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Monographs on Invasive Plants in Europe: *Baccharis halimifolia* L.

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ABSTRACT
This account presents information on all aspects of the biology and ecology of *Baccharis halimifolia* L. that are relevant to understanding its invasive behaviour. The main topics are presented within the framework of the new series of *Botany Letters* on *Monographs on invasive plants in Europe*: taxonomy, distribution, history of introduction and spread, ecology (including preferred climate and habitats, responses to abiotic and biotic factors, ecological interactions), biology (including physiology, phenology and reproductive biology), impacts and management. *Baccharis halimifolia* L. (Asteraceae), groundsel bush, is a broad-leaved shrub native to the coastal area of southeastern North America. Introduced for ornamental and amenity purposes during the nineteenth century, it has become naturalized in several coastal habitats, as well as in disturbed areas of western Europe. The shrub is now common on the Atlantic coast of Europe from northern Spain to Belgium and it is an emerging problem on the Mediterranean coast. *Baccharis halimifolia* is a light-demanding pioneer species that colonizes following disturbance but can then become dominant in natural habitats. The shrub can grow on a large range of soil types but prefers moist soils with high organic content and it is well adapted to poorly drained saline soils. In contrast to its native range, where it is in competition with other coastal shrubs, populations in the secondary range have almost no native analogues across most of its ecological niche except for *Tamarix gallica* in Mediterranean areas. *Baccharis halimifolia* reproduces sexually, but it has a high resprouting ability following mechanical damage or fire. Very high seed production, coupled with dispersal by wind and water, ensure a good colonization capacity of suitable habitats. The species shows a relatively high plasticity for both morphological and ecophysiological traits, which is probably the basis for its tolerance to a wide range of ecological conditions, including salinity and light availability. *Baccharis halimifolia* is host to a limited number of insects, both in the native and introduced ranges, but a number of highly specific agents have contributed to the control of this plant following its introduction to Australia. In Europe, *B. halimifolia* is considered an invasive non-indigenous plant and the shrub is the object of control programmes. Negative impacts include the addition of a new canopy layer in formerly open habitats (e.g. *Juncus maritimus* communities), which causes a strong decrease in species richness and herbaceous cover and poses a threat to some birds by modifying habitat quality, mainly in priority habitats and in many natural protected sites. Most efficient control methods are mechanical removal and herbicide application either on leaves or stumps. Due to the high cost of mechanical removal and the unintended effects of herbicide application on other species, alternative management methods such as controlled inundations and biological control could also be considered. The plant is legally prohibited in several countries and it is prelisted on EU Regulation 1143/2014.

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Biogeography; climate; ecophysiology; environmental impacts; germination; habitats; invasion history; management strategies; natural enemies; reproductive biology; salinity; species distribution modelling

Taxonomy

Names and classification

Scientific name: ***Baccharis halimifolia*** L., 1753
Synonym: *Baccharis cuneifolia* Moench, 1794
Taxonomic position: Eudicotyledons, Order: Asterales, Family: Asteraceae, Tribe: Astereae
Common names: Kreuzstrauch [DE], eastern baccharis, groundsel baccharis, groundsel bush, seepwillow, silverling, sea myrtle, manglier, consumption weed, saltbush [EN], tres Marías, bácaris, chilca de hoja de orzaga, carqueja [ES], baccharide à feuilles d'halime, séneçon en arbre [FR]
EPPO code: BACHA

Baccharis halimifolia is the type species of the genus *Baccharis*, i.e. the species on which the concept of the genus is based (Nesom 2006).

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Figure 1. Habit of *Baccharis halimifolia* L. in *Juncus maritimus* communities, 04/X/2012, Torreilles (France). © Guillaume Fried.

Morphological description

Species description

Baccharis halimifolia is a branching shrub or small tree, usually growing to between 1 and 3 m but sometimes to 4 m (Sundberg and Bogler 2006), being classified as a nanophanerophyte (Tison and de Foucault 2014). The stems are erect or ascending, often densely branched from the base (bushy habit, see Figure 1), sometimes with a single stem (small tree habit). Young stems are 'slender, striate-angled, glabrous or minutely scurfy, sometimes resinous' (Sundberg and Bogler 2006). On mature, single-stemmed plants, the trunk can reach 16 cm in diameter, with a deeply fissured bark. The leaves are alternate, pale green, thick (Figure 2); those of the stem and lower branches are obovate to elliptic or oblanceolate, 2–7 cm long and 1–5 cm wide; those of the branchlets are smaller, cuneate at the base, several-toothed above the middle.

Baccharis halimifolia is dioecious. Flowers are small; flower heads (capitula) are situated in terminal or axillary clusters of one to five. Achenes are 1–2 mm long and the pappus is bright-white, 8–12 mm long (Weber 2003; Sinnassamy 2004; Nesom 2006; Sundberg and Bogler 2006). During the flowering period, female individuals are whitish, due to the color of the pappus, which is much longer than the involucre (Figure 3); male individuals are yellowish due to the copious production of pollen (Figure 4).

Figure 2. Leaves of *Baccharis halimifolia* L., 04/X/2012, Torreilles (France). © Guillaume Fried.

Distinguishing features

In its native range, non-botanists can confuse *B. halimifolia* with *Iva frutescens* L., which often co-occurs, but the latter has opposite (alternate on *B. halimifolia*) and more lanceolate leaves. The Mexican species *Baccharis heterophylla* Kunth. is much more readily confused with *B. halimifolia*. Where both occur in the region of Veracruz (Mexico), *B. halimifolia* can be distinguished by its habitat along the coast or coastal plain, and its more gradate, blunt-tipped involucral bracts, and longer pappus (Nesom 2006).

Variations at the infraspecific level

No subspecies or varieties are currently recognized within the species. Plants described from the West Indies have been called *Baccharis halimifolia* var. *angustior* DC., but there appears to be little justification for their formal recognition and this name is now considered as a synonym of *B. halimifolia* (Nesom 2006).

Figure 3. Female inflorescence of *Baccharis halimifolia* L., 04/X/2012, Torreilles (France). © Guillaume Fried.

Figure 4. Male inflorescence of *Baccharis halimifolia* L., 04/X/2012, Torreilles (France). © Guillaume Fried.

Distribution and status

Native range

Baccharis halimifolia L. is a North American species (Sundberg and Bogler 2006). Its native distribution includes: Canada (Nova Scotia), Mexico (Mexico, Nuevo Leon, San Luis Potosi, Tamaulipas, Veracruz), the USA (Alabama, Arkansas, Connecticut, Delaware, Florida, Georgia, Louisiana, Maryland, Massachusetts, Mississippi, New Jersey, New York, North Carolina, Oklahoma, Pennsylvania, Rhode Island, South Carolina, Texas, Virginia, West Virginia). It is also native in the Caribbean: Bahamas (Correl and Correl 1982), Cuba (Weber 2003; USDA National Genetic Resources Program 2012).

In Canada, *B. halimifolia* reaches its northern range limit and it is considered as an extremely rare Atlantic coastal plain species, occurring only in the Tusket River estuary and its vicinity. Official conservation programmes are being implemented in this area (COSEWIC 2011).

Introduced range

Baccharis halimifolia has been introduced on three continents. In Oceania, it is invasive in Australia (Queensland, New South Wales) and locally established in New Zealand (South Island) where, according to Webb, Sykes and Garnock-Jones (1988), the species was recorded on Banks Peninsula (Canterbury) only. There are approximately 40 known sites consisting mostly of old scattered plants on the Porthill area near Sumner (Lynne Huggins, Department of Conservation, New Zealand, pers. comm. 2012).

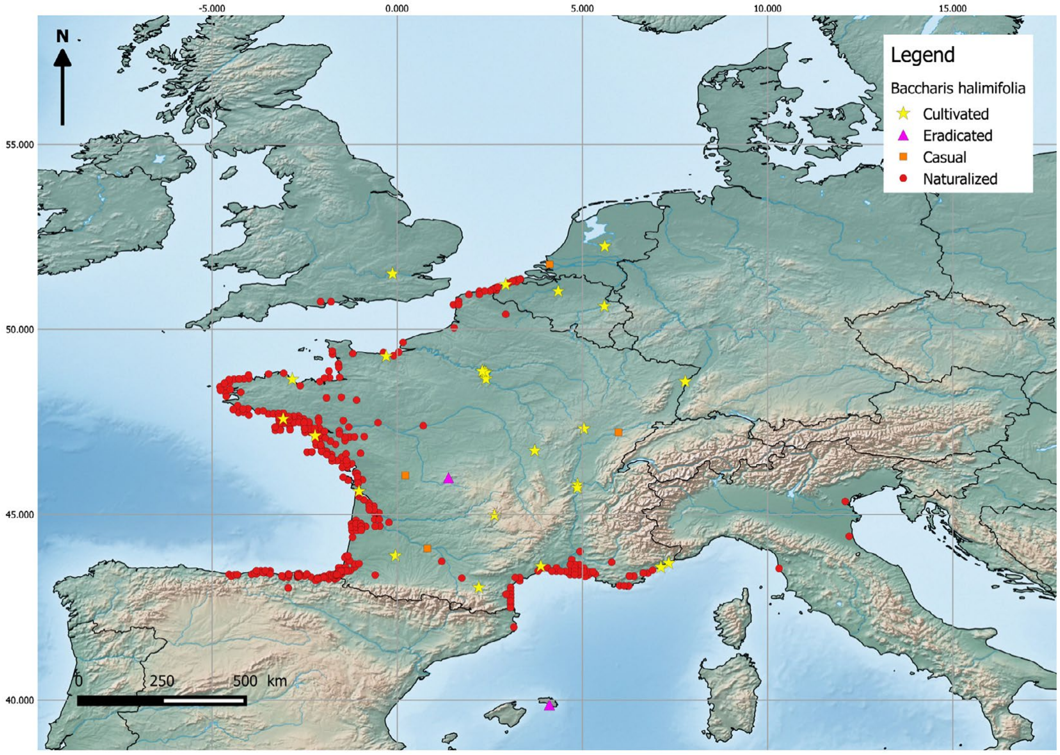

Figure 5. Distribution map of *Baccharis halimifolia* L. in western Europe. The map is given according to GBIF (2016) with corrections based on our expertise on the species. For Spain, we used Caño et al. (2013) and the BIOVEG database (Biurrun et al. 2012). For France, we used the Système d'information « Flore, Fonge, Végétation et Habitats » de la Fédération des Conservatoires botaniques nationaux (2016), Jovet (1947), Dupont (1952), Dupont (1966) and herbarium specimens from P and MPU; Rappé et al. (2004) was used for Belgium and van Valkenburg, van Duistermaat and Meerman (2014) for The Netherlands; Arrigoni & Viegi (2011), Coaro (1987), Minelli (2009), Pizzo and Buffa (2009), Tomé (2010), Zanetti (1997) were used for Italy.

In Asia, *B. halimifolia* is recorded only in Georgia (in Abkhasia, on the eastern coast of the Black Sea) (Westman, Panetta and Stanley 1975; Kikodze et al. 2010). The plant is also recorded as planted in the Ataturk arboretum in Istanbul, but has so far not been recorded as naturalized (EPPO 2013).

In Europe, *B. halimifolia* is distributed along the Atlantic coast from northern Spain to the Netherlands, and along the Mediterranean coast from Spain to Italy, where it is much more scattered (Figure 5). It is established in Belgium (Verloove 2008), and very locally in the United Kingdom (Clement and Foster 1994). It is considered invasive mostly in France (Thellung 1916; Sinnassamy 2004), and in Spain (Allorge 1941) and more recently in Italy (Zanetti 1997; Arrigoni and Viegi 2011). The species had been recorded as casual in the Netherlands and it is not known to be present anymore in this country (van Valkenburg, van Duistermaat and Meerman 2014).

History of introduction and spread

From different bibliographic and herbarium sources, it seems that *B. halimifolia* has been cultivated in Europe in different botanic gardens, at least since the seventeenth century, with a first record in 1688 in London, UK (Miller 1807 in Caño et al. 2013). In France, the plant was mentioned in the Jardin du Roi in Paris (Lamarck 1783) and in Montpellier in 1824 (Agence Méditerranéenne de l'Environnement, Conservatoire Botanique National Méditerranéen de Porquerolles 2003).

During the nineteenth century, the cultivation of *B. halimifolia* as an ornamental plant was recommended in several horticultural books (Duhamel du Monceau 1800; Dupuis and Hérincq 1884) and it started to be grown in private gardens. For example, Langlois (1877) states in his book *Le nouveau jardinier fleuriste* that *B. halimifolia* should be planted as a hedge plant. Specific indications of places where it was cultivated could be found in the southwest of France (Guillaud 1887), in Paris (Pardé 1902) and in Brittany: Carnac, Saint-Quay-Portrieux (Hibon 1938). Thellung (1916) indicates that the plant was cultivated in Provence since its introduction. Here it was first introduced in 1863 at Villa Rothschild (Saint-Jean-Cap-Ferret) from Carolina (USA) (Sauveigo 1899). A few years later (1889) it was also recorded in Antibes in Villa Thuret garden (Jeannel 1890).

