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Assessing the effects of *Carpobrotus* invasion on coastal dune soils. Does the nature of the invaded habitat matter?

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Abstract: We investigate the modifications of soil factors in *Carpobrotus* invaded sites by evaluating differences between non-invaded and highly invaded plots in three habitats of coastal dune ecosystems in Central Italy. Nitrogen content, organic matter content, pH and salinity were measured in three coastal habitats: shifting dunes along the shoreline with *Ammophila arenaria*, *Crucianellion maritimae* fixed beach dunes and fixed coastal dunes with *Juniperus* spp. Soil variables of the invaded plots were compared to non-invaded ones using two-way factorial ANOVAs and post-hoc Tukey HSD tests. We found significant differences between invaded and non-invaded plots for nitrogen content, organic matter content and pH in both foredune habitats. On the other hand, no differences were revealed on fixed dunes. Thus, we found distinct responses of soil factors to *Carpobrotus* invasion depending on the habitat. Pioneer habitats with very poor soils are more sensitive to invasion probably because the production of litter by *Carpobrotus* is considerably higher than for native species. Therefore, for the establishment of efficient alien control programs of those habitats of conservation interest, it is imperative to take into account the relationship between invasive species presence and the top soil characteristics. For instance, particular attention is required in the foredune zone (pioneer habitats), where *Carpobrotus* invasion is more likely to affect the parameters of the soil.

Introduction

Alien species (*sensu* Pyšek et al. 2004) have caused consistent environmental changes throughout the world, and represent an important threat to biodiversity conservation (Sala et al. 2000, IUCN-CMP 2006). In particular, the spread of alien plants has been claimed to produce a wide range of impacts, including changes in community diversity and alterations of ecosystem processes (Vitousek et al. 1997, Ehrenfeld 2003). For example, alien plants can influence the plant-soil relationship in the invaded habitats (Levine et al. 2003, Kulmatiski et al. 2008) modifying the soil biota diversity and composition (Wolkovich et al. 2009).

Two succulent species of the genus *Carpobrotus* (*C. acinaciformis* and *C. edulis*), both of which originate from South Africa (Wisura and Glen 1993), are among the most widespread alien plants in the Mediterranean coastal ecosystems around the world and are currently considered a severe threat to native plant communities in these habitats (Campos et al. 2004, Weber 2005, Traveset et al. 2008). These alien plants are known to negatively influence the diversity of native species (Vilà et al. 2006, Carboni et al. 2010), the fitness of native neighbors (D'Antonio and Mahall 1991) and the pollination network in the invaded communities (Bartomeus et al. 2008). In addition, it has been shown that in some cases *Carpobrotus* is capable of altering the characteristics of the invaded soils. Conser and Connor (2009) found that *Carpobrotus edulis* can significantly affect some soil parameters in a coastal habitat in California: invaded soils had higher organic matter content and lower pH values. Vilà et al. (2006), using a paired plot design in different islands across the Mediterranean Basin, found that in certain sites *Carpobrotus* invasion was associated with changes in soil parameters. The authors hypothesized that these results were due to local characteristics of the study sites, including the invaded habitat in question, the age of the mat and the taxonomic identity of the invader.

In this study, we aim to increase understanding the invasion process by investigating soil characteristics of the invaded communities. This provides crucial information for defining effective conservation actions to address invaded communities. We investigate the modifications on top soil parameters in *Carpobrotus* invaded sites across different types of coastal dune habitats. In particular, we analyze soil differences between non-invaded and *Carpobrotus* highly invaded plots in three habitats of coastal dune ecosystems in the Circeo National Park (Central Italy). We hypothesize a non uniform modification of soil parameters and thus that the presence of significant differences between invaded and non-invaded soil parameters varies with the type of invaded habitat.

Materials and methods

Study area and nomenclature

In the present study, the nomenclature of Habitat types conforms with the "Habitats" Directive (EC 1992). The Habitats Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora), adopted in 1992 as a response to the Berne Convention, is one of the more effective conservation instruments in Europe. The Directive specifies a list of habitats and species of conservation interest in Europe to help implement the necessary local conservation policies. The Directive also provides a key for the identification of habitats on the basis of typical and diagnostic plant species (Council Directive 92/43/EEC Annexes I and II, EC 2007).

