

# Understanding the influence of urbanization on invasibility: *Carpobrotus edulis* as an exemplar

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**Abstract** Coastal dune areas are valuable ecosystems, generally impacted by habitat destruction and invasive alien species. In this study, we assessed how human disturbance and invasion by *Carpobrotus edulis* impact the soils and the establishment of native flora in the north-western coastal regions of Spain. We compared soil characteristics (pH, conductivity, water content, nutrients and enzymatic activities) and native plant as well as *C. edulis* fitness correlates (germination and early growth) between uninvaded and invaded soils from urban and natural coastal dune areas. We found that human disturbance impacts coastal soils by increasing organic matter and water content, modifying soil nutrients and cycles, and reducing the pH in urban soils. The presence of invasive *C. edulis* further increases these impacts.

These changes in soil characteristics allow for the establishment of the native, but ruderal, *Scolymus hispanicus* and non-native *C. edulis*, both of which are not adapted to the typically limiting conditions of coastal dunes. In some instances, the coastal dune endemic, *Malcolmia littorea*, showed no fitness effects in response to urbanization or the presence of *C. edulis*. These results suggest that human disturbed coastal areas might be more easily invaded than natural areas. More broadly, our findings of differential responses of different native species to disturbance and invasion, illustrate the need for multi-taxon approaches when assessing the impacts of invasive species.

**Keywords** Enzymatic activities · Ecological impacts · Germination · Invasive species · Nutrients · Urban areas

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## Introduction

Coastal dune ecosystems provide a broad range of socio-economic services such as erosion control, water purification, aesthetic value, etc. (Everard et al. 2010), as well as critical habitats for a highly diverse fauna and flora (Maun 1994). As for all ecosystems, coastal dunes and their associated biodiversity are threatened by human-mediated habitat destruction and the impacts of invasive alien species (Carboni et al. 2009). These two threats are not mutually exclusive, with invasive species often benefiting from disturbance, to the detriment of native species. Another synergy between disturbance and invasions is that densely human populated areas may act as sources for the introduction and dissemination of non-native species to surrounding areas (Dehnen-Schmutz et al. 2007; Gaertner et al. 2016). For example, coastal urban areas are often important sources of non-native species propagules to neighbouring semi-natural habitats, especially through gardens (Sullivan et al. 2005; Foxcroft et al. 2008; Akasaka et al. 2015) and urbanized beaches. Soil, habitat and climate disturbances associated with anthropogenic habitats, e.g. heat islands in urban areas, may further enhance the establishment of non-native species (Nobis et al. 2009; Kowarik 2011) as these species are often well-adapted to survive under these conditions (Klotz and Kühn 2010).

It is well documented that invasive species may have a large variety of environmental and socio-economic impacts in coastal dunes systems, such as changes in the physical–chemical properties of soils, biodiversity losses, or soil erosion (Richardson and Rejmánek 2011; Staudhammer et al. 2015). Nevertheless, studies on the effects of urbanization and disturbances created through recreational activities on non-native plant recruitment and performance are scarce. Coastal dune systems generally represent hostile (windy, salty and sandy) and nutrient-poor environments (Cao et al. 2011). It is therefore conceivable that, when dominated by dense stands of invasive plants or modified by humans for recreational purposes, soil characteristics will be heavily impacted in these systems through e.g. leaf litter feedbacks, changes in soil moisture content, pH, erosion, loss of sediment, compaction, etc. (D'Antonio and Vitousek 1992; Ariza et al. 2010). These impacts can have multiple knock-on effects such as altered soil

microbial community structure, and thus nutrient cycling. This in turn may positively impact on non-native plant performance, while negatively impacting on the performance of native plants. For example, weedy species (native or alien), not typically found in coastal dune ecosystems, may benefit by invader-induced changes to these systems (Rousset and Lepart 2000). On the other hand, native dune plants, while adapted to the hostile and nutrient-poor conditions of coastal dunes, especially to reoccurring sand burial or high tolerances to salinity and drought (Maun 1994), might not be strong competitors against such weedy species (Novoa et al. 2013b).

