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Monographs of invasive plants in Europe: *Carpobrotus*

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ABSTRACT

This report synthesizes all aspects of the taxonomy, distribution, history of introduction and spread, ecological constraints (including preferred climate, substratum and habitats), responses to biotic and abiotic factors, biology (including phenology, vegetative and reproductive biology), economic importance and human uses, ecological impacts, legislation and management of *Carpobrotus* N.E.Br. (Aizoaceae), a prominent invasive plant in Europe.

Carpobrotus species are mat-forming trailing succulent perennial herbs native from South Africa, introduced in Europe for ornamental and soil stabilization purposes since the beginning of the seventeenth century, now widely naturalized on coastal habitats of southern and western Europe. *C. acinaciformis* and *C. edulis* are the main species recognized outside South Africa, together with their hybrids and potential hybrid swarms. Identification conflicts both in the native and invaded areas raise doubts on the taxonomy of these taxa, but hybridization processes may boost adaptive changes in the invaded range.

The release of *Carpobrotus* in natural environments and protected areas is prohibited in several European countries, but this taxon is not included in the list of invasive species of Union concern. *Carpobrotus* is a pioneer of disturbed sites and coastal areas including cliffs and sand dune systems, due to its tolerance to stress factors such as salinity, drought and excess of light. *Carpobrotus* invasion ultimately affects patterns of native species diversity. Moreover, it has been recognized as a major driver of soil conditions shifts and soil geochemical processes disruptions, representing a serious threat for coastal habitats.

Management plans for *Carpobrotus* must consider its high plasticity for morphological and ecophysiological traits, which may probably explain its tolerance to a wide range of ecological conditions. Its flexible mating systems, which represent an optimal strategy to facilitate local adaptation and habitat colonization, include ability to produce apomictic seeds, self- and cross-pollination, and an intense vegetative clonality. In addition, *Carpobrotus* produces a large seed bank with a moderate short-term persistence, and fruits are effectively dispersed by mammals. The most efficient control methods are physical removal and herbicide application on leaves, whereas integration of biological control with other conventional management methods are likely to be most effective. A long-term monitoring of control actions and restoration of soil conditions are needed to prevent recovering from clonal parts, seed bank or mammal faeces as well as potential new invasions by other opportunistic species.

Taxonomy

Names and classification

Scientific name: *Carpobrotus edulis* (L.) N.E.Br., 1926

Basionym: *Mesembryanthemum edule* L., 1759

Taxonomic position: Eudicotyledons, Order *Caryophyllales* Juss. ex Bercht. & J.Presl

Family: *Aizoaceae* Martinov, subfamily *Ruschioideae*

Common names: sour-fig, cape-fig, Hottentots-fig, ice plant [EN], fico degli Ottentotti (IT), uña de gato, bálsamo [ES], figue marine, griffes-desorcières [FR], hottentottenfeige, pferdefeige [DE], chorão-da-praia [PT].

EPPO code: CBSSE

Type: the type of *C. edulis* is an iconotype, ie the drawing of "*Mesembriathemum falcatum majus, flore amplo luteo*", table 212 in Dillenius, Johann Jakob.

Hortus Elthamensis [...] Tomus alter, 1732 (Wisura and Glen 1993).

Scientific name: *Carpobrotus acinaciformis* (L.) L.Bolus, 1927

Basionym: *Mesembryanthemum acinaciforme* L., 1753

Taxonomic position: Eudicotyledons, Order Caryophyllales Juss. ex Bercht. & J.Presl

Family: Aizoaceae Martinov, subfamily Ruschioideae

Common names: sour-fig, cape-fig, Hottentots-fig, ice plant [EN], fico degli ottentotti (IT), uña de gato, bálsamo [ES], figue marine, griffes-de-sorcières [FR], hottentottenfeige, pferdefeige [DE], chorão-da-praia [PT].

EPPO code: CBSAC

Type: the type of *C. acinaciformis* is an iconotype, ie the drawing of “*Mesembriathemum acinaciforme flore amplissimo purpureo*”, table 211 in Dillenius, Johann Jakob. Hortus Elthamensis [...] Tomus alter, 1732 (Wisura and Glen 1993).

Identification conflicts

Aizoaceae *sensu* Hartmann (1993, 2012) is the largest family of leaf succulent plants and consists of about 2,500 species in 127 genera. Members of this family are predominantly perennial shrubs or subshrubs, rarely annual or biennial herbs. The primary centres of diversity are South Africa and Southern Europe, but a few species are native to America, Australia and New Zealand (Hartmann 1993; Klak et al. 2003). Within the family Aizoaceae, the subfamily Ruschioideae contains about 1,585 species in 112 genera including *Carpobrotus* N.E.Br. (Hartmann 1993). Approximately 20–25 species are recognized in the genus, most from South Africa, four from Australia and New Zealand and one from South America. However, there are several taxonomic uncertainties and a full review of the genus is needed.

The taxonomic identity of the invasive *Carpobrotus* species in Europe and the Mediterranean has long been a subject of debate. Two species are most often included in the European floras: *C. edulis* and *C. acinaciformis* (Cabello 2009; Clement and Foster 1994; Gonçalves 1990; Pastor 1987; Tutin 1993).

According to the original descriptions and floras, the main diagnostic character for these species is petal colour, yellow in *C. edulis*, purple in *C. acinaciformis*. However, there are reasonable doubts on the validity of flower colour as a reliable character for identification. Strid and Tan (1997) suggest that records of *C. acinaciformis* from Greece correspond to *C. edulis* var. *rubescens* Druce, a purple-perianth variety of *C. edulis*. The occurrence of this variety, commonly used in gardening (Cullen 2011) has been reported in Europe (eg Crete, Fielding and Turland 2005; Ireland, Parnell and Curtis 2012). Preston and Sell (1988) also treated the variation in flower colour within the *C. edulis* complex in the British Isles, recognizing three varieties including *C. edulis* var. *edulis* with pure yellow petals, *C. edulis* var. *rubescens* with purple flowers, and *C. edulis* var. *chrysophthalmus* C.D.Preston & P.D.Sell, with petals yellow at base and purple at apex. They suggest a possible hybrid origin for this variety. More recently, some authors have confirmed the occurrence of another taxon with an unclear identity, generally described as close to *C. acinaciformis*. This has led to the use of a *C. aff. acinaciformis* entity in the scientific literature (eg Suehs, Médail, and Affre 2003; Ortiz, Lumbreras, and Rosselló 2008; Traveset, Moragues, and Valladares 2008). According to Suehs, Affre, and Médail (2004a, 2004b) this could be a hybrid form between the two species. Intercrosses between *C. edulis* and *C. acinaciformis* have been reported in South Africa (Wisura and Glen 1993) and in Europe (Ortiz, Lumbreras, and Rosselló 2008; Andreu et al. 2010; Suehs, Affre, and Médail 2004a, 2004b) (*see reproductive biology section*).

Wisura and Glen (1993), in their monograph on South African species of *Carpobrotus*, used a number of morphological characters for the identification of *C. edulis* and *C. acinaciformis*, synthesized in Table 1. These characters were partly tested in introduced populations of southern France by Suehs, Affre, and Médail (2004a, 2004b), who concluded that both species are present in the area, although a wide hybridization zone has produced a hybrid swarm between *C. edulis* and *C. acinaciformis*, hampering identification. Preston and Sell (1988) developed their own key for *Carpobrotus* but, as noted by Hartmann (2001),

Table 1. Main diagnostic characters for *Carpobrotus edulis* and *C. acinaciformis* from Wisura and Glen (1993) with an addition from Gonçalves (1990).

CHARACTER	CARPOBROTUS EDULIS	CARPOBROTUS ACINACIFORMIS
LEAVES	Straight or very slightly curved	Scimitar-shaped
LEAVES (GONÇALVES 1990)	Green with equilateral triangular section	Glaucous with isosceles triangular section
RECEPTACLE	Receptacle turbiniform, 20–40 mm long, tapering gradually into the pedicel	Receptacle oblong or subglobose, 12–20 x 12–18 mm, abrupt joint with the pedicel
CALYX	Calyx lobes unequal, the longest 30–70 (80) mm, the shortest 10–35 mm	Calyx lobes sub-equal, the longest 10–35 mm
COROLLA	Petals yellow, fading to pink when aging	Petals rose purple
OVARY	With 9–11 loculi	With 12–16 loculi

discrimination between the different taxa is unclear. In the key of Gonçalves (1990) and in other floras from the Iberian Peninsula (eg Cabello 2009) the section of the leaf is considered as a discriminant character (an equilateral triangle for *C. edulis*, isosceles for *C. acinaciformis*), already suggested by Marloth (1913) but not considered by Wisura and Glen (1993).

Several other *Carpobrotus* species have been recorded as alien to Europe, but many are a result of misidentifications or nomenclature ambiguity (Preston and Sell 1988; López González 1995; Hartmann 2001). *Carpobrotus chilensis* (Molina) N. E.Br. is a smaller species with an unknown origin that occurs in the Pacific coasts of western South America, and introduced in California, where it is known to hybridise with *C. edulis* (Vilà, Weber, and D'Antonio 1998). Reports in Europe are from the Balearic Islands, but these occurrences have not been confirmed (Akeroyd and Preston 1990; López González 1995). *Carpobrotus glaucescens* (Haw.) Schwantes and *C. virescens* Schwanthes, two species from Australia (Blake 1969), have also been reported from the British Isles (Preston and Sell 1988). Unless otherwise stated, we refer to the *C. edulis* – *C. acinaciformis* complex throughout this monograph, with specific comments for a given taxon (eg *C. edulis*, *C. acinaciformis*, *C. aff. acinaciformis*) reproduced as in the original source (Figure 1).

Morphological description

The genus *Carpobrotus* consists of mat-forming trailing succulent perennial herbs, with opposite leaves, somewhat connate at the base, sharply 3-angled, with a triangular cross-section, ranging from isosceles to equilateral depending on the species (Table 1). The chlorenchyma occurs all-round the periphery and colourless water-storage tissue in the core. The water-storage tissue may account for 69% of the leaf fresh weight as opposed to 30% of the leaf dry weight (Earnshaw, Carver, and Charlton 1987). The main vascular bundles run through the water-storage tissue with a large bundle occurring in the centre and a smaller bundle near each corner (Earnshaw, Carver, and Charlton 1987). The chlorenchyma of *C. edulis* contains numerous secretory cells with mucilaginous contents, which are released when fresh material is cut. These cells also occur sporadically in the water storage tissue (Earnshaw, Carver, and Charlton 1987).

The flowers of *Carpobrotus* are among the largest in the subfamily Ruschioideae. They are pedicellate, terminal, solitary, up to 120–150 mm in diameter (Wisura and Glen 1993). Each pedicel has a pair of leaf-like bracts, usually borne at the midpoint. The calyx in *Carpobrotus* is almost always composed of five lobes (sepals), which may be sub-equal (*C. acinaciformis*) or very unequal (*C. edulis* subsp. *edulis*). The receptacle is considered a very important character in this genus, turbiniform



Figure 1. The *Carpobrotus* complex in the invaded range at different development stages. a) Detail view of *C. edulis* flowers with yellow petals, fading to pink when aging, and leaves with equilateral triangular section; b) Detail view of *Carpobrotus* sp., tentatively identified as *C. acinaciformis* with petals rose purple and yellow filaments, and leaves with isosceles triangular section. See section on taxonomy for a more detailed information on identification conflicts of the species.

and tapering into the pedicel in *C. edulis*, while not tapering into the pedicel in *C. acinaciformis* (Wisura and Glen 1993; Table 1). The multi-locular ovaries are characteristic of the genus *Carpobrotus*, with the number of locules varying within species and sometimes even on a single plant. The number of styles corresponds with the number of locules (Wisura and Glen 1993). The fruit is fleshy, pulpy, indehiscent, without valves and bearing many glossy, brown, obovoid and slightly compressed seeds (Wisura and Glen 1993).

Carpobrotus edulis is the only member of the genus to have distinctly yellow flowers, fading to pink when aging (Wisura and Glen 1993) (Figure 1). In its native range, two subspecies have been described, notably *C. edulis* subsp. *edulis* and *C. edulis* subsp. *parviflorus* Wisura & Glen. The former is the most widespread in both its native and invaded range; the latter has smaller flowers and its habitat seems to be limited to the mountains of the south-western Cape above 800 m a.s.l. (Wisura and Glen 1993).

Carpobrotus acinaciformis occurs in abundance on the Cape Peninsula, although conflicts in the identification of *Carpobrotus* species persist even in its native range (A. Novoa pers. observ.). Its petals are rose purple, filaments pinkish, pallid towards the base. The distinctly scimitar-shaped leaves and the oval fruit distinguish this species from other *Carpobrotus* species (Table 1). However, in the native range, there is a considerable variation in the appearance of the plant in contrasting habitats (A. Novoa pers. observ.).

Distribution and status

Native range

Carpobrotus edulis is native to the Eastern Cape, Northern Cape and Western Cape in South Africa, where it has been reported as growing mainly on coastal and inland slopes at low altitudes (Manning and Paterson-Jones. 2007), although it can grow in the mountains of the south-western Cape above 800 m a.s.l. (subsp. *parviflorus*, Wisura and Glen 1993). On the other hand, the native range of *C. acinaciformis* is restricted to the Western Cape, from Saldanha to Mossel Bay, where it grows in coastal sandy soils near the sea (Wisura and Glen 1993; Raimondo et al. 2009). Both species (and probably their hybrids) have been intensively planted as ornamental plants all over South Africa, especially in coastal areas. In fact, it is almost impossible to find any large area in the South African coast devoid of *Carpobrotus* (A. Novoa, pers. observ.) (Figure 2).

Introduced range

Carpobrotus species have been introduced in all five continents and they are widely naturalized on many coastal habitats outside their native range.

