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From global to local scale: where is the best for conservation purpose?

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Abstract

Demographic analysis of plant populations represents an essential conservation tool allowing to identify the population trends both at global and at the local level. In this study, the population dynamics of *Helianthemum caput-felis* (Cistaceae) was investigated at the local level by monitoring six populations distributed in Sardinia, Balearic Islands and Ibero-Levantine coast (Alicante). Demographic data for each population were analysed by performing Integral Projection Models (IPMs). Our results showed that, although the local trend of the main basic demographic functions was similar, vital rates and demographic dynamics varied among populations indicating high variability. In fact, asymptotic growth rate in Spanish populations widely varied both between years and populations (some populations growth, decline or strongly decline), while Sardinian populations showed greater equilibrium or a slight increase. Also, the typical pattern of a long-lived species was not supported by the results at the local scale. These results indicated that different populations of the same species can present extremely different population dynamics and support the belief that, for conservation needs, local studies are more informative than global ones: the conservation status of *H. caput-felis* could notably vary at a small spatial scale and, accordingly, the conservation efforts must be planned at the population level and supported by local analysis.

Keywords Demographic analysis · *Helianthemum caput-felis* · Long-lived plant · Mediterranean vascular flora · Population dynamics

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Introduction

Demographic studies on threatened plants, are a pivotal element for both population management and effective conservation efforts (e.g. Godefroid et al. 2011; Menges et al. 2016) since demographic studies are a powerful tool for detecting and diagnosing the decline of plants populations (Menges 1990). A recovery plan for a threatened plant is impossible without a good knowledge of population demography (Schemske et al. 1994; Menges and Dolan 1998; Bell et al. 2003; Cogoni et al. 2019). Therefore, demographic analysis, combined with extensive ecological and genetic studies, constitute an essential conservation tool allowing to identify the long-term population trends, the contribution of particular life history stages to the population growth rate, and causes and consequences of differences in life stages among populations and years (Caswell 2001; Morris and Doak 2002; Dibner et al. 2019; Cogoni et al. 2019). In addition, management actions for species recovery require understanding differences among populations in different parts of the species range, especially if the range includes distinct ecosystems. Particularly for endemic and/or threatened plants, the difference in population trends at the local level must be evaluated in order to understand the mechanisms driving the vital rates in different populations. Indeed, previous studies demonstrate as populations of the same species, despite the proximity to the areal of distribution, could show strong local adaptations and a low correlation with the overall population performance (e.g. García 2008; Abeli et al. 2014; Dibner et al. 2019). This adaptation to local conditions at range edges (e.g. Giménez-Benavides et al. 2007; Villellas et al. 2013), has proven to be a probable consequence of geographical and ecological gradients (e.g. Giménez-Benavides et al. 2007; Sulis et al. 2017), such as distinct ecological niche (Papuga et al. 2018), but also of different levels of human-related disturbance.

Although demographic analysis have been successfully applied in plant ecology and evolutionary biology (e.g. Rees and Rose 2002; Williams 2009; Coulson 2012; Dibner et al. 2019), their use in conservation biology remains still lacking (e.g. Zuidema et al. 2010; Nicolè et al. 2011; Ferrer-Cervantes et al. 2012), especially in the Mediterranean Basin (e.g. Belaid et al. 2018; Sulis et al. 2018; Cogoni et al. 2019). Indeed, although much interest has been devoted to the Mediterranean vascular flora (e.g. Médail and Quézel 1997; Nikolić et al. 2008; Bacchetta et al. 2012; Iliadou et al. 2014), demographic studies on endemic and/or threatened plant populations are uncommon, even more so at the local level (e.g. Pino et al. 2007; Iriondo et al. 2009; Pisanu et al. 2012; Cursach et al. 2013; Cursach and Rita 2014; Belaid et al. 2018; Sulis et al. 2018; Marrero et al. 2019; Gauthier et al. 2019; Cogoni et al. 2019).

Recent studies indicated that the conservation needs vary at the small local level in the Mediterranean territories since a plant species could need different conservation attentions depending on the particular conditions of the locality on which it grows (Fenu et al. 2020), and thus, the local demographic trends should be the main guide to plan conservation measures at the restricted local scale. Consequently, the pivotal question is to know whether having data and general assessments on a threatened species are (or not) determinant to identify effective conservation measures for such species. To test this question, *Helianthemum caput-felis* (Cistaceae) represents an emblematic plant species because it is distributed in several countries, presents populations isolated from long distances and, locally, grows in very different ecological conditions (Sulis et al. 2020).

H. caput-felis is a long-lived half shrub that mainly grows in coastal environments, under the direct influence of the sea, but some populations are also found in other

ecological contexts such as sand dunes or rocky slopes (Sulis et al. 2020). It is distributed throughout the western Mediterranean Basin in several fragmented populations (Sulis et al. 2020); the widest distribution and the largest populations are located in Spain, whereas the presence of this species in Sardinia and northwest Africa is restricted to small areas in unique or reduced places where often few mature plants are present (Sulis et al. 2020). A recent demographic study carried out considering the whole population of this plant species highlighted that, despite inter-annual fluctuations mainly related to the reproductive traits, the population was at equilibrium under the simulated environmental stochasticity. In fact, the population dynamics of *H. caput-felis* followed the general pattern typical for long-lived Mediterranean plants: populations with growth rates closer to the equilibrium in the long term, the determinant role of the survival-growth transitions for the population growth rate, slow growth and stasis, longevity of established individuals, shrinkage of medium-large plants, low recruitment rate, high generation times and mean long lifespans (Sulis et al. 2018).

