



Reproductive performance of *Helianthemum caput-felis* along its fragmented distribution in the Mediterranean coasts



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ABSTRACT

Plant's reproductive success is determined by intrinsic characteristics of the reproductive system of the species, as well as by extrinsic abiotic and biotic factors. Reproductive traits can vary along different gradients (e.g. ecological, geographical, etc.) and several studies revealed that the most favourable conditions (i.e. greater densities, fitness and genetic diversity) will be found at the core of a plant distribution range than in marginal or isolated populations. In this study the phenological and reproductive traits of several fragmented populations of *Helianthemum caput-felis* Boiss. (Cistaceae), a perennial Mediterranean plant were investigated. Six populations, covering the entire distribution range of the species were studied over two years (2013–2014). The phenology and reproductive outputs were analysed considering ecological and climatic factors, and human trampling intensity by fitting Generalised Linear Mixed Models (GLMMs).

The results indicated that geomorphology, substrate, slope and human trampling intensity affected the reproductive traits of *H. caput-felis*. An ecological gradient, mainly linked by the interaction of temperature and precipitation regimes could explain this finding. Plants growing at the eastern edge of the distribution range (Sardinia; geographically marginal) produced more fruits than those growing in the other populations. Conversely, plants growing in arid substrate showed a negative correlation with fruit production and viable fruits. The reproductive outputs of the populations located in the core of the distribution range (Cabo Roig and Moraira; ecologically marginal) were lower than those of the other populations. On the other hand an ecological gradient dominated by the precipitation and temperature regimes was detected. In addition, a positive effect of the high and moderate level of human trampling on the reproductive output was found. Further studies, based in particular on the habitat fragmentation, are needed to understand the complex interactions that govern the reproductive output of *H. caput-felis* in the Mediterranean region.

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1. Introduction

A fundamental issue in ecology and conservation biology is how evolutionary processes shape variation across the whole geographical range of a plant's distribution (Gaston, 2009; Grant and Antonovics, 1978; Holt and Keitt, 2005; Sexton et al., 2009). Several plant species are characterised by a fragmented and/or disjunct distribution, in which peripheral populations are isolated from the main home range (e.g. Gargano et al., 2007; Pouget et al., 2013; Thompson, 2005). Plants that display a fragmented distribution are of interest to practitioners in the fields of ecology, evolution-

ary biology and genetics (Eckert et al., 2008; Pouget et al., 2013; Sexton et al., 2009) because they can provide insights into critical phenomena, such as speciation, adaptive radiation and natural selection (Fenu et al., 2015; Grant and Antonovics, 1978; Holt and Keitt, 2005).

Several plant species are characterised by this type of distribution in the Mediterranean Basin (e.g. Gargano et al., 2007; Thompson, 2005) as a consequence of evolutionary process related to the paleogeographical events such as the separation of land-masses caused by tectonic events and the consequent insularity condition of several areas (e.g. Mansion et al., 2008; Bobo-Pinilla et al., 2016). In addition, particularly in the recent decades and specifically along the coastal area, the human-related activities strongly modified the natural condition leading often a great fragmentation of natural plant population, so that the human activities

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are currently considered one of the most prevalent threats in the Mediterranean Basin (e.g. Rossi et al., 2016; Fenu et al., 2017). In particular human trampling was considered a severe threat for the persistence of the several coastal Mediterranean plants (e.g. Quilichini and Debussche, 2000; Fenu et al., 2013, 2015). In this context, several studies investigated how plant traits (e.g., morphology, breeding system, genetic settings, ecology and demography) vary across the distribution range of a species and, also, in relation with the effects of human disturbance.

Many studies analysed the Abundant Centre Model (ACM) that assumes that the most favourable conditions will be found at the core of a species' range and that the centre will support greater densities, fitness and genetic diversity than peripheral sites (e.g. Alexander et al., 2007; Grant and Antonovics, 1978; Jump and Woodward, 2003; Sagarin and Gaines, 2002; Vaupel and Matthies, 2012). However, the findings of several studies have diverged from these classical predictions, with the researchers highlighting the impact of specific local environmental conditions on populations (Doak and Morris, 2010; Sagarin and Gaines, 2002; Samis and Eckert, 2007; Vilellas et al., 2013a,b). Furthermore, recent literature reviews raised considerable doubts about the generality of the ACM model in nature (Castilla et al., 2011; Eckert et al., 2008; Gaston, 2009; Sagarin and Gaines, 2002; Sagarin et al., 2006; Sexton et al., 2009), suggesting that not all geographically marginal populations are ecologically marginal but these may be adapted to local conditions (e.g. Abeli et al., 2014; Barton, 2001).

The existence of ecological gradients that could affect the phenological and reproductive traits of plant populations has been widely studied; geographical gradients are important in plant population ecology, with several studies attributing variation in reproductive traits among populations to such gradients (e.g. Eckhart et al., 2011; Schemske et al., 2009; Vilellas et al., 2013a). Several authors have also investigated plants' phenological and reproductive traits along latitudinal and altitudinal gradients (e.g. Abbott and Brennan, 2014; Giménez-Benavides and Milla, 2013; Giménez-Benavides et al., 2007a, b; Schemske et al., 2009). However, to the best of our knowledge, the study of longitudinal gradients among plant populations, especially Mediterranean ones, has been less well documented.