There is some evidence to suggest that *B. halimifolia* probably became naturalized at the end of the nineteenth century in the Basque region (Dupont 1952). A specimen of *B. halimifolia* without any reference to date and place has been found in the herbarium of a Basque naturalist, L. Prestamero (1733–1817). This could be the first record of the presence of this species in the Basque coast because Prestamero lived in Vitoria in the Basque Country (Uribe-Echebarria 2015). However, the oldest known record with clear evidence of escape in the wild was found on a herbarium specimen collected on the cliffs of 'la Chambre d'Amour' in Biarritz (Pyrénées-Atlantiques, France) in 1903 (Neyraut 5062 P, see Figure 6).

Baccharis halimifolia was collected (de Vergnes s.n. P) at about the same time (1907) as a casual escape in a damp wasteland at La Teste de Buech (Gironde, France). In the same area, a herbarium specimen conserved in Montpellier (MPU) was collected even earlier, in 1890 in Arcachon (Gironde, France), but without an indication of its naturalization status. From the addition and corrections to the three volumes of the *Flore illustrée de la France* (Coste 1906), it is clear that the plant was already completely naturalized in the Gironde and Pyrénées-Atlantiques departments. A few years later, in 1913, a third establishment locus was observed in the south of Brittany, where it was recorded as abundant in thickets of cliffs in Pornic (Ducellier s.n. MPU) and in a pine forest along railways between Pornic and Paimboeuf in the South of Brittany (Anonymous 1916).

In the 1940s, *B. halimifolia* was already considered as locally invasive and spreading rapidly: Jovet (1947, 4) describes the situation, stating that it "is now very common in the South-West", especially abundant all around the Arcachon basin (Gujan, between Andernos and Arès, around Pitchourlin). In some locations, for example in the Courant d'Huchet (Léon, Landes, France), *B. halimifolia* forms "impenetrable thickets" (Jovet 1947, 4). At the same time in Brittany, it also showed similar signs of invasiveness, for example in *Juncus maritimus* marshes in Carnac, precisely where it was previously observed as cultivated (Hibon 1938). Des Abbayes (1947) indicated its presence in many localities between le Pouliguen and le Croisic (Loire-Atlantique) and, for the first time, in the Finistère at Guilvinec. Dupont (1952) summarized the situation in Brittany, pointing out new locations around Carnac, 30 km westwards (Larmor, Morbihan) and 10 km eastwards (Arzon, Morbihan). He also reported that *B. halimifolia* was common along 40 km of coast between Piriac-sur-Mer and Saint-Nazaire (Loire-Atlantique). A dozen new locations were then cited between Pornic (Loire-Atlantique) and Royan (Charente-Maritime) (Dupont 1966). Thus, in the middle of the 1970s, *B. halimifolia* was considered as completely naturalized along the French Atlantic coast (Jovet and de Vilmorin 1975) and occurred in nine departments: Ille-et-Vilaine, Côtes-d'Armor, Finistère, Morbihan, Loire-Atlantique, Vendée, Gironde, Landes and Pyrénées-Atlantiques.

During the 1980s, the first records of *B. halimifolia* were reported along the Mediterranean coast, in the Roussillon (Amigo 1983). In the Camargue, an age estimation of individuals by counting growth rings dated colonization to the early 1980s (Charpentier, Riou and Thibault 2006). *Baccharis halimifolia* was recorded more recently along the Languedoc coast (Salabert and Gastesoleil 1991). During the 2000s, it also appeared on the shores of the North Sea in Pas-de-Calais in the estuary of the Slack (Ambleteuse) and Wimereux (Benoît Toussaint, Conservatoire Botanique National de Bailleul, pers. comm. 2012) as well as on the Provence coast (SILENE 2016). As observed in the native range (Ervin 2009), an increasing number of locations are recorded inland (Figure 5). All of these floristic data (herbarium, literature, data sets) can be used to reconstruct the invasion dynamics of *B. halimifolia*. The cumulative number of localities over time (using French *commune* as a unit) showed that the start of the exponential phase of invasion occurred in the 1940s (Figure 7). During the first 40 years, there were 0.32 new locations per year. A second inflexion point is detected in the 1990s, with a dramatic increase in the number of new localities. Whereas between 1940 and 1990, 0.83 new locations were detected each year, after 1990 the rate reached 11.3 new locations per year. These invasion dynamics are similar to those of other major invasive plants in Europe, such as *Impatiens glandulifera* Royle (Pyšek and Prach 1993). However, increased attention on the species during the 2000s as well as the development of communal

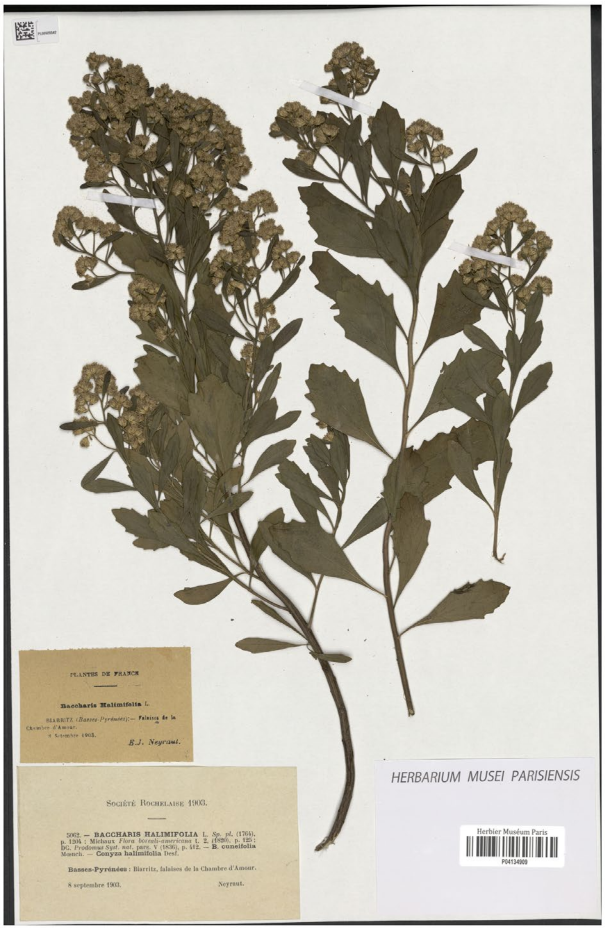

Figure 6. Herbarium specimen corresponding to the probable oldest individual collected in the wild in Europe: Falaises de la Chambre d'Amour, Biarritz (France), 8/IX/1903, Neyraut N°5062, Herbarium P. © Muséum National d'Histoire Naturelle (MNHN).

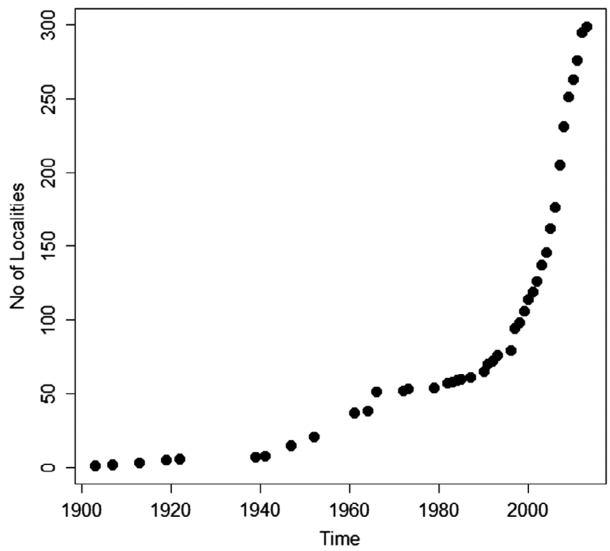

Figure 7. Invasion curve of *Baccharis halimifolia* L. in France based on herbarium and literature surveys and the database *Système d'information « Flore, Fonge, Végétation et Habitats » de la Fédération des Conservatoires botaniques nationaux* (2016). Total cumulative number of localities is given on the *y*-axis. A regression tree analysis identified two main breaks in 1940 and 1990. The slope of the three separated regression lines performed for each period is respectively: 0.32 (1900–1940), 0.83 (1940–1990) and 11.3 (from 1990 on) new locations/year.

inventories by the National Botanical conservatories could also have contributed to the observed pattern.

In Spain, *B. halimifolia* was first reported in 1941 in Lekeitio in the Basque Country (Allorge 1941). It is currently widely naturalized on the Atlantic Coast of the Basque Country and of Cantabria. It occurs in almost all estuaries of the Cantabric coast, from the Ría of Tina Mayor at the border with Asturias east to Txingudi in Guipuzcoa (Caño et al. 2013). In Cantabria it was first recorded in 1958 in the bay of Santander (Guinea 1953) and in Asturias it was recorded in 1998, in the marshes of Tina Mayor (Campos et al. 2004). A few locations with only some individuals or some scattered thickets are found at other points in Asturias (including Avilés, the marshes of the rivers Sella and Navia, the Ría of Villaviciosa) but *B. halimifolia* does not seem to have yet established in Galicia. Since it has been recently cited in the Bidasoa River in Navarre (Lorda 2013) we cannot exclude the possibility that it could be currently spreading into inner areas through riversides. However, *B. halimifolia* is rare along riversides at present. It is also present to a lesser extent on the Mediterranean coast (comarque of Baix Empordà, Catalonia, Barriocanal et al. 2005). On the island of Menorca *B. halimifolia* appeared as naturalized, forming a small population (< 10 individuals) that was totally eliminated in 2005 (Podda et al. 2010; Pere Fraga i Arguimbau pers. comm.) Since then, it has not been observed in the wild although it is sporadically cultivated in gardens.

In Italy, *B. halimifolia* has been recorded in the Veneto region (Zanetti 1997; Pizzo and Buffa 2009; Minelli 2009) and in the Tuscany region (Coaro 1987; Arrigoni and Viegi 2011), in coastal areas in both cases. According to Zanetti (1997) the species was introduced in Veneto in the forest plantations along the coastal wetlands, especially in the delta area of the rivers Piave and Po. Also in the Veneto region, in 2010 *B. halimifolia* was recorded inside the nature reserve (riserva naturale) Valle Averto, a Site of Community Interest (SIC IT3250030), according to Tomé (2010). In the Tuscany region, the taxon is considered invasive. Near Livorno, it is recorded as massively present in the vicinity of *Salicornia* spp. communities (Coaro 1987).

In Belgium, *B. halimifolia* was first planted in botanic gardens in the nineteenth century (Rappé et al. 2004). During the first half of the twentieth century, it was intentionally introduced as a windbreak in coastal dunes (e.g. in Raversijde in 1924). It was then recorded as a casual escaped species in the port of Oostende in 1948 (Lambinon 1957). In the past decades, it has been increasingly planted ornamentally in public parks in coastal areas. It is now naturalized in numerous, widely scattered localities along the Belgian coast, concentrated between Adinkerke and Oostduinkerke, around Blankenberge and between Zeebrugge and Knokke (Verloove 2011).

In the Netherlands, a few individuals were collected in 2003 in the nature reserve "Kwade Hoek" (coordinates 51°50.689 N, 3°59.387 E) and a herbarium sample had been deposited at the Nationaal Herbarium Nederland, Universiteit Leiden branch (L.) by R. van de Meijden. The plant could not be relocated during targeted surveys in this nature reserve in September 2012 and is considered to be locally extinct (van Valkenburg, van Duistermaat and Meerman 2014).

In the United Kingdom, there are two records. According to Clement and Foster (1994), *B. halimifolia* is established on the shore at Mudeford, South Hants (known since 1942) and is also known from the shore at Hamworthy, Dorset, where Bowen (2000) in *The Flora of Dorset* says it was recorded as a self-sown plant in 1958. A third record from Scotland is regarded as dubious by the New Atlas editors (Chris D. Preston, Centre for Ecology and Hydrology, pers. comm. 2012).

The history for *B. halimifolia* clearly is one of intentional introduction with two main purposes: (a) for ornamental use in private gardens or (b) as an amenity plant cultivated on a moderate to large scale in public places for landscaping purposes, including soil stabilization, aesthetic enhancement or windbreaks. From these plantings in gardens, but also on roundabouts or along roads and along pathways close to shorelines, the species has spread to semi-natural and natural habitats, first along roadsides or disturbed grasslands, then into coastal wetlands (Le Moigne and Magnanon 2009). In many places, such as Carnac, La Teste de Buech, there are clear records of the plant being cultivated in gardens or as a hedge a few years before the first records of naturalized populations. In his early survey of the plant along the Atlantic coast, Dupont (1952, 1966) often reported the presence of *B. halimifolia* in private gardens near places where he found the plant in the wild. Interestingly, Dupont (1966) also observed *B. halimifolia* in green waste disposal sites and proposed that it could also have spread through disposal of garden wastes.

Ecology

Response to abiotic factors

Climate

According to the World Map of Köppen-Geiger Climate Classification (Kottek et al. 2006), *B. halimifolia* occurs mainly in warm temperate climate, fully humid with hot summers as well as in equatorial climate type with a dry winter (e.g. in Florida). In Australia, it occurs in both humid subtropical (Cfa) and marine temperate or oceanic (Cfb) climate types. A large part of Europe is under oceanic (Cfb), hot-summer Mediterranean climate (Csa) and warm-summer Mediterranean climate (Csb) types, and therefore is presumably suitable for the establishment of *B. halimifolia*.

