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REGULAR ARTICLE

The impact of *Carpobrotus* cfr. *acinaciformis* (L.) L. Bolus on soil nutrients, microbial communities structure and native plant communities in Mediterranean ecosystems

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Abstract

Background and aims *Carpobrotus* spp. are amongst the most impactful and widespread plant invaders of Mediterranean habitats. Despite the negative ecological impacts on soil and vegetation that have been documented, information is still limited about the effect by *Carpobrotus* on soil microbial communities. We aimed to assess the changes in the floristic, soil and microbial parameters following the invasion by *Carpobrotus* cfr. *acinaciformis* within an insular Mediterranean ecosystem.

Methods Within three study areas a paired-site approach, comparing an invaded vs. a non-invaded plot, was established. Within each plot biodiversity indexes, C and N soil content, pH and microbial biomass and structure (bacterial and fungal) were assessed.

Results Invaded plots showed a decrease of α-species richness and diversity. The least represented plant species in invaded plots were those related to grassland habitats. In all invaded soils, a significant increase of carbon and nitrogen content and a significant decrease of pH were registered. *Carpobrotus* significantly increased bacterial and fungal biomass and altered soil microbial structure, particularly favoring fungal growth.

Conclusions *Carpobrotus* may deeply impact edaphic properties and microbial communities and, in turn, these strong modifications probably increase its invasive potential and its ability to overcome native species, by preventing their natural regeneration.

Keywords Mediterranean islands · Biological invasions · Carbon and nitrogen content · Biodiversity loss

Introduction

The increasing distribution of invasive alien plants is one of the main factors of ecosystem degradation and of biodiversity loss at global scale (Mack et al. 2000). Some invasive species are particularly able to quickly spread, may replace whole plant communities and habitats over wide areas and therefore are denominated transformer species (Pyšek et al. 2004) or ecosystem engineers (Molinari et al. 2007). Apart from threatening biodiversity, such species can deeply modify chemical, physical and biological soil characteristics, soil erosion rate and water runoff, microclimatic substrate conditions, water content along soil profile, ecosystem food webs, nutrients cycle as well as organic matter decomposition (Vilà et al. 2011; Nanko et al. 2015). This explains why many experimental studies and research have been addressed to identify such taxa, to assess their impacts and to understand the reasons for their relevant invasive success.

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Some species belonging to the genus *Carpobrotus* fall within this category of introduced plants. *Carpobrotus* spp. are well-known mat-forming succulent invaders of Mediterranean-type ecosystems, where they compete aggressively with native plants, strongly hindering their growth and establishment and deeply changing the characters of whole ecosystems over large areas (D'Antonio and Mahall 1991; Albert 1995; Suehs et al. 2004; Vilà et al. 2006). The two most widespread naturalized species of the genus, *Carpobrotus edulis* (L.) Nebr and *C. acinaciformis* (L.) L. Bolus, are both native to coastal areas of South Africa (Malan and Notten 2006); however, the identification of the two species has been complicated by the frequent hybridization events that raise a hybrid complex named *C. affine acinaciformis* (Delipetrou 2006; Andreu et al. 2010). Although the introduction of Carpobrotus spp. in Europe is relatively ancient, dating back to the 17th century (Fournier 1952), the naturalization and the subsequent spread in the Mediterranean Basin began between the end of the 19th century and the beginning of the 20th century (Lojacono-Pojero 1891; Sanz-Elorza et al. 2004). Nowadays *C. edulis*, *C. acinaciformis* and their hybrids forms are considered a major threat to biological diversity and ecosystem functioning of Mediterranean islands (Brundu 2013), where they are undergoing a number of control and eradication programs in order to protect native biodiversity (Brunel et al. 2013).

If the spread of *Carpobrotus* spp. in the Mediterranean has been undoubtedly favoured by their extensive use for the stabilization of sand dunes in many coastal areas (La Mantia 2011), a number of biological traits are underlying their outstanding invasive potential. Traveset et al. (2008), for instance, highlighted the remarkable plasticity of *Carpobrotus* aff. *acinaciformis* with respect to light availability, because it grows well in full light conditions, but tolerates partial shading. *Carpobrotus* spp. are capable of rooting at nodes even without a direct contact with the ground, radially spreading with growth rates equal to 1 m per year in the native range (Wisura and Glen 1993), and exceeding 30 cm per year in the Mediterranean (Traveset et al. 2008; Passetti et al. 2012). Sexual reproduction is equally effective. The flowers are frequently visited by native pollinators (Bartomeus et al. 2008), seed production is particularly abundant, reaching an average of 1000 seeds per fruit (Carta et al. 2004; Bartomeus and Vilà 2009), and a high proportion of seeds is stored in the soil seed bank and in litter (Chenot et al. 2014). Seed dispersal is then carried out mainly by small mammals such as rats and rabbits, whose ingestion causes an increase in the germination percentage and therefore the chance for new individuals to become established (D'Antonio 1990a; Bourgeois et al. 2005; Novoa et al. 2012).

In invaded Mediterranean ecosystems, *Carpobrotus* spp. possess many unique traits, typically different from those of native Mediterranean species, such as life form, size, spatial distribution and litterfall dynamics; these differences are expected to bring about important changes in the quality of soil microsites as well as in resident plant communities. Such marked differences with the local biota may be important for the widespread presence and the recognized negative ecological impacts displayed by *Carpobrotus* spp. in many Mediterranean island ecosystems, which generally do not host *Carpobrotus*-like species (Heywood 1995). Phylogenetic relatedness between native and introduced species has been recently considered a valuable tool to forecast which introduced species are more likely to have higher ecological effects on recipient ecosystems. For instance, introduced grass species less closely related to native grasses were found to be those having the most relevant impacts and tending to spread much further in California grasslands (Strauss et al. 2006). From an ecological point of view this could be explained, for instance, by the reduced likelihood that parasites as well phytophagous insects may specialize and attack host plants far different from native species. Even the plant-mediated introduction of a new biochemical process, which reflects the adaption and evolution in a given habitat, may have catastrophic consequences for invaded ecosystem functioning. *Myrica faya* Ait. is such an emblematic case in this respect because it has been capable of quadrupling the nitrogen content of the recent lava flows in Hawaii, where normally no nitrogen-fixing native species occurs (Vitousek et al. 1987).