Nevertheless, considering their distribution, the observed decline in several populations, and the deteriorating status of the habitat quality as well as the quasi-extinction risk probability, *H. caput-felis* was categorized as "Endangered" (EN) according to the IUCN protocol (Sulis et al. 2020). Accordingly, since *H. caput-felis* is also included in the Berne Convention and Appendix II of the Habitats Directive (European Community Council Directive 92/43/EEC), a transnational conservation strategy was proposed (Sulis et al. 2020); this strategy should include both translocation programs and the protection of each locality in which this plant occurs, to avoid further decline or extirpations, habitat restoration in degraded localities and reduction of the impacts of recreational activities (Sulis et al. 2020).

However, further analysis at the small-scale level were needed to evaluate each local situation and to plan adequate conservation measures related to local environmental needs. In other words, are these indications obtained by analyzing the global population *H. caput-felis* also consistent at the local level and useful to plan the conservation measures of single populations? Using demographic analyses, plant performance and population dynamics were investigated in six populations representative of the European distribution of *H. caput-felis* in an attempt to verify if the local population dynamics of *H. caput-felis*, follow the same pattern obtained for the global population and, as a consequence, if the conservation requirements are similar for local populations along the western Mediterranean Basin.

Materials and methods

Study species

Helianthemum caput-felis is a half-shrub that grows to a height of 35(50) cm. Its flowers are hermaphrodite and have a short lifespan (3–4 days; Rodríguez-Pérez 2005). The flowering period is from March to June, and the fruiting season runs from late April to the beginning of August (Fenu et al. 2015; Sulis et al. 2017). *H. caput-felis* is an entomophilous, mostly self-incompatible, plant species (Agulló et al. 2015). Fruits are capsules that detach at maturation, and seed germination takes place in autumn, at the onset of the rainy season (Rodríguez-Pérez 2005). Seeds exhibit a high germination rate after scarification (Rodríguez-Pérez 2005; Sulis et al. 2017).

Ecologically, *H. caput-felis* is a thermophilous plant with a growth preference for coastal areas under the direct influence of the sea, mostly on calcareous rocky cliffs (0–200 m a.s.l.) with garrigues or scrublands; it also grows on other, more idiosyncratic habitats, such as sand dunes, rocky slopes bordering inland ravines and, rarely, in open wooded areas (Sulis et al. 2020). *H. caput-felis* is distributed throughout the western Mediterranean Basin (Iberian Peninsula, Mallorca, Sardinia, Morocco and Algeria; Fenu et al. 2015; Sulis et al. 2020).

Data collecting

Demographic data were collected in 98 permanent plots placed in six different populations along the overall European distribution range of the species and representative of the full ecological range in which the plant grows. Two populations are located in Sardinia (Italy), at the eastern margin of its distribution range: Capo Mannu and Su Tingiosu (CM and ST, hereafter); two in Majorca's island, in the middle of its range: Sa Ràpita and Colònia de Sant Jordi (SR and SJ, hereafter); two in and Ibero-Levantine coast (Alicante, hereafter), at the western part of its distribution: Moraira (MO hereafter), in the north of Alicante's coast and Cabo Roig and Punta de la Glea (CR hereafter), which represent the southern population (Table 1).

In each population, after selecting the most appropriate/undisturbed areas, the permanent plots (2 × 1 m in size) were randomly placed in the area where the plant was found. Demographic censuses were carried out during two consecutive transitions (i.e. plant

Table 1 Geographical and ecological traits of *Helianthemum caput-felis* populations: coordinates, altitudinal range (m a.s.l.), substrate type, number of plots and number of plants within the monitored plots

Region	Population (code)	Coordinates U.T.M (time zone)	Altitudinal range (min–max)	Substrate type	N. plots	N. plants
Ibero-Levantine coast (Alicante)	Cabo Roig and Punta de la Glea (CR)	700,388.62 m E, 4,198,390.09 m N (30 S)	3–15	Limestone	15	116
Ibero-Levantine coast (Alicante)	Moraira (MO)	250,226.01 m E, 4,285,845.34 m N (31 S)	3–15	Limestone	15	56
Majorca	Sa Ràpita (SR)	496,897.00 m E, 4,356,780.00 m N (31 S)	0–5	Sand and limestone	15	252
Majorca	Colònia de Sant Jordi (SJ)	500,074.00 m E, 4,352,060.00 m N (31 S)	0–5	Sand and limestone	13	65
Sardinia	Capo Mannu (CM)	447,428.00 m E, 4,432,412.00 m N (32 S)	5–55	Limestone	20	146
Sardinia	Su Tingiosu (ST)	449,657.67 m E, 4,428,538.64 m N (32 S)	5–25	Limestone	20	186

Detailed information and a precise map on the investigated populations are reported in Sulis et al. (2018)

change—in terms of growth, stasis or reduction in size—from t in a year to $t + 1$ in the consecutive year; cycles hereafter), covering a total of 3-year period (2013–2015). Within the plots, all plants (821 in the first census) were marked, mapped and regularly monitored. All new seedlings that appeared inside the plots were also counted, measured, and mapped.

Demographic data have been collected following the same methodology reported in Sulis et al. (2018). Specifically, surveys took place three times *per* year. In early March, all plots were surveyed for the first time to locate all previously mapped individual plants and to map any new seedlings; during the flowering peak (March–April), when all the plants were fully grown, the plots were surveyed a second time to measure each plant (i.e. height, minimum and maximum diameter), to count the number of flowers per plant and to check for the occasional new individuals, which were added to the data set. Finally, during the fruiting peak (late May–early June), the last survey was oriented to estimate the number of fruits per plant. In this case, 10 mature fruits were randomly collected from each plot to estimate the mean number of seeds per fruit (n = 980 fruits in total). The number of seeds per fruit was directly counted in the laboratory, and subsequently, the number of seeds for each plant was estimated by multiplying the average number of seeds per fruit and the number of fruits per plant.