In its native area, *B. halimifolia* is found from Florida, which has a humid subtropical to tropical climate, to as far north as Massachusetts, where snowfall commonly occurs during winter (USDA-ARS Website). It covers four plant hardiness zones (from 9 to 6) with mean annual minimum temperatures of −17.8°C to −23.3°C in the last zone (Ervin 2009). The species is considered to be resistant to −15°C (Huxley 1992).

In Australia, optimal climatic conditions for *B. halimifolia* include long warm summers and an annual precipitation of > 900 mm, mainly occurring in summer (Westman, Panetta and Stanley 1975). It is assumed to grow more vigorously under subtropical conditions and to be particularly invasive in the wetter parts of the country (Sims-Chilton, Zalucki and Buckley 2010). Westman, Panetta and Stanley (1975) found that optimal germination occurs between 15 and 20 °C after cold pre-treatment at 5 °C. This explains the temperate to subtropical range of the species. Because *B. halimifolia* is a late flowering and fruiting species, it is not known how the date of first frost and duration of freezing in winter could limit its extension northwards in Europe. Self-sown individuals are recorded in Belgium up to Knokke-Heist in the north at latitude 51°20' N. In the Netherlands, a few individuals were observed on sand dunes in "Kwade Hoek" in 2003, but they did not persist. The hypotheses are that the species did not persist because the winters were too cold, or that competition with native communities of *Elaeagnus rhamnoides* (L.) A.Nelson excluded it (van Valkenburg, van Duistermaat and Meerman 2014). Of course, these hypotheses are not mutually exclusive (see the next section, *Response to biotic factors*, for other examples supporting the second hypothesis).

Maxent modelling has been undertaken using the 18 Bioclim variables (Hijmans et al. 2005) at a 2.5 arc min resolution scale, i.e. approximately 4 km^2 (Fried, unpubl. work), using all *B. halimifolia* naturalized points (Figure 5) on a background that included the full geographic extent of Europe, to assess how well these climate variables explain the current European distribution of the species. This model is useful for identifying which climate variables contribute to the current distribution of *B. halimifolia* in Europe, but is not appropriate for predicting further range expansion because *B. halimifolia* is probably still spreading (Figure 7). Highest relative contributions showed that *B. halimifolia* is sensitive to variables representing seasonality (isothermality, precipitation seasonality), reflecting its association to oceanicity, but also to annual trends (mean temperature) and limiting factors (minimum and maximum temperature) (Table 1). Response curves indicated a higher probability of presence when Minimum Temperature of Coldest Month > 0 °C and when Maximum Temperature of Warmest Month is between 20 °C and 30 °C.

Sims-Chilton, Zalucki and Buckley (2010) elaborated a CLIMEX climatic projection for *B. halimifolia* for the world. The potential distribution of *B. halimifolia* was projected for Europe with the software CLIMEX using the parameters of this previous study (EPPO 2013, see Table 2). This projection may overestimate the potential range of the species in Europe (Figure 8), particularly in northern countries. Furthermore, consideration of the distribution of suitable habitat types would be required for a more realistic projection (Kriticos et al. 2015). As a rough estimate, the most suitable areas are the Mediterranean basin (Albania, Bosnia & Herzegovina, Croatia, Greece, Slovenia), the Atlantic Western Europe (Belgium, France, Ireland, the UK, Portugal, Spain) and the eastern part of the Black Sea (Georgia, Turkey, Russia). Other countries may be at risk, including Germany, Denmark and the Netherlands. Uncertainties remain on the cold and drought resistance of the species.

Substratum

Baccharis halimifolia can be found on a wide range of soil types with regard to texture and pH (Westman, Panetta and Stanley 1975), as well as other characteristics. Paudel and Battaglia (2015) found that *B. halimifolia* occurrence in coastal Mississippi, USA, increased with percentage increase of sand, decreased with percentage increase of silt, but remained invariant with carbon to nitrogen ratio. In Australia, it is recorded from dry infertile forest soils to rich volcanic loams and low-lying clay soils with high moisture content (Winders 1937, cited in Sims-Chilton and Panetta

Table 1. Estimates of the relative contributions of Bioclim climate variables to an explanation of the current distribution of *Baccharis halimifolia* in Europe.

Code	Variable	% contribution	Permutation importance
BIO19	Precipitation of the Coldest Quarter	18.4	7.3
BIO1	Annual Mean Temperature	16.5	5
BIO3	Isothermality ((BIO2/BIO7)*100)	12	19.6
BIO15	Precipitation Seasonality (cv)	11.8	4.4
BIO6	Min Temperature of Coldest Month	11.8	13.1
BIO7	Temperature Annual Range (BIO5–BIO6)	9	5.7
BIO4	Temperature Seasonality (sd*100)	7.9	5
BIO8	Mean Temperature of Wettest Quarter	5.3	2.6
BIO5	Max Temperature of Warmest Month	4	4.2
BIO13	Precipitation of Wettest Month	1.1	6.5
BIO2	Mean Diurnal Range	0.8	7.1
BIO10	Mean Temperature of Warmest Quarter	0.8	8.8
BIO12	Annual Precipitation	0.2	0
BIO16	Precipitation of Wettest Quarter	0.1	8
BIO9	Mean Temperature of Driest Quarter	0.1	0

Percent contribution is the relative contribution of each variable to the Europe-trained model during the model-training process. Permutation importance was estimated as the relative loss in area under the curve (AUC) value of the final model when the values of a given variable are permuted randomly among the presence points and random background points. Higher per cent permutation importance means greater relative loss in AUC value after random permutation, hence a greater reliance on the particular variable.

Table 2. CLIMEX parameters for *Baccharis halimifolia* according to Sims-Chilton, Zalucki and Buckley (2010) used to predict potential distribution in Europe as shown in Figure 8.

Description of the parameter	Parameter	Value
Temperature parameter (°C)		
Lower threshold of temperature for population growth	DV0	5
Lower optimal temperature for population growth	DV1	12
Upper optimal temperature for population growth	DV2	27
Upper threshold of temperature for population growth	DV3	35
Moisture		
Lower threshold of soil moisture	SM0	0.3
Lower limit of optimal range of soil moisture	SM1	0.6
Upper limit of optimal range of soil moisture	SM2	1.5
Upper threshold of soil moisture	SM3	2.5
Stress indices		
Threshold of cold stress (°C)	TTCS	−4
Weekly accumulation of cold stress (week^{-1})	THCS	−0.009
Threshold of heat stress (°C)	TTHS	38
Weekly accumulation of heat stress (week^{-1})	THHS	0.015
Threshold of dry stress	SMDS	0.2
Weekly accumulation of dry stress (week^{-1})	HDS	−0.01
Threshold of wet stress	SMWS	3
Weekly accumulation of wet stress (week^{-1})	HWS	1

2011). Similarly, a survey along the French Atlantic coast (Dupont 1966) indicated that *B. halimifolia* occurs on sand, on rocks (granite or limestone), on dry soils or in wetlands. Despite its presence on such a large gradient of soil types, it preferentially grows on moist soils with high organic content, temporarily covered by brackish water (Young, Erickson and Semones 1994; Sims-Chilton and Panetta 2011; Caño et al. 2013). Indications on the nature of soils on which *B. halimifolia* has been found are summarized below.

Soil moisture. *Baccharis halimifolia* grows most typically in moist soils with high organic content (Westman, Panetta and Stanley 1975; Boldt 1987; Sims-Chilton and Panetta 2011). However, in salt marshes, *B. halimifolia* is rather associated with high elevations and coarse sand, with fewer plants found in waterlogged conditions and high soil silt content and conductivity (Onaindia, Albizu and Amezaga 2001).

Soil pH. The plant is observed on soils with pH values in the A horizon ranging from 3.6 to 9 (Westman, Panetta and Stanley 1975). These results were obtained from 22 sites in Florida (pH 5–9) and 14 sites in Queensland (pH 3.6–8.2).

Soil nutrients. Based on 14 sites in Queensland where the species is present, Kjeldahl nitrogen ranged from 560 to 5500 ppm where the plant was recorded, whereas available phosphorus ranged from 4 to 73 ppm (mean: 15 ± 5) (Westman, Panetta and Stanley 1975).

Salinity. In both its native (Florida) and exotic (Australia) ranges, *B. halimifolia* is often found in soil covered by water with salinity ranging from 0 to 3.6%, i.e. 36 g/l (from chlorinities of 0.06–1.78 and 0.0–1.98%, in Florida, USA and in Queensland, Australia, respectively, according to Westman, Panetta and Stanley 1975). In the native range, along a 11.3-km transect in coastal Mississippi, USA, the highest occurrence of *B. halimifolia* was recorded under moderate levels of salinity (Paudel and Battaglia 2015). Also in its native range, in North American marshes, *B. halimifolia* colonizes sites with groundwater salinity levels < 15 g/l (Young,

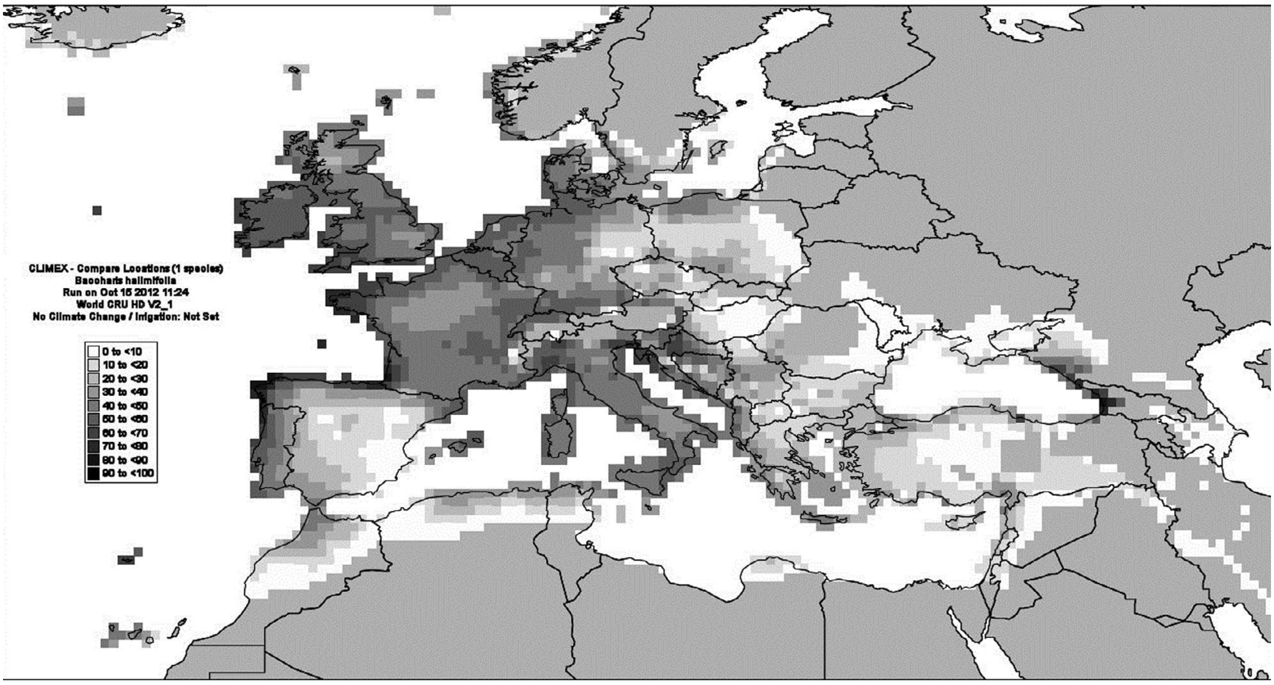

Figure 8. Potential distribution of *Baccharis halimifolia* L. in the EPPO region. The colour corresponds to the Ecoclimatic Index (EI), which summarizes the suitability of the area. Darker grey indicates increasing suitability of areas. It is considered that a species can persist where EI > 20 (corresponding to the second lightest grey colour on this figure).

Erickson and Semones 1994), although Tolliver, Martin and Young (1997) showed that under glasshouse conditions this plant can survive concentrations of 20 g/l.

In Europe, *B. halimifolia* is found on soils with even higher salt concentrations. For instance, in Oyambre estuary (Cantabria, Spain), Frau et al. (2014) found that *B. halimifolia* develops in areas with salinity values of up to 25 g/l. Moreover, in the Basque region it can invade sub-halophytic rush communities with a salinity range between 4 g/l and 33 g/l, with mean salinities between 9% and 22% (Caño et al. 2014). However, fine-scale increase in edaphic salinity limits the exotic shrub invasion, since average *B. halimifolia* cover in invaded plots is eight or nine times lower in the high-salinity (mean salinity of 22 g/l) than in the low-salinity (9 g/l) communities (Caño et al. 2014).