Much effort has been either devoted to understanding the biological reasons for *Carpobrotus* spp. invasive success (D'Antonio 1990b, 1993; D'Antonio et al. 1993; Novoa et al. 2012) and to assessing the ecological consequences associated with their invasion on floristic richness and diversity (Carta et al. 2004; Vilà et al. 2006; Andreu et al. 2010; Novoa et al. 2013; Chenot et al. 2014; Fried et al. 2014), on soil properties (Vilà et al. 2006; Conser and Connor 2009; de la Peña et al. 2010; Santoro et al. 2011; Novoa et al. 2013, 2014) or on both (Vilà et al. 2006; Novoa et al. 2013). In all previous references, *Carpobrotus* spp. were found to exert a strong impact on the composition, diversity and dynamics of plant communities, and generally lead to a significant decrease of species richness as well as diversity of invaded habitats. Recently, a number of works have focused on the impact of invasive alien species on local soil characteristics (Heneghan et al. 2006; Rout and Chrzanowski 2009; Osunkoya and Perrett 2011; Perkins et al. 2011; De Marco et al. 2013), and such effects are considered particularly important in determining the invasive success of *Carpobrotus* spp. as well (Vilà et al. 2006; Novoa et al. 2014). For instance, Novoa et al. (2014) found a large variation in soil pH, enzymatic activity, nutrient, salinity and moisture content in a dune ecosystem invaded by *Carpobrotus edulis*. Novoa et al. (2013) showed that these effects influence the function of soil microbial communities and constrain the establishment of native plants in dune communities. Increasing importance has been given to the role played by soil microbial communities (van Grunsven et al. 2009; de la Peña et al. 2010), to the changes of these communities as a result of the invasive establishment and to the plant-soil feedback mechanisms that may enhance the competitive ability of this invasive species with respect to native species (de la Peña et al. 2010). In addition, *Carpobrotus* litter is well known to exert a strong allelopathic effect on native species by reducing their germination rate, growth and establishment, and such effect is highly species-specific (Novoa et al. 2012; Novoa and González 2014). One of the most important consequences of *Carpobrotus* invasion is the significant alteration of soil nutrients dynamics that lead in most cases to an increase in the organic matter and nitrogen content and a decrease in pH, with clear long lasting ecological consequences (Vilà et al. 2006; Conser and Connor 2009; de la Peña et al. 2010; Santoro et al. 2011; Novoa et al. 2013, 2014). These changes, combined with shifts in microbial communities assemblage, make soils much more conducive to the establishment of the alien species and generally adverse for germination and/or growth of native species (de la Peña et al. 2010; Conser and Connor 2009; Novoa et al. 2013; Novoa and González 2014). The intensity with which invasive alien species are capable of altering the physical and chemical characteristics of soils appears to be strongly dependent on the identity of the invaded habitat (Forey et al. 2009; Maestre et al. 2009; Santoro et al. 2011; Fried et al. 2014); however, time since invasion could be considerably important as it is recognized that impacts may change over time (Dostál et al. 2013; Marchante et al. 2015). Although the invasive process by *Carpobrotus* spp. in the Mediterranean has been documented, information is still limited whether or not and how soil microbial communities are affected. More in detail, the impact on the structure of soil microbes, for instance on bacteria/fungi ratio, has never been assessed, even though it is well recognized that soil microbes are important in affecting plant performance as well as the competitive interactions between co-occurring species. With this regard, the phospholipid fatty acid analysis (PLFA) is a promising tool as fatty acids are considered valuable bioindicators of soil quality and they could be used for the development of soil quality indices (Kaur et al. 2005). The knowledge of the overall ecological impacts on soils by *Carpobrotus*, and its characterization in terms of type and magnitude, may play a key role in developing an effective strategy to control this invasive species. In fact, the germination, growth and establishment strategies of plants, as well as their competitive dynamics in the field, are deeply influenced and regulated by physical, chemical and biological characteristics of soil. This is particularly true for sensitive species of fragile ecosystems such as coastal habitats of Linosa island (La Mantia et al. 2009). Many precious species of dune ecosystems, for instance, are strictly linked to low nutrient as well salinity levels in soils (Santoro et al. 2012; Novoa et al. 2013), whereas ruderal, opportunistic and/or nitrophilous species are enhanced by nutrient enrichment (Marchante et al. 2015). The altered edaphic conditions due to *Carpobrotus* invasion, may affect the success of sowing and/or planting interventions of some native species in eradicated areas, compromising the chance for native habitat restoration and thus having clear management implications (Ruffino et al. 2014). The aim of the research was to assess the changes in the content of soil carbon and nitrogen, in the floristic richness and diversity, and in the microbial communities structure following the invasion by *Carpobrotus* cfr. *acinaciformis* at Linosa, an insular Mediterranean ecosystem.

Materials and methods

Study area and vegetation surveyed Our survey was conducted in Linosa, a 5.45 km^2 island of the Pelagie Archipelago where *Carpobrotus* cfr. *acinaciformis* is widespread. This alien species has successfully invaded coastal habitats and seminatural grasslands, among the richest in endemic species and species of particular conservation value. In fact, 36 out of 74 of the vascular plants and mosses of main biogeographic and/or conservation interest occurring on Linosa island, and listed within the SCI Management Plan (La Mantia et al. 2009), are more or less exclusively linked to annual therophytic grasslands. They include: *Astragalus peregrinus* subsp. *warionis* (Gand.) Maire, *Avena saxatilis* (Lojac.) Rocha Afonso, *Bellium minutum* (L.) L., *Catapodium hemipoa* subsp. *occidentale* (Paunero) H. Scholz & S. Scholz, *Erodium neuradifolium* var. *linosae* (Sommier) Brullo, *Logfia lojaconoi* (Brullo) C. Brullo & Brullo, *Lotus halophilus* Boiss. & Spruner., *Lotus peregrinus* L., *Reichardia tingitana* (L.) Roth, *Serapias parviflora* Parl.