The impacts of invasive species on coastal dunes systems have been well-demonstrated for various plants (Millenium Ecosystem Assessment 2005). A poster child for dune invasions is *Carpobrotus edulis*, a succulent plant native to South Africa (Albert 1995), that has been intentionally introduced globally as an ornamental and/or to prevent soil erosion in coastal areas (Gallagher et al. 1997; GEIB 2006; Pyšek et al. 2008). As a result, *C. edulis* is a major invader of many natural and urban coastal ecosystems globally, especially in Mediterranean-type climate regions (Albert 1995; D'Antonio 2006; Novoa et al. 2012). *Carpobrotus edulis* can reproduce both sexually and vegetatively, which allows it to invade areas at a fast rate, and to successfully compete with native dune flora (de la Peña et al. 2010; Lechuga-Lago et al. 2016). *Carpobrotus edulis* has a wide variety of negative impacts on the ecosystems it invades, often to the detriment of native species, many of which are endangered or of special concern. *Carpobrotus edulis* reduces soil pH, modifies nutrient dynamics, prevents sand movement, and competes with native species for space and water, reducing their growth, survival and reproduction rates (D'Antonio and Mahall 1991; D'Antonio and Haubensak 1998; D'Antonio 2006; Conser and Connor 2009; Novoa et al. 2012).

While human-mediated disturbance often facilitates invasions in urban ecosystems (e.g. beaches with high human traffic, urban furniture, and utilities with recreational function), it is, to our knowledge, unknown whether impacts on the performance (positive or negative) of native species are greater in these areas (hereafter referred to as urban areas) compared to non-urban areas (hereafter referred to as natural areas).

Here we studied the impacts of *C. edulis* invasions on soil conditions in urban and natural coastal areas in the north-west coast of Spain, and how these may impact two native species; *Malcolmia littorea* (L.) R.Br., a coastal dune endemic, and *Scolymus hispanicus* L., a widespread ruderal/weedy but native species, not typically found in coastal dune systems. Specifically, by comparing soil characteristics (pH, conductivity, water content, nutrients and enzymatic activities) and native plant fitness correlates (germination and early growth kinetics) between uninvaded and invaded soils from urban and natural coastal dune areas we (1) aimed to assess whether the impact of *C. edulis* on the soil characteristics and the performance of the two native species is different in these two areas. Then, by comparing the performance of *C. edulis* in response to these different soil conditions we aimed to determine whether (2) urban coastal areas leads to higher performance of *C. edulis* than natural areas and (3) whether *C. edulis* invasions lead to positive invader feedbacks, i.e. higher performance in previously invaded areas. Overall, our aim is to test if human disturbance (urban/natural areas) and invasion status (*C. edulis* uninvaded/invaded areas) play a role in the performance and impacts of *C. edulis* invasions in coastal dune systems. We predict that urban areas, irrespective of invasion status, will lead to soil nutrient enrichment, in turn leading to enhanced performance of invasive *C. edulis* and the adventive and weedy, but native, *S. hispanicus*.

## Materials and methods

### Study sites

This study was conducted in Galicia, Spain. The coastline in Galicia is 1720 km in length and it is penetrated by a series of flooded tectonic valleys that allowed the formation of beaches and coastal dunes. The climate is classified as Oceanic and is temperate and rainy, with markedly drier summers.

We selected a total of six dune areas that presented zones invaded by *C. edulis* in close proximity to uninvaded zones (Fig. 1, Table 1): three in urban (sensu Jiménez et al. 2011) and three in natural dune areas. The three selected urban areas presented a high level of urban infrastructure (housing, parking spaces, streets, and boardwalks) characterised by habitat

fragmentation, high human traffic during the summer season, and high disturbance (personal observation). The length of these three urban beaches varied from 20 to 140 km. The three selected natural areas were semi-pristine beaches representing well-preserved dune systems belonging to the Red Natura 2000 Network. In these beaches, habitats are not fragmented and have no manmade infrastructure. These sites typically have soils that are highly restrictive to the establishment and performance on non-dune species. Uninvaded zones in both urban and natural areas were dominated by native species, including *Pancreatium maritimum*, *Eryngium maritimum*, *Malcolmia littorea*, *Euphorbia paralias* and *Ammophila arenaria*. Invasive *C. edulis* completely dominated the invaded zones (Fig. 1).

