

ORIGINAL PAPERS

Combined effects of deer, mice and insect seed predation on the reproductive success of a Mediterranean shrub



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Abstract

The sum of fruit and seed predation by multiple species may strongly affect plant reproduction and population dynamics. We evaluated the combined effects of ungulates, seed-eating rodents and insect pre-dispersal seed predators on the reproductive success of the Mediterranean gum cistus shrub (*Cistus ladanifer*), over two consecutive years within a long-term ungulate-exclusion experiment. We compared fruiting success in shrubs exposed and protected from ungulates by examining fruit abortion and fruit production. We also investigated the effect of insect predation on seed production (i.e. proportion of depredated fruit and seed loss) and measured fruit weight, seed number per fruit, and seed weight of unpredated fruits. Ungulate browsing directly removed 42.3% of the plant reproductive structures, early in the reproductive season and insect predation reduced mature seeds by over 40%. Results also emphasize the additive effects of ungulate browsing on pre-dispersal insect predation and fruit abortion which increased by 74.7% and 60.9%, respectively. Rodents, which only occurred in ungulate-excluded plots, had a limited and later effect on seed production with 6% of mature fruit loss. Fruit weight, seed weight and number were higher in shrubs protected from ungulates. Our study indicated that seed predation by mice was irrelevant, but ungulate and invertebrate seed predation interacted to strongly limit the reproductive success of *C. ladanifer*, potentially affecting plant population dynamics in the long-term.

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Introduction

Seed predation by vertebrates and invertebrates critically limits the recruitment and dynamics of many plant popula-

tions (Fedriani & Manzaneda, 2005; Mezquida & Benkman, 2010; van Klinken & White, 2014). Seed predation often occurs during the plant pre-dispersal phase, when seeds are removed from the mother plant, and is mostly reported in birds, rodents and invertebrates (Hulme & Benkman, 2002; Fedriani et al., 2004; Fedriani & Boulay, 2006). Browsing ungulates, however, often depredate plant seeds both

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before and after fruits and seeds have completed their development (Malo & Suárez, 1995; Gómez & Zamora, 2000; Gómez 2003a). In most systems, there are a diversity of fruit and seed consumers with potential to limit fruit and seed production and, ultimately, plant recruitment. This potential to impact plant population dynamics is particularly strong when multiple seed predators (e.g. vertebrates and invertebrates) act synergically over time (e.g. Louda, Potvin, & Collinge, 1990; Strauss, 1991; Palmisano & Fox, 1997).

Ungulates (e.g. red deer, wild boar), which have recently increased worldwide because of favorable habitat changes and under-harvesting (see Côté, Rooney, Tremblay, Dussault, & Waller, 2004), prey upon fruits and seeds of various flowering plant species (Gómez, 2005; Perea, Girardello, & San Miguel, 2014; Suárez-Esteban, Delibes, & Fedriani, 2014). Pre-dispersal seed predation by ungulates may strongly affect plant recruitment and growth, phenology, number and size of flowers and seeds and even plant size, although these effects remain temporally and spatially dependent (Kolb, Ehrlén, & Eriksson, 2007). In addition, pre-dispersal seed predation by invertebrates also affects plant recruitment negatively by reducing seed sets (von Zeipel, Eriksson, & Ehrlén, 2006; Dahlgren & Ehrlén, 2009; Ramírez & Traveset, 2010). Thus, reproductive success of most plant species results from multiple consumers feeding on the same plant host which can lead to intriguing direct and indirect cascading effects (*sensu* Terborgh & Estes, 2010). For instance, ungulates can affect the whole faunal assemblage, including insect populations, by reducing overall vegetation cover and altering plant community structure (Bugalho, Lecomte, Gonçalves, Caldeira, & Branco, 2011; Foster, Barton, Lindenmayer, & Du Toit, 2014; Van Klink, Van der Plas, Van Noordwijk, WallisDeVries, & Olf, 2015). Ungulates can directly ingest and kill significant fractions of insect seed predators (e.g. Or & Ward, 2003; Gómez & González-Megías 2007). Ungulates can also reduce fruit crops to such an extent that the resulting diminished crops are unlikely to satiate invertebrate seed predators (Mezquida & Olano, 2013; Peguero, Bonal, & Espelta, 2014) which often deplete remaining fruits and seeds. Additionally, ungulates can affect rodent populations, by altering vegetation cover (Parsons, Maron, Martin, & Pelletier, 2013) or by reducing food availability (Keesing 1998). However, few studies have documented the joint effect of different mammals and insect pre-dispersal seed predators on plant fitness (Strauss 1991; Sallabanks & Courtney 1992; Palmisano & Fox, 1997). For instance, additive effects of deer herbivory and insect pre-dispersal seed predation reduced the reproduction of *Ipomopsis aggregata*, a native flowering plant from Colorado, USA (Irwin & Brody, 2011). Yet, to fully understand plant reproduction and population dynamics it is essential to investigate combined effects of multispecies interactions.