The three following native vegetation types were taken into account:

A). Patchy vegetation near the coast with discontinuous coastal sub-halophilous scrub with *Lycium intricatum* Boiss. and *Senecio cineraria* subsp. *bicolor* (Willd.) Arcang. (which is ascribed to the phytosociological class *Crithmo-Limonietea* and corresponds to the EU habitat 5320 'Low formations of *Euphorbia* close to cliffs') and annual and perennial salt-tolerant herbs (mainly *Daucus gingidium* L. and *Euphorbia pinea* L.) in the gaps, which can be referred to the priority EU habitat 6220 (Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*);

B). Patchy vegetation with dwarf annual herbs linked to acidic and sandy soils (phytosociological class *Tuberarietea guttatae* and priority habitat 6220 'Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*') and annual and biennial sub-nitrophilous plants typical to fallow areas (e.g. *Brassica fruticulosa* Cirillo, *Lupinus cosentinii* Guss., etc.);

C). Patchy vegetation dominated by few grasses and sub-shrubs (*Hyparrhenia hirta* (L.) Stapf, *Dactylis hispanica* Roth., *Phagnalon saxatile* (L.) Cass.) typical to the *Lygeo-Stipetea* phytosociological class and to the priority EU habitat 6220 ('Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*'), encroached by some shrubs typical to the local thermo-xerophilous maquis communities like *Pistacia lentiscus* L. and *Periploca angustifolia* Labill. (class *Quercetea ilicis*, order *Quercetalia calliprini*, alliance *Periplocion angustifoliae*, referred to the EU habitat 5330 'Thermo-Mediterranean and pre-desert scrub').

The island is characterized by a markedly Mediterranean climate, with a dry season lasting for about 6 months, concentrated in the hottest period of the year, followed by a cool and wet winter season (La Mantia et al. 2009). As concerns bioclimate, Linosa lies within the infra-mediterranean belt, according to the climatic indices proposed by Rivas-Martínez et al. (1999). In particular, during the study year (2014) the rainfall was 308.4 mm (http://www.infoclimat.fr/climatologie/annee/2014/lampedusa-e-linosa-linosa/valeurs/MNWSCL078.html), resulting in a dry year, respect to the annual average of about 458 mm (Duro et al. 1997). The average annual temperature is 20.2 °C, with an annual thermal excursion equal to 13 °C (Duro et al. 1997). According to Fierotti (1988), the soil types occurring in Linosa island are Typic Xerorthents, Lithic Xerorthents and Andic Xerochrepts.

Study design Three study areas differing in habitat characteristics and in time since *Carpobrotus* cfr. *acinaciformis* invasion were investigated (Fig. 1; Table 1; additional data are given in Online Resource 1): (A) invaded 20 years before; (B) invaded 15 years before and (C) invaded 8 years before. Field surveys were carried out during May 2014, when most of the local annual species are still present or at least recognizable. Based on the previous surveys carried out in the surroundings of the three study areas (La Mantia et al. 2009), very few or no species with autumn or winter life-cycle might be missing.

Within each area an invaded plot (I) was compared to a non-invaded (NI) neighboring plot according to a paired-site method (Conteh 1999; Novara et al. 2012). The invaded plot was characterized by a cover value by *Carpobrotus* cfr. *acinaciformis* higher than 80 %. The non-invaded plot was covered by native vegetation, it was no more than 5 m far away from the paired invaded plot and was characterized by the same microclimatic conditions (aspect, slope, etc.). Time since invasion was assessed by means of available aerial orthophotos (sources: Regione Siciliana ATA2008 and IT2000), with the integration of field observations carried out during the preparation of the management plan of "Isola di Linosa" SIC ITA040001 (La Mantia et al. 2009) and during field surveys carried out in 2014 within LIFE11+ NAT/IT/000093 "Pelagic Birds" project (available at http://www.pelagicbirds.eu/).

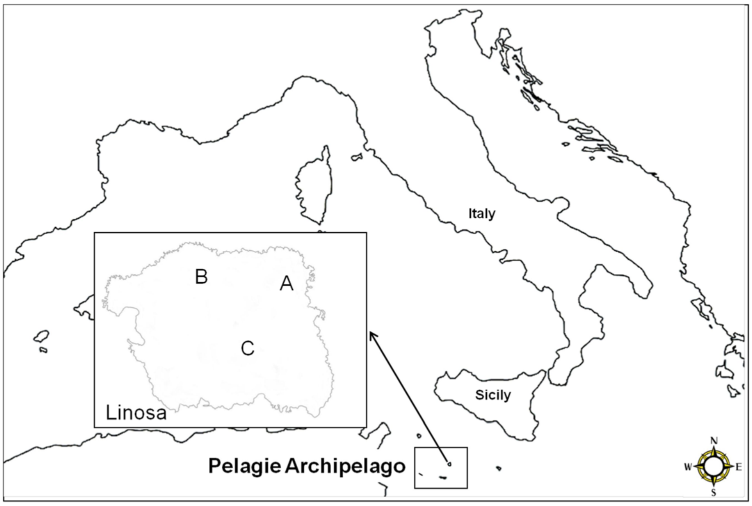

Fig. 1 The three study areas within Linosa island: **a**) invaded 20 years before; **b**) invaded 15 years before; **c**) invaded 8 years before

Phytosociological surveys Phytosociological relevés (Braun-Blanquet 1932) were carried out on May 2014 in the three study areas and within three 50 m^2 wide (5 × 10 m) paired invaded vs. non-invaded plots. Within each plot the following physical and biological parameters were registered: altitude (m a.s.l.), mean slope (°), outcropping rock (%), litter thickness (cm), average height of shrub layer (m), average height of herb layer (m), total vegetation cover (%), shrub layer cover (%), herb layer cover (%) and taxonomic diversity (i.e. number of infrageneric taxa). Moreover, life forms spectrum (i.e. the percentage rate of each life form sensu Raunkiær 1934), phytosociological spectrum (i.e. the percentage rate of each phytosociological class), Shannon diversity index (H': Shannon and Weaver 1949) and Evenness index (J) were calculated after converting Braun-Blanquet values according to Tüxen and Ellenberg (1937). Furthermore, the same cover values were used to estimate the Relative Impact (RI) on α-species richness, Shannon and Evenness index, and on life forms as well. The RI expresses the variation in a given parameter as a consequence of the invasion process and it is computed, according to Vilà et al. (2006), with the following formula:

$$RI(a) = \frac{a_{NI} - a_I}{a_{NI} + a_I}$$

in which a is the estimated parameter within non invaded (NI) and invaded (I) areas. RI is a number ranging from −1 to +1; a positive and a negative value of RI indicate a decrease and an increase of the considered parameter, respectively. The Jaccard dissimilarity index (D_J) was also computed as follows:

$$D_J = 1 - J$$

where

$$J = \frac{a}{a + b + c}$$

a is the number of species occurring in either invaded and non-invaded plots, b is the number of species occurring only in the invaded plots and c is the number of species occurring only in the non-invaded plots (Fried et al. 2014). Such index expresses the magnitude of the variation in invaded areas based on plant species identity.