### Soil collection

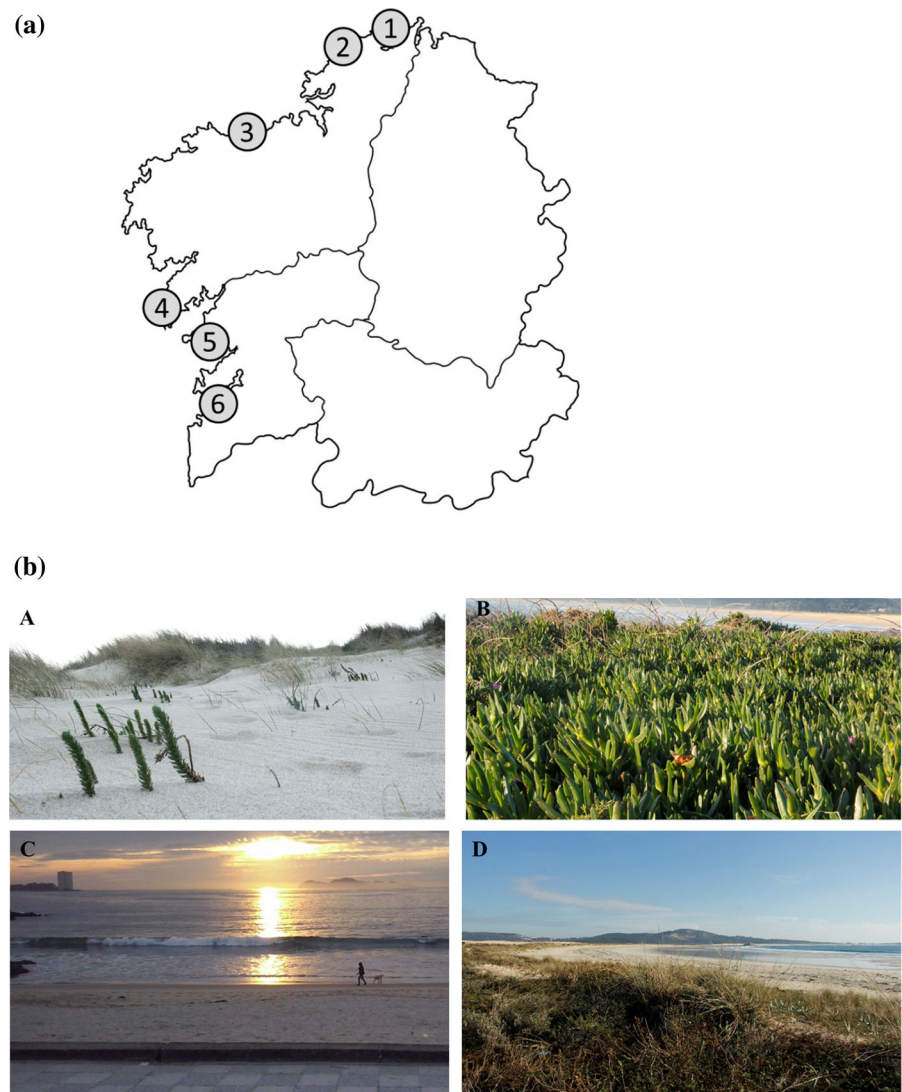
Soil samples were collected at the six selected areas in invaded and uninvaded zones (Table 1). In each zone, we randomly established five plots of 0.5 × 0.5 m, 10 m apart from each other between the 29th of March 2016 and the 4th of April 2016. In each plot, plants and litter were carefully removed and five soil sub-samples taken from the top 10 cm using a shovel. These samples were air-dried and sieved through a 2.0 mm mesh.

Each soil sample was used in subsequent measures of (1) pH, conductivity, water content, and nutrients (2) soil enzymatic activities and (3) germination performances of *C. edulis* and two selected native species (see below). Soils used for pH, conductivity, water content, and elemental soil and germination analyses were kept at room temperature until needed, and soils used for enzymatic activity analysis were refrigerated at 4 °C and analysed within 3 days from collection.

### Soil pH, conductivity, water content, and nutrients

Soil pH was determined by dilution with water (1:2.5; soil: distilled water) (Gutián and Carballas 1976; Allen 1989; Maun 2009), using a Crison Basic 20 pH meter (Crison, Spain). Conductivity was measured using a Crison CDTM-523 instrument (Crison, Spain). Following drying of three replicates of each soil sample at 70 °C for 48 h, percentage (%) water content was calculated as: (Fresh soil weight-Dry soil weight)/(Fresh soil weight) \* 100. Available soil