Data analyses

Collected data have been analysed following the same methodology reported in Sulis et al. (2018), where it is also described how the model was built. In this study, data from each population were analysed separately in order to detect the population trend at the local level and to elucidate differences among populations and cycles, if present. Integral Projection Model (IPM) has been particularly advocated for small demographic datasets (less than 300 plants; Ramula et al. 2009), and therefore it is very useful for this study case. Accordingly, the dynamic patterns of each population were investigated, and the population growth rate (λ) and the stable size distribution with damping ratio (ρ) were evaluated by performing IPMs (Easterling et al. 2000; Ellner and Rees 2006). IPMs describe how a population structured by a continuous individual-level state variable changes in discrete time (Easterling et al. 2000) using a continuous projection kernel to describe the population size distribution by a density function (Easterling et al. 2000; Ellner and Rees 2006). The chosen continuous state variable for evaluating the demographic dynamics of the *H. caput-felis* populations was plant size (i.e. plant volume, hereafter), which has been demonstrated to be positively correlated with its reproductive capacity (Fenu et al. 2015; Sulis et al. 2017), following the same approach in Sulis et al. (2018).

The life cycle of *H. caput-felis* includes a continuous stage, in which this plant grows and reproduces, combined with a discrete stage, with seeds that can either enter in the soil seed bank or germinate in the next autumn after dispersion (Sulis et al. 2018). Both continuous and discrete stages were considered in the analyses, following the method for species with complex life cycles (Merow et al. 2014; Salguero-Gómez 2014), specifically adapted to our study species as reported in Sulis et al. (2018).

The growth, survival, and fertility functions were obtained from statistical models of the census data: constant, linear and quadratic models were fit, and the best was selected based on the lowest Akaike Information Criteria (AIC; Dauer and Jongejans 2013).

Additional population traits were extracted by the IPMs: the λ calculated excluding the soil seed bank stage ($\lambda_{continuous}$), in order to analyze any potential differences with λ, and the stochastic rate of increase (λ_S). The stochastic rate of increase (λ_S) was calculated as

the geometric mean proportional change in population size over 50,000 model iterations, where one yearly projection kernel was randomly drawn for each iteration.

Moreover, demographic perturbation analysis was performed: elasticity (proportional sensitivity) provided details on the size range having the greatest effect on λ (Dauer and Jongejans 2013), which is a prospective analysis. Conversely, Life Table Response Experiments (LTREs) are retrospective analyses that quantify the contribution of each demographic process to the actual differences found in λ (Caswell 2001) by analyzing the observed variation.

In this study, elasticity and the LTRE were derived or calculated from the IPMs, following the same approach used in previous studies (e.g. Ramula et al. 2009; Merow et al. 2014; Sulis et al. 2018). Elasticities were partitioned into survival-growth (*P*) and reproduction (*F*) components in each studied cycle. LTRE was verified by a cross-check as recommended by Salguero-Gómez (2014). Due to the strong low values and/or the presence of an excessive number of zeros of some populations, plots were scaled in order to display the main differences. Elasticity was used to identify potential management targets, as changes in vital rates with high elasticity produce large changes in λ (Caswell 2000).

All the analyses were performed using the "IPMpack" package, version 2.1 (Metcalf et al. 2014), and the kernels were plots with the "image" function of the "fields" package (Nychka et al. 2014) in R version 3.1.2 (R Core Team 2014).

Results

As expected, vital rates models show that plant volume was generally correlated with survival, growth, flowering probability, and fruit number in both studied cycles (Figs. 1, 2, 3 and 4).

Survival rate positively correlates with plant size (Fig. 1) but some exceptions to this pattern were detected: CR in cycle 2 and SR and SJ in both cycles. During cycle 1, plants of SR showed the lowest survival for little-intermediate sizes, but high survival for lowest and highest volumes, whereas in SJ no relationship between survival and plant size was observed. In cycle 2, an exception was represented by CR: survival initially decreased and then, in correspondence of high volumes, increased; during cycle 2, SR plants showed a
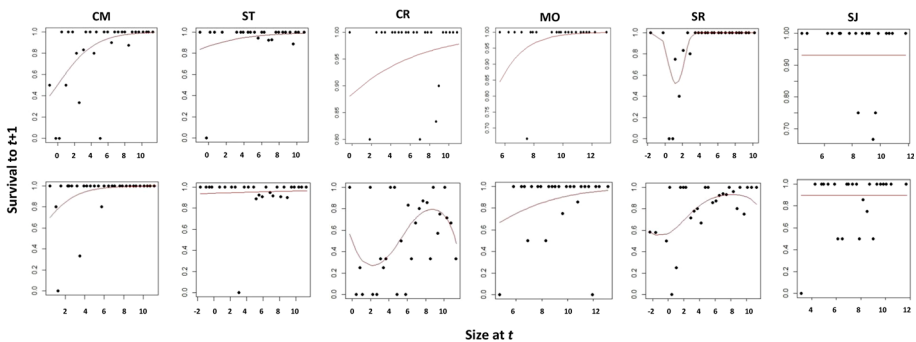

