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Constraints to native plant species establishment in coastal dune communities invaded by *Carpobrotus edulis*: Implications for restoration

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ABSTRACT

Carpobrotus edulis, an alien chamaephyte species from South Africa, severely invades and represents one of the greatest threats to coastal plant biodiversity in regions with Mediterranean climate worldwide. Although actions have been promoted to eliminate it, these efforts have failed to restore dunes to the natural, preinvasion stage.

We tested, by means of field and laboratory experiments, how *C. edulis* alters soil chemistry by causing residual effects on soil, and examined whether these effects decrease germination, survival and growth of a common native chamaephyte dune species *Malcolmia littorea*. We also recorded species diversity to find out which species can establish after the removal of the invasive *C. edulis*. To link both measures, we monitored changes in soil characteristics over 1 year after the removal of the invader, by analyzing both soil chemical properties and extracellular enzymes.

C. edulis lowers soil pH, Ca and Na content and increases organic content, salinity and nitrogen and phosphorus concentration. The effects of the invader on the growth of *M. littorea* during the first growing season were very weak, despite strong negative effects in the early stages of this species' population development that decreased total germination and survival.

Overall, the soil characteristics and activity of the microbial community tend to recover back to preinvasion conditions in plots from which *C. edulis* is removed. In contrast, the establishment of native dune vegetation is constrained, as indicated by lower species diversity in restored compared to non-invaded areas. This is because regenerating dunes are occupied by opportunistic ruderal species that compete with native dune plants of conservation value and restrict their establishment.

1. Introduction

Invasive plant species are among the most serious environmental problems of today worldwide (Simberloff et al., 2005; Richardson and Pys, 2006; Hulme et al., 2012), including in the Mediterranean region (Hulme et al., 2012; Novoa et al., 2012; Gaertner et al., 2009). Invasive plants affect resident species and communities through a wide range of impacts, including marked reductions in native biodiversity (Pysek and Richardson, 2010; Watling et al., 2011; Gioria et al., 2012; Pyšek et al., 2012a; Pyšek et al., 2012b; Simberloff et al., 2012). This brings about not only ecological effects but also huge economic costs. Despite the assessment of economic consequences of biological invasions being still in its infancy, available estimates suggest that the costs are substantial, be it assessed at the global (Pimentel et al., 2005) or regional scale (McConnachie et al., 2012). In Europe, a conservative estimate of costs of biological invasions reaches at least 12.7 billion euro annually (Kettunen et al., 2009), and in Spain alone, 10.1 million euro (Andreu and Vilà, 2007). Therefore the study of invasive species' removal and subsequent restoration of invaded areas has become an important and promising line of research in invasion ecology in the last decade (D'Antonio and Meyerson, 2002; Bakker and Wilson, 2004; Vosse et al., 2008; Selge et al., 2011; Daehler, 2012).

Mediterranean coastal primary dunes are rather homogeneous ecosystems with very little variation in local ecological conditions (Maun, 2009), since they are influenced by the same extreme environmental factors such us salt spray, high winds or high insolation. They are of a high cultural and ecological value, and support many threatened and endemic species ("Council Directive 92/43/EEC, 1992). One of the major invaders of Mediterranean ecosystems is

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a South African succulent species, *Carpobrotus edulis*, considered by the GEIB (2006) as one of the 20 most aggressive invasive species of coastal dunes. Invasion by *C. edulis* in coastal habitats (Carranza et al., 2011) has a great impact on community composition, diversity and succession (Donath and Eckstein, 2009) via its modification of soil properties (Novoa et al. 2012; Conser and Connor, 2008). In many parts of the world where *C. edulis* invades natural dune ecosystems (e.g. Southern Europe, California, Australia) removal projects have been carried out in order to restore invaded dunes, but these efforts have failed to restore dunes to the natural, pre-invasion stage (A. Novoa, personal observation). Due to the changes in the soil, ruderal nitrophilous species typically replace the native dune species (Maurel et al., 2009)

Andreu and Vilà (2007) evaluated the ecological success of the manual removal of *Carpobrotus* species by comparing treated, non-invaded, and invaded plots in southern Spain. Treated plots from which *C. edulis* was removed harbored a higher number of species than invaded plots, especially of annual plants, but both types of plots had the same native plant cover and species diversity. Conser and Connor (2008) examined the residual effects of *C. edulis* on soil and found strong negative effects on the germination, survival and growth of *Gilia millefoliata*, an annual plant native to the northern coastal region of California. Moreover, it has been shown that the effects of *C. edulis* on pH and nitrogen compounds persist over time. After *Carpobrotus* removal, opportunistic ruderal species can have an advantage over native dune species because of the effect of modified soil characteristics, presence of litter, and their ability to compete. Increasing evidence for the residual effects of *C. edulis* invasion, including possible allelopathic effects of its litter (Novoa et al., 2012), suggests that to improve restoration success, it is necessary to understand how this invasive plant affects co-occurring plant species by inducing changes in soil and what the duration of this impact on the invaded ecosystem is. Understanding these effects will help land managers, restoration practitioners, and scientists to more effectively manage and restore dune plant communities and create suitable conditions for native plant species (Cox and Allen, 2008).