**Fig. 1** **a** Distribution of sampling points along the coast in Galicia, Spain. 1: Cariño. 2: Cedeira. 3: Baldaio. 4: Corrubedo. 5: Ardía. 6: Samil. **b** An example of uninhabited (A) invaded by *Carpobrotus edulis* (B) Urban (C) Natural (D) in Galicia, Spain



nutrients ( $\text{Ca}^{2+}$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$ ,  $\text{P}$ ,  $\text{NO}_2^-$ ,  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ ) and total organic carbon (TOC) were extracted using the rhizo method, also known as the low molecular weight organic acid (LMWOA) method (Wang et al. 2003; Feng et al. 2005). For this, we made an aqueous solution consisting of organic acids (acetic acid + lactic acid + citric acid + malic acid + formic acid) in a ratio of 4:2:1:1:1 to 10 mM, followed by shaking for 16 h to simulate rhizosphere conditions (Feng et al. 2005). Inductively coupled plasma optical emission spectroscopy (ICP-OES) was used to quantify  $\text{Ca}^{2+}$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$  and  $\text{P}$ , an Autoanalyzer AA3 instrument (Bran and Luebbe, Elmsford, New York) for nitrogen compounds ( $\text{NO}_2^-$ ,  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ),

and a Multi N/C 2100 instrument (Analytik Jena, Germany) for TOC.

#### Soil enzymatic activities

We analysed the activities of  $\beta$ -1,4-glucosidase (Carbon, EC 3.2.1.21), urease (Nitrogen, EC 3.5.1.5) and alkaline phosphatase (Phosphate, EC 3.1.3.1). The substrates for the  $\beta$ -glucosidase, urease and alkaline phosphatase assays were 4-nitrophenyl (pNP)  $\beta$ -D-glucopyranoside, urea and pNP-phosphate, respectively. For  $\beta$ -1,4-glucosidase, urease, and alkaline phosphatase analyses we followed the methods described by Tabatabai and Bremner (1969), Kandeler

**Table 1** Description and characteristics of the sampling sites along the coast in Galicia, Spain, included in this study

Site name	GMS	Köppen climate classification	AAT (°C)	AAP (mm)	Beach type	Distance to the nearest human settlement (m)	Presence or absence of infrastructure (Promenade, walkway, benches, beach bar, good access to the beach)
Cariño (1)	43°44'20.874"N 7°52'11.464"W	Csb	14.2	969	Urban	81	Yes
Cedeira (2)	43°39'5.316"N 8°3'2.812"W	Csb	14.2	985	Urban	49	Yes
Baldaio (3)	43°18'5.603"N 8°39'26.632"W	Csb	11.5	1318	Natural	115	Non
Corrubedo (4)	42°34'36.056"N 9°4'1.972"W	Csb	14.8	1146	Natural	250	Non
Ardia (5)	42°28'14.304"N 8°51'22.758"W	Csb	14.8	1211	Natural	472	Non
Samil (6)	42°12'27.5"N 8°46'36.5"W	Csb	14.9	1303	Urban	92	Yes

GMS degrees, minutes and seconds, Csb mild temperate with dry and warm summer, AAT average annual temperature, AAP average annual precipitation

and Gerber (1988) and Allison and Vitousek (2004), respectively. Following the recommendation of German et al. (2011), the enzyme assays were run at environmental pH conditions and within less than 48 h of collection of soils.

#### Selected species and seed collection

*Malcolmia littorea* (L.) R.Br. and *Scolymus hispanicus* L. were selected as native target species because they represent two distinct functional groups and have different physiological responses to the presence of *C. edulis* (Novoa and González 2014). *Malcolmia littorea* is native to Southern Europe (Tutin et al. 1993) and, as a dune-endemic, is commonly found in coastal dune systems and in the same habitats typically invaded by *C. edulis* (Thuiller et al. 2005). On the other hand, *S. hispanicus* is a native but ruderal/weedy species (Grime 1997) and commonly establishes in coastal dunes following the removal of *C. edulis*. Seeds from *M. littorea* and *S. hispanicus* were supplied by Semillas Silvestres S.L. (<http://www.semillasilvestres.com>).

*Carpobrotus edulis* fruits were collected in the invaded area of Cabo Estai (Vigo, Pontevedra) between August and September 2014. The seeds were

separated from the rest of the fruit and stored in the dark at 4 °C until needed.

