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The role of alien plants in the natural coastal vegetation in central-northern Spain

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Abstract. Alien plants in coastal habitats and their influence on natural vegetation are studied. After 5 years working on this subject in the Basque Country and surrounding areas, a number of results from the coastal ecosystems are presented. These ecosystems are one of the most threatened and affected by the invasion of alien plants, especially shore dunes, saltmarshes and cliffs. These kinds of habitats, especially the dunes, experience significant pressure from human activities which favours the expansion of some of these species: *Arctotheca calendula*, *Sporobolus indicus* and *Oenothera* spp. The presence and abundance of these invasive plants and others such as *Baccharis halimifolia*, *Cortaderia selloana*, *Spartina patens* and *Carpobrotus edulis* in the plant communities in an area between the French border and the western part of the region of Cantabria have been studied. The degree of invasion of each plant in each syntaxonomic unit has been analysed.

Glossary

Alien plants	Synanthropic species of exotic origin, deliberately or accidentally introduced.
Archaeophytes	Alien plants permanently established but older immigrants, before 1500 A.C.
Ephemerophytes	Alien plants not permanently established, introduced temporarily.
Epoecophytes	Xenophytes established only in ruderal and/or segetal communities
Ergasiophygophytes	Alien plants not permanently established, escaping from cultivation.
Hemiagriophytes	Xenophytes established in semi-natural communities.
Holoagriophytes	Xenophytes established in natural communities.
Synanthropic plants	Plants linked to the voluntary or involuntary actions of man which generally modify their natural distribution by extension.
Syntaxonomy	Taxonomy of plant communities following the phytosociological system of Braun-Blanquet.
Xenophytes	Alien plants permanently established, but newcomers (after 1500 A.C.).

Introduction

Alien plant species are increasing in frequency and abundance in many natural areas in Spain, often favoured by disturbance and habitat fragmentation

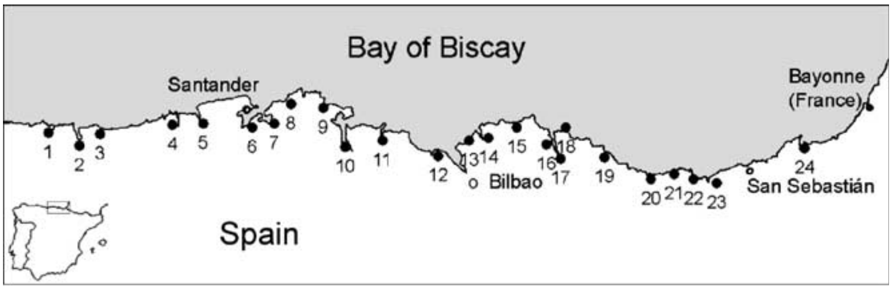

Figure 1. Locations sampled. Cantabria: 1. Nansa river estuary, Tina Menor. 2. San Vicente de la Barquera. 3. Ría de la Rabia. 4. Saja river estuary. 5. Pas river estuary. 6, 7. Santander, ría de Cubas. 8. Galizano, ría la Canal. 9. Noja. 10. Asón river estuary. 11. Agüera river estuary. Basque Country: 12. Muskiz, La Arena. 13. Getxo. 14. Plentzia. 15. Bakio. 16–18. Gernika, Urdaibai. 19. Lekeitio. 20. Deba. 21. Zumaia. 22. Zarautz. 23. Orio. 24. Hondarribia-Irun, Txingudi.

(Heywood and Iriondo 2003). Despite that, studies about them are very recent (Casasayas 1989; Campos and Herrera 1997; Meaza et al. 1997; Dana et al. 2001; Sanz Elorza et al. 2001; Vilà et al. 2001; Sobrino et al. 2002). The presence of alien plants in coastal habitats in the eastern Cantabrian fringe of the Iberian Peninsula (Bay of Biscay) and their effect on natural vegetation have been studied. Intensive data compilation was carried out on all types of coastal habitats. Main dunes, saltmarshes and cliffs with natural vegetation were studied, 24 localities in total, in the regions of Cantabria and the Basque Country (Figure 1). These habitats are seriously threatened (Fernández Prieto and Bueno 1997; Meaza et al. 1997), and it is essential to determine the degree of alien plant invasion and its effect on plant communities (loss of biodiversity and changes of community dynamics and structure) so that conservation programmes can be initiated, following the guidelines of the Convention on Biological Diversity (art. 8 h, 5 June 1992). Most of these coastal plant communities are included as 'Natural habitats of European Community interest' in Annex I of the Habitats Directive 92/43/EEC. Two of them, 'fixed coastal dunes with herbaceous vegetation (grey dunes)' and 'dry Atlantic coastal heaths with *Erica vagans*' (see Appendix 1), are considered within the category of 'priority habitat' (Loidi 1999). Moreover, many vascular plants that occur in these coastal habitats are included in the 'Basque Catalogue of threatened species of wild and marine Fauna and Flora' (BOPV no. 129, 2 July 2003).