Studies on the reproductive biology of endangered plants are crucial for predicting their survival capacity (Evans et al., 2003; Fenu et al., 2015; Morellato et al., 2016; Zhao et al., 2013). However, to date, few exhaustive studies have explored the phenological and reproductive patterns of Mediterranean coastal plants (Cogoni et al., 2015; Estiarte et al., 2011). In particular, such studies are lacking for plants that show a fragmented distribution, with marginal and disjunct populations, isolated by great distances. In this context, *Helianthemum caput-felis* Boiss. (Cistaceae) represents an interesting study case because of its fragmented distribution throughout the coasts of the western Mediterranean Basin (Fenu et al., 2015 and references therein). The actual fragmented distribution of this plant could be related both to the paleogeographic and to human factors; in fact *H. caput-felis* is considered the only extant plant of an ancient lineage (Arrigoni, 1971) which could suffer the same evolutionary processes of several palaeoendemic Mediterranean plants (e.g. Mansion et al., 2008; Bobo-Pinilla et al., 2016); in addition, this plant suffers at local level the direct pressure of urban expansion (Padilla et al., 2014) and also the impact of tourism and human trampling (Fenu et al., 2015).

This study explored the phenological and reproductive patterns of *H. caput-felis*. Two ecological gradients that could influence the reproductive performance of the species were considered: a geographical gradient based on the ACM model and an ecological (longitudinal) gradient, analysing differences in phenological and reproductive patterns of central and marginal populations, across its entire distribution range; in addition the effect of human distur-

bance intensity was considered in this study. Specifically, the main questions were: (1) are there differences in phenological periods and reproductive output among populations and in relation with the local ecological and climatic conditions? (2) could human trampling intensity affect reproductive outputs at population level? (4) are the assumptions of the ACM model confirmed? and (5) is there a longitudinal gradient in reproductive output for *H. caput-felis*?

2. Materials and methods

2.1. Study species

Helianthemum caput-felis Boiss. is a perennial half shrub, which ranges in height from 35 to 50 cm. Flowers are arranged in inflorescences at the tip of new branches and are generally yellow and hermaphroditic, although Agulló et al. (2015) detected a variability in flower morphology in some Spanish populations. They open at dawn and close at dusk and have a short lifespan (three or four days; Rodríguez-Pérez, 2005). Local phenological studies carried out in Majorca and Sardinia reported that the flowering period is from late February to late May, with a fruiting season from late April to July–August (Fenu et al., 2015; Rodríguez-Pérez, 2005). Rodríguez-Pérez (2005) reported the allogamous character of this species, being a generalist entomogamous plant; in particular, Agulló et al. (2015) demonstrated a partial self-compatibility of this species and a pollination system mainly mediated by Hymenoptera and Coleoptera. Fruits are capsules that detach at maturation, and seed germination takes place in autumn, at the onset of the rainy season (Rodríguez-Pérez, 2005).

From an ecological point of view, *H. caput-felis* is a thermophilous plant that preferably grows in coastal environments under the direct influence of the sea, mostly on calcareous rocky cliffs with garrigues or scrublands; peculiar populations also grow on sand dunes (Majorca), or rocky slopes bordering inland ravines (Fenu et al., 2015 and references therein).

Helianthemum caput-felis is distributed in several disjunct and fragmented populations throughout the coasts of the western Mediterranean Basin (SE Iberian Peninsula, Balearic Islands, Sardinia and NW Africa; Fenu et al., 2015 and references therein; Sulis, 2016; Fig. 1). In this study, the Alicante coast was considered the centre of the plant's distribution range due to the high number of localities where this plant grows and due to the total number of individuals recorded in this site, while Majorca and Sardinia were considered geographically marginal populations at the edge of the species distribution range (Sulis, 2016). A local genetic study, which considered only few Spanish and Moroccan populations, showed genetic similarities among Alicante and Balearic Islands populations, while the Moroccan one represented a genetically isolated group (Agulló et al., 2011).

2.2. Data collection

In this study, six populations, covering the entire geographical range of this plant species (Fig. 1) and corresponding to the eastern, central and western parts of the distribution range of *H. caput-felis* were analysed: Capo Mannu and Su Tingiosu (CM and ST, respectively) in Sardinia, Sa Ràpita and Colònia de Sant Jordi (SR and SJ, respectively) in Majorca's island and Cabo Roig and Moraira (CR and MO, respectively) in Alicante's coasts (see details in Table 1).

Over a two-year period (2013–2014), data sampling was carried out from March to August in 98 permanent plots of 2 × 1 m, which were randomly stratified and selected only in areas where the plant was found along the six selected populations. Within the plots, a total of 821 plants were monitored fortnightly (Table 1).

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