



Original Research Article

Evidence for age-structured depensation effect in fragmented plant populations: The case of the Mediterranean endemic *Anchusa sardoa* (Boraginaceae)[☆]



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ABSTRACT

Depensation in a population growth rate, well-known as *Allee effect*, has dramatic implications for the dynamics and conservation of small or sparse populations, as it can drive low-density populations to extinction when their demographic size is below a critical threshold. Although rarely detected, depensation effects are believed to be common in nature. Here we present experimental evidence for Allee effect in one Mediterranean endemic plant: *Anchusa sardoa*. Depensation in the population growth rate is demonstrated through a density-based approach by showing the fingerprinting relationship which ties the population density to its *per capita growth rate (pgr)* during specific stages of the plant life-cycle. The *pgr*-density plots derived from observational data qualitatively compare with a general 2nd order polynomial function which features one of the peculiar trends underlying an Allee mechanism. We found strong evidence for depensation in the seedling and sapling classes, whereas no-depensation effect could be clearly observed in the adult classes. We also point out a characteristic demographic structure of *A. sardoa* (i.e. number of juveniles > number of adults) which reflects a not common life strategy with respect to Mediterranean endemic plants. By combining dynamical and demographic information, the results of this study suggest a possible scenario by which *A. sardoa* population could go extinct, and are discussed in the context of the increasing mass tourism in Mediterranean coastal environments.

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1. Introduction

Historically biophysical variables have been shown to influence the spatial and temporal distribution of anthropic activities in human dominated ecosystems. Vice versa, Earth's ecosystems are increasingly and dramatically affected by human activities: in the Mediterranean, biomes threats to biodiversity increased from 1900 to 2000, and were always related to the augmentation of human population density (Underwood et al., 2009). This trend is even more critical in coastal areas which are the preferred by tourists

(Davenport and Davenport, 2006; Pulselli et al., 2007). As a consequence of mass tourism development, urban sprawl and invasive alien species propagation, in the last 65 years the dunes located on the Northern edge of the Mediterranean Basin experienced high levels of land consumption and degradation, that caused a loss of about 70% of dune systems during the last century (Feola et al., 2011).

The impact of anthropic activities can be responsible for the loss of biodiversity in particular at the regional scale, for instance by inducing a strong fragmentation on the surrounding habitat.

In this context mathematical approaches are playing an important role in the analysis of a population dynamics and to address conceptual and practical conservation issues. Multivariate statistics (Feinstein, 1996) allowed to isolate the fragmentation of territory as one of the principal human-related factor which mainly affects the population growth (Chen and Lin, 2008; Chen and Hui, 2009) and rises the risk of extinction for many species,

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among which those distributed in small and isolated populations appear as the most threatened (Cheptou and Avendano, 2006; Wagenius et al., 2007).

Several mathematical models (Edelstein-Keshet, 1987), often based on a statistical platform, describe through demographic projections the susceptibility of these small and fragmented populations to go extinct (Terry, 2011). For example many species (and probably most rare species) may be more influenced by environmental factors and interspecific competition than by their own densities. Typical demographic studies for these plants parametrize density-independent models at realized levels of interspecific and intraspecific competition and provide reliable indicators of the population dynamics (Crone et al., 2011). The projection matrix model (Bierzychudek, 1999) is a very popular method which allows one to build a transition matrix to describe the evolution between successive stages of age-structured populations. By using elementary linear algebra, one can predict asymptotic population growth rates and stable stage distributions from the spectral properties of the matrix. This approach gives a sensitive and flexible tool to determine how small changes in life history parameters can effect the asymptotic population growth rate. In their simplest form, the entries of a projection matrix are constant parameters accounting for the survivorship probabilities and fecundity. Generally speaking, this formalization implies a linear description of a population evolution and cannot catch the nature of the dynamics when their growth rate is nonlinearly sensitive to the actual population size, such as in the presence of an Allee effect. In this context a density-dependent description appears to be necessary for a correct modelling of the population dynamics.

Most of confined plant populations developed a life strategy based more on local persistence than colonization ability (Thompson, 2005), as a result of adaptation to severe habitat conditions (Kawecki and Ebert, 2004; García, 2008; García et al., 2010). The spatial distribution of individuals can affect some reproductive phases such as pollination efficiency, flower production, seed production and vitality, seedling establishment and survival, challenging the persistence of the population (Colas et al., 2001; Shaw et al., 2010; Quilichini and Debussche, 2000). These mechanisms are well-known to be at the basis of the so-called Allee effect (Allee et al., 1949) which describes a dramatic and nonlinear dependence of the demographic growth upon the actual size of a population. In practical terms, the Allee effect introduces an intrinsic multistability (including the null-density equilibrium) by which a population could go extinct whenever its demographic size is led below a critical threshold due to external agents (Lande, 1993, 1998; Ferdy and Molofsky, 2002; Liebhold and Bascompte, 2003; Clerc et al., 2010; Shi and Shivaji, 2006; Dennis, 1989; Amarasekare, 1988; Budroni et al., 2011; Saha et al., 2013). This effect is believed to be common to many low-density populations (Le Cadre et al., 2008; Forsyth, 2003; Arrigoni and Diana, 1999) but quite difficult to isolate, particularly in plant species.