#### Germination and early growth experiments

Seeds were surface-sterilized for 5 min in 1% sodium hypochlorite, rinsed 3 times in distilled water and dried at room temperature prior to the experiment to avoid fungal contamination. Fifteen randomly selected seeds of *M. littorea*, *S. hispanicus* and *C. edulis* were sowed in Petri dishes filled with equal volumes of soil from natural dunes (invaded and uninvaded zones) and soils from urban beaches (invaded and uninvaded zones). Each treatment was replicated seven times. Petri dishes were moistened with 2 mL of distilled water every 2 days and incubated in a germination chamber with periods of 12/12 h of light/dark and 25/15 °C day/night temperatures. Seeds were considered germinated when the seed coat was broken and a radicle was visible (Posmyk et al. 2009). The number of germinated seeds was recorded every 2 days for 21 days. At the end of the experiment, the shoot and root length (mm) of ten randomly selected seedlings/per replicate were measured on graph paper. Total and speed of accumulated germination indices (Gt and AS, respectively) were calculated following the equations of Chiapusio



et al. 1997). These indices are representative of the germination pattern followed in each treatment and are two of the most widely cited and used in the literature (Chiapusio et al. 1997). Total accumulated germination was calculated as  $G_t = [N_T \times 100]/N$ , where  $N_T$  is the proportion of total germinated seeds in each treatment and  $N$  is the number of seeds used in the treatment. Speed of accumulated germinations was calculated as  $AS = [N_1/1 + N_2/2 + N_3/3 \dots + N_n/n]$ , where  $N_1, N_2, N_3, N_n$  is the cumulative number of seeds which germinated at 2-day interval 1, 2, 3, ...  $N$ .

### Statistical analyses

Data were analysed with a two-way ANOVA using the base package of the R statistical environment (R Development Core Team 2016), with area (urban vs. natural) and status (invaded vs. uninvaded) as fixed effects. Kruskal–Wallis non-parametric analyses of variance were performed for data that were not normally distributed.

## Results

### Soil pH, conductivity, water content, nutrients and enzymatic activities analysis

We found significant differences between status (invaded vs. uninvaded) for water content, conductivity, alkaline phosphatase activity,  $\beta$ -glucosidase activity, urease activity,  $K^+$ ,  $Mg^{2+}$ ,  $Na^+$ ,  $P$ ,  $NO_3^-$  and  $NH_4^+$  ( $p < 0.05$ ;  $n = 15$  for all parameters). We also found significant differences between area type (urban vs. natural) for pH, water content, conductivity, alkaline phosphatase activity,  $\beta$ -glucosidase activity, urease activity,  $Ca^{2+}$ ,  $K^+$ ,  $Mg^{2+}$ ,  $Na^+$ ,  $P$ ,  $NO_2^-$ ,  $NO_3^-$ ,  $NH_4^+$  and TOC ( $p < 0.05$ ;  $n = 15$  for all parameters). We found lower levels of pH in urban compared to natural areas. Moreover, we found higher water content, conductivity, nutrients and soil enzymatic activities in urban and invaded areas compared to natural and uninvaded areas (Table 2).

### Germination and early growth

The percentage and speed of germination of *C. edulis* were higher in soils from uninvaded compared to soils from invaded zones. We found the opposite pattern for

both native species, that is, percentage and speed of germination were higher in soils from invaded than uninvaded zones (Fig. 2). In general, we found no differences in the percentage and speed of germination of *C. edulis* between urban and natural areas. However, the speed of germination of both native species was higher in urban compared to natural areas. The shoot length of *C. edulis* was higher in urban areas. However, the root length of both *C. edulis* and *S. hispanicus* was higher in natural or uninvaded areas than in urban or invaded areas (Fig. 2). We found no differences in the early growth kinetics of *M. littorea* between areas (urban vs. natural) or status (invaded vs. uninvaded).

## Discussion

Coastal dune ecosystems are particularly vulnerable to disturbance both by urban development and the effects of invasive species. It is important to understand the interplay between these factors in order to stimulate or restrict the establishment of native plant species in support of in situ conservation or restoration of dune ecosystems (Schemske et al. 1994) or to control biological invasions (Novoa et al. 2012, 2013b). Nutrient deficiency, lack of moisture, and salt spray are among the most important limiting factors for the survival and establishment of plant species in coastal dune areas (Maun 2009). Here, soil physicochemical factors, soil enzymatic activity, germination, and early growth of native plants were used as impact correlates of urbanization and *C. edulis* invasion on native biodiversity.