Caño and colleagues (Caño, Garcia-Magro and Herrera 2013; Caño et al. 2014) also assessed the growth of individuals of *B. halimifolia* occurring in communities on low, medium and highly saline substrates. Shoots of *B. halimifolia* grew from May to December in the low- and medium-salinity communities but in the high-salinity community shoots showed almost no growth from early August (Caño, Garcia-Magro and Herrera 2013). Moreover, the height, seed production and specific leaf area of *B. halimifolia* decreased as salinity and waterlogging increased, whereas the percentage of leaf drop increased under more physiologically stressful conditions (Caño et al. 2014). Interestingly, they detected significant differences between sexes in response to edaphic stress because, in comparison with males, females displayed lower shoot elongation and leaf production rates during summer and higher leaf drop rates in high-salinity sites (Caño, Garcia-Magro and Herrera 2013).

Concerning germination requirements in a greenhouse experiment, Paudel and Battaglia (2013) showed that percentage germination in native populations of *B. halimifolia* did not differ between the control (0 g/l) and salinity treatments up to 20 g/l but it significantly declined at 30 g/l. However, in another study, Caño et al. (2010), using invasive populations of *B. halimifolia*, showed that low concentrations of salt (approx. 2 g/l) in irrigation water can decrease the probability of germination to about 20%; concentrations > 10 g/l seem to inhibit germination. This suggests that for *B. halimifolia* to colonize the most halophytic communities, recruitment must happen under specific rainfall, temperature and soil conditions that result in lowest salinity values.

Polluted soils. *Baccharis halimifolia* has been observed to naturally grow on explosive-contaminated soil near munitions sites, which indicates that it might be tolerant to TNT and RDX (Ali et al. 2014).

Hydrodynamic regimen. Frau et al. (2014) showed that *B. halimifolia* develops in areas that are inundated < 26% of the year, with water speed and water flow of < 0.1 m/s and < 0.85 m^3/s, respectively. Habitat suitability modelling indicated that *B. halimifolia* was not equally represented over the estuary, preferring areas with lower than average hydrodynamic values (Frau et al. 2014).

Light

Baccharis halimifolia can produce seeds at various degrees of shade and under light intensity as low as 3% of open light (Westman, Panetta and Stanley 1975), even if the yield of viable seed is reduced (see also Panetta 1979a, 1062). In coastal Mississippi, USA, the peak of occurrence for *B. halimifolia* was recorded at low to moderate levels of canopy openness (Paudel and Battaglia 2015).

Response to biotic factors

Co-occurring plants can have a significant influence on the suitability of the habitat for the establishment of *B. halimifolia*. As for many invasive plants, *B. halimifolia* has a number of biological characteristics adapted to pioneer stages in succession (Westman, Panetta and Stanley 1975). At the germination stage, the species takes advantage of open areas and disturbances (including micro-disturbances) and is dependent on such situations. However, once established, it is able to outcompete other species.

Baccharis halimifolia shows a degree of shade-tolerance during establishment (Panetta 1977). However, the relative lateness of stem growth indicates that seedlings are not able to rapidly escape shade conditions in the field (Panetta 1977). Compared with tropical pasture species in Australia, *B. halimifolia* is at a disadvantage in terms of establishment (through both lower seed weight and lower relative seedling growth rate). During early development (before the five-leaf stage), heavy shade can affect root and leaf allocation and root establishment, leading to seedling mortality (Panetta 1977). However, the critical factor for *B. halimifolia* establishment will not be the available photon flux, but rather drought and/or lack of nutrients resulting from competition with established plants.

In its native range *B. halimifolia* inhabits the intermediate marsh zone, together with the salt-tolerant shrub *Iva frutescens* (Young, Erickson and Semones 1994); competition between these two species may prevent the formation of monospecific stands. In contrast, on the Atlantic Coast of Spain and France, shrub and tree vegetation is absent in the sub-halophilous zone of the marsh, as other native European shrubs or trees, such as *Salix atrocinerea* Brot. and *Alnus glutinosa* (L.) Gaertn., are mostly restricted to the freshwater-influenced upper salt marsh. Although elevated, well-drained areas seem to provide the most suitable growth conditions for this facultative halophyte (see section on *Physiology* below) (Lozano Valencia and Alagón Cardoso 1995; Onaindia, Albizu and Amezaga 2001). Competition with other woody species (e.g. *Alnus glutinosa*, *Salix atrocinerea*) is likely to limit species presence or abundance in these areas (Caño et al. 2013). However, in low-salinity sites in the upper salt marsh, *B. halimifolia* does outcompete the dominant species (*Phragmites australis* (Cav.) Trin. ex Steud. and *Juncus maritimus* Lam.), and so it manages to establish in small soil gaps and to spread in these communities, even in almost undisturbed sites (Caño et al. 2013; Fried and Panetta forthcoming).

In Mediterranean coastal wetlands, *B. halimifolia* is able to grow and outcompete native vegetation in salt-marshes dominated by *Juncus maritimus*, *Spartina versicolor* Fabre or *Elytrigia* spp. (Fried et al. 2014; Fried and Panetta forthcoming), but areas where dense stands of *Phragmites australis* dominate are more rarely colonized.

In summary, *Baccharis halimifolia* has the ability to invade habitats where native vegetation is periodically disturbed, either naturally, e.g. by fire, flooding or animal activity (Panetta 1977), or through human activities. The management of roadsides (e.g. mowing) or any soil disturbances altering the native vegetation cover and creating bare soil will favour *B. halimifolia* in infested areas because of the promotion of seed germination upon exposure to light (Westman, Panetta and Stanley 1975; Anonymous 2007a). As an example, in its native range, the current subcoastal range expansion of *B. halimifolia*, from its original distribution restricted to coastal areas, is occurring along disturbed habitats, such as highways, power line rights-of-way and pine plantations (Ervin 2009). However, frequent management actions (e.g. roadside mowing twice a year) would disfavour the species. Several current management actions in wetlands are also assumed to favour the establishment of the species: (a) by developing irrigation channels and canals, which are favourable habitats for *B. halimifolia* (Westman, Panetta and Stanley 1975), such human infrastructure can enhance the spread of the species; (b) water management: the introduction of freshwater as in the Camargue (and probably in other coastal areas) influences the soil water balance in such a way that establishment is favoured due to the water becoming less brackish; (c) artificial fire regimens (sometimes used to control *B. halimifolia*) have a positive influence on the germination success of this species (Panetta 1977); (d) in Australian pastures under conditions of over- or under-grazing, in recently cleared areas and forestry plantations, or in fertilized areas, the species was identified as particularly invasive (Ensbey 2009); (e) disturbances associated with *B. halimifolia* control programs may also favour the establishment of new seedlings (Ihobe 2014).

Habitats and syntaxonomy

Baccharis halimifolia can be found in several coastal habitats, including salt marshes, coastal swamps, coastal forests, tidal rivers and sandy places (Weber 2003). It can also colonize disturbed habitats, even far from the coast.

North America

In its native range, according to Sundberg and Bogler (2006), *B. halimifolia* occurs in open sandy places, wet fields, marshes, beaches, disturbed sites, roadsides, old fields, from 0 to 100 m above sea level. It is considered as a common species in upland fringes of coastal saline marshes and back dune habitats (Cronquist 1980). It is

Table 3. List of EUNIS Habitats where *Baccharis halimifolia* has established in Europe.

EUNIS Habitats	Level 3 EUNIS Habitat type	References
Marine habitats	A2.5: coastal saltmarshes and saline reedbeds	Campos et al. (2004); Caño et al. (2013); Fried et al. (2014); Sinnassamy (2004); Le Moigne and Magnanon (2009)
Coastal habitats	B1.43: Mediterraneo-Atlantic fixed grey dunes	
	B1.8: moist and wet dune slacks	Sinnassamy (2004); Le Moigne and Magnanon (2009)
	B3.3: rock cliffs, ledges and shores, with angiosperms	Campos et al. (2004); Caño et al. (2013)
Inland surface waters	C3.2: water-fringing reedbeds and tall helophytes other than canes	Herrera & Campos (2010)
	C3.3: water-fringing beds of tall canes	
Mires, bogs and fens	D5.2: beds of large sedges normally without free-standing water	Zendoia et al. (2006)
Grasslands and lands dominated by forbs, mosses or lichens	E3.1: Mediterranean tall humid grasslands	Sinnassamy (2004); Fried and Panetta (forthcoming)
	E3.4: moist or wet eutrophic and mesotrophic grassland	Herrera and Campos (2010)
Heathland, scrub and tundra	F4.234: Northern [*Erica vagans*] heaths	Campos et al. (2004)
	F9.3131: West Mediterranean thickets	Fried et al. (2014)
Woodland, forest and other wooded land	G.1.4: Broadleaved swamp woodland not on acid peat	Caño et al. (2013)
Constructed, industrial and other artificial habitats	J4.2: road networks	Le Moigne and Magnanon (2009)
	J4.3: rail networks	
	J4.5: hard-surfaced areas of ports	Sinnassamy (2004); Le Moigne and Magnanon (2009)
	J4.6: pavements and recreation areas	Sinnassamy (2004); Le Moigne and Magnanon (2009)
	J5: highly artificial man-made waters and associated structures	Le Moigne and Magnanon (2009)
Habitat complexes	X03: brackish coastal lagoons.	Caño et al. (2013)

also capable of establishing in disturbed habitats such as fallow fields and hedgerows, as well as inland saline soils (Krischik and Denno 1990a), especially in areas outside its native range, where it is currently expanding (Ervin 2009). *Baccharis halimifolia* is abundant in swamps dominated by *Melaleuca leucadendra* (L.) L. and along sandy shorelines consisting of *Casuarina equisetifolia* L. (Westman, Panetta and Stanley 1975). It is commonly associated with *Iva frutescens* (McCaffrey and Dueser 1990; Young, Erickson and Semones 1994; Tolliver, Martin and Young 1997) and *Morella cerifera* (L.) Small (McCaffrey and Dueser 1990; Young, Erickson and Semones 1994; Tolliver, Martin and Young 1997; Wang et al. 2006), both perennial shrubs found along the east coast of North America. In a vegetation survey in the Kissimmee River floodplain (south-central Florida), *B. halimifolia* was found to dominate the community, along with *Paspalum notatum* Flüggé, *Rubus cuneifolius* Pursh, *Morella cerifera* and *Thelypteris interrupta* (Willd.) K. Iwats. (Toth 2005).

Australia

Baccharis halimifolia is found in similar habitats in Australia where it invaded a wide variety of plant communities, from dry *Eucalyptus* forests to native tea-tree (*Melaleuca quinquenervia* (Cav.) S.T. Blake) swamps (Westman, Panetta and Stanley 1975). It is particularly suited to moist gullies, salt marsh areas and wetlands. As in its native range, *B. halimifolia* is also found in disturbed habitats, including cleared unused land, cleared slopes (Anonymous 2007a), subtropical pastures (Westman, Panetta and Stanley 1975) or exotic pine plantations, e.g. *Pinus elliottii* Engelm. (Panetta 1979a, 1979b). Westman, Panetta and Stanley (1975) observed that irrigation channels and coastal canals provide favourable man-made habitats for the species.

Europe

On the Atlantic coast of Europe, *B. halimifolia* is known to escape from cultivation (private gardens, hedges, roundabouts and central reservations of road) and to establish first in artificial habitats, along roadsides, along canals and irrigation channels, in agricultural, industrial or on old saltworks wastelands (Le Moigne and Magnanon 2009), in hard-surfaced areas of ports and in pavements and recreation areas, from which it can invade coastal wetlands, tall humid grasslands and open woodlands (Sinnassamy 2004; Le Moigne and Magnanon 2009). Although occurring preferentially in wetlands, it is also found in drier habitats such as heathlands with *Ulex europaeus* L. or in the upper beach area (Anonymous 2007b) and occurs from 0 to c. 200 m above sea level.

In the Basque regions (France and Spain), the communities most affected by *B. halimifolia* invasion are the sub-halophilous communities, particularly, sea rush communities dominated by *Juncus maritimus* (Campos et al. 2004; Caño et al. 2013). It also invades water-fringing reedbeds with *Phragmites australis*, communities of *Elytrigia acuta* (DC.) Tzvelev and humid prairies of *Calthion palustris* communities (Herrera and Campos 2010), as well as in marshes

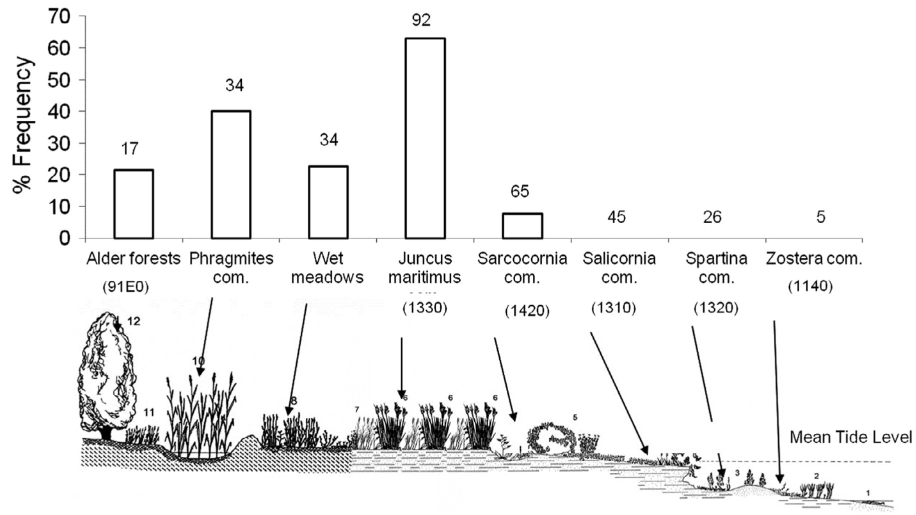

Figure 9. Frequency of presence of *Baccharis halimifolia* in estuarine communities in northern Spain based on 318 floristic relevés. Numbers above bars indicate the total number of relevés per community type used to calculate the frequency of *B. halimifolia*. Figure modified from Caño et al. (2013). Figures under community names refer to the codes of the related habitat in Annex I of the EC Habitats Directive (European Commission 2007, see Table 5)

with *Cladium mariscus* (L.) Pohl. (Zendoia et al. 2006). It is also found in dunes and coastal cliffs, with halochasmophytic communities of *Crithmo-Armerion* or aerohaline heathlands with *Dactylido-Ulicion* communities (Valle, Varas and Sainz 1999; Campos & Herrera 2009). *Baccharis halimifolia* is also reported to establish in woodland estuarine communities such as *Alnus glutinosa*, and can colonize sparsely the halophilous communities of the lower marsh zone dominated by *Sarcocornia fruticosa* (L.) A.J.Scott (Caño et al. 2013). In France as well (e.g. in the Domaine de la Palissade), some individuals of *B. halimifolia* are growing in *Sarcocornia* communities, although these are the less invaded communities owing to high salinity.