Through coastal rocky and sandy habitats which characterize the Mediterranean areas, different potential study cases of Allee effect in small populations can be found. As a model species we chose *A. sardoa*, a narrow endemic plant that grows in a limited area where the touristic impact is very high both in habitat loss and in human trampling (Farris et al., 2013). Genetic data showed that this species has low levels of genetic variation due to bottleneck events caused by loss of habitat and natural stochastic factors (Bacchetta et al., 2008; Coppi et al., 2008). Morphological and biological features also make *A. sardoa* a potential vulnerable species (Farris and Filigheddu, 2008).

In this paper we use observational time series of *A. sardoa* population density to identify the characteristic relationship existing between the population size and its per capita growth

rate, *pgr* (Brauer and Castillo-Chavez, 2001; Sibly et al., 2005). This method allows us to extract the dynamical model underlying the temporal evolution of *A. sardoa* populations from descriptive trends in their *pgr*-plots. With respect to the pure time series analysis, a *pgr*-density study is able to distinguish between a population decrement due to accidental factors in density-independent models and the decline of a population size associated to the intrinsic nature of the population dynamics.

Beyond dynamical implications (i.e. a striking evidence for Allee affected population growth of *A. sardoa* populations), the study of the *pgr*-density relationship features a first step towards elucidating the nonlinear dependence of the growth rate of *A. sardoa* populations upon the population size to be implemented for a more quantitative description of the population dynamics.

This method paves the way for a deterministic evaluation of the extinction risk of rare and sparse populations, detecting demographic thresholds at which a population is endangered or threatened. Indeed, at an advanced level, our density-based approach structured on the different life stages of a population can be used to make predictions and optimize the management of critical areas where conservation has to be preserved (Sibly et al., 2005; Garrett and Bowden, 2002; Davis et al., 2004; McCormick et al., 2010; Beissinger and McCullough, 2002; Caughley and Sinclair, 1994; Pastorok et al., 2002).

2. Materials and methods

2.1. Biogeographical area and study species

Corsica and Sardinia are two of the major biodiversity hotspots of the Mediterranean basin (Lavergne et al., 2004; Suárez-Santiago et al., 2007) where plant populations have grown confined and scattered as a consequence of the past geological history of these lands (Gueguen et al., 1998; Hellwig, 2004; Oberprieler, 2005). The Corsican-Sardinian system is a main center of diversity for the *Anchusa* genus, with seven allopatric taxa occurring in either coastal or mountain habitats of the two islands (Bacchetta et al., 2008).

A. sardoa (Illario) (Selvi and Bigazzi, 1998) is a narrow endemic plant, exclusive of the Porto Conte Bay in north-western Sardinia (municipality of Alghero – province of Sassari at 40°37'2.59"N; 8°12'15.66"E): the site is included in the Natura 2000 site SIC ITB 010042 “Capo Caccia (con le isole Foradada e Piana) e Punta del Giglio” and in the Natural Regional Park of Porto Conte. *A. sardoa* is a perennial plant, with erect-ascending to reptant stems up to 30(40) cm that increase in number and length with age. (Selvi and Bigazzi, 1998; Bacchetta et al., 2008; Farris and Filigheddu, 2008). Flowering occurs during April–June, pollination is entomophilous, whereas fruiting (mericarps 2.5 mm × 1.5 mm) happens during June–July and seed dispersion is carried out by ants (authors' personal observation). *A. sardoa* grows preferably on the continental side of sea dunes, on stable and wet sands at the contact of retro-dunal wetlands, at an average distance of 22.6 m from the seashore (min 6.2–max 53.4 m). It takes part in herbaceous communities that can be referred to the European habitat 2220 – Dunes with *Euphorbia terracina* (European Commission, 1992, 2007). It can also survive under the canopy of *Pinus* plantations. The individuals of *A. sardoa* can be classified into four life stages: (1) seedlings (sdl), still with cotyledons (often with one or two pairs of leaves but without stalks); (2) saplings (sap), non-reproductive individuals; (3) 1st class adults (ad-1), reproductive individuals with only one erect flowering stem (probably at their first reproduction event); and (4) 2nd class adults (ad-2), with one erect and several reptant flowering stems. The juvenile individuals (seedlings and saplings), with no stems and with a very weak and no deep roots, are very vulnerable by human interventions on

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