In Oceania, *C. edulis* was introduced in Australia (Weber 2003) where it is naturalized along the southern and eastern coast, being recorded on South Australia, New South Wales, Victoria, and Tasmania. In the northeast of the country, it has also been documented on the south coast of Queensland (Atlas of Living Australia Website 2017); in Western Australia, it is

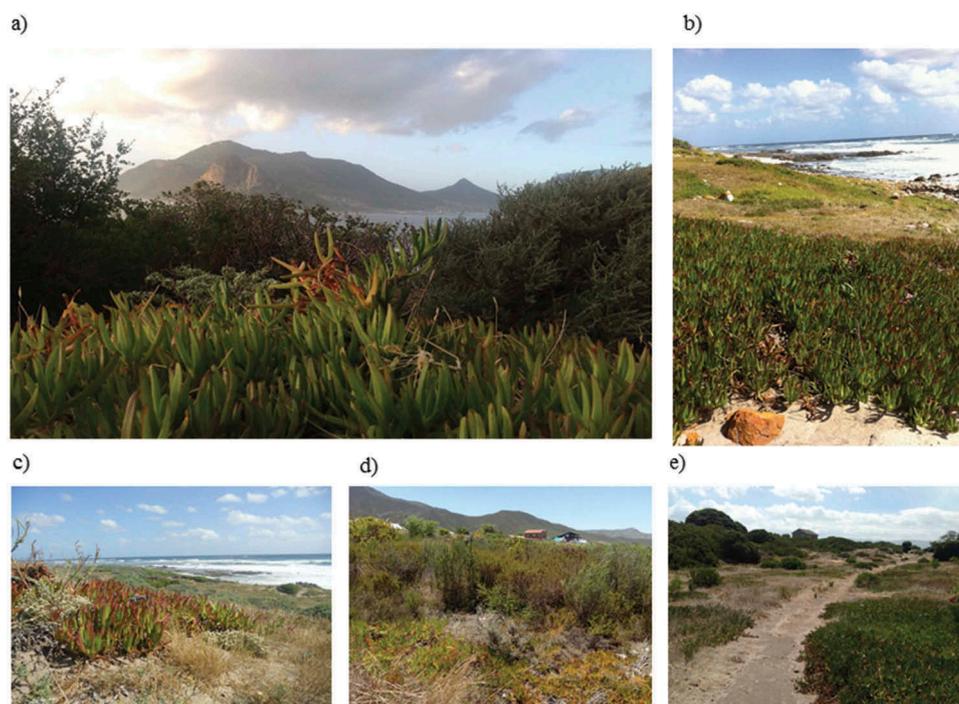


Figure 2. Coastal areas inhabited by *Carpobrotus* in its native range (South Africa). a) View to Hout Bay; b-c) Cape Point; d) Kleinmond; e) Hawston.

naturalized along the west coast from Perth to Albany (Malan and Notten 2006). This species was also cultivated and recorded on French Polynesia; in Tahiti Island, it has a restricted distribution (Florence 2004) but in Pitcairn Island it occurs in a wider area and is considered as a potential invader in cliffs (Meyer 2000). In New Zealand, *C. edulis* is considered invasive (Howell 2008) and it has established on many parts of the coast; it occurs in “cliffs and sand dunes, coastal and inland on railway and roadside cuttings” and it spreads from the North Island (Northland, Auckland, Bay of Plenty, Wellington, Wairarapa) to the South Island (Nelson, Marlborough, Canterbury, Otago, Southland) (Webb, Sykes, and Garnock-Jones 1988).

In Northern Africa, *C. edulis* is naturalized in Algeria and Morocco (USDA National Genetic Resources Program 2012; GBIF.org 2017b) and it has been introduced in Lybia (Delipetrou 2009). It can also be found naturalized along coastal areas of Sousse, Tunisia (Brandes 2001; Greuter and Domina 2015; GBIF.org 2017b).

In North America, it is naturalized in Florida (Wunderlin et al. 2018) and is considered invasive in California (CAL-IPC 2006) from the Northwest coast (Eureka) to Mexico (Rosarito bay, Lower California) (Albert, D’Antonio, and Schierenbeck 1997). In South America, *C. edulis* has been planted extensively as an ornamental in Argentina (Schmalzer and Hinkle 1987). In Chile, *C. edulis* has naturalized in the Juan Fernández Archipelago and coastal areas of Valparaiso and Biobío regions (Sotes, Cavieres,

and Rodríguez 2015). It has also been introduced in Bolivia (Jørgensen, Nee., and Beck 2014) and Uruguay (Masciadri, Brugnoli, and Muniz 2010) where it was only recorded in Punta Ballena, Maldonado (Ríos et al. 2010).

In Western Asia, *C. edulis* has become an invader over large natural areas in Israel (Dufour-Dror 2013). It was also recorded in Lebanon, Syria and Cyprus (Delipetrou 2009) and it is considered as alien on Turkey (Arslan, Uludag, and Uremis 2016).

In Europe, the presence of two hybridizing taxa (*C. edulis* and “*C. aff. acinaciformis*”) in the Mediterranean basin is well documented (Suehs, Affre, and Médail 2004a, 2004b; Verlaque et al. 2011). They are widely distributed along the Mediterranean coast from Spain to Greece and along the Atlantic coast from Gibraltar to the United Kingdom (Figure 3).

In Spain, *Carpobrotus* has invaded most coastal regions (Gonçalves 1990) along the Cantabrian, Atlantic (eg Campos et al. 2004; Campos and Herrera 2009; Torre Fernández 2003; Fagúndez and Barrada 2007) and Mediterranean coast (eg Dana et al. 2005) including the Balearic Islands (Moragues and Rita 2005). In Mainland Portugal, *Carpobrotus* is also considered invasive in coastal ecosystems and both taxa occur from the North (Minho) to the South (Algarve) (Marchante et al. 2014). In Mediterranean France they are widely spread in the Albères Coast, Provence-Alpes-Côte d’Azur, Bagaud and Porquerolles (Hyères archipelago, Provence) and Corsica, which is particularly invaded by these two taxa (Suehs, Affre, and Médail

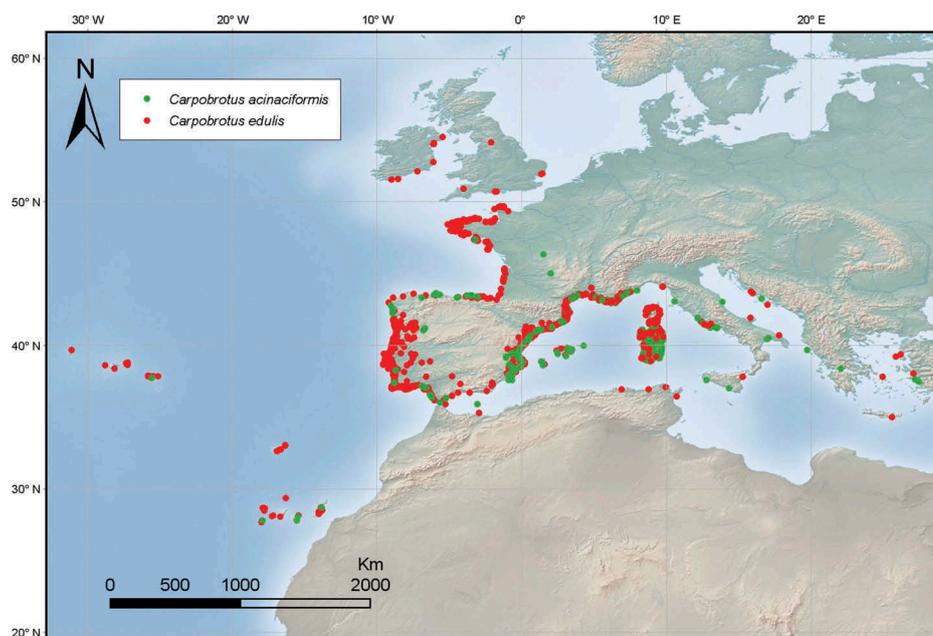


Figure 3. Distribution map of *C. edulis* and *C. acinaciformis* in Western Europe. The map is given according to GBIF (2017) and the Fédération des Conservatoires botaniques nationaux (2013) with some modifications based on our unpublished data on the species. Species as in the original source, see text for identification problems.

1999; Suehs, Médail, and Affre 2001). In Sardinia, *Carpobrotus* has also naturalized (Camarda et al. 2016; EPPO 2006), and in Sicily both *C. aff. acinaciformis* and *C. edulis* are reported as frequent on beaches throughout the Island (Giardina, Raimondo, and Spadaro 2007). *Carpobrotus* is one of the most threatening invasive species on Central Italy, where it is particularly widespread along the Tyrrhenian coast (Acosta, Izzi, and Stanisci 2006; Carranza et al. 2010; Santoro et al. 2011). *Carpobrotus edulis* is also expanded along the coast from Croatia to Albania (Barina et al. 2014; Boršić et al. 2008). In the alien flora of Greece, only *C. edulis* was catalogued as naturalized with invasive behaviour (Arianoutsou et al. 2010). However, both taxa can be found invading coastal ecosystems including some Aegean Islands as Crete and Lesbos (Vilà et al. 2006). *Carpobrotus edulis* was also introduced into Malta where it has naturalized throughout the Maltese islands (Malta Environment and Planning Authority 2013).

In Northwestern Europe, *Carpobrotus* is present in the British Isles. In England, it is mainly found in Cornwall (SW) and in the Channel Islands it has spread widely on Guernsey Island (Varnham 2006), but other occurrences are reported from scattered places along the coast (Preston and Sell 1988). In Ireland, *C. edulis* is locally naturalized and often abundant on coastal cliffs (Reynolds 2002). In Belgium, *Carpobrotus* is not yet naturalized but it is considered to have a high invasion potential in coastal dune ecosystems (Invasive Alien Species in Belgium Website 2013). Along the Atlantic coast of France, *Carpobrotus* is reported from Basque country to Cotentin, with higher densities in Brittany. Schmalzer and Hinkle (1987) reported that *C. edulis* has been planted extensively as an ornamental plant in Germany.

In the Atlantic islands, *Carpobrotus* has been reported in the Azores archipelago, although not among the most frequent alien species (Silva and Smith 2006), and in Madeira and Porto Santo islands (Jardim et al. 2003; Marchante et al. 2014; GBIF 2017). In the Canary archipelago, *C. edulis* has been reported as casual in all islands (Gallo, de la Torre, and Rodríguez 2008) while *C. acinaciformis* is locally established in Gran Canaria Island (Sanz-Elorza, Dana, and Sobrino 2005). Outside Europe, the Cape Verde, Santo Antão and Fogo Islands have also been colonized by *Carpobrotus*. In St. Helena Island, *C. edulis* occupies large areas especially in the north (Ashmole and Ashmole 2000).

History of introduction and spread

South African Aizoaceae have been grown in Europe for ornamental purposes since the beginning of the seventeenth century, and a thorough description of the botanists, scientists and plant collectors involved in these early activities can be found elsewhere (Codd

and Gunn 1985; Gunn and Codd 1981). Among the South African Aizoaceae, *Carpobrotus* is one of the earliest arrivals since its presence in European gardens dates back to the late seventeenth century (Preston and Sell 1988). Retracting the history of spread in Europe is challenging. There is evidence of naturalized populations at the mouth of the English Channel (Channel Islands, West Cornwall coast, Isles of Scilly, northern Brittany) by the end of the nineteenth century (McClintock 1975; Le Sueur 1984; Lousley 1971; Davey 1909; GBIF.org 2017b; Preston and Sell 1988). These naturalized populations are very likely the result of propagule escapes from private botanical gardens and from the horticultural industry. For example, Aizoaceae were grown in gardens on the south Cornish coast at least since 1871 (Baker 1871). A few decades later, *Carpobrotus* could be collected from several naturalized populations around the area (Davey 1909; Thurston and Vigurs 1922). Also, the Isles of Scilly, 28 miles off South-West England, have a reputation for an exotic flora that owes much to a private botanical garden established in the islands by the mid-nineteenth century, and to the flower industry that flourished in the archipelago later in that century. By the early 1920s, naturalized *Carpobrotus* was common in the islands (Lousley 1971). On the french side of the entrance to the English Channel (France), there has been another private botanical garden in the Island of Batz (near Roscoff, Brittany) since 1897 (Clavreul 2008). Interestingly, Batz already had a rich exotic flora before the garden was created because sailors from the island had acclimated locally plants from all over the world. Nonetheless, gardening might not be the only origin for the established populations since the plant may have also been deliberately released at some sites for soil and sand dune stabilization (Preston and Sell 1988). In other areas of the world (eg California), several *Carpobrotus* species have been used for soil stabilization since the early twentieth century (Albert, D'Antonio, and Schierenbeck 1997).

Given the above, it is unsurprising that the oldest European record of *Carpobrotus* in GBIF is from the island of Batz (GBIF.org 2017b): a preserved specimen collected in 1889 and housed in the MNHN in Paris (Museum National d'Histoire Naturelle 2017) (Table 2). Records of *Carpobrotus* from European countries stored in GBIF (> 3000 records as *C. edulis* and > 350 records as *C. acinaciformis*; accessed on 1 May 2017) reveal that naturalized populations could be found in regions as far apart as the English Channel and the northern coast of the Western Mediterranean by the beginning of the twentieth century (GBIF.org 2017a, 2017b). The collection from Batz is nearly contemporaneous with a preserved specimen from the French Mediterranean coast (1903: Toulon, Provence-Aspes-Côte-d'Azur) (Museum National d'Histoire Naturelle 2017), and

Table 2. Oldest records for *Carpobrotus* from Europe stored in GBIF as of 1 May 2017. Only collections dated before 1950 are included. Complete data sets available at <http://doi.org/10.15468/dl.hzsn8l> (as *C. acinaciformis*) and at <http://doi.org/10.15468/dl.lkncy> (as *C. edulis*).