Methods

Three hundred phytosociological relevés (Braun-Blanquet 1951) have been made and classified according to the typology of Rivas-Martínez et al. (2001, 2002) and are shown in the syntaxonomical scheme (see Appendix 1). In the plant communities studied, the abundance of each alien species was estimated according to the following scale:

1. Very rare: known only at one or two localities; always little coverage.
2. Rare: known at few locations where it can be locally abundant.
3. Sparse: neither rare nor frequent.
4. Frequent: high probability of appearing in the community; never dominant.
5. Common: always or nearly always present in the community; little coverage.
6. Very common: always or nearly always present; high coverage, sometimes dominant.

A Principal Components Analysis (PCA) (Ter Braak and Smilauer 1998) was used for the ordination (centring and standardization by species) and to show the affinities of each species to different ecological conditions, and their degree of concurrence. A square-root transformation was applied to the species abundance data of Table 1. Graphic outputs were completed using the computer programme Canodraw 3.1 (Smilauer 1992). The acronyms of the species are given in Table 1. Aizpuru et al. (1999) was used for species nomenclature except for *Aloe vera* (L.) Burm. fil., *Conyza sumatrensis* (Retz.) E. Walker, *Oenothera* × *fallax* Renner and *Spartina patens* (Aiton) Muhl. The xenophytes were defined and categorized (see Glossary) according to Kornás (1990).

Results

Fifty-four alien species were found in littoral ecosystems of the studied area. They are listed in Table 2, where different features are given. In the life form spectra of alien species (Figure 2), dunes show the biggest proportion of therophytes and biennial hemicryptophytes, well adapted to very dynamic ecosystems with many open spaces. In saltmarshes, on the other hand, geophytes and rhizomatous hemicryptophytes dominate, better adapted to the sea water flooding stress typical of these environments, where competition for space and resources is very high. Chamaephytes and nanophanerophytes are well represented both in cliffs and dunes.

Figure 3 shows the different life form spectra of alien species in coastal habitats of the studied area (Figure 1) and in all types of habitats in the Basque Country (Campos and Herrera 1997). Here, the larger frequency of hemicryptophytes and the lower presence of phanerophytes in coastal habitats can be seen.

The alien flora of the littoral environment has a rather diverse origin (Figure 4). Many of the species come from temperate and subtropical areas of the New World (56%), where they usually occupy similar habitats. Species coming from the Mediterranean Region form another important group (22%); in this case the geographical proximity makes it easy for some species with strong colonizing capacity to expand out of their natural distribution area.

The most outstanding feature about the status of the alien plants found in the studied area (Figure 5) is the scarcity in coastal habitats of the species ephemerophytes (2%) and ergasiophygophytes (7%), which are not permanently established. These results differ remarkably from those obtained by Campos and Herrera (*op. cit.*), according to which these groups form half (56%) of the alien flora present in all types of habitats of the Basque Country. The most important group is constituted by the holoagriophytes (31%), which are able to successfully invade rather well preserved communities.

As for the way these species have been introduced (Figure 6), the biggest percentage (65%) corresponds to species that arrived in our territory in an accidental way. Those species cultivated as ornamental plants are also important.

The 54 species catalogued belong to 18 families (Figure 7). The most important ones are Asteraceae (25%), which shows effective mechanisms of dispersal by wind and by water, and Poaceae (18%). Many of the latter that live in coastal habitats have C4 metabolism, and are very competitive in environments under the influence of sea water.

Figure 8 shows the results of the PCA using a matrix of data from Table 1. Two trends can be observed: on one hand dune plant communities are represented to the right of axis 1. A lot of alien species (Figure 8b) are frequent in these types of habitats; many of these species (e.g., *Euphorbia polygonifolia*, *Oenothera drummondii*, *Arctotheca calendula*) are exclusive to dunes, some of them with a clear ruderal behaviour (e.g., *Oenothera glazioviana*, *Sporobolus indicus*, *Conyza* spp.). On the other hand, the plant communities of saltmarshes (*Salicornion fruticosae*, *Spartinion maritimae*, *Limonio–Frankenion*) and cliffs (*Dactylo–Ulicion*) appear grouped on the left of axis 1 (Figure 8a) because they have very few alien species and besides, these only appear in these communities. This could be due to the hard environmental conditions occurring in saltmarshes that allow the survival of only a few well-adapted species (e.g., *Spartina alterniflora*, *Baccharis halimifolia*, *Cotula coronopifolia*) that come from similar habitats in their native country.

Different factors such as salinity, flooding frequency and level, trampling intensity and nitrification seem to be the main variables which determine the abundance of many alien species in these kinds of habitats. The abundance of each species in different plant communities is shown in Table 1.

Most dangerous species

Some of the taxa included in this work are able to transform the environmental conditions and processes and the structure of littoral ecosystems, thus they have a strong impact on coastal vegetation. They are the so-called 'transformers' (*sensu* Richardson et al. 2000), and are listed below.

Table 1. Occurrence of alien species in coastal communities. The numbers belong to the following scale: 1: very rare; 2: rare, 3: sparse; 4: frequent; 5: common; 6: very common (explained in section 'Methods').