In agreement with previous findings under greenhouse conditions, our results suggest that human disturbance reduce the limiting factors typical of coastal dune systems (Novoa and González 2014). That is, we found urban areas, irrespective of the presence of invasive *C. edulis*, have higher levels of nutrients, conductivity, enzymatic activities and water content and lower pH (reduced alkalinity) (Novoa et al. 2013b). Moreover, *C. edulis* invasions often lead to a thick leaf litter layer in invaded areas (Badalamenti et al. 2016). This litter layer shields the underlying soil from rainfall, wind and sun, simultaneously increasing the water content (Novoa et al. 2013b), soil aggregation, aeration, water infiltration, resistance to erosion, and dune stability (Bot and

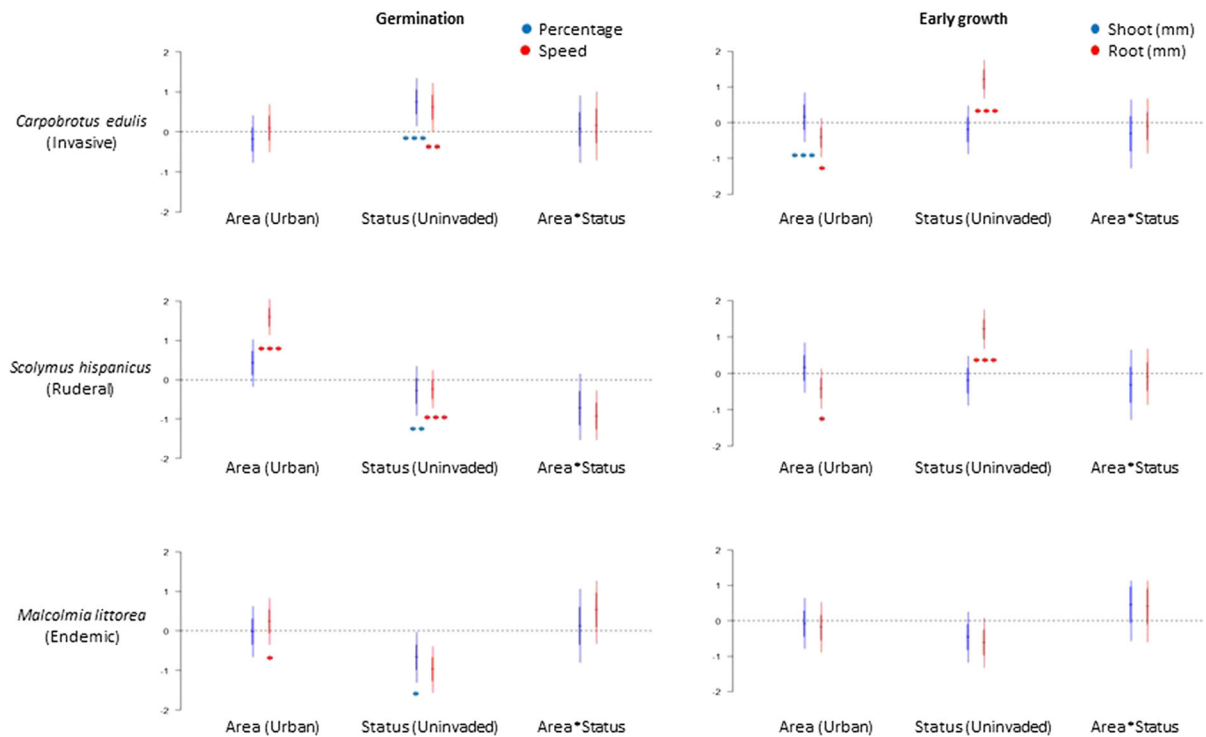
**Table 2** Mean ( $\pm$  SE) of pH, water content (%), conductivity ( $\text{mS cm}^{-2}$ ), alkaline phosphatase ( $\mu\text{mol/g h}$ ),  $\beta$ -glucosidase ( $\mu\text{mol/g h}$ ), urease ( $\mu\text{mol de N-NH}_4^+/\text{g h}$ ),  $\text{Ca}^{2+}$  (mg/g),  $\text{K}^+$  (mg/g),  $\text{Mg}^{2+}$  (mg/g),  $\text{Na}^+$  (mg/g), P (mg/g), TOC (mg/g),  $\text{NO}_2^-$  (mg/g),  $\text{NO}_3^-$  (mg/g),  $\text{NH}_4^+$  (mg/g) in uninverted and inverted urban and natural areas