The study was carried out on the Tyrrhenian coast of Central Italy (Latium region) where the latest vascular flora survey (Izzi et al. 2007) revealed the widespread presence of *Carpobrotus* aff. *acinaciformis* and where a selective distribution of this alien species on the different coastal dune habitats of European interest (*sensu* Habitats Directive - EC 1992, 2007) has been demonstrated (Carranza et al 2008). In fact Carboni et al. (2010) and Carranza et al. (2010) have recently observed that *Carpobrotus* aff. *acinaciformis* tends to be mainly associated with the shifting dunes along the shoreline with *Ammophila arenaria* (EC Habitat 2120) and with the Crucianellion maritimae fixed beach dunes (EC Habitat 2210), and secondarily with the fixed coastal dunes with *Juniperus* spp. (EC Habitat 2250).

A test area including about 22 kilometers of Tyrrhenian sandy shores in the Circeo National Park (Central Italy) was selected for the analyses (Figure 1). In the Circeo National Park, *Carpobrotus* invasion is a relatively recent phenomenon (around the late 70's according to observations by the park staff and local knowledge). In fact, it was initially introduced for dune stabilization by the park managers when the issues related to biological invasions where not yet fully understood.

The taxonomy of *Carpobrotus* on the Mediterranean coasts is problematic and partially unresolved (Suehs et al. 2004), but in this area only magenta flowered *Carpobrotus* (generally considered *C.* aff. *acinaciformis*, see Traveset et al. 2008) were introduced and consequently are now present and widespread. Therefore in the present study the issue of taxonomic identity raised by Vilà et al. (2006) is negligible.

In accordance with a previous study (Carranza et al. 2008), the Circeo coastal dune system belongs to a single environmental unit called "Recent coastal dunes under thermo-Mediterranean subhumid climate" with a characteristic edaphic coastal dune zonation. The dunes of the study area have an average width of 250 m and an average altitude of ca. 15 m (Acosta et al. 2000) and are made by sandy regosols, which are very porous and dry. These soils have a poorly differentiated profile in which we can recognize a thin horizon above the sandy sediment with variable humus content, depending on the density of vegetation cover. The physical and chemical composition is rather uniform, being always rich in bioclastic calcium carbonate, with an alkaline reaction, and low nutrient content (Dowgiallo and Bottini 1998). The mentioned sea-inland soil zonation is matched by a vegetation gradient that goes from annual communities on the upper beach (EC Habitat 1210), through the perennial geophytic communities of the embryo (EC Habitat 2110) and mobile dune (EC Habitat 2120) and the chamephytic communities of the transition dune (EC Habitat 2210), to shrubby communities on the inland back dunes (EC Habitat 2250) (Stanisci et al. 2004, Carranza et al. 2008) (Figure 1).

Nomenclature of native species conforms to the checklist of the Italian vascular flora (Conti et al. 2005). Nomenclature of alien plants follows the work of Celesti-Grapow et al. (2009).