In Mediterranean France, *B. halimifolia* colonizes especially Mediterranean saltmarshes with *Juncus maritimus* and *Juncus acutus*, water-fringing reedbeds with *Phragmites australis*, Mediterranean tall humid grasslands of the *Molinio-Holoschoenion*, Tamarisk thickets (Fried et al. 2014; Fried and Panetta forthcoming) and marshes with *Cladium mariscus* and *Schoenus nigricans* L. In the Crau, the species is particularly invasive at the junction of marshes with *Cladium mariscus* and *Molinio Holoschoenion* humid grasslands (Marc Thibault, Tour du Valat, pers. comm.). It is also present along ditches and irrigation canals. A study conducted in coastal saltmarshes of the Camargue and Pyrénées-Orientales (Fried et al. 2014) showed that the most common species associated with *B. halimifolia* were *Juncus maritimus*, *Phragmites australis*, *Elytrigia acuta*, *Althaea officinalis* L., *Sonchus maritimus* L. and *Juncus acutus*.

As in France and Spain, in Belgium *B. halimifolia* grows in a wide range of coastal habitats, including the upper fringes of irregularly flooded tidal fresh and brackish marshes, dunes and open woods (Rappé et al. 2004). It colonizes man-made as well as natural habitats: cracks in pavement, quays and walls, sea dunes and beaches, saltmarshes and open woods (Rappé et al. 2004; Verloove 2011).

Table 3 summarizes the main habitats in which *B. halimifolia* is known in Europe according to the EUNIS habitats classification. This includes habitats that are protected by the Habitat Directive, which are reviewed in more detail in the section on *Negative impacts*, below. Caño et al. (2013) indicate that the communities most often replaced by monospecific stands of *B. halimifolia* are wet meadows and *Juncus maritimus* communities, as shown in Figure 9.

In summary, the suitable habitats for *B. halimifolia* are distributed along the coasts of European and Mediterranean countries, estuaries being particularly suitable (e.g. in France in the Rhône, Gironde and Loire Estuaries, in Spain in Galicia, in Italy in the Veneto region, etc.). Moreover, anthropogenic habitats (e.g. road networks, rail networks and wasteland) suitable for the establishment of the species are widespread and distributed throughout Europe, and can favour colonization inland as observed in the native range (Ervin 2009).

Ecological interactions

Herbivory (mammals and insects)

In its native range, various species of beetles and moths feed on *B. halimifolia* as larvae or adults. Based on a survey on *B. halimifolia* and *Baccharis neglecta* Britt. in Texas, Louisiana and northern Mexico, Palmer (1987) collected 133 phytophagous insects (including mainly Lepidoptera, Hemiptera and Coleoptera) of which 11 were considered specific to *B. halimifolia*. This survey also provided a list of 55 non-phytophagous species of insects collected on *Baccharis* spp., including predators

Table 4. List of natural enemies with high specificity (host plants restricted to the genus *Baccharis)* found on *Baccharis halimifolia*

Species (Order: Family)	Origin	Type of damage	Biological control	Pest status
Slaterocoris pallipes Knight, 1926 (Hemiptera: Miridae)	N. Am.	Ectophagous		No
Stobaera pallida Osborn, 1905 (Homoptera: Delphacidae)	N. Am.	Ectophagous		No
Lorita baccharivora Pogue, 1988 (Lepidoptera: Cochylidae)	N. Am.	Ectophagous (inflorescence)	Yes	No
Prionoxystus piger Grote, 1865 (Lepidoptera: Cossidae)	N. Am.	Endophagous		No
Aristotelia ivae Busck, 1900 (Lepidoptera: Gelechiidae)	N. Am.	Ectophagous (leaf skeletonization)	Yes	No
Itame varadaria Walker, 1860 (Lepidoptera: Geometridae)	N. Am.	Ectophagous		No
Bucculatrix ivella Busck, 1900 (Lepidoptera: Lyonetiidae)	N. Am.	Endo- and ectophagous (leaf mining)	Yes	No
Hellinsia balanotes Meyrick, 1908 (Lepidoptera: Pterophoridae)	N. Am.	Endophagous (stem borer)	Yes	No
Epiblema discretivana Heinrich, 1921 (Lepidoptera: Tortricidae)	N. Am.	Endophagous (stem borer)		No
Amniscus perplexus Haldeman, 1847 (Coleoptera: Cerambycidae)	N. Am.	Endophagous		Yes
Megacyllene mellyi Chevrolat, 1862 (Coleoptera: Cerambycidae)	S Am.	Endophagous (stem borer)	Yes	
Trirhabda bacharidis Weber, 1801 (Coleoptera: Chrysomelidae)	N. Am.	Ectophagous (leaf holes)	Yes	
Neolasioptera baccharicola Gagne, 1971 (Diptera: Cecidomyiidae)	N. Am.	Endophagous		
Neolasioptera lathami Gagne, 1971 (Diptera: Cecidomyiidae)	N. Am.	Endophagous		
Rhopalomyia californica Felt, 1908 (Diptera: Cecidomyiidae)	N. Am.	Ectophagous (galls on growing point / leaves / inflorescence)	Yes	No
Tephritis subpura Johnson, 1909 (Diptera: Tephritidae)	N. Am.	Endophagous		
Puccinia evadens Harkn., 1884 (Pucciniales: Pucciniaceae)	S. & N. Am.	Pathogen (sori abundant on leaves and stem)	Yes	

Taken from Palmer and Bennett 1988 and Sims-Chilton, Zalucki and Buckley 2009, 2010.
Origin indicated where the species has been recorded: North America (N. Am.), South America (S. Am.).

(16 species) and pollen feeders (15 species). In a second survey on the eastern coast of the USA, Palmer & Bennett (1988) collected 108 phytophagous species, of which 14 were considered monophagous and restricted to the genus *Baccharis* (see Table 4). Overall, Westman, Panetta and Stanley (1975) considered that the level of consumption of *B. halimifolia* is low even in its native range (1.95% foliar loss). This can be explained by the secretion of a sticky resin that deters herbivory by all but the most specialized insects (Krischik & Denno 1990b, see also section on *Biological control* below).

The monarch, *Danaus plexippus* (Linnaeus, 1758), and other butterflies feed on the nectar produced by *B. halimifolia* (Brown and Cooperrider 2011). For some wild mammals, such the white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780), *B. halimifolia* is considered as a "desirable" browse species. However, it seems to have little or no value for other wild species and may be toxic to some (Van Deelen 1991).

In its introduced range, several natural enemies, including mealybugs and aphids, have been identified in France (Fried, Balmès and Germain 2013) and Spain (Caño, Garcia-Magro and Herrera 2013).

Mealybugs. *Ceroplastes sinensis* Del Guercio, 1900 (Hemiptera: Coccidae), the Chinese wax scale, was first identified on the species in Gironde (Dauphin and Matile-Ferrero 2003) and more recently in the Roussillon (Fried, Balmès and Germain 2013); *Saissetia oleae* Olivier, 1791 (Hemiptera: Coccidae), the black scale, which leads to the development of fungi (sooty mould) has also been observed on *B. halimifolia* in the Camargue and on the Atlantic coast (Dauphin and Matile-Ferrero 2003).

Aphids. Two species were recorded on *B. halimifolia* in France (Fried, Balmès and Germain 2013), *Aphis fabae* Scopoli, 1763 (Hemiptera: Aphididae), which is a very polyphagous species, recorded in the Camargue and in the Pyrénées-Orientales; *Aphis spiraecola* Patch, 1914 (Hemiptera: Aphidiae), which is a moderately polyphagous species, recorded in the Pyrénées-Orientales.

Dauphin and Matile-Ferrero (2003) also state the presence of an undetermined Agromyzidae larva on *B. halimifolia* in Gironde. Despite the fact that strong infestations of *Ceroplastes sinensis* locally affect the reproduction output of young *B. halimifolia* individuals (Fried, Balmès and Germain 2013), their impact seems not sufficient to control *B. halimifolia* populations. In a recent experimental study Lovet (2015) showed that, in the short run and with low larvae densities, the direct impact of *Ceroplastes sinensis* on *B. halimifolia* growth, water content and number of dry leaves was not significant. In the Basque region, *B. halimifolia* is also attacked by *Ceroplastes* although their exact identity has not been determined (Caño, Garcia-Magro and Herrera 2013). Scale insects were present on new shoots from August to December and scale-excreted honeydew supported the growth of sooty mould during autumn. Male individuals showed more scale insects per shoot and higher levels of fungal infection than females (Caño, Garcia-Magro and Herrera 2013). However, the impact of wax scale insects and sooty mould on *B. halimifolia* individuals remains unknown.

Plant parasites

Fewer nematodes were found in the soils under *B. halimifolia* in the introduced range in Australia compared with native soils in Florida (Porazinska et al. 2014), as expected according to the hypothesis of higher invasiveness resulting from release from soil-borne disease and plant parasites. However results were inconsistent, with different patterns according to years and experimental conditions, so no general conclusions can be drawn regarding the importance of natural enemy release in *B. halimifolia* invasion.

Fungi, bacteria, viruses

There are almost no serious diseases that appear to affect this plant in its native range (Gilman 1999). However, a rust fungus, *Puccinia evadens* Harkn., native to South America up to southwestern USA and specific to the *Baccharis* genus (Groundsel bush rust), acts as both a leaf and a stem pathogen and causes defoliation during summer and winter; in extreme cases stems can die back over summer (Sims-Chilton and Panetta 2011; F.D. Panetta, pers. obs.). *Baccharis halimifolia* is a natural host of *Xylella fastidiosa* Wells et al., 1987 but the identified strains do not cause Pierce's disease (Hopkins and Adlerz 1988).

In its native range, the roots of *B. halimifolia* are colonized by arbuscular mycorrhizal fungi (AMF), that may help to increase plant access to limiting nutrients, and total biomass of seedlings of *B. halimifolia* was positively correlated to the percentage of colonization by AMF (Paudel, Baer and Battaglia 2014). Studies are lacking in the introduced range to test whether the development of mutualism with AMF occurs at a higher rate than in co-occurring native species and can hence contribute to the invasiveness of *B. halimifolia* (Richardson, Allsopp et al. 2000).

Biology

Phenology

In Australia, most germination occurs during the autumn and early winter months, soon after seed is released from plants (Panetta 1979a). In the Atlantic coastal habitats in Spain, germination can occur from spring to early summer (Caño et al. 2010).

In the cooler part of its distribution range, *B. halimifolia* is deciduous. In the Mediterranean region, leaves fall late in autumn (November) and new leaves are produced at the end of winter (February). A similar period of leaf drop (from December to February) has been observed in Gainesville, Florida (Van Deelen 1991). In the Basque region, leaves are reported to fall earlier, from late summer (Caño, Garcia-Magro and Herrera 2013). In this region *B. halimifolia* shoot growth occurs from May to December, flower buds are produced at the end of July (Caño, Garcia-Magro and Herrera 2013), but males flower earlier than females. *Baccharis halimifolia* flowers from August to October and seeds are produced from October to November both in its native range (Van Deelen 1991) and in its introduced range in Spain and France. However, fine-scale variations in edaphic conditions can alter the phenology of *B. halimifolia*: stem elongation and leaf production cease earlier as salinity increases and salinity overall promotes earlier flowering (Caño, Garcia-Magro and Herrera 2013). In addition, females and males show different phenological responses to environmental conditions.

Physiological data

Several studies have showed that plasticity of both morphological and ecophysiological traits may be underlying mechanisms for the relative tolerance of *B. halimifolia* to a wide range of ecological conditions.

Leaf lifespan and climate

The relative adaptability of *B. halimifolia* can be seen through its leaf lifespan: although it exhibits a semi-deciduous growth habit in the northernmost portions of its North American range, and in Europe, it may retain its leaves year-round throughout most of its global distribution, particularly in Australia (Sims-Chilton and Panetta 2011).