In the present paper, we used a combination of: (i and ii below) soil and enzymatic activities analysis, (iii) seed and seedling addition field experiments, (iv, v) biodiversity analysis and (vi) laboratory germination experiments to test the following hypothesis: (a) *C. edulis* has strong effects on chemical properties and microbial activity of soils. (b) These effects persist after the removal of *C. edulis* from invaded plots, creating residual effects of the invasion. (c) Residual effects on soil inhibit re-establishment of native dune plant species after *C. edulis* has been removed. (d) Species composition of communities that establish after the removal of the invader is different from that of natural communities in non-invaded sites that harbour typical native dune species. (e) Changes in soil properties resulting from *C. edulis* invasion promote the emergence of seedlings of ruderal nitrophilous species that establish in removal sites, and by competing with typical native dune species, prevent their establishment.

2. Materials and methods

2.1. Study species

C. edulis (L.) N. E. Br. (Aizoaceae), native to South Africa, has become one of the most invasive plants of rocky shorelines and dunes. It is one of the most thoroughly studied invasive species (Pysek et al., 2008) and the mechanisms of its invasion and impact have been addressed in a number of studies (Gallagher et al., 1997; Vilà and D'Antonio, 1998; Weber and D'Antonio, 2000; Bartomeus et al., 2008; Novoa et al., 2012). It was originally introduced to Europe, California and Australia to stabilize coastal sand dunes in the early 20th century (Albert, 1995). *C. edulis* invades large areas, changing the dynamics of dunes and displacing the local flora. Its growth pattern results in the building of a thick mat of living and dead plant material of up to 40 cm in depth (D'Antonio and Mahall, 1991).

As a model species to test the effects of *C. edulis* invasion on native dune plants (hypothesis c), we chose *Malcolmia littorea* (L.) R. Br. (Cruciferae), a perennial plant native to the Atlantic and Mediterranean coasts of Italy and Spain. We chose *M. littorea* as a native dune target species because of its occurrence in coastal habitats (thus in habitats commonly invaded by *C. edulis*), and because natural populations of *M. littorea* have declined to the point of becoming an endangered species in some areas of north-western Spain as a result of habitat loss due to human activities and biological invasions (Gobierno del principado de Asturias, 1995).

The target native species used to test the competitive effects of opportunistic colonizers (hypothesis (e) above) are the chamaephyte *M. littorea* and the therophyte *Cakile maritima* Scop. (Brassicaceae), two species common to coastal dunes, typically thriving in non-invaded vegetation (we refer to these hereafter as 'dune species'), and the hemicryptophytes *Scolymus hispanicus* L. (Asteraceae) and *Dactylis glomerata* L. (Poaceae), two species with ruderal life strategies (Grime, 1997) that commonly appear in coastal dunes after the removal of *C. edulis* (referred to as 'ruderal species').

2.2. Study site

The experiment was conducted at the coastal dune ecosystem of Punta Ron in O Grove, Pontevedra (42°29′52.91″N8°52′59.77″W), an area with coastal oceanic climate from which *C. edulis* was first reported to occur in Spain in 1900 (GEIB 2006). The annual average temperature is 14.8 °C; it reaches 24.6 °C in warmer months (June–September), and 6.4 °C in colder months (December–March). The average annual rainfall 1263 mm (O Grove meteorological station, 50-yrs average).

2.3. Plant material

Seeds of *M. littorea* and *C. edulis* were collected between 10th September and 10th October 2010 from at least 15 plants from each of 20 different populations of each species, located along 20 km in Pontevedra Coast, Spain The seeds were stored in the dark at 4 °C until assay. Seeds were surface-sterilized for 5 min in 0.1% sodium hypochlorite, rinsed 3 times in distilled water and dried at room temperature prior to the experiment to avoid fungal attack.

The target seeds for testing the role of ruderal (opportunistic) species (hypothesis e) were provided by Semillas Silvestres S. A. (*M. littorea*, *C. maritima* and *S. hispanicus*) and Semillas Cantueso (*D. glomerata*).

2.4. Soil and litter collection

Soil samples were collected from the above coastal dune location in O Grove, Pontevedra and located from invaded and non-invaded areas. We randomly established three plots of 0.5 m × 0.5 m and 10 m apart in each area (invaded and non-invaded). In each plot, five soil samples were collected from the top 10 cm. In the invaded area, *Carpobrotus* plants and litter were removed prior to soil collection. In the non-invaded area (practically devoid of litter), soil was collected following the same process. Samples from both sites were sieved (2.0 mm mesh size), homogenized and pooled within samples from invaded and noninvaded plots.