Table 1 Environmental characteristics of study areas (A = invaded 20 years before; B = invaded 15 years before; C = invaded 8 years before; NI = non-invaded plot; I = invaded plot)

	A		B		C	
	NI	I	NI	I	NI	I
Altitude (m a.s.l.)	10	10	30	30	20	20
Distance to the sea (m)	15	15	349	349	760	760
Mean slope (°)	9	10	3	1	11	12
Outcropping rock (%)	40	45	3	5	20	15
Litter thickness (cm)	0	2	0	2	0	2

Soil sampling and analysis To assess the differences in soil parameters after *Carpobrotus* cfr. *acinaciformis* invasion we sampled soil at paired sites. Soil cores (20 cm deep × 10 cm diameter) were collected in May 2014, with six replicates for each invaded and uninvaded plot (total 36 samples). We used criteria adopted for collection by Conteh (1999), also applied in several research studies (Chan et al. 2010; Kucharik et al. 2003; Murphy et al. 2003; Novara et al. 2012). The soil samples were air dried, gently sieved at 2-mm, ground to a fine powder, treated with HCl 2:1 to remove carbonates and then analysed for C and N content using a CHN-Elemental Analyzer. SOC content was first expressed as a percentage (g of C per 100 g of dry soil × 100) and then converted to Mg per hectare based on bulk density (BD) and soil depth according to:

$$C_{stock}\left(\mathrm{Mg\ ha^{-1}}\right) = BD{*}C_{conc}{*}D{*}CF_{coarse}$$

where BD is bulk density (Mg m^{-3}), C_{conc} is carbon concentration (g/100 g), D is depth thickness (m), and CF_{coarse} is a correction factor [1 - (gravel % + stone %)/100].

Soil bulk density was measured using the tube core method (Baruah and Barthakur 1997), based on the volume of the collected sample and the weight of dry soil in the sample. Soil pH and electrical conductivity (EC) were measured in saturated extracts and soil texture by sedimentation method. We also computed an average index of SOC content change from each invaded (I) vs. non-invaded (NI) plots as follows:

$$\text{Carbon Change Index}(CCI) = (C_I - C_{NI})/C_{NI}$$

where C_{NI} = SOC content in the non-invaded soil and C_I = SOC content in the invaded soil.

Analogously, an average index of Nitrogen content change from each non-invaded (NI) and invaded (I) plot was calculated as follows:

$$\text{Nitrogen Change Index}(NCI) = (N_I - N_{NI})/N_{NI}$$

where N_{NI} = Nitrogen content in the non-invaded soil and N_I = Nitrogen content in the invaded soil. Student *t* test was performed to test differences between invaded and non-invaded plot in each paired-site for comparing SOC, N content, microbial biomass and community structure. Data analysis was carried out using the SPSS statistical package (IBM SPSS statistics 2013).

Fatty acids analysis Fatty acid methyl esters (FAMEs) were extracted by mild alkaline methanolysis method according to Schutter and Dick (2000) and they were detected on a gas chromatograph (Thermo Scientific FOCUS™ GC) equipped with a flame ionization detector and a fused-silica capillary column Mega-10 (50 m × 0.32 mm I.D.; film thickness 0.25 μm). The GC temperature progression was: initial isotherm at 115 °C for 5 min, increase at a rate of 1.5 °C per minute from 115 to 230 °C, and final isotherm at 230 °C for 2 min. Both injection port and detector were set up at 250 °C and helium at 1 mL min^{-1} in a constant flow mode was used as carrier. Nonadecanoic acid methyl ester (19:0; cat no. N-5377, Sigma-Aldrich Co.) was used as an internal standard for quantification of FAMEs. The identification of the peaks was based on comparison of retention times to known standards (Supelco Bacterial Acid Methyl Esters mix cat no. 47080-U and Supelco 37 Component FAME mix cat n^o. 47885-U). The amount of detected fatty acids (FAs) was expressed as nmol g^{-1} of dry soil (105 °C, 24 h). The total amount of PLFAs with a chain length ranging from 14 to 20 carbon atoms was used to estimate the total microbial biomass (Bailey et al. 2002). The FAs i15:0, a15:0, 15:0, i16:0, i17:0, 17:0, cy17:0, 18:1ω7, cy19:0 were used to represent bacterial biomass while 18:2ω6,9 for fungal biomass (Frostegård and Bååth 1996). The FAs i15:0, a15:0, i16:0, i17:0 were chosen to represent Gram-positive (G+) bacteria while 18:1ω7, cy17:0 and cy19:0 for Gram-negative (G-) bacteria (Zelles 1997; Zogg et al. 1997).

Results

Phytosociological surveys Biological forms did not occur in the same way in *Carpobrotus* cfr. *acinaciformis*-invaded areas. In particular, therophytes (T) and hemicryptophytes (H) were the least commonly observed life forms, although showing a different pattern (Table 2). In invaded plots, both the presence (number of species) and the abundance (cover values) of T were higher in areas A and B, while in area C, despite lacking a difference in species number, a higher cover value was found. The opposite trend was detected in chamaephytes (Ch), whose number was higher in both areas A and B, whereas the cover values were lower in areas A and especially C. In invaded plots, the least represented phytosociological classes were those mainly including perennial and annual grassland species, that is *Stipo-Trachynietea distachyae* (S-T) and *Lygeo-Stipetea* (L-S). S-T occurred only in non-invaded plots B and C, while L-S occurred in non-invaded plot B and was less represented in the invaded than in the non-invaded plot C.