GBIFID	Taxon ^a	Year	Country: Region	Locality	Institution ^b	Recorded by	Catalog number/link
438,497,513	<i>C. edulis</i>	1889	France: Brittany	Île de Batz	MNHN	Legris	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00654557
438,497,512	<i>C. edulis</i>	1903	France: Provence-Aspes-Côte-d'Azur	Toulon	MNHN	Legris	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00654556
211,307,378	<i>C. edulis</i>	1911	Spain: Catalonia	Barcelona	MA	F.re Senmen	30,243-1
1,096,871,026	<i>C. acinaciformis</i>	1912	Italy: Liguria	Bordighera	S	Hj. Hafström	S:VascularPlants:S14-50,729
1,096,871,035	<i>C. acinaciformis</i>	1914	France: Provence-Aspes-Côte-d'Azur	Canadel	S	Hj. Hafström	S:VascularPlants:S14-50,731
1,096,871,024	<i>C. acinaciformis</i>	1914	France: Provence-Aspes-Côte-d'Azur	Pardigon	S	Hj. Hafström	S:VascularPlants:S14-50,733
1,096,611,973	<i>C. edulis</i>	1923	Italy: Liguria	Porto Maurizio, Bordighera	S	Arthur Roos	S:VascularPlants:S05-688
1,096,605,964	<i>C. edulis</i>	1926	France: Brittany	Roscoff	S	S. Grapengiesser	S:VascularPlants:S05-1460
1,096,606,490	<i>C. acinaciformis</i>	1928	France: Provence-Aspes-Côte-d'Azur	Cannes	S	H. Lenander	S:VascularPlants:S05-1931
211,307,379	<i>C. edulis</i>	1932	Spain: Galicia	A Lanzada	MA	Gz. Albo	30,244-1
1,138,834,332	<i>C. edulis</i>	1936	Portugal: Centro	Figueira da Foz	Naturalis	Kostermans AJGH	http://data.biodiversitydata.nl/naturalis/specimen/L.1685956
1,138,478,337	<i>M. edule</i>	1936	Portugal: Centro	Figueira da Foz	Naturalis	Kostermans AJGH	http://data.biodiversitydata.nl/naturalis/specimen/U.1057880
1,096,606,481	<i>C. acinaciformis</i>	1936	Spain: Catalonia	Barcelona	S	H. Lenander	S:VascularPlants:S05-1930
1,455,404,892	<i>M. acinaciforme</i>	1938	France: Provence-Aspes-Côte-d'Azur	Menton	NAM	Matagne Henri	FUNDP:NAM:000058
437,824,342	<i>C. edulis</i>	1946	France: Nouvelle-Aquitaine	Biarritz	MNHN	Sag, G.	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00041973

^a *C. edulis* = *C. edulis* (L.) N.E.Br.; *C. acinaciformis* = *C. acinaciformis* (L.) K.Bol.; *M. edule* = *Mesembryanthemum edule* L.; *M. acinaciforme* = *Mesembryanthemum acinaciforme* L.

^b MNHM = Vascular Plants Collection at Herbarium of Muséum national d'Histoire Naturelle (Paris); MA = Vascular Plant Herbarium at Real Jardín Botánico (Madrid); S = Phanerogamic Botanical Collections of the Swedish Museum of Natural History; Naturalis = Naturalis Biodiversity Center (Leiden); NAM = Herbarium of Namur at Université de Namur.

they are closely followed by records from Spain (1911: Barcelona, Catalonia) and Italy (1923: Bordighera, Liguria). Moreover, by the 1930s, the species had been recorded in the Atlantic coasts of Spain (1932: A Lanzada, Galicia) and Portugal (1936: Figueira da Foz, Centro region) while it was collected from Aquitaine by the mid-1940s (1946: Biarritz, Nouvelle-Aquitaine). It seems unlikely that all European naturalized populations of *Carpobrotus* were the result of dispersal from a single introduction event. Rather, several independent introductions and/or human-aided spread within Europe seem a more plausible explanation (Faulkner et al. 2017). Phylogeographic studies using molecular markers with appropriate resolving power are required to elucidate which scenario is most likely.

Fewer references can be found for Eastern Mediterranean countries, revealing a latter arrival and spread, although absence of records does not necessarily imply non-occurrence in the area. For example, the earliest record in Croatia dates back to 1951 as a cultivated species, but most records along the Croatian coasts as naturalized populations are dated after 2000 (Nikolić 2017) while the earliest record in Albania is from 1976 (Barina et al. 2014).

An examination of the records stored in GBIF over time provides a rough image of the spread of *Carpobrotus* across Europe. Any inference derived from this data set must be interpreted with caution, given the limitations of GBIF, a data-gathering platform that combines records from many independent sources with different levels of accuracy. For example, the low number of records gathered in the 1940s should be attributed to a drop in the number of field surveys, probably due to World War II, rather than to actual changes in the occurrence of *Carpobrotus* across Europe. Nonetheless, the 920 records stored in GBIF that provide a collection/observation date suggest some interesting patterns (Table 2 for links to the complete data set). Most records (883 records, 91%) were identified as *C. edulis*, and an overwhelming majority of them are field observations recorded very recently in the 2010s (808 records, 83%). These very recent records are clearly biased by surveys conducted along the Portuguese coast (698 records, 72%). Nonetheless, even excluding the records from 2010s, Portugal still accounts for 36% of the pre 2010 records, and ranks second in the number of records of *Carpobrotus* presence, after Spain accounting for 41% of the pre 2010 records. These data reveal that most of the occurrences of *Carpobrotus* stored in GIBF are from the Atlantic and Mediterranean coasts of the Iberian Peninsula. France (12% of pre-2010 records) and United Kingdom (6%) follow at some distance. As noted above, these four countries (plus Italy) are also the sites where *Carpobrotus* was detected at an early date,

suggesting that Western Europe was the entrance point to the continent and remains the region where this invader is most widely distributed. Before the 2010s, the number of records per decade has remained low for a long time. This may mean that a long phase of acclimatization took place before the invasive phase began. Alternatively, this invader may have gone rather unnoticed due to its restricted habitat. Only from 1980s, a smooth increase is observed in the number of records, mostly from the Iberian Peninsula. Again, the upward trend in the number of records may indicate an actual spread of the invader within the region or the growing interest in the monitoring of alien species.

Western Europe seems the likely source for the introduction of *Carpobrotus* to North Africa for ornamental and soil stabilization purposes. In Morocco, it was collected at the Atlantic coast (Mehdya) as early as 1934, while there is evidence that it was present on sand dunes in Tunisia at least in 1980 (GBIF.org 2017b).

Ecological constraints

Climate

According to the updated Köppen–Geiger Climate Classification (Kottek et al. 2006), the Cape Region is under the influence of a cold semi-arid climate or temperate climate with dry winters and hot and dry summers. Rainfall pattern shows dramatic variations in quantity, dropping from 2000 mm per year in the mountains facing the coast to 200 mm in the areas closest to the coast (Goldblatt 1997; Goldblatt and Manning 2002). Mean annual rainfall is 576 mm, most of which falls in winter (Mostert et al. 2017). The driest month of summer receives less than 30 mm and average month temperatures vary from 12.35 °C (July) to 21.60 °C (February).

As invasive, *Carpobrotus* is distributed in the five worldwide Mediterranean climate regions, all located between about 30° and 45° latitude North and South of the Equator and on the Western sides of the continents. In Europe, *Carpobrotus* occurs both under warm and hot-summer Mediterranean climate (classes Csa and Csb) throughout the Iberian Peninsula except the Cantabrian coasts, and the Mediterranean coasts of all countries, and Oceanic climate (class Cfb) in northern Spain, western France and the British Isles (Kottek et al. 2006).

The distribution of *C. edulis* outside its biogeographical area of origin does not seem to be constrained by the Mediterranean climatic boundaries. In fact, in Europe, *C. edulis* occurs in Northwestern France, the South of UK and occasionally in Ireland and northern Germany (see section *distribution in introduced range*). The potential climatic area suitable for *C. edulis* could increase in the future. According to

Thuiller et al. (2005), it could invade such areas as the North of UK, and the Tejo and Douro river basin in Portugal. The Southwestern coast of America exhibits a very high probability of occurrence including the North coast of Chile, the coast of Perú, Ecuador and Colombia, the entire California and some regions of Mexico. Some biomes of Central East Africa are also suitable to the invasion of *C. edulis*. The rate of spread of *C. edulis* in these areas may also depend on non-climatic factors such as propagule pressure.

Substratum

Soils in native/invaded areas

In the Cape region, the native biogeographic area of *Carpobrotus*, most of the region is covered with a sclerophyllous shrubland called fynbos. Cape Flats Sand Fynbos landscapes consist of predominantly flat plains with acidic, sandy and poor soils (Mostert et al. 2017) with a gradient of nutrient status from the coastal dunes to inland (Witkowski and Mitchell 1987). Typical soil types for Cape region are Chromic Luvisols and Albic Arenosols along the coast ancient dunes (FAO-Unesco 1977).

Out of the Cape region, *Carpobrotus* is mainly found in the five biogeochemically distinct Mediterranean climate areas. *Carpobrotus* seems to have adapted to a wide range of soil types, but there is evidence of preferences for Inceptisols and Mollisols soil orders (Eswaran and Reich 2005).

In Australia, *Carpobrotus* has naturalized mainly along the southern and eastern coast, where the soils are highly variable: planosols, ferralsols, arenosols, cambisols and podzols (FAO-Unesco 1978), usually, associated to the surrounding granitic areas (Isbell and the National Committee on Soil and Terrain 2016). In New Zealand, *Carpobrotus* invades North and South Islands on cambisols and andosols (FAO-Unesco 1978), mainly in dunes and cliffs with soils ranged from sand to sandy loam. In California, *C. edulis* is widely distributed through the coast in sand dunes and coastal scrub and grasslands. Invaded soils are derived from marine deposits and are low in fertility (Zedler and Scheid 1988) with sand and loamy sand soil texture (D'Antonio 1993) belonging to luvisols type (FAO-Unesco 1978). In Central Chile, *C. edulis* appears mainly on luvisols (Sotes, Cavieres, and Rodríguez 2015; FAO-Unesco 1971). In Europe, *Carpobrotus* can be found in different soil types, mainly on arenosols and eutric, humic and calcic cambisols (FAO-Unesco 1981).

Soil pH

Soils invaded by *Carpobrotus* in New Zealand present a pH from 4.8 to 5.9 (CaCl₂) (Liu et al. 2014). These are more acidic than the invaded soils in California, in which the pH is highly variable, ranging from 5.6

to 8.2 (Vilà and D'Antonio 1998c). The invaded region of Biobío in Central Chile has soil pH values ranging from 5.2 to 6.2 (Berti et al. 2011). In Europe, soils with *C. edulis* are arenosols and diverse types of cambisols with different pH in soil solution ranging from 5.8 to 9.2 (Santoro et al. 2011; Novoa et al. 2014). The optimal germination pH value for *C. edulis* is 8. However, plant growth seems to be stimulated at lower pH values (Novoa et al. 2012).

Salinity, soil nutrients and moisture

Carpobrotus edulis is a facultative halophyte (Rodrigues et al. 2014a). It occurs under soils with a seasonal variation in salt concentration, lower in winter due to higher precipitations and higher in summer, under higher evaporation rates (Callaway et al. 1990).

Carpobrotus invades soils with differences in fertility, from the low-nutrient soils of parts of West and South Australia to the nutrient-rich soils of central Chile, California and the Mediterranean Basin (Vilà and D'Antonio 1998c; Stock and Verboom 2012; Liu et al. 2014). *Carpobrotus edulis* is adapted to different soil conditions, and germination and early growth are not constrained by a lack of nutrients (Novoa et al. 2012). *Carpobrotus edulis*, in its native region, grow in well-drained sandy soils with low soil moisture content. During winter, soil moisture reaches 7% and decreases close to 0 during summer (Yelenik, Stock, and Richardson 2004). In the invaded area, *C. edulis* grows in a wide range of soil types, common to Mediterranean climates, with a moderate to pronounced seasonal moisture deficit (USDA, 1999).

Habitats and syntaxonomy

Native range

In its native range, *Carpobrotus* commonly occurs in coastal habitats that often hold other succulent species such as *Drosanthemum*, *Euphorbia* and *Tetragonia* (Mucina et al. 2006). *Carpobrotus* is also part of the Fynbos vegetation (Manning and Paterson-Jones. 2007) where it is commonly associated with *Thamnocortus erectus* (Thunb.) Mast., *Metalasia muricata* R.Br., *Euclea racemosa* L., *Rhus laevigata* L., *Leucadendron coniferum* Meisn., *Rhus glauca* (Thunb.), *Eriocephalus africanus* L., *Agathosma imbricata* (L.) Willd. and *Diosma hirsuta* L. (Cowling, Macdonald, and Simmons 1996).

Invaded range

Carpobrotus can grow and establish in embankments, garden margins and disturbed sites under a wide range of environmental conditions. Previous studies report a preferential distribution of *Carpobrotus* for coastal habitats, both on rocky and sandy coasts and, in the



Figure 4. Coastal areas invaded by *Carpobrotus* at the Iberian Peninsula (a, b, d, f, g, h), Italy (c), France (e), and Azores (i); (a-d) show the species at sand dunes ecosystems; (e-f) at cliffs; (g-i) at rocky coastal habitats.

latter, particularly in the central part of the coastal dune vegetation zonation (Carranza et al. 2011; Bazzichetto et al. 2016; Figure 4). This is probably due to the absence of frost and the tolerance of this genus to salinity (Weber and D'Antonio 1999). The main invaded communities according to the EUNIS, Habitats directive and phytosociological classifications are shown in Table 3. In California, it can likewise be found in dunes, backdunes, sea cliffs, coastal prairies, shrublands and chaparral (D'Antonio 1990a, 1993; Albert 1995a;

Albert, D'Antonio, and Schierenbeck 1997; Vilà and D'Antonio 1998c).

Carpobrotus in Europe occurs in the full mosaic of communities of dune systems, from the early colonizers to the most stabilized woody communities (Santoro et al. 2011). In Portugal, it can be found in pre-forest formations of *Juniperus thurifera* subsp. *turbinata* (Guss.) Nyman, with other shrubs or trees such as *Rhamnus alaternus* L. or *Pinus pinaster* Aiton (Neto 2002), as it can effectively compete in shaded

Table 3. Main habitats invaded by *Carpobrotus* in Europe according to the EUNIS vegetation codes (Moss 2008), Habitats Directive habitats codes (Schaminée et al. 2012) and main phytosociological classes (Mucina et al. 2016).