Fig. 1 Relationship between plant size and survival probability in cycle 1 and cycle 2 (first and second row, respectively). Columns correspond to the six studied populations of *H. caput-felis* (see Table 1). Red lines show the best-fit model prediction. The x-axis represents plant size at *t*; the y-axis represents survival probability of plants at *t* + 1
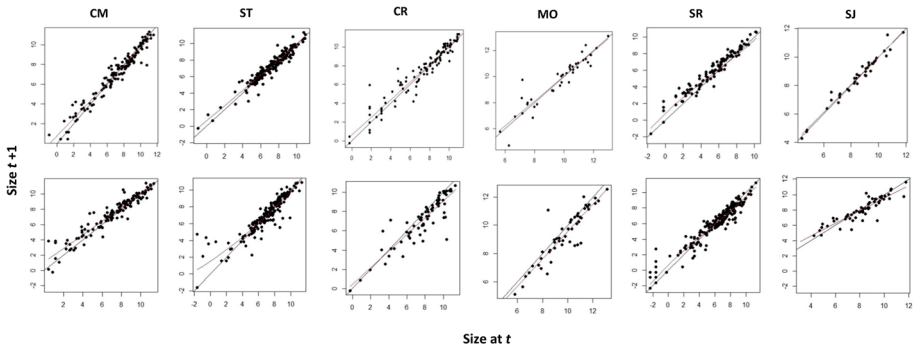
Fig. 2 Relationship between plant size and growth in cycle 1 and cycle 2 (first and second row, respectively). Columns correspond to the six studied populations of *H. caput-felis* (see Table 1). Red lines show the best-fit model prediction. The x-axis represents plant size at *t*; the y-axis represents plant size at $t + 1$
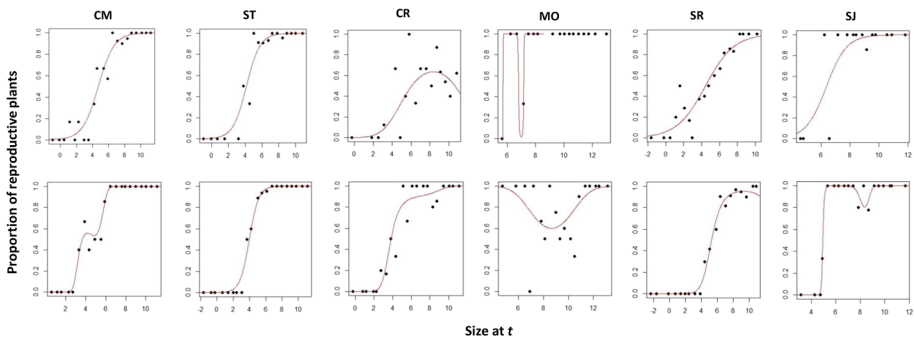

Fig. 3 Plant's flowering probability in cycle 1 and cycle 2 (first and second row, respectively). Columns correspond to the six studied populations of *H. caput-felis* (see Table 1). Red lines show the best-fit model prediction. The x-axis represents plant size at *t*; the y-axis represents the proportion of reproductive plants at $t + 1$
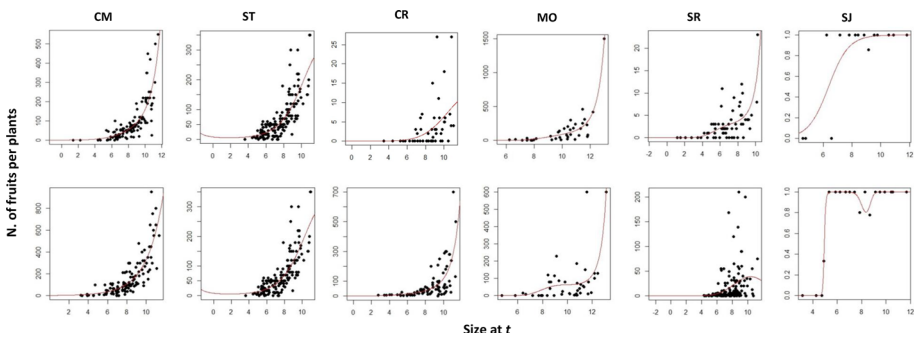

Fig. 4 Relationship between plant size and fruits production cycle 1 and cycle 2 (first and second row, respectively). Columns correspond to the six studied populations of *H. caput-felis* (see Table 1). Red lines show the best-fit model prediction. The x-axis represents plant size at *t*; the y-axis represents the number of fruits per reproductive plant

positive relationship between survival and size until ca. 2900 cm^3 after which it decreases; again no relationship between survival and plant size was observed for SJ (Fig. 1).

The growth rate is always linear dependent on the size in year t and generally follows the same pattern, always with smaller plants that were commonly more likely to grow than larger ones (Fig. 2). Exceptions to this pattern were MO in cycle 2 where there was a linear negative relationship between growth and size (plants reduced their size in the following cycle). Furthermore, growth plots highlighted the general concentration of large plants compared to smaller ones (Fig. 2).

The flowering probability strongly increased with plant volume, with plants larger than ca. 400 cm^3 flowering, except in MO where the probability of flowering decrease for medium-large plants in cycle 2, than increase again for the largest individuals (Fig. 3). Among flowered plants, the number of fruits was exponentially dependent on the plant's volume being larger plants produced more fruits than the smaller ones (Fig. 4).

Asymptotic growth rate values (λ) varied both between cycles (except in ST) and populations (from 0.93 in SJ to 1.65 in MO during cycle 1 and from 0.67 in CR to 1.79 in SJ during cycle 2; Table 2).

Population growth rates considering only the continuous stage ($\lambda_{continuous}$ = excluding the soil seed bank stage) did not change from λ, except in CR during cycle 2, where $\lambda_{continuous} < \lambda$ (-0.08; Table 2). Stochastic growth rates (λ_S) notably varied from 0.80 (CR) to 1.63 (MO; Table 2).

