used for decisions on practical species conservation and management. In the case of the model presented here, it is necessary to point out that all data comes from a single monitoring plot and this lack of replication does not allow us to discern local from environmental variability. However, we were forced to restrict our monitoring to a single location, in order to avoid endangering the species by our own activities. In addition, comparisons between the native and introduced populations were performed for only one year, and relevant vital rates such as the survival of mature adults were not compared. However, we believe that our comparisons of the demographic structure, fruit production and seedling mortality were sufficient to suggest that the dynamics of the natural and planted populations were quite similar. We also assume that herbivores are not a significant factor, because we did not observe any damage that could be attributed to introduced (rabbits, mouflons) or natural herbivores (lizards, insects, etc.), and all observed deaths in the field were caused by summer drought or natural senescence.

In PVA’s, demographic responses to variable environments can be analyzed by prospective or retrospective analyses. Sensitivity or elasticity analyses are prospective and quantify the change in population growth rate given a specified change in one or more elements of the matrix. Retrospective analyses, by life table response experiments, can be used to determine life-history stages or demographic transitions that contributed to differences between populations observed during the observation period (Horvitz et al., 1997; Caswell, 2000). In this paper we resorted principally to prospective analyses because they are the most suitable approach to predict how expected levels of stochasticity will interact with conservation measures to influence the future population growth rate of threatened or endangered species (Menges, 1990; Heppell et al., 1994). The retrospective analyses used in this paper do not clearly coincide with the classical approach. Here, we mainly used it to get an idea of the most likely historical fluctuations in population size.

Elasticity analysis revealed that the most critical stage in the life cycle of H. juliae is the survival of mature reproductive plants, which showed the highest elasticity (31%) in the average matrix. The survival of this stage in natural conditions was 90.8%, and did not show much variation between good and bad years. For management reasons, we periodically visited the natural populations from 1985 onwards, and the planted population from 1989 onwards, when the individuals were three years old. Our field observations indicated that large reproductive plants generally died of senility after 14 years. In contrast, juvenile recruitment was highly variable, with very high values (4.88) in good, and low values (0) in

Fig. 5 – Triangular ordination diagram representing the position of the nine matrices for Helianthemum juliae between 1992 and 2002 with respect to their relative contribution (=summed elasticities) of fecundity (F), Growth (G) and survival (L) to the population growth rate, \( \lambda \). The matrices have been chronologically numbered from 1, 1992–1993 to 9, 2001–2002. Shaded areas enclose matrices that correspond to two precipitation classes, \( P < 350 \text{ mm}, P > 350 \text{ mm} \).
bad years. As expected (Pfister, 1998; de Kroon et al., 2000) this temporally variable transition had comparatively low elasticities (between 0% and 14%). In terms of conservation management, it is therefore most effective to protect the adult reproductive plants from damage by any human-related factors (Oostermeijer, 2003). In the case of H. juliae these factors are restricted to trampling by tourists and occasional herbivory by introduced animals (rabbits and mouflons).

Juvenile recruitment is generally strongly correlated with climatic variability, and more specifically with precipitation, because water is the principal limiting resource in arid regions (Harrington, 1991). Drought effects on fruit production and germination, as shown for another Mediterranean Helianthemum species (Helianthemum squamatum, Escudero et al., 1999), were not observed. Seedlings are generally highly susceptible to drought (Chabot and Mooney, 1985). In bad years (precipitation <350 mm) seedling mortality of H. juliae was high (nearly 100%), but in good years (precipitation >350 mm) mortality decreased to around 90%.

Probably owing to its extreme fluctuations, related to the variation in precipitation, juvenile recruitment has low elasticity (Pfister, 1998; de Kroon et al., 2000). This strong dependency of recruitment on the amount of precipitation is probably the normal situation for H. juliae. Regular recruitment is necessary to maintain viable populations on the long term. However, conservation management can do very little to stimulate recruitment. So, under a scenario of climate change, problems with this vital rate might arise.

The method to simulate stochasticity used in this paper is the simplest: randomly sample from a set of transition matrices and project the population for each year (Beissinger and Westphal, 1998). We preferred this method because it avoids problems of correlation among vital rates (Greenlee and Kaye, 1997; Kaye and Pike, 2003). One of the most important aspects in these models is the duration of demographic monitoring that is needed to adequately estimate environmental variability (Bierzychudek, 1999). The consequences of censusing populations during an insufficient number of years have not been fully explored (Fieberg and Ellner, 2001) but it quite likely leads to unreliable predictions.

Some authors suggest that the estimates of \( \lambda_s \) are likely to be imprecise even with sets of 10 matrices. Following the \( N = (5–10)T \) rule (Fieberg and Ellner, 2000), we would only be able to produce reliable predictions of extinction probability for a 2 years forecast interval with our set of nine matrices. However, for conservation managers and policy makers, predictions over such short intervals (2–3 years) are not very useful, and developing censusing programs that last for 50 years or more generally extend well beyond the time-frame of practical conservation.