Area Zone	Urban		Natural		Status	Area	Test
	Uninverted	Inverted	Uninverted	Inverted			
pH in $\text{H}_2\text{O}$	9.21 ( $\pm$ 0.09)	8.69 ( $\pm$ 0.41)	8.53 ( $\pm$ 1.43)	7.97 ( $\pm$ 1.50)	*	*	KW
Water content (%)	7.12 ( $\pm$ 1.91)	12.84 ( $\pm$ 4.56)	4.10 (2.12)	7.80 ( $\pm$ 2.76)	*	*	KW
Conductivity ( $\text{mS cm}^{-2}$ )	0.05 ( $\pm$ 0.02)	0.17 ( $\pm$ 0.08)	0.09 ( $\pm$ 0.07)	0.17 ( $\pm$ 0.10)	*	*	KW
Alkaline phosphatase ( $\mu\text{mol/g h}$ )	0.64 ( $\pm$ 0.26)	5.28 ( $\pm$ 2.18)	0.72 ( $\pm$ 0.51)	2.35 ( $\pm$ 2.25)	*	*	KW
$\beta$ -glucosidase ( $\mu\text{mol/g h}$ )	0.15 ( $\pm$ 0.00)	0.16 ( $\pm$ 0.02)	0.15 ( $\pm$ 0.01)	0.12 ( $\pm$ 0.05)	*	*	KW
Urease ( $\mu\text{mol de N-NH}_4^+/\text{g h}$ )	0.00 ( $\pm$ 0.00)	0.12 ( $\pm$ 0.14)	0.06 ( $\pm$ 0.08)	0.06 ( $\pm$ 0.05)	*	*	KW
$\text{Ca}^{2+}$ (mg/g)	832.09 ( $\pm$ 51.04)	775.34 ( $\pm$ 101.40)	601.52 ( $\pm$ 382.92)	573.10 ( $\pm$ 382.88)	*	*	KW
$\text{K}^+$ (mg/g)	5.36 ( $\pm$ 2.07)	13.12 ( $\pm$ 4.58)	3.76 ( $\pm$ 2.07)	7.29 ( $\pm$ 3.34)	*	*	KW
$\text{Mg}^{2+}$ (mg/g)	26.93 ( $\pm$ 11.37)	40.69 ( $\pm$ 9.16)	17.37 ( $\pm$ 5.98)	20.36 ( $\pm$ 9.27)	*	*	KW
$\text{Na}^+$ (mg/g)	11.85 ( $\pm$ 0.94)	16.99 ( $\pm$ 7.16)	8.42 ( $\pm$ 3.86)	10.53 ( $\pm$ 3.77)	*	*	KW
P (mg/g)	1.01 ( $\pm$ 0.34)	6.21 ( $\pm$ 0.77)	1.43 ( $\pm$ 0.29)	2.35 ( $\pm$ 0.27)	*	*	ANOVA
$\text{NO}_2^-$ (mg/g)	0.07 ( $\pm$ 0.10)	0.09 ( $\pm$ 0.07)	0.00 ( $\pm$ 0.00)	0.01 ( $\pm$ 0.02)	*	*	KW
$\text{NO}_3^-$ (mg/g)	0.06 ( $\pm$ 0.09)	0.19 ( $\pm$ 0.07)	0.02 ( $\pm$ 0.03)	0.03 ( $\pm$ 0.04)	*	*	KW
$\text{NH}_4^+$ (mg/g)	2.12 ( $\pm$ 1.56)	3.14 ( $\pm$ 1.21)	1.12 ( $\pm$ 1.31)	1.78 ( $\pm$ 1.38)	*	*	KW
TOC (mg/g)	298.43 ( $\pm$ 45.24)	315.22 ( $\pm$ 38.96)	245.95 ( $\pm$ 68.21)	245.28 ( $\pm$ 79.11)	*	*	KW

Asterisks indicate significant differences at 5% level based on two-way ANOVA and Kruskal–Wallis (KW) results