The observed stable size distribution was generally skewed towards large adult plants (Fig. 5); hence, under deterministic conditions, *H. caput-felis* populations could include larger numbers of plants with a volume ranging from $\sim$ 400 to $\sim$ 60,000 cm^3. However, the predicted stable size distributions slightly differed from the observed ones for CR, MO and SR in cycle 1, and for CR, MO SR and SJ in cycle 2.

The damping ratio values range from 1.03 (SJ in cycle 1) to 2.14 (MO cycle 2). Populations had values close to 1, indicating a very slow convergence to the stable stage distribution. Exceptions were represented by MO (both cycles) and SJ (cycle 2), which has large values indicating rapid convergence on the stable stage structure.

Elasticity values were high along the diagonal representing the survival of medium-large individuals in stasis; exceptions were CR (in cycle 2) MO (in both cycles) and SJ (cycle 2) where the highest elasticity values involving small plants (Fig. 6).

Table 2 Population growth rate (λ), population growth rate excluding the soil seed bank stage ($\lambda_{continuous}$), stochastic population growth rate (λ_S), elasticity partition (P and F components) and damping ratio value (ρ) of the six analysed populations in the two transitions (C = cycles)

| Population (code)	λ		$\lambda_{continuous}$		λ_S	P component		F component		ρ	
	C1	C2	C1	C2		C1	C2	C1	C2	C1	C2
Capo Mannu (CM)	0.98	1.06	0.98	1.06	1.03	0.98	0.94	0.02	0.06	1.23	1.23
Su Tingiosu (ST)	1.01	1.01	1.01	1.00	1.01	0.97	0.97	0.03	0.03	1.15	1.18
Cabo Roig (CR)	1.02	0.67	1.02	0.59	0.80	0.97	1.00	0.03	0.00	1.18	1.14
Moraira (MO)	1.65	1.61	1.65	1.61	1.63	0.43	0.39	0.57	0.61	1.71	2.14
Sa Ràpita (SR)	1.13	0.97	1.13	0.96	1.03	0.91	0.93	0.09	0.07	1.17	1.42
Colònia Sant Jordi (SJ)	0.93	1.79	0.93	1.79	1.30	1.00	0.44	0.00	0.56	1.03	1.84
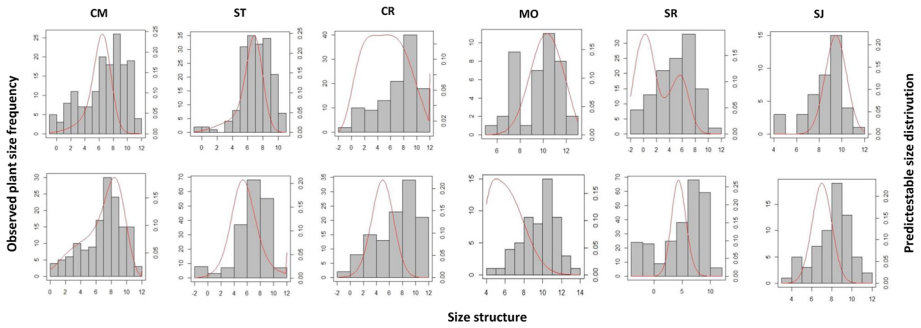
Fig. 5 Histogram distribution of plant sizes (log of plant volume in cm^3) and stable size distribution (red lines) for the IPM fitted for cycle 1 and cycle 2 (first and second row, respectively). Rows correspond to the six studied populations of *H. caput-felis* (see Table 1)
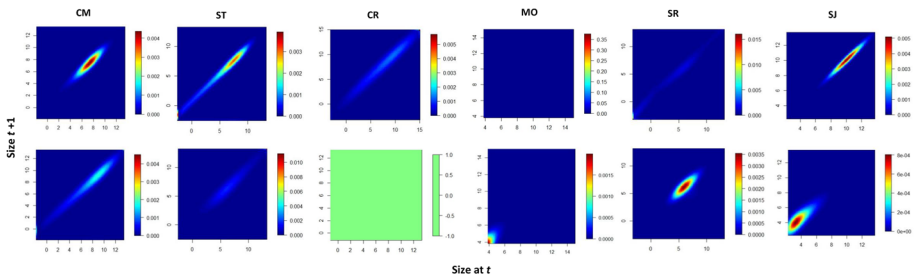

Fig. 6 Relationship between plant size and elasticity from cycle 1 and cycle 2 (first and second row, respectively). Columns correspond to the six studied populations of *H. caput-felis* (see Table 1). The x-axis represents plant size at t; the y-axis represents plant size at $t + 1$

The breakdown of elasticity revealed that P component (survival-growth) is much higher than F component (reproduction) in almost all populations, indicating that the survival-growth transition was the critical determinant of λ (Table 2). In two cases (CR in cycle 2 and SJ in cycle 1) the F component is totally absent. The F component is higher than the P component (fecundity contributed more than survival/growth to the projected λ) only in MO (in both cycles) and SJ (cycle 2; Table 2).

The kernel's plots showed the importance of medium-large size's plants (high values near the diagonal central area); indeed, they were dominated by the survival function, representing individuals in stasis (plants that do not change size in the next year (Fig. 7).

The slight evidences in the bottom-right region represent the F portion of the kernel. The high peak was $\sim$ 22,000 cm^3 (Fig. 7), indicating that individuals of this size contributed most to reproduction. Furthermore, the absence of evidence in the bottom left area, which represents new seedlings entering the smaller size class, indicating that only a few seedlings appeared and a low percentage of these survived, confirm the high mortality rate of smaller plants.