		Dunes									Marshes							Cliffs	
ACRONYM	TAXA	Cakiletalia	Ammophiletalia	Crucianelletalia	Elytrigion athericae	Dauco-Melilotion	Sisymbrietalia	Trifolio-Cynodontion	Polygono-Poetea	Molinio-Holoschoenion	Paspalo-Agrostion	Glauco-Juncion	Baccharis community	Scirpion compacti	Limonio-Frankenion	Salicornion fruticosae	Spartinion maritimae	Crithmo-Armerion	Dactylo-Ulicion
ACAMOL	*Acanthus mollis*				1														
ANARAD	*Anacyclus radiatus*						2												
ASPFIS	*Asphodelus fistulosus*						2												
CARDRA	*Cardaria draba*						4												
EMESPI	*Emex spinosa*						1												
AMBART	*Ambrosia artemisiifolia*				1	2													
CENTRUB	*Centranthus ruber*		2			3													1
CHASUA	*Chamomilla suaveolens*						2		4										
DATSTR	*Datura stramonium*					2	1												
GAMSPI	*Gamochaeta coarctata*							1	2										
OENDRU	*Oenothera drummondii*		2	2		2													
SOLPTE	*Soliva pterosperma*						2		3										
DITVIS	*Dittrichia viscosa*					5	1			5									
EUPPOL	*Euphorbia polygonifolia*	2	2				1												
MIRJAL	*Mirabilis jalapa*				2		2	1											
TETTET	*Tetragonia tetragonoides*	1	2		2	2	2												
ARCCAL	*Arctotheca calendula*	1	2				5	4	2										
ARUDON	*Arundo donax*		3	2						2		1							
CHENAMB	*Chenopodium ambrosioides*					3	2	2		2									
CORONODID	*Coronopus didymus*						4	1	5		1								
LEPVIR	*Lepidium virginicum*					4	5	3	3										
MEDSAT	*Medicago sativa*					4	5	2											
OENFAL	*Oenothera x fallax*		3	3		3		2											
OENGR	*Oenothera gr. biennis*		2	3		3		1											
YUCGLO	*Yucca gloriosa*			3	2	2				1									
CAREDU	*Carpobrotus edulis*		4	4		1	1											3	
DORREC	*Dorycnium rectum*					4	2			5	2	2							
LOBMAR	*Lobularia maritima*			4	3	3	2	2											
PASDIL	*Paspalum dilatatum*					2	2	4		4	4								
SOLASUB	*Solanum chenopodioides*				3	5	3			3		2							
BROWIL	*Bromus catharticus*				3	3	5	2	2		2								
CORTSEL	*Cortaderia selloana*				2	5				5	1	4	2						
CYPERA	*Cyperus eragrostis*					3	2	1		3	6	3							
PASPAS	*Paspalum paspalodes*					3	1	2		3	6	2							
CONYCAN	*Conyza canadensis*					6	3	2	3	4	3	3							
OENGLA	*Oenothera glazioviana*		3	4	3	5	3	2		2									
SPOIND	*Sporobolus indicus*				2	4	3	6	4	2	2								
CONYBON	*Conyza bonariensis*			3	1	2	3	3	3	1		1						1	
STESEC	*Stenotaphrum secundatum*		4	4		2	2	4	3	4		6						4	
CONYSUM	*Conyza sumatrensis*			2	2	6	4	3	2	4	1	1						1	
PASPVAG	*Paspalum vaginatum*	2			3	3	2	5	2	2	3	6	2	4	4	1		2	
ASTSQU	*Aster squamatus*				2	5	3	4	3	4	4	5	2					1	
BACHAL	*Baccharis halimifolia*				4	2				3		6	6	4				1	2
SPAPAT	*Spartina patens*		3		3					3		4				1			
ASPAOFF	*Asparagus officinalis*				2					2			1						
COTCOR	*Cotula coronopifolia*										3	4		3					
SPAALT	*Spartina alterniflora*											2		1		2	3		
MATINC	*Matthiola incana*					3	2		1									4	
AGAAME	*Agave americana*				1														1
ALOVER	*Aloe vera*		1															2	
PITTOB	*Pittosporum tobira*			1														1	1
SENBIC	*Senecio bicolor cineraria*																	3	
RUT CHA	*Ruta chalepensis*																	1	
LEPLAT	*Lepidium latifolium*				1	1						1							

Table 2. Geographical and biological features of species appearing in Table 1, arranged in alphabetical order. Explanation of abbreviations: bi – biennial, cad – deciduous, cras – succulent, herb – herbaceous, pf – evergreen, rhz – rhizomatous, ros – rosette plant, scad – scandent, scap – scape plant, sufr – suffruticose.

