

Soil-dependent growth strategy of invasive plants: empirical evidence and model predictions using *Carpobrotus edulis* as target species

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Introduction

Plants experience different soil conditions that may influence several aspects of their biology such as nutrient uptake, root competition, growth and even floral display (Mal & Lovett-Doust 2005). For clonal plants, the relative investment in sexual reproduction or vegetative growth can vary according to the context in which they grow (e.g. invaded soil vs. non-invaded) since environmental constraints may result in contrasting dispersal strategies due to differential cost-benefit balances (Kot et al., 1996). *Carpobrotus edulis* (L.) N. E. Br., is considered a highly invasive species in coastal areas of Southern Europe because it forms dense fast-growing mats that displace the native dune vegetation (Vila et al., 2006). *Carpobrotus edulis* can change drastically the characteristics of the invaded soil and the long-term occurrence of the species has been associated with a decrease in pH and increase in organic content (Conser in press; D'Antonio & Mahall, 1991). Nevertheless, and in spite of the large dense patches of *C. edulis* formed in invaded areas, there is no information available about how these changes in soil may affect the posterior growth and colonization rate of the species. The objective of the present study was to evaluate whether the residual effects on soil after *C. edulis* invasion affect the growth plasticity of the species and to model the long-term consequences of such growth responses. Our working hypothesis was that soil modification introduced by *C. edulis* leads to plant growth responses oriented to maximize the colonization rate of invaded areas.

Material and Methods

Using a lab experiment we assessed whether the residual effects on soil caused by the invasion of *Carpobrotus edulis* would affect the vegetative and reproductive traits of the species and ultimately the dynamics of establishment. We compared *C. edulis* performance on rhizosphere soil collected under native vegetation in the Quiaios dunes (Portugal) that has never been occupied by *C. edulis* (virgin soil, VS), which was used as a reference situation, with the performance of plants on soil collected under monospecific patches in the same locality where the species grew vigorously (*Carpobrotus* rhizosphere soil, CRS) or was dying-back after a long period of establishment (CDS). After four months growing *C. edulis* in controlled conditions plants were harvested and different plant-growth related features were assessed (e.g. biomass, root length, production of flowers). To understand the long term consequences of the observed plant responses, we built up a Monte-Carlo simulation model in which we integrated clonal growth and seed dispersal under different soil scenarios (absence or presence of residual effects). We modeled the spreading of the plant in a grid of 300*300

grid cells, with one grid equaling $0.3 \times 0.3 \text{ m}^2$, being the species annual growth rate as assessed by Sintès et al. (2007). Each grid cell was characterized by soil type: either virgin (VS), occupied (CRS) or previously occupied soil (CDS). We consequently analyzed the rate of colonization (or coverage) in a hectare. The rate of colonization is followed for one seed entering the center of the landscape for three scenarios: colonization of virgin soil without residual effects, colonization of soil where the species is present and colonization of soil where *C. edulis* has been removed as a restoration measure (hence leaving behind formerly occupied soil). For each scenario we ran 100 replications and calculated average occupancy rates as the number of occupied grid cells/total number of grid cells. Soil status changes according to the emerging plant dynamics. Local plant spreading occurs by clonal growth and by seed dispersal (D'Antonio 1990). With exception of the initial seedling, we introduced a grid cell-extinction rate ε of 0.1 in all situations. Seed dispersal is modeled as a stochastic process where seeds are distributed according to a Gaussian distribution $N(0, \sigma^2)$ from the mother plant in all directions. We chose $\sigma^2=10$ (i.e. variance of the dispersal function approximates 3 meter in a thin-tailed dispersal kernel) in the simulation program because this accords with dispersal distances in similarly dispersed plant species (Cain et al. 1998). We did not model data on the effective number of produced seeds because earlier studies already indicated mass seed production per flower (>1000), with only moderate variance according to different environmental parameters (Suehs et al. 2004) and extremely low survival and germination rates (D'Antonio et al. 1993). Instead, we decided to emphasize on relative differences according to the differences in flower production (number of flowers per grid \sim number of flowers per plant in the experiment), which consequently would determine the number of seeds. Annual clonal growth in *C. edulis* follows fractal rules concentrically from a central branching node and is strongly related to biomass (Sintès et al. 2007). Because annual growth rates are estimated ~ 0.3 meter/year (Sintès et al. 2007) we allowed *C. edulis* to spread clonally one grid cell a year in the four direct neighboring grid cells. This corresponds with the star-shaped growth at maturity (Wisura 1993). Clonal growth was modeled as a decreased probability of 0.2 to colonize each of the adjacent cells based on the results of biomass obtained in the lab experiment with different rhizosphere soils (data not shown).

Results

Experiment

The type of soil in which plants were grown affected the production of flowers (Figure 1A). In that sense, *C. edulis* plants growing on soil collected from the native plant community (VS) produced a greater number of flowers ($P=0.001$, $F_{2,35}=4.026$ Figure 1A) than plants growing on soil collected from the two *C. edulis* patches (i.e. CRS, CDS). The average number of flowers produced in plants growing on virgin soil was 1.8 whereas for the other two types of soil, CRS and CDS, plants presented only 0.4 and 0.6 flowers respectively.