Perturbation analysis

Sensitivity of the arithmetic mean IPM kernel included soil seed bank dynamics showing the importance of the emergence of seeds from the soil seed bank to λ are reported in
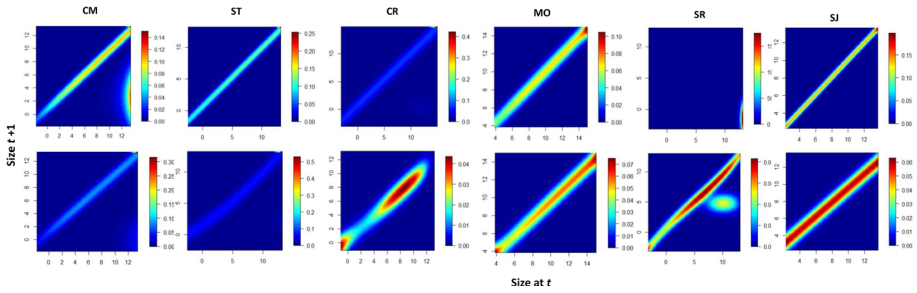
Fig. 7 IPM kernels from cycle 1 and cycle 2 (first and second row, respectively). Columns correspond to the six studied populations of *H. caput-felis* (see Table 1). The x-axis represents plant size at *t*; the y-axis represents plant size at *t* + 1. The F component is difficult to observe in the kernels because its values are extremely low compared to those from P component, which dominate the IPMs. Note that the kernels don't show the discrete stage (soil seed bank) for display reasons, but it is included in all the analyses
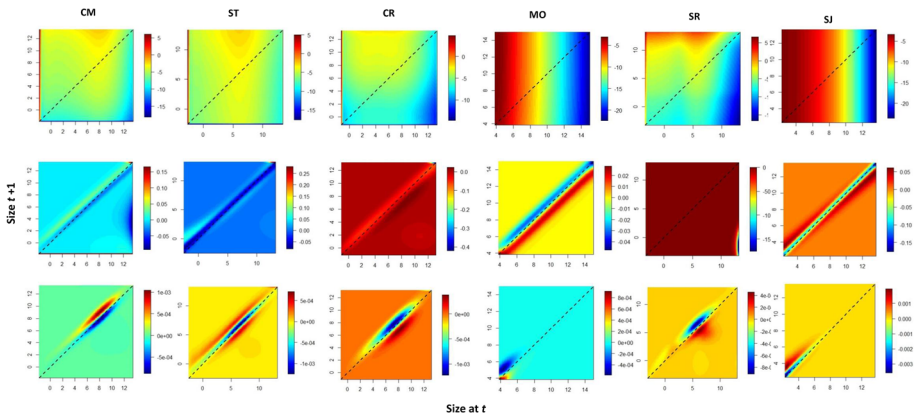
Fig. 8 LTRE outputs. Columns correspond to the six studied populations of *H. caput-felis* (see Table 1). For each population were represented: **a** Sensitivity of the arithmetic mean IPM kernel, including seed bank dynamics; **b** difference between the kernels cycle 1 and cycle 2; **c** contributions to the difference in λ between the two *H. caput-felis* IPMs. The x-axis represents plant size at *t*; the y-axis represents plant size at *t* + 1

Fig. 8a; the sensitivity was high, with values that increase with plant size. Nevertheless, also the new seeds entering into the soil seed bank denotes a low impact on λ: $\lambda_{continuous}$ (calculated considering only the continuous stage) does not change from λ calculated including the soil seed bank dynamics (Table 2).

Accordingly, the soil seed bank dynamics were cancelled in the kernel of differences (Fig. 8b) and their contribution to the difference between $\lambda_{cycle\ 1}$ and $\lambda_{cycle\ 2}$ was null (kernels show only the continuous stage). The contributions of the single part of the life cycle to differences in λ between the two cycles are reported in Fig. 8c.

Populations whose $\lambda_{cycle\ 2}$ was lower than $\lambda_{cycle\ 1}$ (CR, MO and SR) displayed a shrinkage of individuals in the cycle 2, particularly in MO, where the shrinkage involved both larger and small plants (whereas, in CR only medium-large individuals shrink; Fig. 8b). In the case of SR, differences between cycles are due to the high fecundity of large plants in the first census.

A different trend was observed in CM and ST, described by a strong growth of both smaller and large individuals, especially in CM, which λ slightly increases in cycle 2, due to the contribution of medium and large individuals (Fig. 8c). Likewise, ST stayed at equilibrium (λ = 1.01 in both cycles), but in cycle 2 plant stasis involves a bigger range of size. Conversely, in CR and MO there was a high shrinkage (medium-large and smaller plants, respectively), which have a stronger impact on λ compared to the growth of individuals in the past transition. The same pattern occurred in SR, where the highest shrinkage of medium size plants contributed most to the lowest $\lambda_{cycle\ 2}$. The shrinkage of individuals in the second cycle could be considered the main responsible of the lowest λ in MO (small plants), CR and SR. In SJ $\lambda_{cycle\ 2}$ was higher than $\lambda_{cycle\ 1}$ due to a marked growth in size involving smaller plants, with shrinkage only in large individuals.