Fieberg and Ellner (2001) suggest that modelling with environmental covariates may help overcome the requirements with respect to the sampling intensity using the environmental variables that have major effects on vital rates. Through the analysis of these variables we can model the relationship between demographic rates and environment, and knowing the distribution over time of the environmental variables we can obtain better estimates of population viability. For Helianthemum juliae, we have followed this alternative approach. We show that the population growth rate is strongly correlated with the annual precipitation and censused during a sufficient number of years to collect several good as well as bad years. In addition to the standard approach with random selection of matrices, we conducted an alternative random sampling strategy based on the frequencies of good and bad years observed during the last century.

Introducing stochastic variability by a random selection of matrices offered results similar to the deterministic analysis, and predicted a very low extinction risk. When we simulated the population dynamics in relation to climatic variability, the results were quite different. Under the climate scenario of the past 85 years (30% chance of good years) the simulations indicated a high extinction risk over the next 100 years. Simulating the future tendency for the three natural populations using this model, we obtain a regressive dynamic too. Of course, this result needs to be considered with caution because our model did not include the total complexity of the climatic variables and its future changes.

Anthropogenic climate change is a rapid process (N.R.C., 2002; Overpeck et al., 1991; Root et al., 2002), and the survival...
of many plant species may depend on the rates at which they are able to migrate to more favourable areas (Graham and Grimm, 1990; Kutner and Morse, 1993).

Our exploration of the climatic data revealed a significant increase in temperature ($r = 0.480$, $P < 0.05$) over the past 85 years that agrees with the global trend of climate warming (Graham and Grimm, 1990; Schneider, 1989). Precipitation, however, did not change significantly over time ($r = 0.038$, $P > 0.5$). Our analysis showed that $\lambda$ was only significantly correlated with precipitation and not with temperature.

Several models predict changes in precipitation and temperature in the Canary Islands climate zone for the next 100 years. The UK Met Office Hadley Centre for Climate Change (http://www.met-office.gov.uk/research/hadleycentre) predicts a 3–5 °C increase in the average annual temperature. Future changes in precipitation are less clear (−0.2 to 0.2 mm/day), but are predicted to be low. Hence, we could argue that global change will not affect precipitation in the Teide National Park. However, even if precipitation remains the same, a temperature rise will most likely increase evapotranspiration, and thus lower water availability in the soil (Lavender et al., 1998; Rosenzweig and Hilil, 2000). Using the more common equations (Thornthwaite, Turc, Coutagne, Penman, etc.) to calculate the theoretical evapotranspiration (Sánchez, 1992), a 3–5 °C temperature increase could result in a 20–35% increase in evapotranspiration over the current values.

Our retrospective simulations suggest that $H. juliae$ is currently recovering after a strong decline induced by several consecutive bad years at the start of the 20th century. Further climate warming could stop this recovery process. Under these conditions, we predict a problematic future for $H. juliae$, and most likely this is also true for other endemic species in this vulnerable ecosystem.

4.1. Conservation strategies

To test possible conservation strategies, we used the Stella model with climatic restrictions to simulate a worst-case scenario in which the probability good years is 30%, reflecting the data for Diego Hernández extrapolated from the Izaña meteorological station in the last 85 years, and incorporate several population reinforcement campaigns in this scenario. The experimental augmentation of the population with subadult individuals did not result in a significant reduction in the extinction risk, but only increased the time to extinction (Fig. 4). This implies that population reinforcement is not an effective tool to increase population viability. However, increasing the time to extinction can perhaps provide more opportunities for incidental good years, which would yield a more substantial reduction of extinction risk.

Another management strategy could be to increase the number of populations of $H. juliae$ on Tenerife. Seeds of $H. juliae$ do not disperse easily, judging from the observation that most seedlings are found in the direct neighbourhood of (their) mother plants. Hence, we consider the natural ability to colonize other sites with suitable climatic conditions to be limited.

In situ propagation of threatened species is becoming a more important conservation strategy (Maunder, 1992; Falk et al., 1996; Oostermeijer, 2003). In a rapidly changing climate, the founding of new populations in suitable areas could be a good strategy to spread risks of local extinction (Kutner and Morse, 1993). For this strategy to work, the new populations should preferably not be subject to the same climatic fluctuations. For $H. juliae$, this means that selecting new sites with adequate climatic conditions is more difficult, because available options are restricted to the Teide caldera, to which the species is endemic. However, sites with a probability of good years >40%, or sites with lower evapotranspiration can probably be found in the Teide caldera. Such sites might be found at the northern slopes or in sectors in the Southwest and Southeast of the National Park, where a lower altitude and more favourable orientation permit a greater incidence of clouds and fog than inside the Teide Caldera. Such locations form good candidates for founding new viable populations, which would significantly increase metapopulation viability (Fig. 4).

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References