Benites 2005). *C. edulis* litter decomposition also lowers soil pH as a result of high levels of tannin (Van der Watt and Pretorius 2001) and can increase certain soil nutrients such as C, S, N, P, K, Ca and Mg. Despite being at low levels, these nutrients enhance the activity of soil microorganisms by increasing their primary energy source. For example, P is often only available at low pH levels (Grootjans et al. 2004). Physical impacts of *C. edulis* leaf litter includes shading effects that devoid native plant species of sunlight (Berendse et al. 1998). Therefore, human-mediated disturbance and the invasion of *C. edulis* in urban areas might prevent the establishment of those native plant species adapted to the limiting conditions typical of coastal dune systems (Olf et al. 1993), while allowing for the establishment of non-dune plant species (García-Mora et al. 2001; Martínez et al. 2004b). Our results, showed a higher total and speed of germination of both native species in soils from zones invaded by *C. edulis* compared to those from uninverted zones. Such enhanced germination kinetics may

be the result of lower pH, higher water content, and higher nutrients in these zones (Ungar 1978; Kachi and Hirotsu 1983; Novoa et al. 2013b). *Carpobrotus edulis* is considered a transformer invasive species (Richardson and Pyšek 2004), since it can modify the conditions (increased water content and nutrients) of the invaded ecosystems to its own benefit, i.e. establish positive feedback loops (Novoa and González 2014). However, contrary to our predictions, we found *C. edulis* to have reduced germination performance (lower and slower) in invaded soils. A possible explanation might be the allelopathic nature of dense *C. edulis* stands, so that these allelopathic compounds may even retard the performance of the invader (Novoa et al. 2012). On the other hand, we found *C. edulis* to invest less in belowground (root) and more in aboveground growth in urban and in invaded areas, possibly in response to elevated nutrients levels and water content in these areas compared to natural areas (Maun 1994). While the coastal dune adapted *M. littorea* appears to perform equally well (root and shoot



**Fig. 2** Regression estimates showing the effect of Area (Urban/Natural) and Status (Uninvaded/invaded) on the establishment of the invasive species *Carpobrotus edulis*, the ruderal species *Scolymus hispanicus* and the endemic species *Malcolmia littorea* based on two-way ANOVA (for the speed of germination of *S. hispanicus* and the shoot and root length of *M. littorea*)

investment) in urban and natural areas, irrespective of status (uninvaded vs. invaded), *S. hispanicus* showed lower investment in belowground (root) biomass in both invaded and urban soils, possibly also as a response to higher nutrients and water availability. This supports previous work suggesting that such plastic responses may give *S. hispanicus* a competitive advantage over the endemic *M. littorea* under soil conditions altered by invasive *C. edulis* (Novoa et al. 2013b). *Scolymus hispanicus* often colonize and become dominant in coastal dunes areas following the clearing of invasive *C. edulis* populations (Novoa et al. 2013a).

The aims of coastal dune management actions have changed over time. Historically management actions aimed to stabilize coastal dunes, often using non-native species like *C. edulis* that later became invasive (Martínez et al. 2004a). This has led to changes in community assemblages of dunes (Santoro et al. 2012). For example, *C. edulis* induces water stress as

and Kruskal–Wallis (for the percentage of germination of all 3 species, the speed of germination of *C. edulis* and *M. littorea*, and the shoot and root length of *C. edulis* and *S. hispanicus*) results. Asterisks indicate significant differences at 0.01 (\*), 0.001 (\*\*) and 0 (\*\*\*) level

it is capable of storing surface water in its tissue and can therefore strongly compete for this limited resource with native species in dune systems, allowing only the co-existence with species capable of utilizing groundwater.(Santoro et al. 2012). Nowadays, management actions primarily aim at preserving rare and endangered species (Martínez et al. 2004a), or restoring dune ecosystems. Our results illustrate the complexity faced by conservationists due to the interplay between urbanization, increased tourism and anthropogenic disturbance, and invasive species. That is, urbanization and invasive species may have unpredictable and unwanted biodiversity consequences.

## Conclusions

In this study, we aimed to assess whether (1) soil disturbance in urban coastal areas may facilitate the invasion success of *C. edulis*, and (2) the impacts of *C.*



*edulis* on the invaded soils is higher in urban than in natural coastal areas. Our results suggest that both human disturbance and invasive species presence impact soils in a manner that create conditions favouring the establishment of invasive (*C. edulis*) and native species with broad ecological tolerance (*S. hispanicus*), while not affecting the early growth of endemic plant species that are specifically adapted to coastal dune areas (*M. littorea*). These are important findings, as the impacts of invasive species are often determined in isolation, i.e. a single invasive species affecting a single native species. Our results show the dynamic and multiple dimensions of invasive plant impacts and have important considerations for conservation and restoration efforts.

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