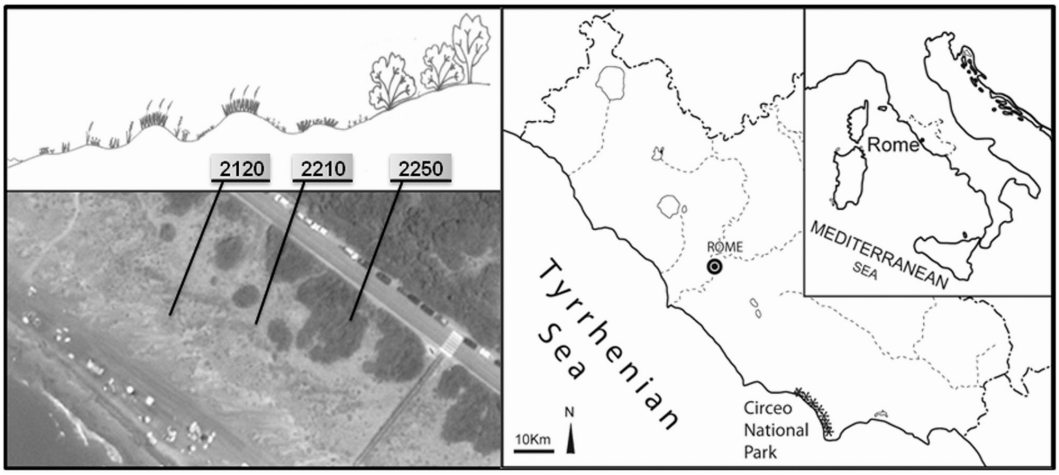

Figure 1. Study area. The cross-sectional diagram indicates the location of the three habitat types: EC Habitat 2120 - Shifting dunes along the shoreline with *Ammophila arenaria*; EC Habitat 2210 - Crucianellion maritimae fixed beach dunes; EC Habitat 2250 - Fixed coastal dunes with *Juniperus* spp. The sea shore is located on the left side of the orthophoto. The mean dune widthin the study area, from the sea shore to the road that runs on the top of the dune, is 80 meters. All our plots were located between the sea shore and the road. The mean dune height at the top is about 15 meters (Acosta et al. 2000).

Soil sampling

First, we selected a set of *Carpobrotus* invaded vegetation plots (4 m^2) taken in the Circeo National Park in 2009 from a larger existing vegetation database (more than 700 random vegetation plots collected along the entire Latium coast by the Plant Ecology Laboratory of "Roma Tre" University). In order to avoid the influence of the age of the mat (Vilà et al. 2006), we only considered plots which had high percent cover and abundant litter stratification of *Carpobrotus* aff. *acinaciformis*. This allowed us to identify 25 plots performed in the coastal dunes of the Park where invasion was not recent. Then, for each of the invaded plots, we measured the topsoil parameters according to a paired sample design: we collected data inside each *Carpobrotus* invaded plot and in an adjacent non-invaded native habitat placed in the same topographic position. Soil samples were collected in the center of each plot (invaded and non-invaded) drawing about 1000 g of soil (after removing litter) from the profile between 5 and 15 cm depth. We determined the dune habitat type (*sensu* Habitats Directive - EC 1992, 2007) of each paired sample in the field following the most abundant diagnostic native species according to the Italian Habitats Directive Interpretation Manual (Biondi et al. 2009). The 25 paired samples of soils were distributed as follows: 11 in the shifting dunes with *Ammophila arenaria* (EC Habitat 2120), 8 in the *Crucianellion maritimae* fixed beach dunes (EC Habitat 2210) and 6 in the fixed coastal dunes with *Juniperus* spp. (EC Habitat 2250).

Soil analyses

The samples were air-dried and passed through a 2 mm sieve before laboratory analyses. Then, a set of parameters commonly used to analyze the effects of plant invasion on soil processes (Ehrenfeld 2003) were measured: content in total nitrogen, content in organic matter, pH and salinity. Total nitrogen content (N) was determined using the Kjeldahl method, which includes three main steps: digestion, distillation, and titration. The organic forms of N in the soil sample are all converted to ammonium by digestion with H_2SO_4 (in presence of a catalyst), the ammonium is then liberated by distillation of the digest with NaOH. Finally, the amount of ammonium in the distilled liquid is determined by titration. To estimate the organic matter content, the Walkley-Black method was used, based on the principle of oxidation of the organic substance by 10 ml of $K_2Cr_2O_7$ in 20 ml of H_2SO_4 at 96%, at the temperature reached due to the effect of the sudden dilution of the sulfuric acid. Salinity and pH were instrumentally measured after dilution of the samples in distilled water. All the soil analyses were performed in a Laboratory of Pedology ("La Sapienza" University, Rome).

Data analyses

In order to determine whether *Carpobrotus* invasion affected the soil parameters of interest and how this effect varied according to the habitat subject to invasion, statistical models were fit using the software R (R-Development-Core-Team 2009). Firstly, to account for non-normality each response variable was appropriately transformed (square root transformation for nitrogen content; log transformation for organic matter content and salinity; pH did not require transformation) and subsequently model residuals were checked to confirm constancy of variance and normality of errors. Pearson's correlations (r) between each response variable were also tested.