Table 2 Floristic parameters of the three study areas (NI = non-invaded plot; I = invaded plot). Life forms abbreviations: P = phanerophytes; Ch = chamaephytes; H = hemicryptophytes; T = therophytes. Percentage values concerning the spectrum of life forms and phytosociological classes are based upon total species number. Extended name of the abbreviations referred to different phytosociological classes: SM = *Stellarietea mediae* (ruderal communities dominated by annual or short-lived pioneer herbs adapted to tolerate strong anthropogenic disturbance); C-L = *Crithmo-Limonietea* (salt-tolerant communities of coastal rocky cliffs); L-S = *Lygeo-Stipetea* (thermo-xerophilous perennial grasslands); QI = *Quercetea ilicis* (evergreen or summer-deciduous maquis and scrub); SaM = *Saginetea maritimae* (ephemeral annual communities prone to salt-spray and linked to muddy and/or sandy coastal soils); S-T = *Stipo-Trachynietea distachyae* (thermo-xerophilous annual prairies typical of oligotrophic and base-rich soils)

		A		B		C	
		NI	I	NI	I	NI	I
Average height shrub layer (m)		0.0	0.4	0.0	0.0	0.6	0.6
Average height herb layer (m)		0.5	0.3	0.2	0.3	0.8	0.4
Shrub layer cover (%)		0	5	0	0	5	5
Herb layer cover (%)		100	95	90	100	65	95
Total vegetation cover (%)		100	100	90	100	70	100
Life form (%)[a]	T	70.6	37.5	83.3	44.5	30	33.3
	H	11.8	12.5	16.7	33.3	40	44.5
	CH	17.6	50	–	11.1	10	11.1
	P	–	–	–	11.1	20	11.1
Phytosociological class (%)[a]	SM	35.3	12.5	58.4	66.7	30	44.5
	S-T	11.8	12.5	33.3	–	10	–
	C-L	17.6	50	–	11.1	–	11.1
	L-S	11.8	12.5	8.3	–	40	33.3
	QI	5.9	12.5	–	22.2	20	11.1
	SaM	17.6	–	–	–	–	–

a: *Carpobrotus* cfr. *acinaciformis* was not taken into account in invaded plots

In terms of relative impact, invaded plots showed lower α-species richness, diversity and evenness (Table 3). The Jaccard index, too, indicated considerable differences in plant species identity between invaded and non-invaded plots. However, areas A and B have proven to be much more differentiated from invaded areas than area C, having the highest values for all the investigated parameters. Despite this, a large difference in life forms was also found within area C. For what concerns plant species of particular conservation value, listed in the regional Red List (Conti et al. 1997), the impact of *Carpobrotus* cfr. *acinaciformis* seemed to be strongly selective so that some species have been considerably more affected than others (see additional data in Online Resource 1). *Rumex bucephalophorus* L. was the most affected species, occurring only in the three non-invaded plots. *Periploca angustifolia* and *Phagnalon saxatile* subsp. *saxatile* were found either in invaded and non-invaded plots, but they reached a higher cover value in non-invaded ones. Furthermore, *Phagnalon saxatile* subsp. *saxatile* occurred only in the early phases of invasion process (area C), suggesting *Carpobrotus* cfr. *acinaciformis* may exert a direct effect on its persistence in a long-term perspective. By contrast, no effect was found against *Senecio cineraria* subsp. *bicolor* and *Trigonella maritima* Poir., both occurring in one area with the same cover value, and in *Lycium intricatum* that occurred only in one invaded plot.

Soil carbon and nitrogen properties Soils of the three areas were characterized by different texture showing silt values ranging from 21.0 % (area A) to 7.5 % (area B) (Table 4). The evidence of texture on both soil carbon and nitrogen determined great differences among areas. Within the three study areas, invasion process significantly increased soil fertility, reduced soil reaction, and increased C/N ratio (Table 4). Soil carbon and nitrogen stocks (Fig. 2) showed, as well as carbon and nitrogen content, different values in the three areas. The differences between invaded and non-invaded plots tended to

Table 3 The Relative Impact (RI) on life forms and Biodiversity indexes within the three study areas (A-B-C) between non-invaded (NI) and invaded (I) plots

	A			B			C		
	NI	I	RI (%)	NI	I	RI (%)	NI	I	RI (%)
Life form									
Phanerophytes	–	–	–	0	2.5	−100	17.5	2.5	75.0
Chamaephytes	20	10	33.3	0	0.1	−100	15	2.5	71.4
Hemicryptophytes	40	15	45.5	17.5	30.1	−26.5	70	20.1	55.4
Therophytes	5.9	0.2	93.4	32.7	20	24.1	0.3	5.1	−88.9
Biodiversity indexes									
α-species richness	17	9	30.8	12	10	9.1	10	10	0.0
Shannon index (H’)	1.37	0.82	25.1	2.03	1.24	23.8	1.25	0.99	11.6
Evenness index (J)	0.49	0.39	11.4	0.82	0.54	20.6	0.54	0.43	11.3
Jaccard index (D_J)	0.61	0.76	0.42						

be higher in the areas with younger time since invasion and lower in the oldest. As a consequence, carbon and nitrogen indexes were negatively correlated with time since invasion (Fig. 3). Both indexes showed a similar pattern, being significantly higher 8 years after invasion had started.

Fatty acids Soil microbial biomass ranged from 96.2 to 488.6 nmol FAs kg^{-1} in non invaded soils and from 241.8 to 787.0 nmol FAs kg^{-1} in invaded ones; it was always significantly higher in invaded plots. Bacteria, bacteria gram + and fungi followed the same pattern, being significantly more abundant in invaded plots (Table 5). Bacteria gram- were significantly increased within invaded plots in areas A and C, but significantly reduced within invaded plots in area B. Soil colonization by *Carpobrotus* cfr. *acinaciformis* also changed the microbial community structure. Indeed, bacterial mass was relatively less increased than fungal mass so that the bacteria/fungi ratio was significantly lower in invaded plots. The gram+/gram- ratio was significantly higher within invaded plots in area A, but significantly lower within invaded plots in areas B and C.