EUNIS Code	EUNIS Code level 3	Habitats directive code	Phytosociological class
B1.3 Shifting coastal dunes	B1.311 Atlantic embryonic dunes, B1.312 Western Tethyan embryonic dunes, B1.321 Atlantic white dunes	Embryonic shifting dunes (2110), Shifting dunes along the shoreline with <i>Ammophila arenaria</i> ("white dunes") (2120)	<i>Ammophiletea</i> , <i>Cakiletea maritima</i>
B1.4 Coastal stable dune grassland (grey dunes)	B1.42 Biscay fixed grey dunes, B1.43 Mediterraneo-Atlantic fixed grey dunes, B1.48 Tethyan dune deep sand therophyte communities	Fixed coastal dunes with herbaceous vegetation ("grey dunes") (2130), <i>Crucianellion maritima</i> fixed beach dunes (2210), Dunes with <i>Euphorbia terracina</i> (2220), <i>Malcolmietalia</i> dune grasslands (2230)	<i>Helichryso-Crucianelletea</i>
B1.5: Coastal dune heaths	B1.52 <i>Calluna vulgaris</i> brown dunes	Atlantic decalcified fixed dunes (<i>Calluno-Ulicetea</i>) (2150)	<i>Calluno-Ulicetea</i>
B1.6: Coastal dune scrub	B1.64 Dune sclerophyllous scrubs and thickets	Coastal dunes with <i>Juniperus</i> spp. (2250), <i>Cisto-Lavanduletalia</i> dune sclerophyllous scrubs (2260)	<i>Cisto-Lavanduletea</i>
B1.7: Coastal dune woods	B1.74 Coastal brown dunes covered with natural or almost natural thermophilous pines	Wooded dunes of the Atlantic, Continental and Boreal region (2180)	
B3.3: Rock cliffs, ledges and shores, with angiosperms	B3.31 Atlantic sea-cliff communities, B3.33 Tethyan sea-cliff communities, B3.34 Canary Island and Madeiran sea-cliff communities, B3.35 Azorean sea-cliff communities	Vegetated sea cliffs of the Atlantic and Baltic coasts (1230), Vegetated sea cliffs of the Mediterranean coasts with endemic <i>Limonium</i> spp. (1240), Vegetated sea cliffs with endemic flora of the Macaronesian coasts (1250)	<i>Crithmo-Staticetea</i>

and open habitats (Moragues, Traveset, and Valladares 2005). It also occurs in coastal dry heaths dominated by *Corema album* (L.) D. Don., *Stauracanthus* spp., *Thymus* spp. and *Cistus* spp. of the *Cisto-Lavanduletea* phytosociological class, and dry dune heaths (*Calluno-Ulicetea*) over podzolic soils with *Calluna vulgaris* (L.) Hull and *Ulex australis* Clemente (Neto, Capela, and Costa 2004; Neto, Arsénio, and Costa 2009). *Carpobrotus* invades grey dunes, relatively stable communities with high plant cover values and soil development such as the dune pastures of the *Koelerio-Corynephoretea* class. It also occurs in the foredune vegetation of marram grass (*Ammophiletea*) of the Mediterranean and Atlantic biogeographic regions (Neto, Arsénio, and Costa 2009) and in other communities with low plant cover from the foredune (*Cakiletea maritimae*). In addition, *Carpobrotus* can grow on wet soils of dune valleys, where it competes with sedges, rushes and tall grasses of dune slacks (*Molinio-Holoschoenion*), and even marshes (Bech and Hernández 1976), although it seems to prefer well-drained soils.

In cliffs, it grows with many different species at different stages of vegetation development, from the *Festuca* grasslands of the coastline to the shrub heath or scrub communities of *Calluno-Ulicetea* and *Cisto-Lavanduletea* (Costa et al. 1997). Mats of *Carpobrotus* can spread to the vertical cliffs and cover the open vegetation community of adapted species such as *Armeria maritima* Willd., *Limonium* spp. or *Crithmum maritimum* L. (Fernández Prieto and Loidi 1984). On the Roussillon coast (Southern France), it has been reported in the cliffs competing with the rare species *Armeria ruscinonensis* Girard (Rioux, Roux, and Pignatti 1955). It also displaces the endemic *Limonium emarginatum* (Willd.) Kuntze, the dominant species in the cliffs of Algeciras, at the Strait of Gibraltar (Garzón, Castillo, and Figueroa 2005).

Responses to environmental factors

Biotic factors

In California, D'Antonio (1993) demonstrated that factors governing *C. edulis* ability to colonize are community-dependent. In the backdune and coastal scrub sites, *C. edulis* seedlings become successfully established, despite some reduction in growth due to competition with shrubs. In grasslands, annual grasses inhibit *C. edulis* seedlings establishment, but *C. edulis* may succeed if there is any disturbance (such as gophers or ground squirrels). In such cases, *C. edulis* competes successfully and limits grass development.

Facilitation by co-occurring exotic or native species can boost the invasion process of *Carpobrotus*. For example, *Pinus halepensis* Mill., growing close to the coast in Mediterranean forest, facilitates the inland

spreading of *C. aff. acinaciformis* by protecting it from an excess of light without lessening its growth (Traveset, Moragues, and Valladares 2008). The impact of *Carpobrotus* on native community structure and diversity has been widely studied. In the Tyrrhenian coastal dunes of Italy, diversity patterns of focal species were significantly reduced in *C. aff. acinaciformis* invaded areas compared to non-invaded. However, taking into account only native species, no differences in diversity parameters were found (Santoro et al. 2012a). Maltez-Mouro, Maestre, and Freitas (2010) reported similar results in coastal Portuguese dune systems. On the contrary, Vilà et al. (2006) and Fried et al. (2014) observed a significant decline in diversity patterns when *C. acinaciformis* and *C. edulis* invaded coastal habitats of Mediterranean islands or mainlands.

Herbivory

The “natural enemies hypothesis”, an explanation for the success of introduced species (Elton 1958; Russo, Mazzeo, and Suma 1999) may apply to *Carpobrotus* either for aboveground herbivores (Maron and Vilà 2001) or soil-borne diseases (Van Grunsven et al. 2009). Yet, D'Antonio (1993) and Vilà and D'Antonio (1998b, 1998c) demonstrated that generalist herbivores can strongly limit *C. edulis* initial establishment in coastal California.

In its native range, numerous species feed on different parts of *Carpobrotus*. Leaves are eaten by different tortoise and snail species. Flowers are eaten by diverse antelope species and baboons (*Papio* sp.), while fruits are eaten by baboons, several rodent species, porcupines (*Hystrix africae australis* (Peters, 1852)), springbok (*Antidorcas marsupialis* (Zimmermann, 1780)) and humans (Wisura and Glen 1993; Vilà et al. 2009).

In Mediterranean islands, *Carpobrotus* fruits are consumed by introduced mammals as European rabbit and black rat (Bourgeois et al. 2005). In California, several rabbit species such as jackrabbit and brush rabbit, as well as mule deer and Californian ground squirrel also feed on *C. edulis* fruits (Vilà and D'Antonio 1998b; D'Antonio 1990b) (for more details see fruit/seed dispersal section). Other generalist herbivores can feed occasionally on *Carpobrotus* fruits and leaves in non-native areas such as small rodents (Bourgeois et al. 2005), snails as *Theba pisana* (Müller, 1774), and *Helix aspersa* (Müller, 1774) (Rodríguez et al. 2017), spittlebugs (*Hemiptera*) as *Aphrophora punctipes* (Walley, 1928) (Knapp 2014) and *Philaenus spumarius* (Linnaeus, 1758) (Silva et al. 2015; Rodríguez et al. 2015, 2017). *Philaenus spumarius* can be found in a variety of terrestrial plant communities and habitats (Rodríguez et al. 2014b) including areas invaded by *C. aff. acinaciformis* and *C. edulis* but damages on plants are not apparent.

In Europe, insects feeding on *Carpobrotus* such as the native *Aphis fabae* (Scopoli, 1763) and the exotic *Pulvinariella mesembryanthemi* (Vallot, 1829) have been described (Majer 1982; Rodríguez et al. 2017). Two predatory mites belonging to the family Phytoseiidae, namely *Typhlodromus phialatus* (Athias-Henriot, 1960) and *Euseius stipulatus* (Athias-Henriot, 1960), are reported as natural enemies feeding on *C. edulis* (Vilà et al. 2008).

The occurrence of the scale insects (Hemiptera: Coccidae) *Pulvinaria delottoi* (Gill, 1979) and *Pulvinariella mesembryanthemi* on *Carpobrotus* has been reported in native (Delotto 1979) and non-native areas including Australia (Collins and Scott 1982), America (Washburn and Frankie 1981; Washburn, Grace, and Frankie 1987) and Europe (Mazzeo, Suma, and Russo 2008). They are sap-feeding insects with a range of hosts restricted to the Aizoaceae and Crassulaceae families (Washburn, Grace, and Frankie 1987). Few studies have evaluated the impact of these scale insects on *Carpobrotus*. It has been reported that *P. mesembryanthemi* retards plant growth and may cause the death of the plant (Collins and Scott 1982). According to Washburn, Frankie, and Grace (1985), the survival of insects and host plants is inversely related to scale densities. Therefore, intra-specific scale competition, the decline or death of host plants, and natural enemies pressure, operate regulating the scale insect populations and their impact.

Diaspine scale insect species (Hemiptera, Diaspididae) feeding on *C. edulis*, namely *Aonidiella mesembryanthemi* (Vallot, 1829), *Aonidia mesembryanthemae* (Brain, 1919) and *Entaspidiotus lounsburyi* (Marlatt, 1908) are reported from South Africa and California (Schmalzer and Hinkle 1987) and the later species also occurs in Italy on the non-native Mesembryanthemaceae, *Disphyma crassifolium* (L.) L. Bolus (Russo, Mazzeo, and Suma 1999; Mazzeo et al. 2014). Like *P. mesembryanthemi*, the above mentioned diaspine scale insects are uncommon and highly parasitized in their natural environment in the Cape Provinces, but *E. lounsburyi* can be very destructive in plantings, even parasitized (S. Naser, pers. comm.). White Spot Moth, *Mesocelis monticola* (Hübner, 1820) (Lepidoptera, Lasiocampidae) (Mountain White Spot) is a host-specific phytophagous insect reported from South Africa, which defoliates *Carpobrotus* almost completely (Prinsloo and Uys 2015).

Plant parasites and diseases

No severe plant parasite or disease infecting *Carpobrotus* in its native distribution range has been reported, although it has been shown that high humidity could cause bacterial leaf rot or fungal diseases (ie *Botrytis cinerea* (Pers., 1974)) in plants growing in shady positions or poorly drained sites (Malan and Notten 2006). However, those pathogens have

not been isolated from affected tissues of *Carpobrotus*.

In the Mediterranean area, Van Grunsven et al. (2009) demonstrated that *C. edulis* and the hybrid are free of soil-borne enemies. Nevertheless, an exhaustive evaluation of diseases affecting *C. edulis* in California was performed in the 1980s by MacDonald et al. (1983) and MacDonald, Hartman, and Shapiro (1984) and then compiled by Schmalzer and Hinkle (1987). Table 4 summarizes the information contained in the above-mentioned reports, reflecting disease symptoms, favorable conditions and confirmation by pathogenicity tests. MacDonald et al. (1983) also performed tests for mycoplasma, spiroplasma, rickettsia, virus, and nematode detection, but all of them were negative. McCain, Raabe, and Wilhelm (1981) reported *C. edulis* as a species susceptible to *Verticillium* wilt, caused by the microsclerotial form of *Verticillium* species, known as *Verticillium dahliae* (Kleb, 1913) or *V. albo-atrum*, (Reinke and Berthold, 1879). See *biological control section* for recommendations about their use as control agents.

Abiotic factors

Both *Carpobrotus edulis* and *C. acinaciformis*, are C3-CAM facultative species (Treichel and Bauer 1974; von Willert et al. 1977; Sanz-Elorza, Dana, and Sobrino 2004). CAM is a specialized photosynthetic CO₂ fixation pathway that improves water use efficiency by uptaking part or all of the net atmospheric CO₂ at night, when plant evaporative demands are lower. This facultative C3-CAM physiology is an important feature to consider in understanding how *C. edulis* responds to such environmental factors as light, water, temperature, salinity, and nutrient availability.

Light

Differences between *C. edulis* and co-occurring native species in their physiological performance in response to varying light conditions may be critical for a mechanistic understanding of its success. Falleh et al. (2012) found that *C. edulis* from provenances differing in rainfall and length of light periods significantly differed in their antioxidant activity and their polyphenol profiles, with long light period provenances exhibiting stronger antioxidant activity together with higher phenolic content. Based on these data, Falleh et al. (2012) suggested that *C. edulis* may adapt to environmental stress inducing changes in phenol composition and improving its antioxidant capacities in order to protect plant tissues against oxidative stress. A similar strategy of increased flavonoid production in response to oxidative stress by excessive light, especially at sub- and supra-optimal salinities, has been documented for *Carpobrotus rossi* (Haw.) Schwantes (Pirie et al. 2013). Some

Table 4. List of pathogens found on *Carpobrotus edulis* collected along roadsides in California (MacDonald et al. 1983; MacDonald, Hartman, and Shapiro 1984; Schmalzer and Hinkle 1987).