We then proceeded to fit mixed-effects models for each response variable with "invasion status" and "habitat" as fixed factors and "paired plot" as a random factor (models fit with REML - Restricted Maximum Likelihood; R package "nlme", Pinheiro et al. 2009). The AIC value (Akaike 1974) of these models was then compared to that of Generalized Least Squares (GLS) models. This allowed us to determine whether the response to invasion was influenced by the paired plot being examined. Since the AIC values of GLS models were always lower than those of the mixed models, the simpler models (GLS) were chosen.

Therefore, a two-way factorial analysis of variance (ANOVA) was fit for each response variable with "invasion status" and "habitat" as explanatory variables. To shed light on the interaction terms of interest and to avoid the inflation of type I statistical errors due to multiple comparisons, a post hoc Tukey HSD test (α=0.05) was then applied to each model. By doing so we were able to investigate how the effect of invasion varied among the different habitats.

Results

The analyses highlighted a significant difference in soil variables between invaded and non-invaded plots. Specifically, both nitrogen content (ANOVA F=13.95; P<0.001; partial χ^2=0.24) and organic matter content (ANOVA F=28.47; P<0.001; χ^2= 0.41) were significantly higher where *Carpobrotus* had invaded, whereas pH was noticeably lower (ANOVA F=5.69; P=0.019; χ^2=0.12).

Moreover, results indicate that the effects of invasion vary according to the habitat. Specifically, the results of Tukey HSD test at α=0.05 show that in the shifting dunes with *Ammophila arenaria* (EC Habitat 2120), invaded plots were characterized by a significantly higher organic matter content (P<0.001; Figure 2B) and lower soil pH (P=0.041; Figure 2C) than non-invaded plots. On the *Crucianellion maritimae* fixed beach dunes (EC Habitat 2210) both organic matter content (P=0.002; Figure 2B) and nitrogen content (P=0.005; Figure 2A) were significantly higher in invaded plots. Conversely, in the coastal fixed dunes with *Juniperus* spp. (EC Habitat 2250) no significant differences in nitrogen content, organic matter content or pH values between invaded and non-invaded soils were found (Figure 2).

Comparison of soil characteristics among habitats for both invaded and non-invaded plots instead reveals how invasion alters the normal spatial patterns of organic matter content and pH along the sea-inland gradient (Figure 3).

Mean values of organic matter content and pH in invaded plots are not significantly different among habitat, whereas where *Carpobrotus* is absent organic matter and pH increases and decreases, respectively, along the zonation. This suggests that invasion has lead to a homogenization of both organic matter content and pH among habitats. On the other hand, we do not observe the same pattern for nitrogen content, suggesting a more complex control of this soil variable.

Note that no significant differences in salinity content between invaded and non-invaded plots were found in any of the three habitats (Figure 2D). Of the four soil parameters of interest, salinity was also the least correlated to the others (r=-0.106 pH; r=0.476 organic matter; r=0.528 nitrogen). In contrast, nitrogen and organic matter were strongly correlated (r=0.793) and both were inversely correlated with pH (r=-0.536 nitrogen; r=-0.49 organic matter).

Discussion

The comparisons (*Carpobrotus* invaded *versus* non-invaded) of soil parameters for distinct habitats in coastal dunes gave heterogeneous results. For two of the analyzed habitats we found significant differences in nitrogen content, organic matter content and pH values. We should observe that, due to the strong correlation between organic matter content, nitrogen content and pH, probably only organic matter content is directly influenced by invasion, and the others are indirect effects. Instead, no difference between invaded and non-invaded samples was found for soil salinity (Fig. 2).