Taxa	Biotype	Introducing way	Dynamic	Status	Origin	Family
Acanthus mollis	H	Cult. Orn	Still unknown	Erga	W and C Mediterranean Region	Acanthaceae
Agave americana	F pf	Cult. Orn	Not spreading	Erga	N Ame. Mexico	Agavaceae
Aloe vera	C ros	Cult. Orn	Not spreading	Holo	Afr.	Liliaceae
Ambrosia artemisiifolia	T	Accid	Spreading fast	Epo	N Ame.	Asteraceae
Anacyclus radiatus radiatus	T	Accid	Spreading slowly	Epo	Mediterranean Region	Asteraceae
Arctotheca calendula	T	Accid	Spreading fast	Hemi	S Afr.	Asteraceae
Arundo donax	F herb	Cult.	Still unknown	Arq	E Asia	Poaceae
Asparagus officinalis	G	Cult.	Still unknown	Holo	Pluriregional	Liliaceae
Asphodelus fistulosus	H	Accid	Spreading fast	Epo	Mediterranean Region	Liliaceae
Aster squamatus	H scap (T)	Accid	Spreading fast	Holo	C Ame. and S Ame.	Asteraceae
Baccharis halimifolia	F cad	Cult. Orn	Spreading fast	Holo	E N Ame.	Asteraceae
Bromus willdenowii	H	Accid	Spreading fast	Epo	N Ame. and S Ame. (S EEUU to Chile and Argentina)	Poaceae
Cardaria draba	H rhz	Accid	Still unknown	Epo	Europe and SW Asia	Brassicaceae
Carpobrotus edulis	C cras	Cult. Orn	Spreading slowly	Holo	S Afr. (Cape Region)	Aizoaceae
Centranthus ruber	C	Accid	Spreading fast	Epo	Mediterranean Region	Valerianaceae
Chamomilla suaveolens	T	Accid	Spreading slowly	Epo	NE Asia or W N Ame.?	Asteraceae
Chenopodium ambrosioides	T (C)	Cult.	Spreading slowly	Hemi	Tropical Ame.	Chenopodiaceae
Conyza bonariensis	T	Accid	Spreading fast	Holo	S Ame.	Asteraceae
Conyza canadensis	T	Accid	Spreading fast	Hemi	N Ame.	Asteraceae
Conyza sumatrensis	T	Accid	Spreading fast	Hemi	Neotropical	Asteraceae
Coronopus didymus	H (bi) or T	Accid	Spreading fast	Epo	S Ame.	Brassicaceae
Cortaderia selloana	H	Cult. Orn	Spreading fast	Hemi	S Ame.	Poaceae
Cotula coronopifolia	T	Accid	Spreading fast	Holo	S Afr.	Asteraceae
Cyperus eragrostis	H	Accid	Spreading fast	Hemi	Tropical Ame.	Cyperaceae
Datura stramonium	T	Cult.	Spreading fast	Epo	Ame.	Solanaceae
Dittrichia viscosa	NF scad	Accid	Spreading fast	Epo	Mediterranean Region	Asteraceae
Dorycnium rectum	C	Accid	Spreading fast	Hemi	Mediterranean Region	Fabaceae
Emex spinosa	T	Accid	Still unknown	Ephe	Mediterranean and Macaronesian Regions	Polygonaceae

Table 2. (continued)

Taxa	Biotype	Introducing way	Dynamic	Status	Origin	Family
Euphorbia polygonifolia	T	Accid	Still unknown	Holo	E N Ame.	Euphorbiaceae
Gamochaeta coarctata	T	Accid	Spreading fast	Hemi	N Ame.	Asteraceae
Lepidium latifolium	H	Accid	Still unknown	Otros	E Europe and C Asia	Brassicaceae
Lepidium virginicum	T	Accid	Spreading fast	Epo	N Ame.	Brassicaceae
Lobularia maritima	C herb	Cult. Orn	Spreading slowly	Holo	Mediterranean Region	Brassicaceae
Matthiola incana	C	Cult. Orn	Spreading slowly	Holo	Mediterranean Region; S Europe (Tirrenic)	Brassicaceae
Medicago sativa sativa	H	Cult.	Spreading fast	Epo	C Asia	Fabaceae
Mirabilis jalapa	H	Cult. Orn	Not spreading	Erga	Tropical Ame.	Nyctaginaceae
Oenothera drummondii	C	Accid	Still unknown	Holo	N Ame. Atlantic coast	Onagraceae
Oenothera glazioviana	H (bi)	Accid	Spreading fast	Holo	N Ame.	Onagraceae
Oenothera gr. biennis	H (bi)	Accid	Spreading fast	Holo	N Ame.	Onagraceae
Oenothera x fallax	H (bi)	Accid	Spreading fast	Holo	Hybrid	Onagraceae
Paspalum dilatatum	H	Accid	Spreading fast	Hemi	S Ame. (Brazil to Argentina)	Poaceae
Paspalum paspalodes	G rhz	Accid	Spreading fast	Holo	Tropical Ame. (S EEUU to Uruguay and Chile)	Poaceae
Paspalum vaginatum	G rhz	Accid	Spreading fast	Holo	Tropical Ame. (S and SW EEUU and Mex to Argentina)	Poaceae
Pittosporum tobira	NF pf	Cult. Orn	Still unknown	Erga	E Asia: S Japan and E China	Pittosporaceae
Ruta chalepensis	C	Cult.	Still unknown	Epo	S Europe	Rutaceae
Senecio bicolor cineraria	C sufr	Cult. Orn	Spreading slowly	Epo	C and E Mediterranean Region	Asteraceae
Solanum chenopodioides	NF pf	Accid	Spreading fast	Hemi	SE S Ame.	Solanaceae
Soliva pterosperma	T	Accid	Spreading fast	Epo	S Ame.	Asteraceae
Spartina alterniflora	G rhz	Accid	Spreading slowly	Holo	N Ame.	Poaceae
Spartina patens	H rhz	Accid	Spreading fast	Holo	N Ame.	Poaceae
Sporobolus indicus	H rhz?	Accid	Spreading fast	Hemi	Tropical and Subtropical Ame. (EEUU and Mex. to Brazil)	Poaceae
Stenotaphrum secundatum	G rhz	Accid	Spreading fast	Holo	Tropical and Subtropical Ame.	Poaceae
Tetragonia tetragonoides	T	Cult.	Still unknown	Epo	New Zealand (Oceania)	Aizoaceae
Yucca gloriosa	NF pf	Cult. Orn	Not spreading	Hemi	N Ame. (SE EEUU or Mexico)	Agavaceae