Species	Symptoms	Favorable conditions	Pathogenicity test
<i>Pythium aphanidermatum</i> (Edson) Fitzp.	Yellowing of plants, wilting of leaves, browning lower stems and crowns, slough off cortical tissue in roots, soft rot of succulent tissue.	Poor drained soils, excessive rainfall or irrigation, prolonged periods of soil saturation.	Yes
<i>Phytophthora cryptogea</i> Pethybridge & Lafferty	Wilting and yellowing of leaves, severe decay of roots and lower stems.	Poor drained soils, excessive rainfall or irrigation, prolonged periods of soil saturation.	Yes
<i>Verticillium dahliae</i> Kleb.	Premature foliar chlorosis and necrosis, vascular discoloration on stems. Severely wilted or dead plants.	Verticillium wilt is favored by moist soils and a temperature range between 21–27°C.	Yes
<i>Phomopsis</i> sp.	Wilting branches, turning dull gray-green and then olive as it shriveled. Orange discolored tissue from beneath the surface of the plant.	Prolonged moisture on green tissues is required for infection.	Yes
<i>Fusarium</i> spp.			No
<i>Macrophomina</i> sp.			No
<i>Pestotia</i> sp.			No

photoprotective strategies displayed by C3-CAM facultative species of the Aizoaceae family may be strictly salinity dependent. In C3-CAM facultative species, as *C. edulis*, the induction of CAM might be not straightforward. For example, Gawronska et al. (2013) have reported that strong light stress-causing oxidative damage may not be enough by itself to activate CAM metabolism in *Mesembryanthemum crystallinum* L. Furthermore, these authors documented that under high irradiance and in the absence of salinity, C3-CAM species may show an age-dependent increase in photosystem II energy dissipation.

Fenollosa, Munné-Bosch, and Pintó-Marijuan (2017) have described several photoprotective strategies in *C. edulis*. Under strong irradiance, *C. edulis* activate the xanthophyll cycle to dissipate the excess of energy, registering a two-fold increase in the VAZ xanthophyll pool. This mechanism is used by plants to mitigate the adverse effects of excessive irradiance (Demmig-Adams and Adams 1992, 1996). In addition, Fenollosa, Munné-Bosch, and Pintó-Marijuan (2017) also suggested that the antioxidant activity of the lutein (Dall’Osto et al. 2006) and the antenna size regulation, mainly through the chlorophyll composition, seem to play a key role in the photoprotective strategy of *C. edulis*.

The efficiency in the use of light by *C. edulis*, as estimated by changes in leaf reflectance, has been found to depend on factors as the age of the ramets, the habitat of provenance, and the level of clonal integration (Roiloa et al. 2014). It has also been reported that *C. edulis* respond to high light not only by physiological changes (increasing their photochemical efficiency) but also by morphological variations, increasing the biomass allocated to above-ground structures (Roiloa et al. 2014; Roiloa et al. 2016). Other studies have documented morphological changes in response to light. Traveset, Moragues, and Valladares (2008) showed that the main and lateral shoots of *Carpobrotus aff. acinaciformis* differed in response to light availability. Whereas the main

shoots grew at similar rates under different light environments, the growth rate of lateral shoots was greater in shaded sites. These authors also documented a high phenotypic plasticity in biomass allocation of individuals located in sun and shade. According to Traveset, Moragues, and Valladares (2008), this highly plastic response to light availabilities greatly contributes to a high photochemical performance, even under moderate shade, and allows the species to rapidly colonize the understorey of Mediterranean scrub and woodlands, well beyond the open sand dune systems. Likewise, Fenollosa, Munné-Bosch, and Pintó-Marijuan (2017), using a new approach to compare phenotypic plasticity, based on the analyses of a combination of different traits, found that *C. edulis* follows an “all-in” strategy, using a profusion of photoprotection mechanisms to respond to annual climatic variations. They concluded that the greater phenotypic plasticity found in *C. edulis*, compared to a coexisting native species (*Crithmum maritimum*), could contribute to its success and be advantageous under a scenario of climate change.

Water

MacDonald, Hartman, and Shapiro (1984) observed that excessive rainfall or watering causes the roots of *C. edulis* to get rotten in places where poor drainage resulted in extended periods of soil saturation. On the contrary, *C. edulis* growing in semi-natural, water-stressed conditions may achieve drought tolerance by the induction of Crassulacean Acid Metabolism (CAM) (Earnshaw, Carver, and Charlton 1987). As a succulent C3-CAM facultative plant, *C. edulis* can tolerate severe water restrictions due to its photosynthetic flexibility provided by the optional use of CAM photosynthesis (Winter and Holtum 2014), and through leaf water storage (Farrell et al. 2012). CAM photosynthesis results in a higher water use efficiency by uptaking CO₂ through stomata at night, thus reducing water loss through transpiration

and maximizing the rate of carbon assimilation to the rate of transpiration (Sayed 2001). Plants with greater succulence (expressed as g water cm⁻² leaf area) can generally survive longer periods without water (von Willert 1992). Therefore, the water storage in leaves may enable *C. edulis* plants to survive under dry conditions by providing water that can be used to maintain plant function when water is unavailable for uptake by the roots. Fenollosa, Munné-Bosch, and Pintó-Marijuan (2017) have documented that *C. edulis* growing in a typical Mediterranean climate, with warm and dry summers, was able to maintain a higher level of hydration (> 9 g H₂O g⁻¹ dry mass) in autumn, winter and spring compared to a coexisting native (*Crithmum maritimum*), but differences disappeared during the summer, when both species exhibited their lowest hydration values. In response to water availability, Fenollosa, Munné-Bosch, and Pintó-Marijuan (2017) also showed some changes in *C. edulis* leaf morphology, such as a 30% increase in leaf mass per volume (LMV, an estimate of leaf succulence) in the summer. A strong negative correlation between LMV and the relative water content indicated the dependence of leaf morphology on water content in this plant.

The ability of *C. edulis* to share resources among ramets occupying microhabitats of different quality may be determinant at the time of colonizing water-stressed environments (Lechuga-Lago et al. 2016). Another important determinant of the success of this species in colonizing environments with long periods of drought has been suggested by D'Antonio and Mahall (1991) who found that *C. edulis* reduces the water potential of the native shrubs and changes their rooting profiles.

Temperature

There is a surprising lack of published scientific research on the responses of *C. edulis* to temperature. Most of the existing information comes from non-systematic observations describing its susceptibility to freezing injury (MacDonald, Hartman, and Shapiro 1984), or indirect evidence provided by plant breeders referring to a very general knowledge on the preference of *C. edulis* for temperate climates. It is considered poorly tolerant to low temperatures (apparently, it can be killed by temperatures below about -2°C), but is resistant to high temperatures. To the best of our knowledge, only two studies have explored the effects of temperature on *C. edulis*. Vilà et al. (2008), after conducting field sowing tests in more than 200 sites across six Mediterranean Basin islands differing in climatic conditions, concluded that the establishment rates (ie seedling to sown seed ratio) tended to be positively correlated with the cumulative precipitation and negatively with mean temperature. D'Antonio, Odion, and Tyler

(1993) provided results of laboratory tests showing that *C. edulis* seeds in burned soils were killed by exposition to temperatures of 105 °C or higher for five minutes.

The fact that *C. edulis* is a succulent plant allows us to infer its tolerance to high temperatures. In fact, succulents have been considered among the most tolerant species to high temperatures, with threshold temperature for heat injury that can well exceed 60 °C (Larcher 1995). The high-water content of succulent plants such as *C. edulis* has important implications for their thermal economy due to the high-specific heat of water that allows to buffer plant tissues against rapid changes in temperature (Fitter and Hay 2002).

Salinity

Carpobrotus edulis is strongly influenced by global and local-scale abiotic factors (climate and shoreline distance) (Maltez-Mouro, Maestre, and Freitas 2010). In coastal environments occupied by *Carpobrotus*, plants are subject to varying levels of substrate salinity and salt spray. It has been demonstrated that germination of *C. edulis* seeds is reduced by high salt concentrations (1.5% salt content) (Weber and D'Antonio 1999). At the lower end of the salinity gradient, salt concentrations do not influence *C. edulis* germination or seedling establishment, probably because of its relative high tolerance to salinity (Novoa et al. 2014), which may determine the extent of establishment and distribution along the salt gradient (Weber and D'Antonio 1999).

The inhibition of germination by salt is considered an osmotically enforced dormancy, preventing the establishment of seedlings under unfavorable conditions (Ungar 1978; Zia and Khan 2008). *Carpobrotus edulis* fruits ripen from late spring to autumn in Europe and in late summer in California; seeds remain dormant in the soil until winter rains triggers germination. Therefore, salt stimulates germination in a favorable season in *Carpobrotus*.

Low and moderate salinity causes an enhancement in biomass production with an increase in water use efficiency (Weber and D'Antonio 1999) although it does not affect early growth (Novoa et al. 2014). *Carpobrotus edulis* is well adapted to maintaining high photosynthetic rates under high salinity conditions, even though other metabolic processes and growth responses are affected (Madawala, Hartley, and Gould 2014). *Carpobrotus edulis* can modulate its response to salinity showing a high efficiency of the photoprotection mechanism, resulting in a high carotenoid to chlorophyll ratio increase (Varone et al. 2017). Chlorophyll *a* fluorescence measurements revealed no permanent adverse impacts on photosynthetic efficiency resulting from long-term exposure to salinity (Madawala, Hartley, and Gould 2014).

Seawater submergence of *C. edulis* stolons significantly reduces the amount of light-harvesting antenna pigments, photochemical activity of PSII and growth. This reduction is dependent on the size of the immersed stolon (Roiloa and Retuerto 2016). Despite this damage, *C. edulis* can grow after an event of seawater submergence indicating its extraordinary capacity to tolerate high salt concentrations. *Carpobrotus edulis* grown for 24 days in nutrient solution plus 400 mM of NaCl showed the typical CO₂ gas exchange reactions observed in CAM plants (Winter 1973), demonstrating its C3-CAM facultative metabolism under salt stress.

Carpobrotus edulis is a “transformer” species *sensu* Richardson et al. (2000). It is capable of modifying soil features, although this depends on the characteristics of the invaded habitats (D’Antonio 1990a; Molinari, D’Antonio, and Thomson 2007). Parameters such as soil salinity are not always modified in the same way by *Carpobrotus* invasion as reflected in the different findings by Santoro et al. (2011) and Novoa et al. (2014) and in the variation between sites demonstrated in California (D’Antonio 1990a).

Nutrient availability

The germination process of *Carpobrotus* is influenced by the soil nutrient content. High soil nutrient concentration favours the germination process but does not exert an influence on early growth (Novoa et al. 2014). Nutrient scarcity is ameliorated by the plant through clonal reproduction and physiological integration (Campoy, Retuerto, and Roiloa 2017) that allow *C. edulis* to invade new poor areas as incipient dune systems or even beach berm (Lechuga-Lago et al. 2016). In Europe, the grow-and-die strategy is used by *C. edulis* to colonize new habitats. A rapid turnover of plant biomass that results from rapid growth, death, and regrowth creates an organic layer and transforms a hostile habitat into fertile soil for the next generation. Transmission of epigenetic changes may increase phenotypic plasticity, and fast evolution boosts the rate of local adaptation in the invaded range (Fenollosa, Roach, and Munné-Bosch 2016).

Biology

Phenology

Flowers emerge between February and June in Europe, and between August and October in South Africa (CEEEI 2013; GISD 2017; L. González pers. observ.). In the invaded range, fruits remain attached to the plant until late autumn when animals begin to consume them (GISD 2017).

Vegetative spread is rapid, and clumps can cover several square meters by the expansion of prostrate

stems that take root at each node. Vegetative growth occurs almost all year-round. Roiloa et al. (2010) quantified the expansion rate of *C. edulis* clones colonizing a coastal sand dune in Mata Nacional das Dunas de Quiaios (Portugal). They reported a constant elongation of the clonal fragments averaging 13.75 cm for the time period from March to September. The greatest stolon increase was recorded during the month of May, with an elongation of 4.5 cm. These results are consistent with those proposed by Sintés et al. (2007), who showed a stolon elongation rate of 29.37 cm per year for *Carpobrotus aff. acinaciformis* colonizing a coastal habitat in the Balearic Archipelago (Spain), but slower than rates shown for *C. edulis* in California (53 cm per year) (D’Antonio 1993).

Vegetative growth

Carpobrotus shows a radial clonal growth with a structure of nodes and internodes that form dense mats and spreads horizontally by the production of numerous modules or ramets that remain physiologically integrated by stolon connections. This clonal growth allows *Carpobrotus* to effectively colonize the surrounding area (Roiloa et al. 2010). The importance of the clonal traits linked to the invasiveness of *C. edulis* has been recently tested in a number of greenhouse and field experiments. One of the most striking attributes associated with clonal growth in plants is the capacity for physiological integration (ie the possibility of resources being translocated between connected ramets, Slade and Hutchings 1987). Several studies have demonstrated that this capacity for physiological integration, and in particular the transport of essential resources from established basal ramets to developing ramets, generates a growth benefit in clonal plants such as *C. edulis* (Roiloa, Campoy, and Retuerto 2015). Indeed, Roiloa et al. (2010) found that physiological integration significantly increased the growth and survival of developing ramets of *C. edulis* invading a coastal sand dune in competition with native species. In addition, the benefit of physiological integration in terms of photosynthetic efficiency and growth has been observed in developing ramets of *C. edulis* under water stress conditions (Lechuga-Lago et al. 2016). These results indicate that physiological integration may contribute to the invasiveness of *C. edulis* in sand dune soils with low water retention. Campoy, Retuerto, and Roiloa (2017) reported similar results, showing that physiological integration improves growth and photosynthetic efficiency in *C. edulis*. Interestingly, this study demonstrated the presence of local adaptation producing highly integrated ecotypes in the harsher rocky coastal habitats. Differences in the capacity for physiological integration between *C. edulis* and

the co-occurring invader congener *C. acinaciformis* have recently been detected. Portela and Roiloa (2017) reported in a field experiment a benefit from physiological integration in both species; however, *C. acinaciformis* was more dependent on integration than *C. edulis*. This result is consistent with those of Suehs, Affre, and Médail (2004a), confirming that vegetative propagation is an important reproductive alternative for *C. acinaciformis*. On the other hand, a recent study detected a non-local response to herbivores in *C. edulis*. In particular, it has been shown that the attack of *T. pisana* snails to basal ramets induced a non-local compensatory response in un-attacked apical ramets. However, this non-local response was not mediated by physiological integration, but probably due to signals released by root exudates (Rodríguez et al. 2018).