In contrast with results obtained for other invasive species of the same family (Aizoaceae) for which salt accumulation has been documented (Vivrette and Muller 1977), salinity did not differ between *Carpobrotus*-invaded and non-invaded habitats. In our case *Carpobrotus* aff. *acinaciformis* did not cause a significant difference in the soil salt accumulation, unlike the very similar and related species *Mesembryanthemum crystallinum* (Vivrette and Muller 1977, Adams et al. 1998). On the other hand, we found significant differences in organic matter content and pH between invaded and non-invaded plots for the shifting dunes (EC Habitat 2120), and we found significant differences in nitrogen content and organic matter content for the *Crucianellion maritimae* fixed beach dunes (EC Habitat 2210). On the whole, our results highlight that the changes in soil factors in *Carpobrotus* invaded plots are detectable only in the two pioneer habitats (EC Habitat 2120 and EC Habitat 2210).

These results are in agreement with previous studies (Vilà et al. 2006, Conser and Connor 2009) performed in the Mediterranean region on rocky and sandy substrates. Finding a distinct behavior of soil factors in the different habitat types, we show support for the hypothesis that soil modifications caused by *Carpobrotus* can vary depending on the habitat type. The differences in soil response to *Carpobrotus* invasion could vary with the strong environmental gradient which characterizes the coastal dune zonation. Only the pioneer habitats of the foredune zone, with poor soils (Forey et al. 2008), seem to be affected by *Carpobrotus* invasion. In fact, the well-known abundant production of litter by *Carpo-*

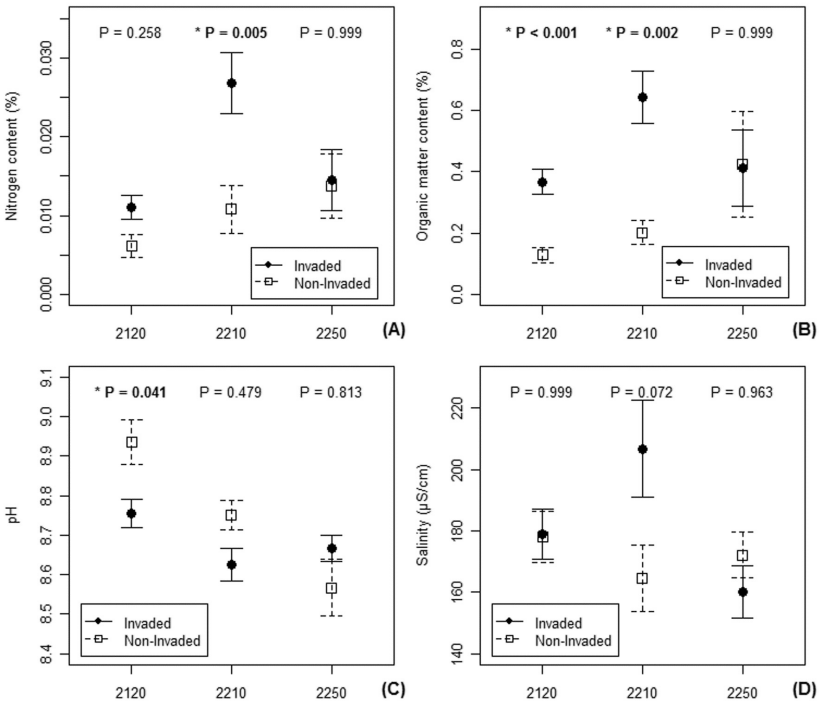

Figure 2. (A) Nitrogen content (mean ± SE) of invaded (full circles) and non-invaded (open squares) plots in each EC habitat (2120, 2210, 2250). (B) Organic matter content (mean ± SE) of invaded and non-invaded plots in each habitat. (C) pH (mean ± SE) of invaded and non-invaded plots in each habitat. (D) Salinity (mean ± SE) of invaded and non-invaded plots in each habitat. P-values refer to within habitat comparison between invaded and non-invaded plots from two-way ANOVA after correction with Tukey HSD test at α=0.05 for multiple comparisons. Significant comparisons are reported in bold and preceded by asterisk.