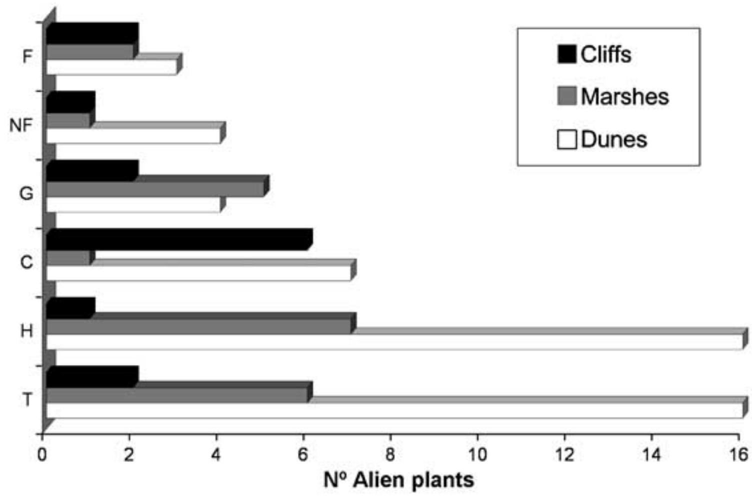

Figure 2. Comparison of life form of alien plants spectra in diverse studied coastal habitats. T: therophyte, H: hemicryptophyte, G: geophyte, C: chamaephyte, NF: nanophanerophyte, F: phanerophyte, Hy: hydrophyte.

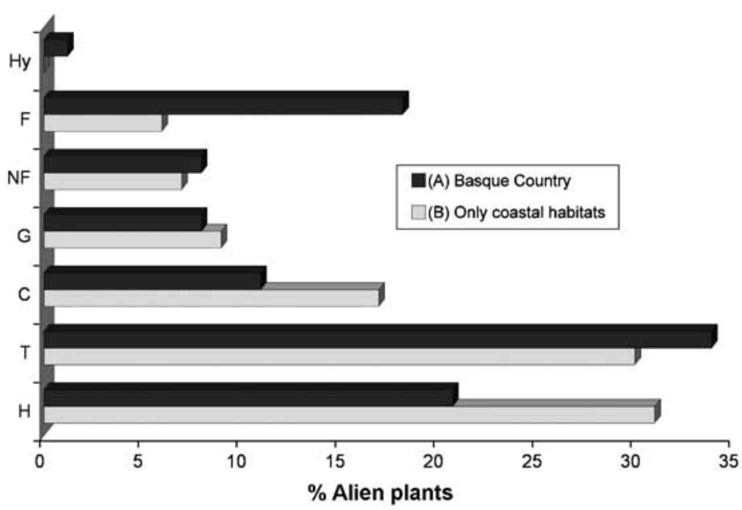

Figure 3. Percentage of life forms (biotypes) of alien plants. A: data from all habitats in the Basque Country (Campos and Herrera 1997); B: data from coastal habitats in the Basque Country and Cantabria regions (data from this work).

Arctotheca calendula

This plant, of South African origin, belongs to the Asteraceae family and has a successful dispersal mechanism due to its woolly seeds; these are able to fix to

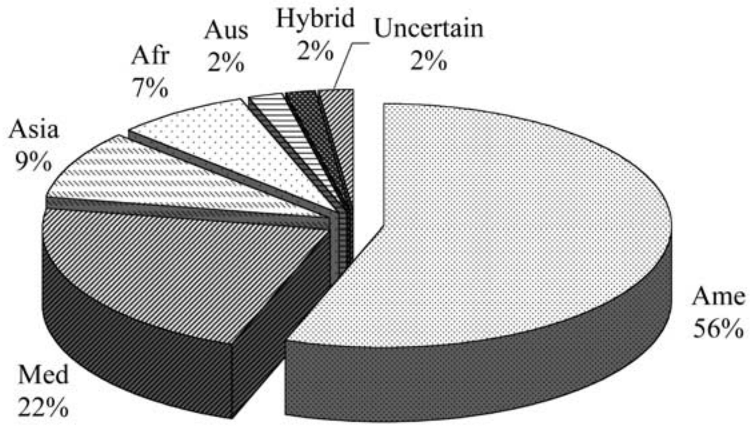

Figure 4. Areas of origin. Med: Mediterranean region, Afr: Africa, Aus: Australia, Ame: America.