Model

The outcome of our simulations indicated that the local spreading of *C. edulis* is faster in the scenarios where there are no residual effects on soil (Figure 1B). Therefore, the fastest covering rate was observed in the model compatible with the responses observed experimentally in which the production of flowers resulted in a higher number of seeds in virgin soils. This is also reflected by the higher slopes of the fitted logistic function

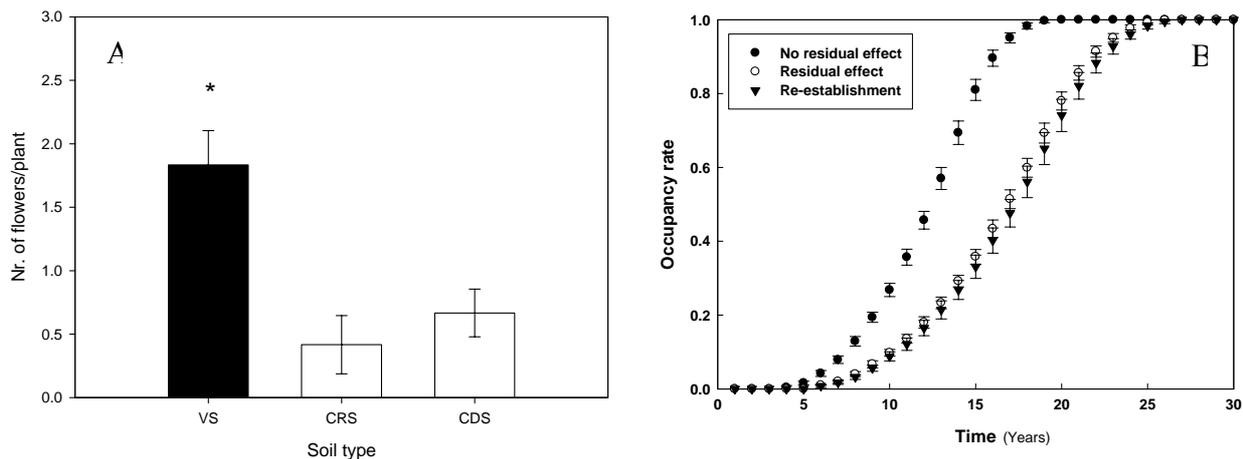


Figure 1. Mean number of flowers (A) for *Carpobrotus edulis* plants growing on Virgin soil (VS); *C. edulis* rhizosphere soil (CRS); *C. edulis* rhizosphere soil from dying mats (CDS). Error bars indicate $\pm SE$. * indicate significant difference after One-Way ANOVA. (B) Occupancy rates of *C. edulis* in a virtual landscape of 1ha under three different soil scenarios: no residual effect on flower production and growth rates, residual effect and residual effect after *C. edulis* removal (re-establishment).

(respectively $r=5.85\pm 0.29SE$). By contrast, on already occupied sites (with residual effects) or after *C. edulis* removal the covering rate decreased ($r=5.19\pm 0.23SE$ and $r=5.23\pm 0.25SE$).

Discussion

The phenotypic plasticity of the plant (individual plant responses in function of soil characteristics) in combination with the resulting contrasting soil environments has interesting consequences in *C. edulis* invasion. In native areas where the plant is not present, investing in the production of flowers is the fastest strategy to occupy a given area. Increasing the number of flowers allows for the formation of a seed-bank after one growing season. A percentage of those seeds would manage to establish (even assuming particularly low germination rates) (D'Antonio, 1990; Vila & D'Antonio, 1998), which would result in a fast short-term spread. On the other hand, in patches where *C. edulis* is already present, investment in vegetative growth would increase the competitive potential against the native plant community (Oftinowski & Kenkel, 2008). If in those already occupied areas the production of seeds were increased, this would result in high kin competition or, alternatively, in less chances of seed germination due to the dense mat formed by the mother plant. As our model supports, in such situations, it is more advantageous to rely on clonal growth as the main means of dispersal. Previous studies have modeled the growth pattern of *C. edulis* in invaded areas however; in those cases the combination of clonal vs. sexual reproduction was not integrated. Interestingly, based on field observations and also model predictions those authors could see that the growth decreased after approximate twenty years (Sintes et al., 2007). This type of pattern is perfectly compatible with the residual effects on formerly occupied soil presented in our model, and therefore, rather than dispute it completes previous observations. The key result of our paper is that the residual effect on soil produced by the species *Carpobrotus edulis* leads to changes in individual plant responses that are oriented to maximize the colonization of invaded areas. In this sense, soil context (invaded vs. virgin) is the factor determining the shift from an enhanced flower production in virgin soils, never exposed to the exotic species, towards the induction of vegetative growth in previously occupied soils. The

changes observed at individual level as a function of soil-context have a dramatic effect on the rates of colonization of invaded landscapes. Our findings reveal a key mechanism to understand the invasion dynamics of *C. edulis*, a species that is a serious threat in the Mediterranean region, and, more importantly, illustrate how some invasive species can quickly respond to soil heterogeneity to maximize the probability of establishing long-term plant populations.

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