Discussion

The knowledge of the ecological impacts caused by invasive alien plant species represents one crucial step if we are to develop appropriate and successful management and control strategies. On the other hand, it is widely recognized that such impacts may deeply vary both in time and space, as invasion is a process involving the dynamic interaction between an introduced species and the recipient ecosystem (Shackleton and Gambiza

Table 4 Soil characteristics in the three study areas. NI: non-invaded plot; I: invaded plot; A) invaded 20 years before; B) invaded 15 years before; C) invaded 8 years before. In the same row, for the same parameter and within each study area, different letters indicate statistical differences for P ≤ 0.05 between non-invaded (NI) and invaded (I) plots

	sand	clay	silt	BD	pH		C (g kg^{-1})		N (g kg^{-1})		C/N	
					NI	I	NI	I	NI	I	NI	I
A	70.5	8.5	21.0	1.59	8.03a	7.87b	28.4b	31.9a	2.9b	3.1a	9.8b	10.3a
B	86.4	3.5	10.1	1.63	7.56a	7.16b	10.1b	13.2a	2.1b	2.5a	4.8b	5.3a
C	86.0	6.5	7.5	1.62	8.28a	8.13b	5.9b	13.9a	1.4b	1.9a	4.2b	7.3a

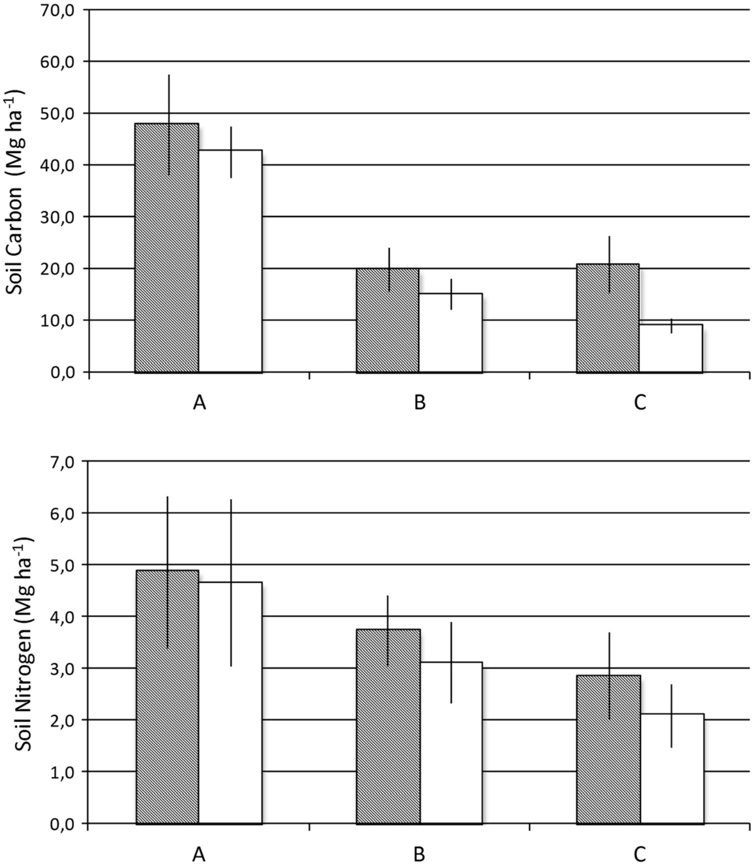

Fig. 2 Carbon stocks (above) and nitrogen stocks (below) in relation to time since invasion. Invaded (grey bar) and non-invaded (white bar) plots are compared. Vertical bars indicate standard deviation (n = 6)

2008; Vilà et al. 2011). While it is acknowledged that the ecological shifts resulting from the spread of invasive species are strongly influenced by the identity of the target habitat, there is still limited knowledge about how impacts change over time (Strayer et al. 2006; Flory and D'Antonio 2015; Marchante et al. 2015). Furthermore, each ecological parameter may be affected to a different extent by invasion and to take into account these differences may provide valuable information on the prevailing impacts (e.g. Vilà et al. 2006), and hence on the ecosystem characters more influenced by a certain invasive species. Although a number of studies has investigated the impacts on soil and vegetation by plant invasions (e.g. Jandová et al. 2014), little research has been addressed to assess the consequences of plant invasion on soil, vegetation and microbial communities at the same time. In this respect, *Carpobrotus* cfr. *acinaciformis* is an excellent case study, due to its ability to completely modify Mediterranean habitats and landscapes, altering ecosystem structure and functioning, as well as biodiversity pattern.

The decrease in α-species richness and diversity in *Carpobrotus*-invaded habitats is a commonly observed effect within insular Mediterranean ecosystems (e.g. Vilà et al. 2006). For instance, the average Shannon index in selected bibliography was 2.67 and 1.90 in non-invaded and invaded sites, respectively (Vilà et al. 2006; Andreu et al. 2010; Novoa et al. 2013; Fried et al. 2014). Our study areas were relatively poorer but showed a similar trend, as Shannon index ranged between 1.25 and 2.03 in non-invaded areas, and between 0.82 and 1.25 in invaded

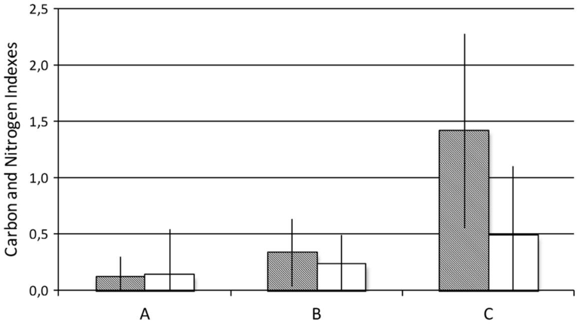

Fig. 3 Carbon (grey bar) and nitrogen (white bar) change indexes in relation to time since invasion. Vertical bars indicate standard deviation (n = 6)

Table 5 Microbial biomass (nmol FAs kg^{-1}) and community structure, as well as bacteria/fungi and gram+/gram- ratios in non-invaded (NI) and invaded (I) soils. Within the same area, different letters indicate significant differences at $P < 0.05$ between non-invaded (NI) and invaded (I) soils