Closely related to the concept of physiological integration in clonal plants, is the concept of division of labor. This has traditionally been defined as the capacity of functional specialization of interconnected ramets to acquire locally abundant resources that increases the overall performance of the clone (Alpert and Stuefer 1997; Hutchings and Wijesinghe 1997). Several studies have demonstrated the capacity of *C. edulis* to show a developmentally programmed (Roiloa et al. 2013) and environmentally induced division of labor (Roiloa et al. 2014; Roiloa et al. 2016). This division of labor was developed by *C. edulis*, both at physiological and morphological level, and enhanced the overall performance of the clonal fragment. Interestingly, Roiloa et al. (2014) demonstrated that the ability for division of labor was positively selected, being more accentuated in patchier environments, where the presence of this trait would be more beneficial. On the other hand, in a recent study, Roiloa et al. (2016) compared division of labor between populations of *C. edulis* from its native and invaded range, demonstrating that the benefit from the division of labor was significantly higher in developing ramets in the invaded area. This finding suggests that *C. edulis* populations might experience rapid evolutionary adaptation in the invaded area, and that division of labor can be considered an important trait for the invasiveness of this species.

Another interesting consequence associated with the capacity for physiological integration in clonal plants is the ability to discriminate between self and non-self genotypes. This ability could be expected to reduce root competition between genets, and as a consequence to increase the performance of the clone. Roiloa, Rodríguez-Echeverría, and Freitas (2014) found in a greenhouse experiment that physiological integration allowed self/non-self genotype recognition in clones of *C. edulis*, leading to a form of division of labor, which reduced intra-genotype

competition, and enhanced the colonization capacity of the species.

The contribution of storage organs, such as stolon and rhizome internodes, to the success of clonal invaders has been considered only recently (Konlechner, Orlovich, and Hilton 2016; Dong et al. 2012; Lin, Alpert, and Yu 2012). The capacity of clonal modules to survive and re-grow after a process of fragmentation could have important implications for the dispersal of clonal invaders. Storage organs of clonal plants can play a crucial role because the stored carbohydrates may be mobilized under unfavourable conditions, allowing the colonization of new habitats. Roiloa et al. (2017) determined the importance of stolons as reserve organs in the colonization of a coastal sand dune by clones of *C. edulis*. They showed that stolons can help to buffer stressful conditions after a process of fragmentation, thus allowing expansion of *C. edulis*. Similarly, Roiloa and Retuerto (2016) simulated in a greenhouse experiment a process of fragmentation and a subsequent event of seawater submergence and de-submergence. Their results suggest the importance of stolons in allowing *C. edulis* to be transported along the shore by the waves and the tide, to colonize new coastal areas.

To summarize, all these recent studies indicate that traits associated with clonal propagation can contribute to the effective colonization of new habitats by *C. edulis*, and therefore contribute to its invasiveness.

Reproductive biology

Floral biology

Flower pollinators recorded in *Carpobrotus* are mostly constituted of Hymenoptera ie, bumblebees, *Apis mellifera* (Linnaeus, 1758), and solitary bees such as *Halictus* sp., *Anthidium* sp. in Provence (France) and *Rhodanthidium septemdentatum* (Latreille, 1809) in Majorca island (Spain) (Suehs, Affre, and Médail 2005; Jakobsson, Padrón, and Traveset 2008). In parallel, flowers visitors are represented by other Hymenoptera (ie, social bees and wasps), Coleoptera and Diptera species. The effects of *Carpobrotus* on plant-pollination networks and on reproduction success of native plants are described in the “Ecological impacts” section.

Reproductive strategies and hybridization potential

Both *C. edulis* and *C. acinaciformis* show flexible mating systems through intense clonality and different sexual alternatives (Suehs, Affre, and Médail 2004a, 2004b; Bartomeus and Vilà 2009) which may have facilitated local adaptation and habitat colonization (Brown and Burdon 1987; Pyšek 1997; Ellstrand and Schierenbeck 2000). Indeed, *C. edulis* shows slight agamospermy (ie asexual seed production, see Vilà, Weber, and D’Antonio 1998) and is completely self-fertile without

inbreeding depression, while *C. acinaciformis* is not agamosperic and only slightly self-fertile (Suehs, Affre, and Médail 2004a). Furthermore, both species show higher fruit and seed sets in intra-specific outcrossing and even more so when they hybridize with each other (Suehs, Affre, and Médail 2004a, 2004b). In Australia, hybrids occur between *Carpobrotus* spp. and *Sarcosoma* spp., and also between *C. virescens* and *C. edulis*, and *C. rossii* and both *C. edulis* and *C. acinaciformis* (Blake 1969; Biffin et al. 2016). Several hybrids are also reported from South Africa (Wisura and Glen 1993): *C. acinaciformis* × *C. edulis*, *C. edulis* × *C. mellei*, *C. edulis* × *C. quadrifidus*. Hybridization between *C. edulis* and *C. chilensis* occurs in California and contributes to invasion success (Albert, D'Antonio, and Schierenbeck 1997; Weber and D'Antonio 2000; Schierenbeck et al. 2005; Gallagher, Schierenbeck, and D'Antonio 1997; Vilà and D'Antonio 1998a, 1998c). Moreover, *C. edulis* and *C. aequilaterus* (Haw.) N.E.Br. have been noted to hybridize with the endemic *Disphyma australe* (Sol. ex Aiton) J.M.Black (Aizoaceae) in coastal areas throughout New Zealand (Chinnock 1972). *Carpobrotus acinaciformis* shows a strong hybrid vigour and significantly introgressed hybrids within a hybrid swarm (named *C. aff. acinaciformis*) that can lead to new chromosomal and phenotypic variants (Suehs, Affre, and Médail 2004a; Verlaque et al. 2011). Hybridization/introgression thus contributes to important evolutionary changes throughout the *Carpobrotus* invasion dynamics (Suehs et al. 2006).

Fruit/seed production

Compared to other representatives of the Ruschioideae subfamily, the genus *Carpobrotus* is distinguished by the presence of fleshy, indeshiscent fruits (Hartmann 1993) known as “Hottentot figs”, “sour figs” or “marine figs”. In Provence (France), seed production is roughly 1000–1800 seeds/fruit in *C. edulis* and 650–750 seeds/fruit in *C. aff. acinaciformis* (Suehs, Affre, and Médail 2004a). *Carpobrotus edulis*, showing higher seed production and germination than *C. aff. acinaciformis*, has more opportunities for long-distance dispersal. Similar situations have been found in California, where the invasive *C. edulis* produces approximately twice the seeds than the less aggressive *C. chilensis* (Vilà, Weber, and D'Antonio 1998) and can be widely dispersed (D'Antonio, Odion, and Tyler 1993). Indeed, differences in seed production affect the relative propagule pressure, considered as an important feature linked to invasive plant establishment and success (D'Antonio, Levine, and Thomsen 2001; von Holle and Simberloff 2005).

Seed bank density and longevity

Few studies have evaluated seed bank densities of *C. edulis* and *C. aff. acinaciformis* (D'Antonio 1990b, 1993; Morzaria-Luna and Zedler 2007; Chenot et al. 2014).

Seed bank density appears to be habitat-dependent and can vary from 556 to 4070 seeds/m² for *C. edulis*. Indeed, this species seems to have a much larger seed bank than *C. aff. acinaciformis* (930 seeds/m² vs. 4070 seeds/m² for *C. edulis*; data gathered on the same island; Chenot et al. 2014). According to Gioria, Pyšek, and Moravcová (2012), *C. edulis* forms a short-term persistent seed bank (1–5 years). Decline in seed germination was observed under *Lupinus chamissonis* Eschsch. bushes, either due to increased mortality or dormancy (D'Antonio 1990b). The same author showed that after two years of storage, 49–80% of *C. edulis* germinated. *Carpobrotus edulis* and *C. aff. acinaciformis* seeds can persist for 5 years after eradication (Ruffino et al. 2015). Studies on a longer span of time are needed, and it is likely that they will show that *Carpobrotus* should be included in the persistent seed bank category (> 5 years).

Fruit/seed dispersal

Carpobrotus fruits are dispersed via endozoochory. All the studied rabbit species (*Lepus californicus* (Gray, 1837), *Sylvilagus bachmani* (Waterhouse, 1839), *Sylvilagus audubonii* (Baird, 1858), *Oryctolagus cuniculus* (Linnaeus, 1758)) widely consume *Carpobrotus* fruits and increase seed germination after gut passage, from as low as 15 and 24% to as high as 58 to 100% (D'Antonio 1990b; D'Antonio, Odion, and Tyler 1993; Bourgeois et al. 2005; Morzaria-Luna and Zedler 2007; Novoa et al. 2012). The maximum distances of seed dispersal by rabbits vary greatly between studies, from 2 to 209 m. *Rattus rattus* (Linnaeus, 1758), *Felis catus* (Schreber, 1775) and *Odocoileus hemionus* (Rafinesque, 1817) also widely consume *Carpobrotus* fruits and increase seed germination while dispersing seeds to a maximum distance of 96, 500 and 800 m, respectively (D'Antonio 1990b; Vilà and D'Antonio 1998b; Bourgeois et al. 2005). Seeds from baboon's droppings collected in the Cape Peninsula also germinated in great numbers (R. Retuerto pers. observ.). On the other hand, *Otospermophilus beecheyi* (Richardson, 1829) also consumes *Carpobrotus* fruits but damages the seeds leaving only 26% of seeds intact (D'Antonio 1990b). In small rodents (*Paragnathus*, *Peromyscus* or *Dipodomys* and *Apodemus sylvaticus* (Linnaeus, 1758)), fruit consumption is anecdotic. *Erinaceus europaeus* (Linnaeus, 1758), *Sus scrofa* (Linnaeus, 1758) and *Vulpes vulpes* (Linnaeus, 1758) were found not to feed on *Carpobrotus* fruits (Bourgeois et al. 2005).

In its native range, *Carpobrotus* offers shelter to snails, lizards and skinks. Native snakes, such as puffadders or Cape Cobras, often hide among *Carpobrotus* clumps to attack the small rodents that are attracted by its fruits (Malan and Notten 2006) (*see herbivory section*).

Economic importance and human uses

Different species of *Carpobrotus* have been commonly used worldwide since the early twentieth century as ornamental plants in gardening, and to stabilize sand dunes and prevent soil erosion (Weber 2003; Chenot et al. 2018). During the last decade, *Carpobrotus* has also been used to establish green roofs (Razzaghmanesh, Beecham, and Kazemi 2014; Vahdati, Tehranifar, and Kazemi 2017). Moreover, the Australian species *Carpobrotus rossii* (Haw.) Schwantes is considered as a promising candidate for the phytoextraction of heavy metals (Zhang et al. 2015).

Carpobrotus is also a traditional medicinal plant. Its leaves are used to treat sore throats, oral thrush, stomach and mouth ulcers, painful lungs, diarrhea and skin ailments such as eczema or burn injuries. These reports come mainly from its native area (Matsiliza and Barker 2001; Van Wyk, de Wet, and Van Heerden 2008), but its use to treat hemorrhoids by local people have also been reported in Campania, southern Italy (Motti, Antignani, and Idolo 2009). *Carpobrotus edulis* has also been credited with anticancer (Ordway et al. 2003), anti-bacterial (van der Watt and Pretorius 2001) and antifungal properties (Omoruyi, Afolayan, and Bradley 2014).

Additionally, *Carpobrotus* is important gastronomically, especially in South Africa. The fruits of *C. acinaciformis* are used to make jam, pickle or chutney (CABI Website 2017), while the fruits of *C. edulis* and *C. deliciosus* (L.) L.Bolus are also eaten fresh or dried (Hartmann 2001). The leaves of *C. edulis* are also edible and they can be used as food preservative (Omoruyi, Bradley, and Afolayan 2012).

Finally, the pollen of *C. edulis* is a good food source for several predatory mite species, and therefore may be used as biological control – ie *C. edulis* may boost the growth of mite predators increasing their effectiveness to control some mite pests (Swirski and Dorzia 1969; Swirski, Amitai, and Dorzia 1970; Ragusa and Swirski 1975; Ragusa, Zedan, and Sciacchitano 1986; Ferragut et al. 1987; Reuveny, Palevsky, and Gerson 1996).

Despite all the uses of *Carpobrotus*, in the invaded range, stakeholders and the public are aware of the invasiveness and negative impacts of *Carpobrotus* and have a positive attitude towards its management (Bardsley and Edwards-Jones 2007; García-Llorente et al. 2008; Dehnen-Schmutz, Chas-Amil, and Touza 2010).

Ecological impacts

Much of the literature regarding *Carpobrotus* report significant changes in the invaded ecosystems at a variety of scales (Vilà et al. 2006; Molinari, D'Antonio, and Thomson 2007; Conser and Connor

2009; Carranza et al. 2011; Santoro et al. 2012b; Fried et al. 2014; Rumlerová et al. 2016). *Carpobrotus* has many indirect negative effects on the invaded native coastal ecosystems (Figure 5). In fact, it has been recognized as a major driver of soil condition shifts and a disruptor of soil geochemical processes, as seen in Santoro et al. (2011), Novoa et al. (2013) and Vieites-Blanco and González-Prieto (2018). There are many studies supporting that *Carpobrotus* invasion changes the soil pH, salt content, moisture level, nutrient content and microbial activity, but the significance of such changes depends on the initial characteristics of the invaded ecosystem. Effects of the necromass of *C. edulis* on soil characteristics in back-dune and rocky coastal habitats have been reported to provide some competitive advantages related to the physiology of this invasive plant. In particular, Vieites-Blanco and González-Prieto (2017) have documented that differences in necromass characteristics from invaded and non-invaded areas are linked to the ability of *C. edulis* to discriminate against Al uptake, while favouring Mg and Ca uptake. It also shows a lower requirement (or higher resorption) of key micronutrients (Co, Cu, Fe, Ni, Zn), when compare to native vegetation. In coastal dune pioneer habitats, *Carpobrotus* invasion is likely to affect the soil physico-chemical and biological processes (D'Antonio 1990a; D'Antonio and Mahall 1991; Vilà et al. 2006; Conser and Connor 2009; Santoro et al. 2011; Novoa et al. 2012; Vieites-Blanco and González-Prieto 2018). These soil modifications could ultimately inhibit germination and 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, Bardgett, and van Straalen 2008). It has been found that different invasive plant species, including *Carpobrotus*, may favour the replacement of typical native dune plants by ruderal nitrophilous species through soil nutrient enrichment (Maurel et al. 2010; Fried et al. 2014; Malavasi et al. 2016).