Discussion

Demographic studies on Mediterranean coastal plants are still lacking and only a few studies have examined endemic and/or threatened plants (e.g. Iriondo et al. 2009; Cursach and Rita 2014; Pisanu et al. 2012; Sulis et al. 2018; Belaid et al. 2018; Marrero et al. 2019; Cogoni et al. 2019; Gauthier et al. 2019; Orsenigo et al. 2020), and even more scarce are the analyses at the population level. In fact, to our knowledge, despite the key role in conservation programs, demographic data and analyses are scarce, even for those plant species for which these activities are mandatory by international or national regulations, with a few exceptions (e.g. Iriondo et al. 2009; Marrero et al. 2019). As far as we know, a recent exception to this general situation in the Mediterranean Basin is represented by the (short-term) demographic study on *H. caput-felis*, which includes plants sampled in different populations along a representative part of the distribution range of this species (Sulis et al. 2018). The *H. caput-felis* global population mainly consists of adult individuals; this pattern of high survival and longevity of adult plants together with the slow growth (frequency of stasis) and fecundity rate generally less important than survival for population growth, represents a typical strategy of long-lived plant species. In this context, seedling emergence and recruitment are absent (or very low) and this rate becomes less important for long-term population persistence (Sulis et al. 2018). The same population traits are also reported, although often not obtained via demographic studies, for other Mediterranean plant species (e.g. Picó and Riba 2002; García 2003, 2008; Fréville et al. 2004; Domínguez Lozano et al. 2011; Pisanu et al. 2012).

In general, the short-term dynamics of the global *H. caput-felis* population was at equilibrium (λ = 1), although this result seems to disagree with the threats and the human disturbance observed in the field (Sulis et al. 2018). This finding shouldn't be surprising because it is not uncommon that long-lived plant populations may be locally adapted and respond differentially to the same overall weather (García 2008). Indeed, differences at the local level, even important ones, have been observed in the populations investigated.

The results of this study showed that the local trend of the four basic demographic functions (i.e. growth, survival, probability of flowering and fruits output) is generally similar to the global population: these functions were size dependent, survival increase with size, smaller plants are generally more likely to grow than larger individuals and larger plants have higher fecundity (Sulis et al. 2018). All populations are mainly composed of large individuals and only few seedlings, and characterized by a high mortality rate of smaller plants; this pattern, together with the slow growth of the plants (frequency of stasis), suggests a low colonization ability and high local persistence (e.g. Thompson

2005; Pisanu et al. 2012; Cogoni et al. 2019). However, vital rates and demographic dynamics varied among populations: some populations growth, some seem at equilibrium and some decline, indicating high variability among them, depending on the zone of origin and environmental or stochastic factors. For example, the survival rate follows the general pattern in all populations except SJ, in which it is not related to size; the growth rate is linear dependent on the size in year t, with smaller plants that were commonly likely to grow than larger ones, except in MO in cycle 2. However, these differences seem to be related to the extremely low size of the population compared with the other populations investigated.

The predicted stable size distributions of all $H.$ $caput$-$felis$ populations were generally skewed heavily towards medium-large adult plants. This indicates that, under deterministic conditions, those populations could include larger numbers of individuals with a medium-large volume, as detected in the Sardinian populations. Generally, there is an 'excess' of mature and reproductive individuals in the original stable stage distribution; these individuals continue to reproduce after the vital rates are changed, resulting in an increase in population size (Caswell 2001). The predicted stable size distribution does not match with the observed size distribution in the Spanish populations, but only in MO and SJ the high damping ratio values highlight that the stable stage distribution is reached fairly soon.

The larger sensitivity of population growth rate to changes in growth and survival of adult plants than to changes in reproduction is a typical property of many long-lived plants (Silvertown et al. 1993). In fact, for long-lived, iteroparous species, fecundity is generally less important for population growth than survival (Silvertown et al. 1993; Franco and Silvertown 2004; Ramula 2008, 2014).

As expected, considering the breakdown of elasticity, the P component is higher than F component in almost all populations, indicating that the survival-growth transitions were the critical determinant of λ and the contribution of growth to λ was dominated by transitions into the larger plants where reproduction occurs, as previously obtained for the global population. However, two populations significantly deviate from this pattern: in MO (both cycles) and SJ (cycle 2) the F is higher than the P component, indicating that the fecundity contributed more than survival/growth to the projected λ. This indicates that in these populations the plant did not show the general pattern of a long-lived and the main contribution to λ is linked to the growth of small plants. Moreover, MO in both cycles and SJ in cycle 2 showed high damping ratio values, indicating that this population can converge fast to the stable stage distribution.

In two peculiar cases elasticity was made up almost entirely of contributions from stasis transitions: in SJ (cycle 1) and CR (cycle 2) fecundity completely fails (F component of elasticity = zero). At low values of λ delay mechanisms such as stasis and retrogression prevail at the expense of reproductive loops, which become important only at the higher population growth rates. These patterns suggest caution to base management on elasticities of a matrix of a single population at a single time, especially for declining population (Silvertown et al. 1996); in fact, in perennial plants, remnant populations with low recruitment may only persist by the survival of some mature individuals (Eriksson 1996).

Considering only the continuous stage ($\lambda_{continuous}$), population growth rates do not change from the total λ, except in CR (cycle 2), where $\lambda_{continuous}$ showed a value inferior to λ, maybe due to the complete failure of the F component.

The absence of recruitment is validated by the LTRE analysis. The transient dynamics can occur if a stage structured population is not at the stable stage distribution, i.e. when the relative proportions of life history stages have not reached constant values. These dynamics include environmental stochasticity and do not depend on the initial size of the

populations, shows a strong long-term increase in MO and SJ, a slight increase in the Sardinian populations and in SR, and a high decline (20%) in CR. It is essential to highlight that as environmental stochasticity increases (i.e. MO and SJ) the importance of mean population growth rate as a predictor of population dynamics declines (Menges and Dolan 1998; Caswell 2001).

Moreover, in semiarid and arid situations (as in CR) characterized by high environmental stochasticity, perennial shrubs usually rely on their longevity to persist over time (García and Zamora 2003), because the effort invested in new plant establishment seems to be high and the allocation of energy to stress tolerance mechanisms is supposed to increase survival but to reduce energy for reproduction (Aragón et al. 2009). Hence, the different population dynamics observed among the analyzed localities of *H. caput-felis* should be correlated to microclimatic and ecological conditions which can affect the relationship among plant size and vital rates.