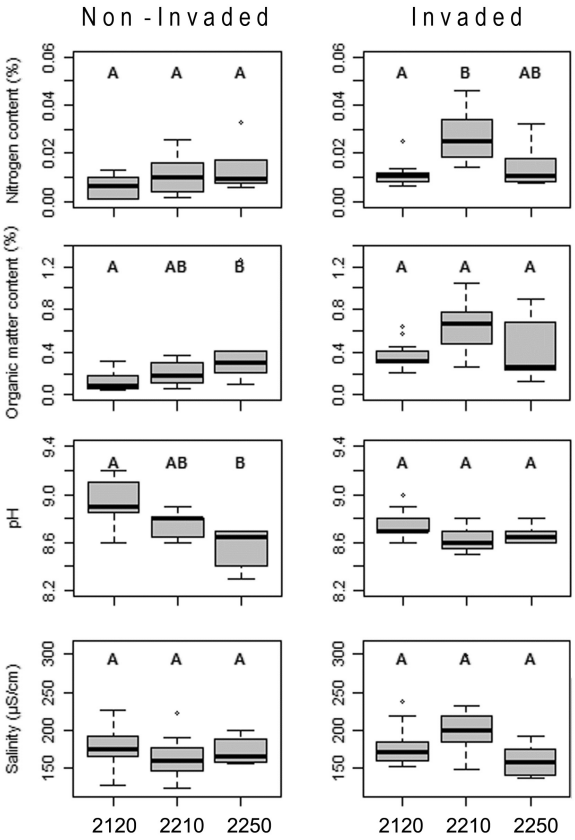

Figure 3. Box and whisker plots of each soil variable (nitrogen content, organic matter content, pH, salinity in order) according to the EC Habitat (2120, 2210, 2250) in both non-invaded and invaded plots. Letters represent homogenous subsets according to Tukey HSD test at α=0.05.

brotus (Wisura and Glen 1993) is very different from that of the dominant native species in the same habitats (e.g. *Ammophila arenaria, Anthemis maritima, Crucianella maritima* or *Pycnocomon rutifolium* practically have no litter deposition). *Carpobrotus* litter may therefore be responsible for the enrichment in organic matter and nitrogen content (and in turn for the acidification) in the soil of these herbaceous plant communities.

It has been previously demonstrated that soil modifications in invaded areas can potentially threaten native plant diversity. In particular, herbaceous communities of coastal dunes are highly susceptible to soil modifications caused by invasive plants with abundant litter production (Isermann et al. 2007). The enrichment in organic matter and nitrogen content could inhibit germination and eventually affect the survival of the specialized native dune species, which spread only in these particularly poor soils (van den Berg et al. 2005, van der Heijden et al. 2008). These soil modifications could alter the turnover of species. For example, ruderal nitrophilous species could substitute the typical native dune species, as recently highlighted in other ecosystems under alien plant invasion (Maurel et al. 2010).

On the contrary, in the fixed coastal dunes with *Juniperus* spp. (EC Habitat 2250), characterized by relatively high plant cover and abundant litter, no significant soil differences between invaded and non-invaded plots were detected. In this habitat, the high levels of litter production by native species, such as the needle-like leaves of *Juniperus*, leaves of *Pistacia lentiscus* and *Phillyrea angustifolia* (McKinley and Blair 2008, Brantley and Young 2010) probably influence the contents of nitrogen and organic matter and the pH of the soil in a similar way as the alien *Carpobrotus* litter.

The effects of the replacement of native habitats by mats of alien species have recently been investigated. Dassonville et al. (2008) in NW Europe showed that, depending on the initial conditions of the invaded site, the same alien plant species may cause different modifications in the soil, leading to a "soil homogenization" in the whole study area. Our results suggest that something similar happens on *Carpobrotus* invaded soils, at least for pH and organic matter content (Fig. 3).

Our results have interesting conservation implications. At present, no management efforts regarding *Carpobrotus* removal are being carried out in the study area. However, if similar actions to those performed in California (Conser and Connor 2009) were to be undertaken in the future, we suggest that particular attention be paid to the foredune zone (Habitat 2120 and Habitat 2210) as the soils of these habitats seem to be more strongly affected by the invasion. In the case of removal of *Carpobrotus* from the foredune zone and subsequent restoration with native plant species, the highlighted modification of soil parameters should be taken into consideration and could require a litter removal associated with the plant removal.

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