Responses of leaves to light availability

In a study characterizing the physiological profiles of three common dominant species along a coastal coenocline in Alabama, spanning changes in salinity, soil water availability and light availability, the specific leaf area of *B. halimifolia* ranged from ~ 10 to ~ 16.5 mm^2/mg^- with decreasing level of light (Pivovaroff et al. 2015). This shows that under low-light conditions *B. halimifolia* produces larger and thinner leaves. Stomatal conductance varied between ~ 100 and 500 mmol m^{-2} s^{-1} during the course of the day and showed adaptation to light availability, with longer periods of stomatal openness in reduced light, and higher, more concentrated peaks of stomatal conductance in sites more exposed to light (Pivovaroff et al. 2015).

Tolerance to salinity

Research work carried out on native populations (Virginia, USA) showed that *B. halimifolia* can resist high salt concentrations in its tissues (> 300 mM), maintaining low photosynthetic activity without necrosis (Zinnert, Nelson and Hoffman 2012). Experiments carried out under controlled conditions using populations from the invasive range (Basque Country, Spain) showed that *B. halimifolia* is a facultative halophyte (i.e. its growth is optimal in the absence of salinity) with strong tolerance to salinity (Caño et al. forthcoming). This is supported by the low mortality found at high salinity levels of 20 g NaCl/l in greenhouse conditions and an ability to reproduce under saline conditions ≤ 15 g NaCl/l. Experimental exposure of *B. hamilifolia* to salt stress reduced growth, decreased its specific leaf area and enhanced leaf drop under greenhouse conditions (Caño et al. forthcoming), all of which are in line with responses documented for adult individuals invading natural salt marshes (Caño et al. 2014). Reduction of specific leaf area probably allows *B. halimifolia* to improve water use efficiency by reducing its stomatal density and so transpiration. Moreover, *B. halimifolia* behaves as a salt-accumulating plant, accumulating sodium ions (Na^+) in leaves as a function of external salinity (Caño et al. forthcoming) and also synthesizing high levels of proline (Fuertes-Mendizabal et al. 2014) that probably acts as an osmolyte or osmoprotectant. These findings provide strong evidence of physiological adaptation of *B. halimifolia* to saline habitats.

Cutting-derived plants seemed to be more salt tolerant than seed-derived plants because total biomass reduction under similar salinity levels in the greenhouse was lower in the former (48%) than in the latter (84%) (Caño et al. forthcoming). This observation indicates that resprouts from plants cut during control procedures will probably display higher growth rates than plants from seeds in saline soils, especially given the low absolute growth rates of seedlings (Panetta 1977). In the same experiments the broad salinity gradient that was created in the greenhouse permitted demonstration that several plant traits displayed a plastic response over the entire gradient (Caño et al. forthcoming). Interestingly, the response to salinity and plasticity seemed to be affected by the maternal salinity (as assessed by parental leaf Na^+ content), both in seed-derived and cutting-derived plants, indicating transgenerational effects.

Drought stress

Plant water potentials along the above described coastal coenocline in Alabama (Pivovaroff et al. 2015) varied between −0.5 MPa (predawn) and −1.9 MPa (midday), with no differences between midday water potentials from the seaward to the landward edge of the distribution of *B. halimifolia* (decreasing water availability), indicating similar water stress. The variation of xylem vulnerability to cavitation (ψ_{50}) showed a physiological adjustment to water stress at the landward edge of its range (Pivovaroff et al. 2015).

Response to nutrient availability

According to Connor and Wilson (1968) quoted by Westman, Panetta and Stanley (1975), the relative dominance of *B. halimifolia* in swamp vegetation increased following fertilizer application.

In an experiment testing the responses of *B. halimifolia* seedlings to various levels of N concentration (0–200 mg/kg$^-$), its biomass was highest at 200 mg/kg$^-$ N (Vick and Young 2013). This study indicated that *B. halimifolia* showed stress response and resource limitation based on physiological responses (photosynthesis and stomatal conductance were reduced by 62% and 76%, respectively), nutrient contents and isotope effects. It also showed signs of co-limitation of both N and P (Vick and Young 2013). This confirms previous observations that *B. halimifolia* is sensitive to low P availability, which may explain its greater sensitivity to flooding (Westman, Panetta and Stanley 1975).

Seeds

Baccharis halimifolia has two seed categories: (1) seeds that respond to temperature fluctuations in the absence of light and (2) seeds that germinate under fluctuating temperature and intermittent light (Panetta 1979c). Seeds buried at depths in excess of 5 cm are probably dormant, lacking light and temperature cues for germination.

Reproductive biology

Floral biology

Female flowers of *B. halimifolia* are wind-pollinated (Krischik & Denno 1990a; Sims-Chilton & Panetta 2011). The flowers can also be pollinated by generalist pollinators such as bees, but such organisms are not necessary for the production of seeds.

Hybrids

Baccharis is a genus of about 400 species, mostly found in the New World tropics and warm temperate regions. In its native range, *B. halimifolia* has been recorded as having hybridized with *B. neglecta* and *Baccharis angustifolia* Michx. in Arkansas, Louisiana and East Texas. In Florida, *B. halimifolia* is known to hybridize with *B. angustifolia* (Sundberg and Bogler 2006). With no native *Baccharis* species in Europe, the risk of hybridization with a native species is nil.

Seed production, dispersal and germination

Achenes are attached to a pappus and are therefore readily dispersed by wind and also by water (Sims-Chilton and Panetta 2011). No other species is necessary for seed dispersal.

The reproductive strategy of *B. halimifolia* has some characteristics that will aid its establishment: (a) the ability, although a woody shrub, to flower after 2 years (Panetta 1979a), (b) high efficiency of pollination mechanisms, with fertility rates of 90% having been observed (Panetta 1979a); (c) the ability to produce many seeds – estimations range between 10,000 (Auld 1970) and 1,500,000 per year for a healthy adult plant growing in full sunlight (Westman, Panetta and Stanley 1975); (d) effective dispersal, including a capacity for long distance dispersal by wind (particularly given the high fecundity of the species), increasing the probability of reaching areas suitable for establishment; (e) the ability to germinate rapidly when conditions are favourable: field observations (Westman, Panetta and Stanley 1975) showed that most of the seeds germinate within 1 month after seed set; (f) the longevity of seed bank, which is expected to persist for a minimum of 2 years (Panetta 1979a, 1979b); and (g) the ability to sprout new shoots from the base following disturbance (fire, management) (Westman, Panetta and Stanley 1975).

Some characteristics are also detrimental, however: (a) *B. halimifolia* is a small-seeded species and consequently has only moderate seedling growth potential (Panetta 1977); (b) low growth during the establishment phase may lead to extended periods of drought susceptibility or, alternatively, increasing mortality under flooding; (c) shade has been found to have a significant impact on seedling growth, particularly during the first 11 weeks (Panetta 1977); (d) high insolation is necessary for initiating flower production (Panetta 1979a); (e) since the species is dioecious, a colonizing female must be within the pollen shadow of a male in order to produce seeds.

Panetta (1979a) estimated that the reproductive output of a *B. halimifolia* population growing within a pine stand before canopy closure was 376 000 achenes/m^2. Even in shaded conditions (Sarlon 92% shade cloth), seed production remains considerable, with about 20 000 achenes produced per m^2 (Panetta 1979a). Seeds are very small: their mass is approximately 0.11 mg (Panetta 1977). Most fall within a few metres of the parent bush (Anonymous 2007a), but records showed that seeds can drift up to 140 m from a 2-m high plant (Diatloff 1964), whereas wind updrafts can carry seeds over many kilometres (Anonymous 2007a). According to Westman, Panetta and Stanley (1975), some remote populations were apparently separated by at least 2–3 miles (3.2–4.8 km). Some isolated populations found during a survey in the Camargue were separated by more than 5 km (Charpentier, Riou and Thibault 2006). *Baccharis halimifolia* is suspected to be continually entering the Spanish Basque Country from wind-dispersed achenes produced in the French Basque region and vice versa (Estela Beteta, Gobierno Vasco, pers. comm. 2012).

Caño et al. (2013) report that over the past 90 years, *B. halimifolia* has invaded all the estuaries along 300 km of coastline in northern Spain, so the mean progression of *B. halimifolia* could be estimated at ~ 3 km/year. In the Urdaibai Biosphere Reserve (Basque Country, Spain), the invaded area has increased from 54 ha in 1996, to 128 ha in 2000 and to 288 ha in 2005. In addition, according to Prieto (2008) *B. halimifolia* totally replaces sub-halophilous plant communities and forms monospecific impenetrable stands over 88 ha. In the National Nature Reserve of Arès–Lège Cap-Ferret (France), *B. halimifolia* has spread over 11.27 ha from 1985 to 2007 with an estimated rate of increase of 0.34 ha/year from 1985 to 2005 and 1.25 ha/year between 2005 and 2007 (GT IBMA 2016).

Perennation

Seedling establishment is the primary method of *B. halimifolia* regeneration. However, if clipped above the ground, *B. halimifolia* is able to resprout. According to horticultural sources in the USA (e.g. Brown and Cooperrider 2011) the lifespan of *B. halimifolia* could be as long as 50 years.

Economic importance and impacts

Uses and positive impacts

In its native range, *B. halimifolia* is occasionally cultivated, but rarely recommended by garden designers or landscape architects (Brown and Cooperrider 2011). It is considered useful as a hedge or border, particularly on the seaside due to its resistance to salt sprays (Brown and Cooperrider 2011). It is also used for reclaiming sites, on moist or wet soils such as drainage ponds or retention areas (Nesom 2006). In Southern Louisiana, *B. halimifolia* has been used traditionally as a medicine to treat inflamed kidneys and fever.

In Europe, the plant has been a popular ornamental species, much appreciated for its hardiness, freedom from disease, autumn flowering and resistance to salt spray. For these reasons *B. halimifolia* has been used largely as a hedge or windbreak in seaside areas. The species is still available in trade as an ornamental. The German shopping guide for ornamental plants (PPP-Index 2016) lists three suppliers of *B. halimifolia* and EPPO (2013) list a number of other suppliers in Europe. However, sales in major French garden centres are minimal, not exceeding a few individuals per year over the whole territory (Manceau 2015). The estimated value of the species to the trade is low and the potential for interference of the prohibition of the species with trade is therefore considered low. Several nurseries and garden centres in France have voluntarily removed *B. halimifolia* from sale because of its known invasiveness. Recently, the voluntary code of conduct of the horticultural sector in France has classified the species on its list of consensus, meaning that the signatories to the code agree on a total ban of use (Manceau 2015). Non-invasive substitution plants may be used for the same ornamental and amenity purposes. In France, recommendations in accordance with nursery professionals suggest that *Atriplex halimus* L., native from the Mediterranean basin, may be used as a wind-break because it is resistant to drought and salt spray. The exotics *Leucophyllum frutescens* (Berland) I.M.Johnst. and *Xanthoceras sorbifolia* Bunge may be used for ornamental purposes (Agence Méditerranéenne de l'Environnement, Conservatoire Botanique National Méditerranéen de Porquerolles 2003).

Negative impacts

Effects on biodiversity and ecosystem functioning

The species forms dense monospecific stands that are persistent: each shrub can live several decades (Brown and Cooperrider 2011). Therefore, the species can have detrimental impacts on native populations and communities.

Impacts on plants and vegetation. *Baccharis halimifolia* is considered as a weedy shrub in its native range (Ervin 2009). In a project of native-prairie restoration in eastern Texas the presence of invading *B. halimifolia* reduced forb diversity (Harcomb 1989). In Australia, *B. halimifolia* is a major pest of native *Melaleuca* wetlands (Westman, Panetta and Stanley 1975) where it forms a thick understorey and suppresses growth of native sedges (Anonymous 2007a in Sims-Chilton and Panetta 2011). In France, Sinnassamy (2004) reports that *B. halimifolia* can outcompete other plants. Once established, the shrub blocks the light to other species, modifying micro-climatic conditions, which leads to a regression of herbaceous species. According to Dupont (1966), in the wettest part of rock, *B. halimifolia* invasion leads to the elimination of spontaneous species such as *Apium graveolens* L., *Apium nodiflorum* (L.) Lag., *Samolus valerandi* L. or *Lysimachia maritima* (L.) Galasso, Banfi & Soldano.