We evaluated the combined effects of deer (*Cervus elaphus* and *Dama dama*), seed-eating rodents and insect pre-dispersal seed predators on the reproductive success of

the Mediterranean native shrub gum cistus (*Cistus ladanifer*). We experimentally compared, over two years, early fruiting success of shrubs exposed and protected from deer herbivory and the combined effect of insect predation on seed production, within a long-term experiment (see Lecomte et al., 2016). We posed two main questions: 1) Does deer browsing affect fruit production, fruit abortion and fruit traits and 2) does deer browsing affect pre-dispersal seed predation by mice and insects? We predicted that deer would be the major cause of seed loss (Lecomte et al., 2016) but also that the combined effect of deer browsing, mice, and insect predation would further reduce fruiting success and seed production of *C. ladanifer*.

Materials and methods

Study site

The experiment was conducted in Tapada Real de Vila Viçosa (“Tapada Grande”), a study site located in south-east Portugal (38°49’N, 07°24’W). The site is an enclosed estate, of approximately 900 ha, predominantly covered by evergreen oak woodlands. The climate is typically Mediterranean characterized by hot and dry summers and cool and wet winters. Mean annual precipitation is 585.3 mm mainly distributed between October and May. Mean annual temperature is 15.9 °C with a maximum of 31.1 °C (July) and a minimum of 5.8 °C (January).

The tree layer consists predominantly of holm (*Quercus ilex* ssp. *rotundifolia* Lam) and cork oak (*Quercus suber* L.) with a mostly monospecific understorey of gum cistus (*C. ladanifer* L.), interspersed with grasslands dominated by grasses (e.g. *Brisa maxima*, *Bromus madritensis*, *Gaudinia fragilis*), with forbs (e.g. *Andryala integrifolia*, *Leontodon taraxacoides*) and legumes (e.g. *Vicia disperma*, *Ornithopus compressus*) occurring in lower proportions. The site is mainly browsed by red deer (*C. elaphus* L.) and fallow deer (*D. dama* L.) with approximate population densities of 0.35 and 0.1 deer per ha, respectively (Bugalho et al., 2011). Small rodents, such as *Apodemus sylvaticus*, *Mus spretus* and *Rattus* spp. (Rosalino, Ferreira, Leitão, & Santos-Reis, 2011) are the likely local consumers of *C. ladanifer* fruits and seeds (personal observation) as they commonly occur in evergreen oak woodlands. Browsing marks left by deer (i.e. ragged edge on damaged stems) are easily distinguished from marks left by mice (i.e. sharp-angled, knife-like cut on ends of stems) (Hodge & Pepper 1998).

C. ladanifer, a Mediterranean perennial and fire-prone shrub, is an obligate seeder recruiting from hard seeds encapsulated in woody fruits and from the soil seed bank. In the last decades, *C. ladanifer* has expanded due to land use (Costa, Pereira, & Madeira, 2009) and climate changes (Acácio, Holmgren, Rego, Moreira, & Mohren, 2009), forming often dense and mono-specific layers. *C. ladanifer* reaches maturity at 2–4 years (Talavera, Gibbs, & Herrera, 1993). *C. ladanifer*

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