In Californian coastal communities, *C. edulis* invasion affected water relationships and plant morphology of the shrub species *Ericameria ericioides* (Less.) Nutt. ex Jeps (= *Haplopappus ericioides* (Less.) Hook. & Arn.) and *Isocoma menziesii* var. *sedoides* (Greene) G.L.Nesom (= *Haplopappus venetus* var. *sedoides* (Greene) Munz), competing directly for water and light (D'Antonio and Mahall 1991). Negative effects of *C. edulis* decomposed tissues on the germination, survival, growth, and reproduction of annual native *Gilia millefoliata* Fisch & C.A.Mey in California, by indirect alteration of soil chemistry (decreased soil pH and increased organic matter content) have also been reported (Conser and Connor 2009). Also in California, *C. edulis* has been shown to alter soil nutrients, pH and litter depth (Molinari, D'Antonio,



Figure 5. *Carpobrotus* competing with endemic species: a) *Ulex europaeus* (A Coruña, Spain), b) *Armeria pungens* (Pontevedra, Spain), c) *Corema album* (Moledo, Portugal), d) *Cistus salviifolius* (Pontevedra, Spain), e) *Euphorbia paralias*, *Aetheorrriza bulbosa* and *Ammophila arenaria* (Lugo, Spain), f) *Centaurea horrida* (Sardinia, Italy), g) *Helichrysum picardii* (Pontevedra, Spain), h) *Medicago marina* (Viana do Castelo, Portugal), i) *Pancratium maritimum* and *Artemisia crithmifolia* (Pontevedra, Spain).

and Thomson 2007). Similarly, in the foredunes of Central Italy, *C. aff. acinaciformis* litter modified significantly soil parameters, increasing nitrogen and organic matter content and decreasing soil pH (Santoro et al. 2011). *Carpobrotus aff. acinaciformis* also affects soil microbial communities, favouring relative increase of fungal with respect to bacterial growth possibly by the increase in total organic carbon and nitrogen (Badalamenti et al. 2016). According to these authors, the change in bacteria/fungi ratio can influence the carbon use efficiency, affecting the behaviour of co-occurring native species and probably favouring the invasion of *Carpobrotus*. *Carpobrotus edulis* also lowers Ca and Na content and increases salinity and phosphorus concentration. Those soil modifications have strong negative effects in the early stages of *Malcolmia littorea* (L.) R.Br. populations, decreasing total germination and survival (Novoa et al. 2013). The litter of the invasive *C. edulis*, which remains on the soil surface for several years, releases allelopathic substances that suppress the native plant germination process and root growth (Novoa et al. 2012) depending on plant species and density (Novoa and González 2014).

Carpobrotus has undesirable direct impacts on native plants, with negative effects on the germination, survival, growth and reproduction (D'Antonio and Mahall

1991; Vilà et al. 2006; Conser and Connor 2009; Affre et al. 2010; Novoa et al. 2013). *Carpobrotus* directly competes with native plants for space, suppressing the growth of mature native shrubs and the establishment of their seedlings (Albert 1995a; Conser and Connor 2009). Additionally, *C. edulis* directly competes with native plant species for water, reducing their growth, survival, and reproduction (D'Antonio and Mahall 1991; Molinari, D'Antonio, and Thomson 2007). Moreover, *Carpobrotus* may affect the quantitative component of pollination. Its influence on the pollination of native plants can be neutral, facilitative or competitive and it is likely to be species specific, depending on the ecological context (ie the environmental conditions prevailing at a given site), and varying from year to year, along with fluctuations in other factors such as insect abundance, composition, and flower abundance of other native plants (Moragues and Traveset 2005; Jakobsson, Padrón, and Traveset 2008; Bartomeus, Vilà, and Santamaría 2008; Bartomeus, Bosch, and Vilà 2008; Morales and Traveset 2009; Vilà et al. 2009). For instance, Bartomeus, Bosch, and Vilà (2008) reported that although *C. aff. acinaciformis* is integrated in pollen transport networks, it did not compete for pollination services on coastal Mediterranean ecosystems dominated by shrubs and annual herbs. In fact, it sometimes facilitated the visit of pollinators to

native species, affecting the structure of Mediterranean plant-pollinators networks (Bartomeus, Vilà, and Santamaría 2008). Similarly, *Carpobrotus* had no effect on the pollination of the rare plant *Dithyrea maritima* (Davidson) Davidson in southern California (Aigner 2004) or on *Cistus monspeliensis* L. in the Balearic Islands (Moragues and Traveset 2005), but it has a competitive effect (ie, fewer visits) on *Lotus cytisoides* L. and a facilitative effect (ie, more visits) on *Cistus salviifolius* L. and *Anthyllis cytisoides* L. (Moragues and Traveset 2005). Likewise, *Carpobrotus edulis* and *C. aff. acinaciformis* compete with native plant species by using their pollinators in Southeast France (Suehs, Affre, and Médail 2005) and the Balearic Islands (Jakobsson, Padrón, and Traveset 2008). If competition dominates, native plant-pollinator networks may be restructured influencing seed production and the dynamics of *Carpobrotus* invasion.

Several studies have shown that *Carpobrotus* invasion ultimately affects patterns of native species diversity (Vilà et al. 2006; Santoro et al. 2012b; Fried et al. 2014), confirming that its successful establishment probably operates through the replacement and exclusion of native species, rather than coexistence. For instance, it has been observed that *C. aff. acinaciformis* represents a serious threat for focal species, characteristic of specific coastal habitats and a major conservation target, representing an early alarm sign of diversity loss (Santoro et al. 2012a). Moreover, *Carpobrotus* may affect community structure and functioning in multiple ways. Molinari, D'Antonio, and Thomson (2007) suggest that *C. edulis* effectively simplifies communities, through its ability both to reduce vegetation height and to homogenize horizontal vegetative cover. In particular, these authors found that *C. edulis* differentially altered vegetation height and distribution in backdune and coastal sage scrub communities with the maximum height of vegetation decline in fully invaded sites (Molinari, D'Antonio, and Thomson 2007).

Changes in vegetation structure due to *Carpobrotus* invasions have only been scarcely studied in other organisms. Galán (2008) found a dramatic decrease on the densities of the Western three-toed skink (*Chalcides striatus* (Cuvier, 1829)) in coastal halophyte grasslands in NW Spain when comparing invaded vs non-invaded spots, and that this decrease correlates with the level of dominance of *Carpobrotus*. Reptiles, amphibians, insects and other groups are sensitive to environmental changes in coastal habitats, thus potentially affected by the invasion of *Carpobrotus*.

In conjunction with the decline in taxonomic diversity, Jucker, Carboni, and Acosta (2013) reported a parallel loss in functional diversity as *Carpobrotus* abundance increased, suggesting that the species is acting as a filter in the process of native community

assembly by preferentially excluding species with specific life-history traits. In particular, on the bases of a plant trait analysis, *Carpobrotus* appears to exclude closely related and ecologically similar taxa (Jucker, Carboni, and Acosta 2013). In fact, according to these authors, low-growing species with small leaf surface area-to-weight ratios seemed much more likely to decrease in abundance in response to *Carpobrotus* invasion. However, *Carpobrotus* also seem to have a strong impact on wind dispersed species, many of which are ephemeral or characterized by annual life cycles, as already reported by Vilà et al. (2006) and Andreu et al. (2010). Thus, it seems that both weaker competitors and ecologically similar species decline in the presence of *Carpobrotus*. Ultimately, it has been shown that *Carpobrotus* invasion in coastal dune plant communities may also affect native assemblages in more subtle and indirect ways, leading to changes in community structure and assembly by disrupting some of the key ecological processes that contribute to determine the pool of plant species present (Santoro et al. 2012a). While uninvaded communities were strongly tied to the sea–inland environmental gradient, *Carpobrotus* invasion may cause a shift to randomness in the species occurrence patterns (Santoro et al. 2012a), an effect generally associated to stress factors such as wildfires (Pitzalis, Luiselli, and Bologna 2010).

Legislation

Since the Bern Convention¹ came into force, European and European Union legislations have been concerned with invasive alien species, ie those animals and plants that, after being introduced accidentally or deliberately into a natural environment where they were not normally found, cause serious negative consequences to the new environment. So far, *Carpobrotus* species have not been specifically taken into account by the Regulation (EU) no. 1143/2014.²

In Portugal, *C. edulis* is listed among the 32 species of plants and animals declared invasive (Royal Decree no. 565/99, 21st December) and as such forbidden to be released in the environment (Marchante and Marchante 2016). *Carpobrotus edulis* is listed under Schedule 9 to the Wildlife and Countryside Act 1981 with respect to England, Wales and Scotland. As such, it is an offence to plant or otherwise cause this species to grow in the wild. In Northern Ireland, the Article 15 (2) of The Wildlife (Northern Ireland) Order 1985 (under review) states that if any person plants or otherwise causes to grow in the wild *C. edulis* or any other species included in Part II of Schedule 9, he shall be guilty of an offence. In the Republic of Ireland, Section 52 (7) of The Wildlife (Amendment) Act 2000 states that if any person who plants or otherwise cause to grow in a wild state any species of flora, or the flowers, roots, seeds or spores

of flora except under and in accordance with a licence granted in that behalf by the Minister shall be guilty of an offence. In Spain, the law no. 42/2007 created the Spanish catalogue of Invasive Alien Species which was put into place by the Royal Decree no. 630/2013³ which lists both *C. acinaciformis* and *C. edulis*. As a consequence, a number of management plans to deal with major invasive species have been developed, including for *C. edulis* and *C. acinaciformis* on sand dune ecosystems. In Italy (Tuscany), since 2000 the regional law of the 6th of April 2000, no. 56 (afterwards converted into the r.l. 19 March 2015, no. 30 – Gazzetta Uff. 25/03/2015, no.14) explicitly put a ban to the introduction, cultivation and release of *Carpobrotus* in protected natural habitats (Habitats Directive, HD⁴).

Outside Europe, in California, *C. edulis* is listed as CalEPPC List A-1 (since 1994) and as CDFA-NL (<http://www.cal-ipc.org/>); on the contrary it is not declared or considered noxious by any state government authorities in Australia. A dedicated search on main legislation databases such as, eg, N-LEX (http://eur-lex.europa.eu/n-lex/index_en) and WorldII (<http://www.worldlii.org/>) did not return any additional information.

Management

Prevention and early detection

In order to facilitate the prevention of invasive species spread, early detection tools were developed to identify areas more susceptible to invasion, and two of them were specifically tested on *Carpobrotus* species. Carranza et al. (2011) used a habitat selection function approach combined with a bootstrap test of significance to identify habitat types where the incidence of invasive species is higher or lower than would be expected from a random null model. A different tool for *Carpobrotus* detection was developed by Calviño-Cancela et al. (2014) consisting in an affordable remote-sensing technique (hyperspectral imaging system operated on board ultralight aircrafts) which allows for accurate spatial and temporal monitoring.

The research program EPIDEMIE (Exotic Plant Invasions: Deleterious Effects on Mediterranean Island Ecosystems) showed that anthropogenic changes in Mediterranean islands increase the invasibility of urban, ruderal and roadside habitats for *Carpobrotus* (Affre et al. 2010; Traveset et al. 2008). Avoiding frequent disturbance events may thus be a first prevention step. Early detection is essential, since *Carpobrotus* can be relatively easy to control if plants are removed when young (D'Antonio and Meyerson 2002) (see section control methods for more information).

Eradication and control plans

Eradication and control plans targeting *Carpobrotus* invasions have been developed in many places around the world (Ruffino et al. 2015) and in Europe (Andreu et al. 2010; Foxcroft et al. 2013; see section on control costs for more information). However, these management actions are carried out mainly by local stakeholders, and precise information on their outcomes is often lacking. In Spain, several plans for control and elimination of invasive plant species in dune systems have been performed in the last 10 years in Andalucía, Asturias, Baleares, Cataluña, Valencia, Galicia and Murcia. In Isla Grosa (Murcia), Cabrera Natural Park (Baleares) and Mondragó Natural Park (Baleares), these actions have been successful (Ministerio de Medio Ambiente y Medio Rural y Marino 2011). In Portugal, *Carpobrotus* control plans were established in Vila Nova de Gaia, in the dune system of Cresmina-Guincho in Madeira Island and in areas of high conservation interest in the Azores archipelago (EPPO 2017, Reporting Service no. 08 – 2013 Num. Article: 2013/178). An EPPO survey in 2010 also reported eradication campaigns for *Carpobrotus* in France (Bagaud Island), Malta (Malta and Gozo islands) and Spain (Andalucía). In Italy, Pontine Archipelago, Tavolara and Carbonara Cape LIFE programs included the eradication of *Carpobrotus* as one of the objectives. Altogether, the European Commission approved four LIFE Nature proposals in Spain (LIFE00 NAT/E/7339, LIFE00 NAT/E/7355 and LIFE04 NAT/ES/000044, LIFE14 NAT/ES/000699), seven in Italy (LIFE08 NAT/IT/000353, LIFE11 NAT/IT/000093, LIFE12 NAT/IT/000416, LIFE12 NAT/IT/000471, LIFE13/NAT/IT/000433, LIFE14 NAT/IT/000544, LIFE15 NAT/IT/000914) and one LIFE BIO proposal in Portugal (LIFE13 BIO/PT/000386) in which control and/or eradication of *Carpobrotus* was involved (Scalera et al. 2017).

