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

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**Introduction**

Several invasive species modify the abiotic composition of the soil, which results in a contrasting mosaic of soil environments within the invaded landscape. However, up to date, it has not been addressed how the mosaic created by the residual effects of these species on soil influence their own establishment. This is particularly important for invasive species that are able to disperse by means of seeds or vegetative growth. *Carpobrotus edulis* is a highly invasive species native to South Africa and introduced in different areas of the Mediterranean for gardening and soil stabilization purposes. It can reproduce very rapidly either clonally or by means of seeds. *Carpobrotus edulis* forms dense fast-growing mats that displace the native dune vegetation. The presence *Carpobrotus edulis* can change drastically the characteristics of the invaded soil and the long-term occurrence of the species is associated with a decrease in pH and an increased soil organic content. Nevertheless, and in spite of the large dense patches of *C. edulis* formed in invaded areas, there is no information available about the putative effects of *Carpobrotus* residual effects on the posterior growth and consequences on the colonization rate of the species.

**Objectives**

To evaluate whether the residual effects on soil after *C. edulis* invasion affect the growth plasticity of the species. Our hypothesis was that soil modification introduced by *C. edulis* leads to plant growth strategies oriented to maximize the colonization rate of invaded areas. Secondly, and in order to understand the long-term consequences of individual plant responses to the different soil environments, we built a model in which the rate of growth and the invasion of a landscape was compared under different scenarios (i.e., presence or absence of soil residual effects) and in function of different dispersal strategies (clonal and/or seed dispersal).

**Results**

<table>
<thead>
<tr>
<th>Soil Characteristics</th>
<th>% Org. Mat</th>
<th>pH</th>
<th>% N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Virgin soil (VS)</td>
<td>0.03</td>
<td>7.5</td>
<td>0.01</td>
</tr>
<tr>
<td>Active growth (CRS)</td>
<td>0.18</td>
<td>5.3</td>
<td>0.02</td>
</tr>
<tr>
<td>Dead patch (CDS)</td>
<td>0.23</td>
<td>5.3</td>
<td>0.02</td>
</tr>
</tbody>
</table>

**Conclusions**

Our results demonstrate that differences in soil attributes resulting from the invasion by *C. edulis* can trigger different responses of this exotic plant. *Carpobrotus edulis* shifted from an enhanced flower production in soils that had not been previously exposed to the invasive species, to vegetative growth on soils previously occupied. Soil-contest is therefore, a fundamental factor to understand not only the responses of *C. edulis* at individual level but also the dynamics of colonization at a landscape level.

**Methodology**

The experiment: We compared plant performance on rhizosphere soils collected under native dune vegetation in Quiaios Portugal (a heavily invaded area) that has never been occupied by *C. edulis* (VS), soil collected under monospecific patches where the species grew vigorously (CRS) or soil where *C. edulis* was dying-back after a long period of establishment (CDS).

The model: We developed a grid-based Monte-Carlo simulation model (in Delphi environment) to infer the importance of residual soil effects on local colonization dynamics. We modeled the spreading of the plant in a grid of 300*300 grid cells, with one grid equaling 0.3*0.3 m². 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. Each grid cell was characterized by its soil type: either virgin (VS), occupied (CRS) or previously occupied soil (CDS). Soils status changes according to the emerging plant dynamics. Local plant spreading occurs by clonal growth and by seed dispersal.