	A		B		C	
	NI	I	NI	I	NI	I
Microbial biomass	488.6b	787.0a	180.0b	241.8a	96.2b	294.6a
Bacteria	203.3b	294.1a	80.3b	80.9a	32.3b	94.9a
Fungi	10.9b	31a	6.3b	16.7a	3.0b	14.0a
Bacteria gram+	113.6b	156.4a	42.6b	51.3a	15.3b	50.2a
Bacteria gram-	48.1b	89.9a	25.0a	19.5b	13.2b	27.1a
Bacteria/Fungi	18.6a	9.4b	12.7a	4.8b	10.9a	6.8b
gram+/gram-	2.4a	1.7b	1.7b	2.6a	1.2b	1.9a

ones (Table 3). Overall, the plant species associated with annual and perennial grasslands (therophytes and hemicryptophytes) were found to be the least represented in *Carpobrotus* cfr. *acinaciformis*-invaded areas. For instance, *Rumex bucephalophorus*, an annual species of particular conservation value (Conti et al. 1997), occurred exclusively within non-invaded plots. Other research has confirmed the sharp decrease of therophytes, and generally also of hemicryptophytes, in *Carpobrotus*-invaded habitats (Vilà et al. 2006; Fried et al. 2014). This is especially worrying because of the large presence of endangered or rare native species within these life forms in the Mediterranean flora (Heywood 1995). Chamaephytes seem to be differently affected by *Carpobrotus* cfr. *acinaciformis* invasion, having been observed either an increase or a decrease of their presence and/or abundance in invaded sites, suggesting the existence of a strongly site-specific response (Vilà et al. 2006; Fried et al. 2014). It is also noteworthy to point out that some native species such as *Periploca angustifolia*, *Senecio cineraria* subsp. *bicolor* and *Lycium intricatum* seem to be quite resistant to invasion by *Carpobrotus* cfr. acinaciformis at the adult stage, but their natural regeneration is severely impacted and seriously hindered by invasive establishment. Interestingly, a similar pattern was found in coastal dunes invaded by *Carpobrotus edulis* in Spain, where adult native plants were not affected by the invasive presence while the establishment of their seedlings in competition with the invasive species was seriously hindered (Novoa and González 2014). These competitive relationships have been put in relation with the altered soil conditions in terms of fertility, reaction and microbial community.

As concerns the impacts on the flora and vegetation, we may argue that a key role may be played by belowground modifications, in terms of chemical properties and microbial assemblage. Apart from direct mechanisms of competition (e.g. for water resources, D'Antonio and Mahall 1991), *Carpobrotus* spp. may compete via indirect mechanisms involving changes in microbial assemblages (de la Peña et al. 2010). In fact, we found significant effects on soil parameters, already 8 years after the start of the invasion, and especially starting from low soil nutrient content, as observed in other invasive species (Dassonville et al. 2008). Our results are consistent with other studies showing a clear increase in soil fertility as a consequence of *Carpobrotus* spp. invasion, especially in terms of C content (Vilà et al. 2006; Conser and Connor 2009; de la Peña et al. 2010; Santoro et al. 2011; Novoa et al. 2013, 2014). Accordingly, a positive value of C index is generally associated to *Carpobrotus* spp. invasion, whereas just three cases, never statistically significant, showed an opposite trend. Overall, in invaded soils of Linosa island N and C reached 0.25 % and 1.97 %, respectively (Tab. 4); values not so far from those registered in islands maquis stands, equal to 0.36 % and 3.21 %, respectively (Schiere 2000). In our study areas, C index decreased in relation to time since invasion (Fig. 3); the mean value was 0.62, lower than 1.05, the overall mean value found in the aforementioned bibliography.

A similar pattern is found taking into account N index, which was positive in most of the examined cases, whereas it was negative just in four, but statistically significant in a single case (Novoa et al. 2014). Overall, mean N index in the selected bibliography was

0.47 (Vilà et al. 2006; de la Peña et al. 2010; Santoro et al. 2011; Novoa et al. 2013, 2014), a value higher than that found in our study (mean value = 0.28) (Fig. 3). These results indicate that on average *Carpobrotus* spp. cause about a doubling in soil carbon content and an increase of almost 50 % in nitrogen content in invaded soils. Several studies reported also the acidification of soil after the invasion by *Carpobrotus* spp. (Vilà et al. 2006; Conser and Connor 2009; de la Peña et al. 2010; Santoro et al. 2011; Novoa et al. 2013, 2014); such effect may, in turn, affect the availability of some elements, such as Ca and Mg (D'Antonio and Haubensak 1998), and especially phosphorous, which generally is increasingly available in invaded areas (Novoa et al. 2014). Also in this case the effect is less marked in our study areas, where on average the pH was reduced by 0.21 compared to an overall average in consulted literature of 0.50. Both time since invasion and the peculiar characteristics of the habitats of Linosa could have determined this difference. Some of the previous studies have generally reported that *Carpobrotus* spp. were introduced in the beginning of the 20th century (e.g. Novoa et al. 2013) while in our case the invasion occurred much earlier, not more than 20 years before.

Soil microbes are essential for soil and ecosystem functioning (Jia et al. 2005; deVries and Shade 2013), particularly for organic matter decomposition and nutrient cycling (Laudicina et al. 2015), but also for the maintenance of plant diversity as plant-plant relationship are often soil microbes-regulated via direct and indirect mechanisms (e.g. van der Heijden et al. 2008). However, they have only recently become a focus of study in restoration ecology and in invasion biology as well (e.g. van der Putten et al. 2007). The functionality of soil microbial communities strongly depends on the dominant plant species and its conditioning on edaphic parameters (Kara and Bolat 2008). An invasive species, due to its ability to dominate plant communities, is expected to bring out deep changes in nutrient cycling processes, especially when it considerably differs from native species (e.g. in life history strategy, litter accumulation, leaf traits, nitrogen fixation activity, ecc.) as in the case of *Carpobrotus* spp. in the Mediterranean basin (Strauss et al. 2006).