Contributions to the difference in λ between cycles highlight that the difference in shrinkage is the leading cause of the difference in λ in Spanish populations, as demonstrated in a previous study (Salguero-Gómez et al. 2016).

Summarizing, we can identify two main groups of populations being the Sardinian ones distinct from the Spanish ones. Sardinian populations seem to have greater equilibrium (λ close to 1), probably due to the reached stable structure of the populations, mainly composed of large individuals, which produce more fruits per plant and, then, more viable seeds per fruit (Fenu et al. 2015). In addition, Sardinian populations are favoured by being included in the Natura 2000 network and being in areas where the impact of tourism and agricultural / forestry activities is managed (Fenu et al. 2015).

Conversely, the dynamics of the Spanish populations showed higher variability of growth rates, both among different localities in the same year and different years of the same population; also values of λ varying between successive cycles. The high differences among these populations seem to reflect the high degree of anthropogenic disturbance to which they are exposed and, specifically, the strong fragmentation linked to the anthropic development of the eighties that turned these localities as one of the principal touristic sites in the western Mediterranean Basin.

Within this group, however, further distinctions can be made; among the Majorcan populations, SJ showed a high variable trend among years, due to the growth of the small plants which contribute to λ with the strong increase of the fecundity. This population seems to benefit from being, at least in part, in private land which therefore limits anthropic disturbance and promotes the protection of the small plants, usually more sensitive to human disturbance. In contrast, SR showed a decline in the short-time, due to the shrinkage of the medium plants; however, when the environmental variability was considered, plants growing in the sand substrate shows equilibrium in the long term (similar to the Sardinian populations) indicating that the species manage to adapt to retrodunal sandy habitat, as long as they are not fragmented and subject to limited human disturbance.

The most variable situation was represented by Alicante's populations. MO shows the highest value of λ, indicating that, despite these values are highly influenced by the F component, the population is now recovering quickly, as also confirmed by the high damping ratio. This positive evolution is most likely the consequence of the establishment of a micro-reserve and the associated conservation program (sensu Laguna et al. 2004). In contrast, the south Alicante's population (CR) showed a strong decline, due to the shrinkage of the medium-large plants, probably related to the high habitat fragmentation mainly linked to a strong touristic exploitation. Although part of the *H. caput-felis* population is included in a large micro-reserve and in a Natura 2000 site (Punta de la Glea),

this conservation measure is probably not sufficient to invert the decreasing rate since the protection has predominantly favored the evolution of the natural vegetation (including the natural competition of other shrubby species).

The *H. caput-felis* populations show variable demography behaviour, close to the equilibrium where the stable size distribution is reached (Sardinian populations and, partially, in Balearic populations growing on sandy substrate), while with high variability in populations far from the stable size structure. In this context, although the Sardinian populations are recognised as extremely threatened of extinction, our results indicated that they could be locally adapted to ecological and microclimatic conditions and low impacted by human-related activities.

Conservation implications

Demographic studies, combined with extensive ecological and genetic studies, are essential tool for an effective plant populations management and conservation, especially at the small local scale (e.g. Godefroid et al. 2011; Menges et al. 2016; Marrero et al. 2019; Cogoni et al. 2019; Fenu et al. 2019). Our study demonstrated that the conservation status of a plant globally considered endangered could notably vary at small spatial scale and suggested that conservation efforts must be supported by local analysis more than global investigation. Such evidence leads us to confirm that the priorities of conservation should vary at the small local level (Fenu et al. 2020), since a population could need different conservation measures depending on the peculiar local conditions.

To ensure the long-term conservation of the natural *H. caput-felis* populations, a unique conservation strategy should be implemented in Sardinia, while population-specific plans in Spain are needed.

At the local level, our results indicated that for Sardinian populations no urgent measures are required to reduce the extinction risk, but continuous monitoring could be an optimal solution to have an updated picture of the local conservation status. Additional conservation actions could be focused to strictly protect and, if possible, enhance the number of medium-large individuals. In addition, this study suggests that the endangered IUCN category at the regional level assessed for this plant in Sardinia was not supported by these demographic analyses, which instead suggests downgrading the risk category.

Conversely, the situation of all Spanish populations required more attention. The same general scheme indicated for the Sardinian populations could be adopted also for the Majorcan populations. However, a translocation program already indicated by previous analysis (Sulis et al. 2020) could be carried out in suitable areas in order to stabilize the population trends by transplanting adult plants carefully selected based on a preliminary and in-depth genetic study. Such conservation actions are urgently needed for Alicante's populations, where a more general approach could be adopted. In this case, our analysis demonstrated that a single passive protection measure is not sufficient to protect a threatened plant as previously demonstrated (e.g. Fenu et al. 2019, 2020): the institution of a micro-reserve could be a relevant conservation measure if connected to a pluri-annual monitoring plan associated to a continuous control of the natural vegetation evolution. The protection in these populations must be primarily aimed to safeguard all the remaining adult plants, specifically those in coastal areas where human-related disturbance is high as previously suggested (Sulis et al. 2020). The conservation measures recently implemented in MO seem to be encouraging and it would be desirable to extend the same approach to

other populations. In addition, specific translocation programs could be carried out in suitable areas mainly based on transplanting adult plants (Sulis et al. 2020).

Finally, monitoring is required of all populations and although it could be challenging to sustain long-term monitoring, it is fundamental for assessment of conservation status and for effective local conservation.

Data availability Due to the sensitive nature of the species locations the datasets from the current study are not publicly available but are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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