In all cases, successful control of *Carpobrotus*, like all other invasive plant species, require long-term management and monitoring to verify the eradication of *Carpobrotus* re-sprouts and new seedlings, the re-establishment of native plant species, and the restoration of ecosystem-level processes (Ruffino et al. 2015; Chenot et al. 2018). Moreover, it is fundamental to establish priorities (with respect to the areas more susceptible to *Carpobrotus* invasion) and to select the most appropriate control methods in each case. Currently the most common methods to control *Carpobrotus* include physical and chemical control, but these methods are sometimes inadequate because they are costly, labor intensive, or may be harmful for native species. The integration of biological control after taking into account potential unanticipated consequences, along with other control methods could

lead to significant cost reductions of invasive plant management (Palmer, Heard, and Sheppard 2010).

Chemical control

The IUCN/SSC Invasive Species Specialist Group has listed several broad-spectrum herbicides that can be used to control *Carpobrotus*, but the standard herbicide is glyphosate. This herbicide has been effective at concentrations of 2% or higher, and the addition of 1% surfactant to break apart the cuticle on the leaves increases plant mortality (Ministerio de Medio Ambiente, y Medio Rural y Marino 2011). Moreover, as of 18 July 2017, the CAL-IPC (California Invasive Plant Council) listed on its website that adding an acidifier to water before mixing with glyphosate can increase the effectiveness of the treatment. In Ireland, *C. edulis* was shown to be also particularly susceptible to the commercial herbicide mix of glyphosate and diquat (Smyth, Jebb, and Booth 2011). In Portugal, Guerreiro (1977) also screened other herbicides to control *C. edulis*. Although glyphosate gave the most rapid and complete control, a mix of paraquat, simazine and benzoylprop-ethyl provided satisfactory results.

In the Natural Park of Albufera (Valencia, Spain), two years after its application, glyphosate persisted in the soil and had a harmful effect on the native flora (*Lotus creticus* L., *Elymus farctus* (Viv.) Runemark ex Melderis and *Malcolmia littorea*). Therefore, despite the effectiveness of glyphosate to control *C. edulis*, it is not recommended to use it in sandy soils (Hueso Alcaide 2017). However, this problem could be solved by adjusting the dose (Fagúndez and Barrada 2007) and by treating the target species in early or mid-winter when most native plants are dormant (Sanz-Elorza, Dana, and Sobrino 2004). For example, Torre Fernández and Alvarez-Arbesú (1999) sprayed *C. edulis* with Roundup Plus (glyphosate 36%) in the Xagó dunes (Asturias, Spain). All *C. edulis* plants died within two or three months while the native species (*Ammophila arenaria* (L.) Link., *Crucianella maritima* L., *Pancratium maritimum* L.) were not affected by the herbicide. In any case, before applying any particular herbicide, it is important to verify that no legislation bans or restricts its use in the area. The current debate over the use of glyphosate in the European Union (Gillam 2017) may altogether restrict or forbid its use in the future.

Overall, since the adjacent vegetation may also be negatively affected by herbicides (Fagúndez and Barrada 2007; Marchante et al. 2014), chemical control may only be useful when *Carpobrotus* is found in pure clumps (Schmalzer and Hinkle 1987). It may also be appropriate to employ chemical control after manual removal of *Carpobrotus*, in order to avoid re-establishment from seeds (Kelly and Maguire 2009). However, physical removal (hand-pulling and buried

stem removal) is still considered as the most effective and cost-efficient method to control the invasion of *Carpobrotus* (Fraga et al. 2005).

Physical control

Hand pulling has been shown to increase plant biodiversity in the controlled areas (Andreu et al. 2010; Krebs et al. 2015). In sandy soils, it does not require a high physical effort. Therefore, it is an effective way for controlling small patches of *Carpobrotus* (Albert 1995b). However, manual pulling can be time consuming when controlling large *Carpobrotus* patches. In such cases, the most effective way of controlling *Carpobrotus* is by rolling up the *Carpobrotus* mat from one side while severing the roots underneath with shovels. Alternatively, removal with a brush rake can also be effective (Albert 1995b).

Once hand pulled, the plant material should be moved to a “secure” place to dry and, if possible, it should be covered with a black plastic to accelerate the drying process and to kill roots and fragments that could otherwise regenerate. However, the transport and disposal of plant material may offer serious logistic problems (Fraga et al. 2005). As of 18 July 2017, “Plantas Invasoras em Portugal” listed on its website that, in these cases, the plant material can be left on site, avoiding the direct contact of the roots with the substrate. Moreover, controlled areas should be monitored for at least a decade to remove seedlings emerging from the seedbank and plants growing from fragments left during the initial clearing (Ruffino et al. 2015).

Prescribed fire. Fire apparently kills *Carpobrotus* seeds stored in the topsoil and this was confirmed by laboratory experiments with exposition at temperatures over 90°C for 5 min (D’Antonio, Odion, and Tyler 1993). However, fire with mild temperatures was found to possibly stimulate the germination of seeds and increase *C. edulis* and *C. modestus* S.T. Blake abundance in California and Australia, respectively (D’Antonio, Odion, and Tyler 1993; Parsons 1997). Moreover, due to an improvement in soil conditions after fire, *Carpobrotus* seedlings establishment and growth may be enhanced (D’Antonio, Odion, and Tyler 1993). Therefore, the use of control burning in areas where *Carpobrotus* is present must be carefully considered.

Solarization. Covering the soil with plastic sheets may also be used to control small *Carpobrotus* infestations. However, it is not a recommended method to control big infestations, since it may cause significant physical, chemical and biological changes in the soil that can last for several years (Tu, Hurd, and Randall 2001). Moreover, Theiss (1994) did not find this method to be particularly effective to control *Carpobrotus* invasions.

Biological control

Biological control may be the best managing option for inaccessible areas and dense, monospecific mats where chemical application or mechanical/manual removal is extremely difficult (see [Figure 3](#)). However, as for many biological invasions, biological control involving *Carpobrotus* remains unexplored and underutilized and little information is available on the issue.

In California, several pathogens have been isolated from the roots and stems of symptomatic *C. edulis* plants (MacDonald, Hartman, and Shapiro 1984). Pathogenicity tests demonstrated that *Pythium aphanidermatum* ((Edson) Fitzp., 1923), *Phytophthora cryptogea* (Pethybr. & Lafferty, 1931), *Phomopsis* sp. and *Verticillium dahliae* (Klebahn, 1913) were the causal agent of diseased individual or patches of plants (wilted, chlorotic or dead) (see *plant parasites and diseases section*). In the Global Invasive Species Database (GISD 2017), it was reported that *Verticillium dahliae* can cause considerable damage to *C. edulis*; however its utilization must be carefully considered because it can also infect some important crop species (McCain, Raabe, and Wilhelm 1981). In Japan, *Botrytis cinerea* Pers. caused damage on the co-occurring Aizoaceae species *Mesembryanthemum crystallinum* (Kuzniak et al. 2010), but again it is not considered appropriate due to its broad host range.

Insects. In the 1970s, two accidentally introduced soft-scale insects (*Pulvinariella mesembryanthemi* and *Pulvinaria delottoi*) caused severe damage to *C. edulis* in California (Washburn and Frankie 1981; Schmalzer and Hinkle 1987), where it had been used in roadside planting to avoid erosion. However, a successful scale management program was developed (Washburn and Frankie 1981, 1985; Tassan, Kenneth, and Cassidy 1982), by introducing several natural enemies (predators and parasitoids) to control the mentioned scale insects because *C. edulis* was considered to be a desirable plant (Schmalzer and Hinkle 1987). These predators and parasitoids were so effective that currently soft scale insects cannot be used as control agent in the invaded Point Reyes National Seashore and other protected areas of California.

In South Africa, two diaspine scale species, *Aonidiella mesembryanthemae* and *Entaspidiotus lounsburyi*, attack the leaves of *Carpobrotus*, although they are usually rare and intensely parasitized in their natural environment in the Cape Provinces. Nevertheless, *E. lounsburyi* can be very destructive on *Carpobrotus* spp. populations grown in Pretoria, even when these insects are severely parasitized (S. Naser pers. comm.).

Since 2015, a biological control program to assess the impact of individual and combined effects of two possible control agents is being developed by the Functional Plant Ecology Group of the

University of Santiago de Compostela, Spain. Under restricted greenhouse conditions, the generalist pathogenic fungus *Sclerotinia sclerotiorum* Lib. ((De Bary), 1884) and the soft scale insect *P. mesembryanthemi* are being tested. Although both agents seem to be able to affect negatively *C. edulis*, only *P. mesembryanthemi* decreased significantly the plant survival over a 6-month period (Vieites-Blanco, Retuerto, and Lema 2017). Also, periodical surveys are being carried out to monitor the effects of *P. mesembryanthemi* on the density, growth and fertility of naturally infested *Carpobrotus* populations occupying Atlantic coastal areas and to determine demographic changes of naturally infested *Carpobrotus* in the Northwest of the Iberian Peninsula. The aim of this biocontrol program is also to define the life cycle of the soft scale insect in the environmental conditions studied and to evaluate the extent of damage caused by natural parasitism in order to assess their use as control agent in this area. The direct or indirect effects on native species and the conservation benefits of biological control programs must be studied in depth.

Since control of many plant invasions has been achieved by introducing natural enemies, new surveys in the native range of *Carpobrotus* might help to find host specific or host restricted biological control candidates (eg *Mesocelis monticola*, see *biotic factors section*).

Grazing. Grazing by generalist species such as deers or rabbits can reduce the establishment and growth of *Carpobrotus* (D'Antonio, Odion, and Tyler 1993; D'Antonio 1993; Vilà and D'Antonio 1998b), although hybrids of *C. edulis* and *C. chilensis* are much less sensitive to grazing than *C. chilensis* (Vilà and D'Antonio 1998c). Despite the potential of grazing to control *Carpobrotus*, if fruits are also grazed, *Carpobrotus* seeds might be dispersed (see *fruit/seed dispersal section*). It is therefore not clear whether grazing can be used for management (D'Antonio and Thomsen 2004) knowing that generalist herbivores may have an overall effect that is facilitative rather than negative on invasive plant abundance (Maron and Vilà 2001).

Control costs

Control and eradication campaigns of *Carpobrotus* have been accomplished in the last two decades in different European countries (see *section on eradication and control plans for more information*) but, in most cases, control costs were not quantified.

In Spain, it has been reported that the total economic costs of *Carpobrotus* control between 2002 and 2007 was € 2,886,683 (0.58 million € per year). These funds were mostly spent in reducing populations through mechanical methods (Andreu, Vilà, and Hulme 2009). According to Andreu and Vilà (2007),

in Spain, *Carpobrotus* has been controlled in eight Autonomous Communities. In Menorca, between 2002 and 2005, *Carpobrotus* was eradicated in a total coastal area of 233,785 m² formerly colonized, for a total amount of 9,041 working hours. As a result of this campaign, 24 out of 27.8 ha of *Carpobrotus* (832,148 kg) were removed (Fraga I Arguimbau 2007).

In Italy, the removal of *Carpobrotus* in several Islands was accomplished under several LIFE funded projects and the costs of its eradication were valued. For example, in Pianosa Island, where 25 ha of land were cleaned, the removal of *Carpobrotus* spp., among other invasive species, was estimated to 9.4 € per m²; in Linosa Island (Strait of Sicily) eradication of alien plants including *C. cf. acinaciformis* was around € 120,000; in Tavolara Island, the elimination of *Carpobrotus* was completed for a total cost of € 50,000; in the Sardinian coast, the removal of 606 ha of *Carpobrotus* spp. charged € 24,362 and in three islands in the Ponziane Archipelago, € 25,000 for cleaning 340 ha, while the expenses in Trapani province (western Sicily) were € 28,664 (Scalera et al. 2017).

In France, control costs for *C. edulis* and *C. acinaciformis* in the Mainland between 2009 and 2013 was € 167,000, with an annual expenditure of € 33,000 (EPPO 2018a, Reporting Service no. 11 – 2015 Num. article: 2015/215). Also, in 2003 a collaboration between a nursery and landscaping industry and “Conservatoire Botanique National Méditerranéen” of Porquerolles was initiated. In this context, local initiatives for *C. acinaciformis* eradication were carried out (Wittmann and Flores-Ferrer 2015).

In Ireland, the Heritage Council provided € 15,000 to control *C. edulis* during 2011 (Kelly et al. 2013). Also, it has been reported that control of *C. edulis* was conducted in Dublin (EPPO 2018b, Reporting Service no. 09 – 2013 Num. article: 2013/208).

Restoration

After the application of any of the above control methods, a specific restoration plan must be implemented. The remaining living parts and litter of *Carpobrotus* should be removed; the controlled areas should be over-seeded with the appropriate native species, and the establishment of opportunistic ruderal species should be avoided (Novoa et al. 2013; Fried et al. 2014).

Legacy effects, including changes in soil characteristics, and accumulation of allelochemicals and *Carpobrotus* seeds on the litter, may persist after the removal (*for more information see negative impacts section*). Ruderal opportunistic species may also benefit from these legacy effects (Novoa et al. 2013; Fried

et al. 2014) due to their greater plasticity and opportunistic strategy or high abundance in the seed bank (Maurel et al. 2010). Therefore, a combination of legacy effects and competition with ruderal species and *Carpobrotus* may prevent the establishment of native dune species in the eradicated or controlled areas (Novoa et al. 2013; Novoa and González 2014).

To successfully restore dune ecosystems invaded by *Carpobrotus*, plants must be removed in the first stages of the invasion, to avoid the strong effects on soil conditions. This should be followed by the removal of necromass to avoid legacy effects (Vieites-Blanco and González-Prieto 2017), and by the removal of opportunistic ruderal species and *Carpobrotus* seedlings that are likely to constrain the establishment of the native dune species (Novoa et al. 2013). However, removing the litter may lead to soil erosion. To reduce such erosion, the bare ground can be covered with geotextile (Bhattacharyya et al. 2010). A different option is to leave a 50 cm strip of *Carpobrotus* plants and only remove it once native species have been established (Chenot et al. 2018). However, this strip needs to be monitored to prevent *Carpobrotus* recolonization.

Notes

1. Convention on the Conservation of European Wildlife and Natural Habitats, Bern, 19.IX.1979Revathy.
2. Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species.
3. <https://www.boe.es/buscar/act.php?id=BOE-A-2013-8565>.
4. HD = Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora.

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