The increase in soil microbial biomass after invasion by *Carpobrotus* cfr. *acinaciformis* is consistent with the observed increase in total organic C and N, being the greatest in the area A. Such results agree with Laudicina et al. (2012) who reported that microbial biomass generally increased by increasing total organic content (TOC), the latter being the food source of the former. Such findings suggest that colonisation by *Carpobrotus* cfr. *acinaciformis* improves the soil environment so hosting a greater amount of microorganisms. However, the effect of colonisation was not uniform among the investigated groups of soil microorganisms. In fact, in invaded soils the decrease of the bacteria/fungi ratio was registered, and it was mainly due to the greater relative increase of fungal biomass with respect to bacterial biomass instead of a decrease of bacterial one. The dominance of either fungi or bacteria in a soil depends on many factors among which soil reaction (Bååth and Anderson 2003), availability of organic C, quality of the plant residues (e.g. C/N ratio), as well as soil moisture and temperature (Strickland and Rousk 2010). Conser and Connor (2009) found that *Carpobrotus edulis* lowers soil reaction and increases organic matter content due to the recalcitrance of its tissue to decomposition. Actually, in our study areas, soil reaction decreased following colonization and the organic C content increased, but such shifts were not so consistent to justify the observed variation of the bacteria/fungi ratio (Strickland and Rousk 2010). On the other hand, the greater relative increase of the fungal biomass could be also ascribed to a cover effect by *Carpobrotus* cfr. *acinaciformis*. In fact, *Carpobrotus* cfr. *acinaciformis* is likely to determine an increase and a decrease of soil moisture and temperature, respectively; these altered microclimatic conditions may favor the fungal growth (Killham 1994). The shift in bacteria/fungi ratio could have affected the carbon use efficiency by microorganisms with fungi being more efficient in utilizing organic C substrates than bacteria (Laudicina et al. 2012). Overall, such findings have a great importance from an environmental point of view as the lower bacteria/fungi ratio has been associated to sites having a greater potential in C sequestrating (Jastrow et al. 2007). The gram+/gram- ratio was also affected by *Carpobrotus* cfr. *acinaciformis* colonisation, although no clear trend emerged comparing invaded and non-invaded plots. Such finding, however, may be of great importance also from an environmental point of view, since bacterial groups also have different C use efficiency (Fierer et al. 2003) and hence they could play a key role in affecting soil C sequestration. Furthermore, gram+/gram- ratio has a strong influence in the resistance and resilience of microbial communities to external disturbances (deVries and Shade 2013). However, further research is needed to understand how this shift in microbial community structure affects the carbon use efficiency and the growth performance of co-occurring native plants, therefore having the potential to modify competitive interactions.

Our results indicate, for the first time, that *Carpobrotus* cfr. *acinaciformis* may impact aboveground as well as belowground community diversity and structure and resources pool; moreover, a residence time of just 8 years was sufficient to modify soil and vegetation characteristics.

The management implications of such deep ecological changes are particularly relevant because *Carpobrotus* cfr. *acinaciformis*, being able to modify nutrient pools, is suspected to leave behind invasion legacies in the invaded ecosystem (Corbin and D'Antonio 2012). This means that some soil conditions, altered by invasion, may persist for a given time even after the removal of the invasive species. For instance, soils invaded by leguminous species, such as *Robinia pseudoacacia* L. (Von Holle et al. 2013) or *Lupinus arboreus* Sims (Maron and Jefferies 2001), have maintained higher N content than non-invaded areas at least for 14 and 5 years after eradication, respectively. The residual effects on soil by *Carpobrotus* spp. have been assessed comparing uninvaded sites (control), invaded sites (altered condition) and restored or treated sites, from which the alien species had been removed. Soil nutrient content and pH were found to be still altered 12 and 18 months after *Carpobrotus edulis* removal (Novoa et al. 2013; D'Antonio 1990b). By contrast, other soil parameters such as salinity, Na^+ and Mg^{++}, were approaching pre-invasion levels and seemed to quickly recover (Novoa et al. 2013).

A substrate so deep altered compared to the pre-invasion status could be not more suitable to host local plant species and could seriously compromise the chances or the required time for the native habitat restoration. Many native species experienced reduced germination, growth, development and reproduction in soils previously occupied by *Carpobrotus* (Conser and Connor 2009; de la Peña et al. 2010; Novoa et al. 2013; Novoa and González 2014). The effect, however, is strongly species-specific (de la Peña et al. 2010; Novoa et al. 2013; Novoa and González 2014). An alteration of interspecific competitive dynamics post-removal may occur, with ruderal and opportunistic species, which may take advantage of soil enrichment, being favored over rare and/or endangered native species (Novoa et al. 2013). One year after the eradication, the recovery by native species was quite slow both in some coastal habitats in Sardinia (Italy) and Pontevedra (Spain) (Carta et al. 2004; Novoa et al. 2013), whereas rapid recolonization processes by local species were observed in Andalucia (Andreu et al. 2010). In the first two cases, habitat restoration planning may not solely rely on eradication interventions but soil amelioration via physical or chemical means and a constant and long-term monitoring of treated areas should also be considered (Ruffino et al. 2014). Therefore, our research provide further evidence of the complicated management of this invasive species, because the changes induced in the soil and belowground communities are much more slow and difficult to recover (Molinari et al. 2007) and they are very likely contributing to the invasive success of *Carpobrotus* cfr. *acinaciformis* in Mediterranean ecosystems.

Conclusions

Carpobrotus cfr. *acinaciformis* is very different from co-occurring native species in our study areas and its invasion significantly increased soil fertility, microbial biomass, decreased soil pH and altered the microbial community structure by favoring the growth of fungi.

It is likely that these altered conditions, or some of them, may persist over a large temporal scale, and the long-term consequences of the invasion may thus affect and/or prevent the establishment of endemic or endangered native plant species of Linosa. In fact, the components of native flora most at risk from extinction are represented by therophytes, which typically grow in Linosean soils characterized by low levels of carbon and nitrogen content.

These results do provide further evidence that *Carpobrotus* cfr. *acinaciformis* may be quite rightly defined an ecosystem engineer, due to its great ability to change the characters of the invaded ecosystem, either at aboveground and belowground level. Furthermore, we found that a residence time of 8 years may be enough to determine significant impacts in vegetation, soil parameters as well as in the structure of microbial assemblages.

The general "benefits" provided by *Carpobrotus* cfr. *acinaciformis*, especially on soil fertility *sensu lato*, do not have to divert the attention from native species and local biodiversity improvement and conservation. In fact, the high competitive ability of *Carpobrotus* cfr. *acinaciformis* is known to drastically reduce biodiversity in the Mediterranean areas and we think that the enhancement of carbon and nitrogen sequestration is not sufficient to counterbalance the negative impacts on species and habitats associated to its uncontrolled spread. Studies on the relationship between time since invasion, soil fertility evolution, the dynamics of vegetation and soil microorganisms, also in the case of *Carpobrotus* cfr. *acinaciformis* removal, are worthy to be further investigated.

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