A recent study conducted in France (Fried et al. 2014), has measured the impact of *B. halimifolia* on native plant communities of Mediterranean *Juncus maritimus* and *Juncus acutus* saltmarshes (A2.522 according to the EUNIS classification). On average, at the plot scale (4 m^2), *B. halimifolia* reduced species richness by 42% and the Jaccard dissimilarity index indicated a difference of 0.64 in species composition. At the habitat scale, total species richness was significantly reduced by 39% from 36 to 22 species (permutation-test on cumulative species-richness curves). The abundance of all life forms (therophytes, geophytes and hemicryptophytes) was significantly reduced under *B. halimifolia* patches, except for the chamaephytes (e.g. *Halimione portulacoides* (L.) Allen, *Sarcocornia fruticosa*, *Limbardia crithmoides* (L.) Dumort). *Baccharis halimifolia* causes especially a decrease in presence of native *Juncus maritimus*, *Elytrigia acuta*, *Lotus jordanii* (Loret & Barrandon) Coulot & Rabaute, *Phragmites australis*, *Limonium narbonense* Mill. and *Sonchus maritimus*. The impacts varied according to the invaded communities with higher magnitude of native species loss in wet meadows on oligohaline soils (*Holoschoenetalia vulgaris*) compared with saltmarsh communities dominated by *Juncus maritimus* (*Juncetalia maritimi*) on mesohaline soils (Fried and Panetta forthcoming). These results were consistent across two different regions (Camargue and Roussillon) and probably due to the higher cover reached by *B. halimifolia* in these communities. Annuals and perennial forbs were more sensitive to increasing cover of *B. halimifolia* compared with perennial graminoids (Fried and Panetta forthcoming). When the cover of *B. halimifolia* exceeds 86%, the total cover of native species begins to decrease more rapidly (Fried and Panetta forthcoming).

In the Spanish Basque region, Caño et al. (2013) have reported that *Juncus maritimus*, *Elytrigia acuta* and *Phragmites australis* communities are the most affected (Figure 9). The average *B. halimifolia* cover in invaded sea rush communities in estuaries of northern Spain ranged from 32.2% (± 4.91 SE) inlow-salinity rush patches to 3.6% (± 2.41 SE) in high-salinity rush patches. However, despite the lower invasibility of high-salinity rush communities, the impact of *B. halimifolia* on estuarine species is more important in these sites than in the low-salinity communities, given that the former harbour most of these singular species. *Baccharis halimifolia* reduced the native species cover, the estuarine native species cover, the native species richness and the estuarine species richness in invaded rush communities (Caño et al. 2014). Another important consequence of *B. halimifolia* invasion in rush communities is the reduction of the area occupied by the herbaceous–subshrub layer. In invaded plots, the average herbaceous–subshrub layer replacement by *B. halimifolia* was approximately 9% in the high-salinity patches and 24% in the low-salinity sites (Caño et al. 2014).

Impacts on animals. A study conducted in Morbihan (Brittany, France) on the insects associated with *B. halimifolia* (Mallard 2008) showed that insect species richness and abundance was reduced on *B. halimifolia*, compared with native shrubs (*Prunus spinosa* L., *Ulex europaeus* L.) and trees (*Quercus robur* L., *Salix atrocinerea*). A particularly strong reduction in phytophagous insects was observed, with Lepidoptera as the most impacted. Modifications in communities of invertebrates and vertebrates are expected, but as yet there are almost no available data on this topic. Galarza and Hidalgo (2005–2006) report that the stands of *B. halimifolia* have an impact on bird populations associated with invaded habitats. The plant is considered to reduce the attractiveness and use of the habitats for nesting, roosting and feeding. A recent study carried out in Urdaibai Biosphere Reserve (Basque Country, Spain) demonstrated that *B. halimifolia* invasion (Arizaga, Unamuno and Clarabuch 2013) affects the abundance, structure and composition of the bird communities associated with common reed stands, because the presence of passerines associated with forest ecosystems is enhanced. *Acrocephalus paludicola* (Vieillot, 1817) is a bird that frequently inhabits the common reed stands of the Cantabrian estuaries and could be one of the species most affected by *B. halimifolia* invasion (Arizaga, Unamuno and Clarabuch 2013).

Impacts on ecosystems. Due to its clear impact on vegetation structure and physiognomy, as well as possible effects on ecosystem processes (e.g. sedimentation), *B. halimifolia* is considered as a "transformer" species, i.e. an invasive alien plant that causes changes in the character, condition, form and nature of the invaded ecosystems (Richardson, Pysek et al. 2000).

Fire regimen. Leaves and wood of *B. halimifolia* secrete an inflammable resin (Bean 1981), so dense

Table 5. List of threatened habitats listed in Annex I of the EC Habitats Directive where *Baccharis halimifolia* L. has established in Europe.

Code	Description
1230	Vegetated sea cliffs of the Atlantic and Baltic Coasts
1330	Atlantic salt meadows (*Glauco-Puccinellietalia maritimae*)
1410	Mediterranean salt meadows (*Juncetalia maritimi*)
1420	Mediterranean and thermo-Atlantic halophilous scrubs (*Sarcocornetea fruticosi*)
2130	*Fixed coastal dunes with herbaceous vegetation (grey dunes)
2190	Humid dune slacks
3130	Oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea*
4040	*Dry Atlantic coastal heaths with *Erica vagans*
6420	Mediterranean tall humid grasslands of the *Molinio-Holoschoenion*
7210	*Calcareous fens with *Cladium mariscus* and species of the *Caricion davallianae*
91E0	*Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*)

*indicates a Priority habitat.

thickets of the species could increase fire frequency in invaded habitats (Sinnassamy 2004), but this has not been observed in Europe.

Sedimentation. Campos and Herrera (2009) suggested that the root system and copious litter production of *B. halimifolia* could cause changes in sedimentation dynamics in salt marshes. Although no measurement has been undertaken to support such statements, Lozano Valencia and Alagón Cardoso (1995) observed that the soils of the areas massively colonized by *B. halimifolia* had a higher percentage of sand.

Light interception. Dense thickets of *B. halimifolia* also reduce the light available for herbaceous species, which is especially detrimental to heliophilous species such as the endangered species *Lysimachia maritima*, *Cochlearia aestuaria* (J.Lloyd) Heywood or *Dryopteris carthusiana* (Vill.) H.P.Fuchs (Campos et al. 2004; Caño et al. 2013).

Succession. In Mediterranean salt marshes, native *Tamarix* (*Tamarix gallica* and *Tamarix africana*) are usually restricted to humid depressions and are not able to establish in the drier parts of salt marshes, where *B. hamilifolia* is the only shrub, therefore changing the natural succession by adding a new vegetation layer (Fried and Panetta forthcoming). In part of the area where these species co-occurred, Fried and Panetta (forthcoming) showed that *B. halimifolia* has stronger impact than *T. gallica* on the herbaceous vegetation.

In the Spanish Basque region, invasion by *B. halimifolia* causes a marked change in the structure and physiognomy of the invaded community (Campos et al. 2004). The impact of *B. halimifolia* on plant communities (including life-form changes) may be also explained by the fact that its presence may favour small herbivores (e.g. rabbits), which reduce the herbaceous cover – also observed in California for the closely related species *B. pilularis* DC. (Hobbs and Mooney 1986).

Colonization of high conservation value habitats and effects on rare or vulnerable species

Presence in habitats of high conservation value. Contrary to the fact that most alien plants are often confined to disturbed habitats, *B. halimifolia* occurs in many "Natural habitats of European Community interest" listed in Annex I of the Habitats Directive 92/43/EEC (European Commission 2007) including especially Atlantic salt meadows (*Glauco-Puccinellietalia maritimae*) [1330] (Invasive Alien Species in Belgium Website 2012) and vegetated seacliffs of the Atlantic and Baltic coast (*Chrithmo-Armerion*) [1230]. Some of these are even considered within the category of "priority habitat": dry Atlantic coastal heaths with *Erica vagans* (*Dactylido–Ulicion*) [1230] (Campos, Caño and Herrera 2004) or *Cladium mariscus* communities [7210] in the Rhone Valley (Anne Charpentier, Montpellier University, pers. comm. 2012). Table 5 summarizes the habitats listed in Annex I of the EC Habitats Directive (Directive 92/43/EEC) colonized by *B. halimifolia*. It is worth highlighting that *B. halimifolia* has already invaded habitats that are located in sites of community importance (SCI) of the Natura 2000 Network and natural protected coastal areas (UNESCO, Ramsar, etc.) such as the Bay of Heist and Zwin Nature Reserves in Belgium, the Camargue Biosphere Reserve in France or the Po Delta Interregional Park and the Venetian Lagoon in Italy (Caño et al. 2013). In Spain, this exotic shrub has already colonized 18 protected areas, including three Natural Parks, one Biosphere Reserve and more than 10 SCI in the Basque Country and Cantabria regions (Campos, Caño and Herrera 2014). A non-exhaustive list of Natura 2000 sites where *B. halimifolia* occurs in Spain, France and Belgium is found in EPPO (2013).

Impact on rare or vulnerable species. In the Spanish Basque region, *B. halimifolia* is thought to have reduced the populations of *Matricaria maritima* L. (Campos et al. 2004), which is included within the category CR (critically endangered) in the "Basque Catalogue of Threatened Species of the Wild and Marine Fauna and Flora", but no measurements of such decline are available. Some of the estuarine species present in invaded rush marshes such as *Cochlearia aestuaria*, *Dryopteris carthusiana*, *Frankenia laevis* L., *Hibiscus palustris* L., *Limonium humile* Mill., *Salicornia* spp. or *Sarcocornia perennis* (Mill.) A.J. Scott are already endangered at the regional or national level (Uribe-Echebarría and Campos 2006; Prieto et al. 2007).

The recent studies conducted in Mediterranean saltmarshes (Fried et al. 2014; Fried and Panetta forthcoming) in France did not reveal a significant impact on rare species. However, dense stands of *B. halimifolia* occur in areas where species of conservation value occur: *Cynanchum acutum* L. (protected in the Provence-Alpes-Côte-d'Azur region), *Iris reichenbachiana* Klatt (protected in the Poitou-Charentes and Pays-de-la-Loire regions), or *Crypsis aculeata* (L.) Aiton. (protected in the Provence-Alpes-Côte-d'Azur region).

The plant is considered to reduce the attractiveness and use of the habitats for nesting, roosting and feeding. *Baccharis halimifolia* is suspected of threatening *Acrocephalus arundinaceus* (Linnaeus, 1758) registered in the Annex 2 of the Bonn and Bern Conventions, registered on the National Catalogue of threatened species in Spain, as well as in France, and categorized as "vulnerable" in the IUCN Red List, and *Emberiza schoeniclus* (Linnaeus 1758), registered in Annex 2 of the Bern Convention, and listed in articles 1 and 5 in France, but which is considered as a minor concern both in France, and according to the IUCN Red List.

Agriculture and other economic impacts

Agriculture. In its native range, *B. halimifolia* is considered a weed due to "infestation" on overgrazed rangeland in the southern United States (Nesom 2006). In Australia, *B. halimifolia* is a pest of pastures, where thick stands can inhibit the movement of stock and reduce the productivity of grazed areas (Ensbey 2001). It has little nutritional value for livestock. There are very few records of livestock poisoning due to the cardiotoxic glucosides present in the leaves of the plant (Boldt 1987, cited in Sims-Chilton and Panetta 2011). This is probably due to the low palatability of the plant: *B. halimifolia* is generally grazed only when grass is scarce (Everist 1974). Other studies have shown no poisoning effect. For example, White (1936) fed *B. halimifolia* to two heifers (*Bos taurus* L.) for 13 days. The animals appeared emaciated, but no symptom of poisoning was evident. In France and Spain, there is currently no record of impacts on pastures.

Other economic losses. In Brittany the species was responsible for slowing salt production (by diminishing wind and the evaporation of water), which resulted in economic losses. The species also limits the access to the salt production areas (Observatoire de la Biodiversité Bretagne website 2012). In addition, the very large number of seeds of *B. halimifolia* increases the insoluble part in the salt production (David 1999 in Sinnassamy 2004).

Health

Seeds are poisonous if eaten (Brown and Cooperrider 2011).

Mosquitoes. Establishment of *B. halimifolia* occurs in areas favourable to mosquitoes. Dense thickets of the species protect mosquito larvae from insecticide treatments and impede access for mosquito control (Bouterin and Canonge 1999 in Sinnassamy 2004).

Hay fever. *Baccharis halimifolia* is also reported to cause hay fever-type allergies (Moss 1967, cited in Panetta 1979a; De Loach et al. 1986) caused by airborne pollen and seed "fluff" (Anonymous 2007a). Green, Simpson and Dettmann (2011) performed a survey on the pollen present in the air in Brisbane. They found that in March and April, the highest concentrations of Asteraceae pollen were predominantly derived from *B. halimifolia*. *Baccharis halimifolia* pollen is reported to be severely allergenic (Pollen library website 2012) and to cause symptoms in *Ambrosia artemisiifolia* L.-sensitive persons (The Asthma and Allergy Foundation of America website 2012).

Control costs

In the 1970s, the cost of a control programme with herbicides (2.4-D and 2,4,5-T) in Queensland was estimated to exceed $500,000 per year (Westman, Panetta and Stanley 1975). This figure largely concerns the control of *B. halimifolia* in pastures, but owing to the legal obligation to control this weed, other land uses would also be involved. In France and Spain, there is no reported impact on pastures, but control programmes are being undertaken for environmental conservation purposes.

In France, in Loire-Atlantique (44), a containment action on a population of 124 trees (spread over 49 locations) was estimated to cost €3,064 (Commission Syndicale de Grand Brière Mottière 2007).