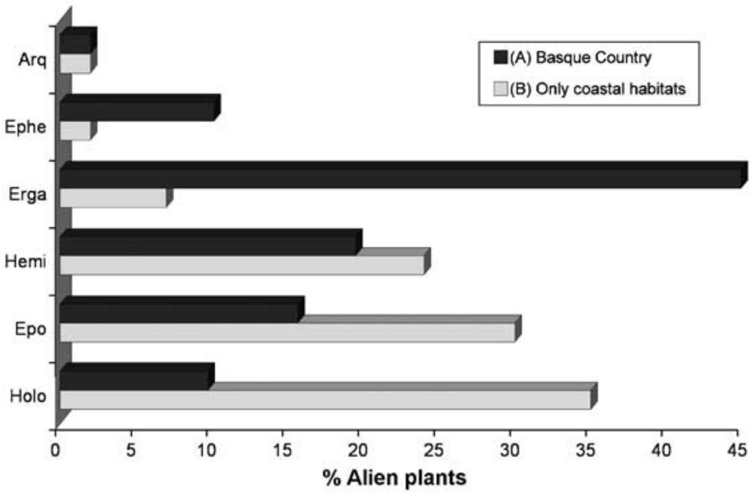

Figure 5. Alien plant status. Hemi: hemiagriophyte, Erga: ergasiophygophyte, Arq: archaeophyte, Ephe: ephemerophyte, Holo: holoagriophyte, Epo: epoecophyte. A: data from all habitats in the Basque Country (Campos and Herrera 1997); B: data from coastal habitats in the Basque Country and Cantabria regions (data from this work).

any surface or to be dragged by the wind. These reproductive features and the type of habitats where it occurs, intensively used by people, give it a strong invasion ability. Its rapid invasion, always on sandy soils, in the southwest of the Iberian Peninsula is well known (Rivas-Martínez 1978). In the Basque

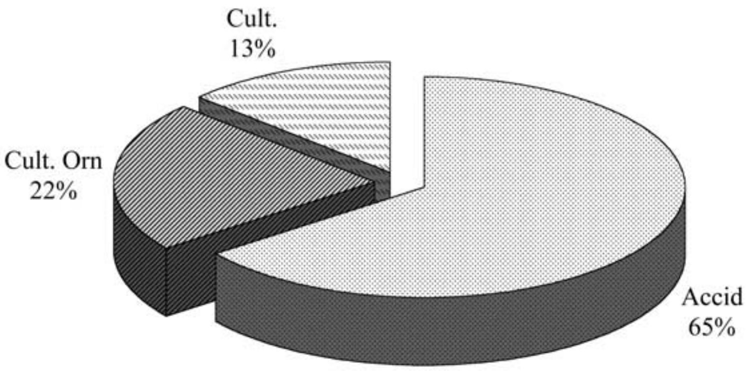

Figure 6. Way of introduction. Cult. Orn: cultivated as ornamental, Cult: cultivated for other purposes, Accid: accidental.

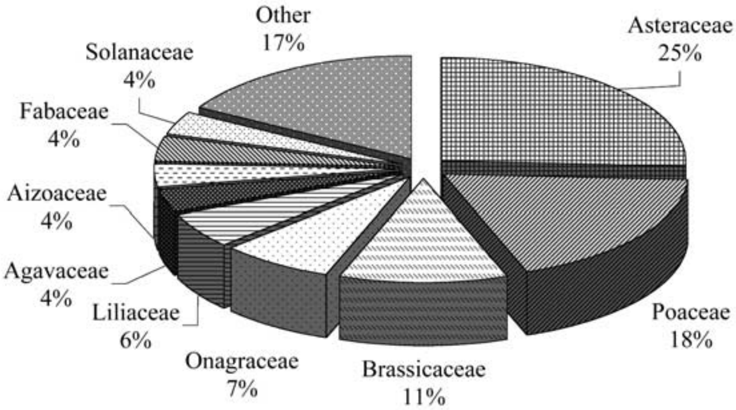

Figure 7. Percentage of families represented in alien flora of coastal habitats in the studied area.

Country it is very abundant in the western littoral (locations 12 and 14, Figure 1) and it also appears in many coastal sandy soils in the regions of Cantabria, Asturias and Galicia.

Baccharis halimifolia

This Asteraceae shrub has its origin in the coastal habitats on the eastern littoral of the USA, from Massachussets to Texas (Tarver et al. 1988). In 1863 it was introduced as an ornamental plant in France. In the Iberian Peninsula it was reported for the first time by Allorge (1941) in the Basque Country (from Lekeitio to Deba). On the Cantabrian coast it is now present in almost all the

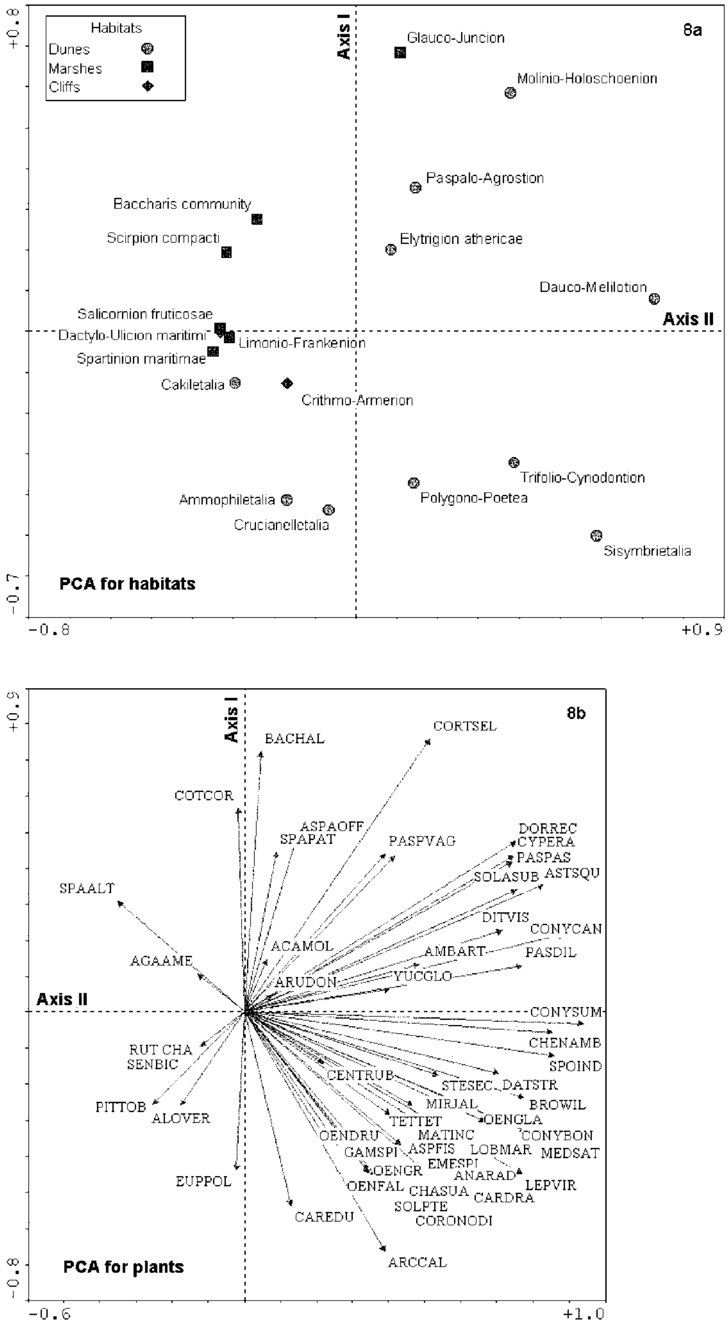

Figure 8. PCA ordination diagrams. First and second ordination axes are shown. (8a) Relationship of studied syntaxa to alien species composition; (8b) relationship of species distribution to environmental conditions.

estuaries from the Ría of Tina Mayor (region of Asturias) to the border with France (see Figure 1). In the Urdaibai Biosphere Reserve (locations 16–18, Figure 1) there are 885 ha of relatively well conserved saltmarshes, where *Baccharis halimifolia* has invaded 128 ha of the subhalophilous saltmarsh (Campos et al. 2000). It is also possible, though less frequent, to find *Baccharis. halimifolia* on cliffs: in halochasmophytic communities of *Crithmo–Armerion* or in aerohaline heathlands with *Dactylido–Ulicion maritimi* communities. The strong salinity and higher level of flooding in the halophilous areas of the estuaries do not currently allow the development of *Baccharis halimifolia* in perennial communities dominated by *Sarcocornia perennis* or *Sarcocornia fruticosa*.

Carpobrotus edulis

This succulent plant of the Aizoaceae family seems to be well adapted to the hard conditions that are found in dunes and cliffs. This species, of South African origin, is very common as a garden plant and is often used to fix dunes and slopes. It frequently appears naturalized in dune ecosystems, eliminating the native species by competition. Many references exist about the patterns and processes of its invasion in the coastal dunes of California (D'Antonio 1990; Vilà and D'Antonio 1998).