In the Basque region, a LIFE+ project has been implemented to suppress *B. halimifolia* from three estuaries (Urdaibai, Txingudi and Lea) (LIFE project Website www.euskadi.eus/life_estuarios). During 2011, control works were carried out in Urdaibai, based on two main methodologies: (a) manual pulling out for specimens shorter than 50–75 cm, completely digging out the root system; (b) using herbicides: adult and resprouting specimens are cut one by one, and brushed with a herbicide (glyphosate 36%) diluted in oil in a proportion of 1 : 1. In 2011, 298.08 ha were treated in this way, at a total cost of €630,000 (Ihobe 2014)

Legislation and management

Legislation

Baccharis halimifolia has been declared an unwanted organism under the New Zealand Biosecurity Act 1993, which makes it illegal to knowingly release, spread, display or sell, breed, propagate or otherwise distribute plants or part thereof. The aim of the management actions where the species is present is eradication (Lynne Huggins, Department of Conservation, New Zealand, pers. comm. 2012). In Australia, the species is considered noxious and is regulated in Queensland and New South Wales as well as in Northern Territory, where it is not recorded as present (Weeds Australia Database 2012).

In Spain, the species is considered as one of the top 20 most invasive species (Grupo Especialista en Invasiones Biológicas 2006) and it is listed as such in the Spanish Catalogue of Invasive Exotic Species. This Catalogue is regulated by the Royal Decree 630/2013 of 2 August that prohibits the possession, transport, traffic and trade of specimens, alive or dead, remains or propagules of all the species listed in the Catalogue (article 7.1). In Germany, the species is listed as "invasive species, black list – warning list" (Starfinger and Nehring 2013).

In Europe, since 2016, *B. halimifolia* is prelisted for being considered as a species of Union concern under the 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. This would imply that *B. halimifolia* "shall not be intentionally: (a) brought into the territory of the Union, including transit under customs supervision; (b) kept, including in contained holding; (c) bred, including in contained holding; (d) transported to, from or within the Union, except for the transportation of species to facilities in the context of eradication; (e) placed on the market; (f) used or exchanged; (g) permitted to reproduce, grown or cultivated, including in contained holding; or (h) released into the environment." (Article 7). In addition, "Member States shall have in place effective management measures for those invasive alien species of Union concern which the Member States have found to be widely spread on their territory, so that their impact on biodiversity, the related ecosystem services, and, where applicable, on human health or the economy are minimised." (Article 19).

Management

Based on previous *B. halimifolia* management programmes (LIFE+ project Estuaries of the Basque Country), some factors should be taken into account before planning the management strategy of invaded areas, such as invaded surface, density, access to work areas, affected habitats, fragility of the ecosystem, human and material resources, or the available budget (Ihobe 2014). Early detection and rapid response of this invasive species is desirable, as its invasion strategies and ability to regrow greatly hinder its subsequent management.

Preventive strategies

In countries where *B. halimifolia* is only in cultivation, it is likely to spread to natural habitats. Prohibition of selling, planting, holding, movement and causing to grow in the wild should be implemented. In countries where the species is already established in the wild, the plant is likely to spread from existing populations present both in gardens and in unintended habitats. Prohibition measures should be combined with surveillance and action plans for early intervention in case the plant is detected beyond cultivation and poses a risk, as well as general containment and control measures. A delimitation survey should be conducted to determine the extent of *B. halimifolia* distribution. Surveillance should be carried out in likely places of introduction of *B. halimifolia*: along roadsides and along canals. Infested areas and adjacent areas that might receive seeds should be monitored. Surveillance is relevant for early detection of *B. halimifolia* and the most appropriate time for it is during the flowering.

Baccharis halimifolia colonizes mainly natural or semi-natural habitats usually subject to no regular pest management practices. Some management practices, such as the removal of invasive alien plants, may leave bare soil and would favour the establishment of *B. halimifolia*. Such management practices are to be considered on a case-by-case basis, and such control actions have been reported in France (e.g. Domaine de la Palissade in Camargue) and Spain (Life project in the Basque region). Minimizing disturbances would lower the probability of establishment of the species (Ihobe 2014).

Chemical control

One of the most effective control methods would be the use of herbicides (Weber 2003), but these are not allowed (e.g. near water courses) or desired (e.g. protected sites) in all situations where the plant occurs. In the European Union, some herbicides have been phased out as they did not gain Annex I listing during the active review process; other active substances may be phased out in the future. Of the currently remaining active substances, availability varies significantly from country to country and the current product approvals are subject to change under the EU review process for plant protection products. Chemical control may in particular not be authorized in nature reserves, especially in humid environments.

Herbicides, although initially expensive to apply, may give long-term control. Treatments of glyphosate, 2,4-D acid or 2,4-D amine achieved over 90% control of *B. halimifolia* in a variety of tests (Auld 1970; Armstrong and Wells 1979). Weber (2003) reported that chemical control provided satisfactory results with 2,4-D, dicamba plus MCPA, glyphosate, picloram plus 2,4-D, and tryclopyr. Gann, Thompson and Schuler (2012) identified that triclopyr was far more efficient in hardwood forest than imazamox, aminopyralid and glyphosate. Combinations of herbicides (e.g. picloram combined with aminopyralid and triclopyr or 2,4-D combined with dichloprop-p) have provided efficient results (still visible after 6 months) in France (Commission syndicale de grande Brière Mottière 2007).

Foliar spraying. Most herbicides are designed for foliar absorption, so spraying on foliage would be the most effective chemical control method in disturbed or low-conservation-value areas. However, foliar spraying may spread the active substances to non-target plants, which could then transfer to soil and water, so it should be avoided in natural or protected areas. A dilution of 2–3% of product seems sufficient for optimal results, and a minimum resprouting may be expected. This methodology has been tested in both estuarine and coastal heathland environment. Spraying may also be performed after a previous clearing, weakening the plant and reducing the number of shoots on which to spray. The best time for application is between August and October (Ihobe 2014)

Application on stumps. Herbicides may also be applied on cut stumps (for plants of more than 1.5 m in height), just after cutting, and this is particularly efficient when the tree is cut at the soil level (Charpentier, Riou and Thibault 2006). The application of glyphosate and ammonium sulfamate (the latter active substance is less toxic than glyphosate) has controlled 90% of the trees treated with the method in an experiment in France (Commission syndicale de grande Brière Mottière 2007). The application of the herbicide should ideally be undertaken within a few minutes. It is recommended to apply such a measure in autumn when sap is going down. Applied in the north of Spain, this methodology showed high effectiveness (97%) in small or medium-sized invasions, and less effectiveness in large and widespread invasions (70–75%). According to the longevity of the seeds (Panetta 1979a, 1979b), reinvasion of the treated area by seedbank germination must be expected for several years after treatment, and manual control can be applied. Further treatments and surveillance are recommended to ensure the total elimination of the invasion.

Based on previous experiences, several considerations regarding herbicide application could be highlighted:

- Although application on stumps greatly reduces the quantities of active substances used and although careful application of herbicides to stumps can minimize the risks for surrounding vegetation in natural or protected areas, for herbicide application to be effective on stumps the concentration of the product has to be much higher than in the case of foliar spraying. Efficient application of glyphosate on stumps requires concentrations 25-fold higher (c. 50% of commercial dilution) than foliar application requires (c. 2% of commercial dilution, Ihobe 2014). Abiotic stress (salinity, anoxia) in natural invaded areas has been shown to prevent resprouting after cutting in some areas (Beteta et al. 2012), suggesting that the use of herbicides on stumps could be reduced or even skipped under particular conditions.
- Herbicides can also be applied on debarked branches; glyphosate has been used in the Basque Country with satisfying results. The application of salt on tree roots has been tested but results still need to be confirmed, and the use of salt could anyway not represent a management measure, because it is not authorized (Commission syndicale de grande Brière Mottière 2007). Moreover, as for herbicide application, the application of salt could negatively affect surrounding vegetation.
- Overall, all financed control programmes should compulsorily include pilot studies to be carried out in every particular context before herbicide application to determine the minimum lethal dose for those particular conditions and that particular strategy (application on leaves versus application on stumps). Control programmes must also be accompanied by monitoring programmes, to verify both the effectiveness of treatments and the possible impact on the environment, especially when working in protected and natural areas.
- Taking into account previous considerations, further control programmes conducted on natural or protected areas might try applying the herbicide locally and carefully on leaves on resprouted stumps to avoid application to already dead stumps (e.g. in harsh, saline or waterlogged areas) and to minimize the herbicide concentration needed while improving the efficiency of the management actions (Campos, Caño and Herrera 2014).

Physical control

Manual removal. On young plants (maximum of 1 to 1.5 m in height) this methodology has provided satisfying results in newly contaminated invaded sites. Manual removal can only be undertaken on new plants resulting from germination, and not on resprouting plants (Commission syndicale de grande Brière Mottière 2007). This method has a low impact on the ecosystem and requires only simple equipment. However, the root system needs to be removed to prevent resprouting and this method is therefore quite expensive and cannot be applied on large, well-developed infestations. This action can be performed all year around and is best done when the soil is relatively moist, which facilitates the total removal of the plant (Ihobe 2014).

Cutting and uprooting. This can locally control the plant, but these expensive measures have to be repeated several times because of the resprouting ability of the species, and its large seed bank. Large plants should be dug out or cut off > 10 cm below ground level. If plants are removed manually, the roots should be cut well below the soil surface to prevent resprouting. When uprooting is not possible, regular cutting of the shrubs before they set seeds can stop the spread of the plant (Charpentier, Riou and Thibault 2006). Clearing can be done in heavily infested sites. Removed plants should be collected and incinerated to avoid any risk of regeneration from this material (Commission syndicale de grande Brière

Mottière 2007). They can also be piled up, placing the roots upwards to prevent contact with the soil and water.

Manual or mechanical stumping of large individuals (> 1.5 m in height) represent efficient punctual measures that have a limited impact on the ecosystem, but require good accessibility and a thorough follow-up control of remaining roots (Charpentier, Riou and Thibault 2006).

Cutting or gyrobroying (i.e. using a rotary flail) large individuals may have varying impacts on the ecosystems. Cutting needs to be repeated several times to exhaust the plant. Plants regrow vigorously after having been the object of gyrobroyage, and more than 10 branch stems may regrow instead of three or four (Commission syndicale de grande Brière Mottière 2007). Gann, Thompson and Schuler (2012) found that two annual cuttings, one during the dormant and one during the growing season, resulted in 43% and 26% mortality, respectively. Mechanical control undertaken during the dormant season could therefore be more effective. Such measures should be repeated every 2 to 3 years as the plant forms new cuttings.

Pruning of the aerial part of the plant to 50 cm can be followed by the covering of the tree root by a black plastic (400-gauge) maintained with ropes. This method is not cost-effective in large infestations and resprouting may be expected.

Containment strategies. Although cutting and manual removal can be efficient methods for *B. halimifolia* control, since they might not be cost-effective in many cases, several strategies could help to increase effectiveness with reduced budgets (Campos, Caño and Herrera 2004):

- When it is not possible to remove all individuals of the population, removing female individuals or even branches on female individuals will avoid seed rain and spreading during one generation.
- According to the longevity of the seeds (Panetta 1979a, 1979b) repeating this procedure for 3–4 years could eliminate partially or totally the seed bank of a population.
- After several years of repeated control of female individuals, when recruitment from the seed bank and female individuals is almost non-existent, budgets could be devoted to the elimination of male individuals.

In the Spanish Basque region, in sites where *B. halimifolia* was removed by control programmes, an increase in the areas covered by two other invasive alien plants [*Lonicera japonica* Thunb. and *Aster squamatus* (Spreng.) Hieron] was observed (Prieto 2008).

Flooding. This method can be effective in areas with appropriate flooding features and can be permanent (as part of a complete restoration project) or temporary. Experiments in France have shown that flooding for several months during winter can eliminate adult plants. In the north of Spain, the permanent flooding method has been used in estuarine environments, with satisfying results, though *B. halimifolia* persists in emerged areas. However flooding also affects non-targeted species, so it could not be recommended in some protected habitats (Ihobe 2014).

Biological control

Grazing. In France, sheep have been used to control resprouting after application of physical methods on large areas. For example, on the Natura 2000 site of 'Ria d'Etel' (Morbihan), two to four sheep were used on 6000 m^2 during 3 years, with two grazing periods of c. 30–50 days each, first in spring and then at the end of summer. First results were mixed due to an insufficient grazing pressure. Since 2012 sheep have grazed continuously on these saltmarshes, with almost no *B. halimifolia* remaining (GT IBMA 2016).

Release of natural enemies. Based on observations of low levels of consumption of *B. halimifolia* by insects in its native range (see section on *Ecological interactions*), Westman, Panetta and Stanley (1975) considered at the time that the prospects of biological control for this species were dubious. However, Australia had launched a biological control programme of *B. halimifolia* much earlier, with the release of the first agent at the end of the 1960s and the final release in 1997 of the Groundsel bush rust (*Puccinia evadens*). These agents were selected on the basis of their high host-specificity to the *Baccharis* genus (Palmer and Bennett 1988) and their potential scope for damaging the plant (see Table 4). From the 13 species that have been initially released (12 insects and one rust), seven have established in Australia. Biological control has not been completely successful (Sims-Chilton, Zalucki and Buckley 2009), but *B. halimifolia* is no longer considered a serious weed in Australia, in marked contrast to the situation in the 1970s, when one of us (FDP) first studied it.

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