In the diverse coastal habitats of Portugal and the Mediterranean basin, *Carpobrotus edulis* forms nearly impenetrable mats that totally eliminate the autochtonous vegetation. The same process can be observed, though to a lesser extent, along the Cantabrian coast. The ecology and genetics of *Carpobrotus edulis* and *Carpobrotus acinaciformis* have been recently studied in some islands of Mediterranean France (Suehs et al. 2001). On the Cantabrian coast, *Carpobrotus edulis* is more abundant in the western part, where it invades well conserved dunes and cliffs.

Oenothera glazioviana and Oenothera × fallax

Oenothera glazioviana and *Oenothera × fallax* (*Oenothera glazioviana × Oenothera biennis*) are the most frequent species of this genus of Asteraceae on the northern Spanish coast. *Oenothera* has already been studied in the context of plant invasions (Frean et al. 1997). Both taxa we are dealing with here are biennial species, which are the most successful invasive species of the genus in central Europe (Mihulka 2001). These biennial species have a ruderal strategy, producing many small seeds without apparent adaptations for dispersal in space; these seeds remain dormant in soil over decades, waiting for the suitable moment for germination (Gross and Werner 1982). In dune systems there is always a chance of germination, because of the high proportion of exposed soil usually found in this habitat, increased by high human pressure. These ruderal species reach high densities which obstruct the native species linked to this environment in becoming established, some of them in danger of extinction on the Cantabrian coast (e.g., *Medicago marina*, *Glaucium flavum*, *Matricaria maritima*).

Paspalum vaginatum

This neotropical grass (Poaceae family) is currently naturalized in Europe, where it is spreading in various brackish environments (Filigheddu et al. 2001). On the Cantabrian coast it finds its optimum in high saltmarshes, where it forms dense grasslands 40 cm high, sometimes monospecific. It often shares biotopes with *Baccharis halimifolia*, and its expansion is also being favoured by the abandonment of formerly exploited marsh areas. There, it colonizes open spaces in rush communities and their pioneer stages, which are the most diverse with regard to typical saltmarsh species, and where rare species such as *Limonium vulgare* and *Glaux maritima* are established; the latter is decreasing rapidly due to the disturbance of its habitat on the Basque coast.

Spartina alterniflora

The North American Poaceae *Spartina alterniflora* substitutes the native *Spartina maritima* in some estuaries of this area. Thus, the intertidal helophytic communities of *Spartinetum maritimae*, which grow mainly in muddy soils, are replaced by communities of *Spartinetum alterniflorae*, especially in better drained muddy–sandy soils. This species is greatly menacing the rare populations of *Limonium humile* which grow in the territory, catalogued as ‘Vulnerable Species’ by the Basque Autonomous Government. For the moment *Spartina alterniflora* has been recorded in Txingudi, Orio, Zarautz and Zumaia in Gipuzkoa and in Sestao in Bizkaia (Campos and Herrera 2000, p. 441). In the bay of Txingudi (location 24, Figure 1) *Spartina* × *townsendii* also grows (Hubbard et al. 1978); it is a rather aggressive spontaneous hybrid of *Spartina alterniflora* and *Spartina maritima*.

Spartina patens

This perennial rhizomatous grass coming from the Atlantic coasts of North America has long been recorded along the western Mediterranean littoral (San León et al. 1999). It has recently reached the Cantabrian coast, from Galicia to the Basque Country, where it has started to naturalize, growing vigorously especially in subhalophilous rush communities and in subhalonitrophilous *Elymus pycnanthus* communities, even in densely populated communities. It also appears in disturbed dune slacks, where it forms dense grasslands that eliminate native species. For the moment no flowering or fruiting specimen has been found on the Cantabrian coast; it probably reproduces by vegetative fragments carried by the tide, which develop roots in suitable habitats. The number and size of known populations in the Basque Country are still small (unlike some places in Cantabria, Asturias and Galicia), so there is still time to take steps to ensure the control of its expansion and to eliminate it.

Stenotaphrum secundatum

This rhizomatous grass, originating in tropical and subtropical areas of America, is often used for lawns in Mediterranean areas, due to its resistance to drought and its efficiency in the use of water. In the study area it frequently appears in subhalophilous marshes, where it is especially common in trampled areas, reaching high densities and heights of 40 cm. It is also common in dune systems, especially in dune slacks, where the soil is always moist, in strong competition with *Carex arenaria*. It is also very abundant in beach entries and dune paths, forming dense grasslands adapted to trampling (*Trifolio–Cynodontion*), together with *Sporobolus indicus*, another introduced grass widespread in the area. *Stenotaphrum secundatum* is also spreading little by little on coastal cliffs, where it forms dense grasslands in suitable moisture and salinity conditions. Thus it sometimes threatens the establishment of rare or threatened native species, such as *Armeria maritima* or *Matricaria maritima*. Arteaga et al. (1999) show its negative effect on a population of the Basque–Cantabrian endemic *Armeria euskadiensis*, by strong competition for space.

Discussion

Among the alien taxa found in littoral ecosystems there are some which are very specific to certain types of plant communities, for example, *Euphorbia polygonifolia*, *Arctotheca calendula* and *Sporobolus indicus*. *Euphorbia polygonifolia* is specific to *Cakiletea* strandline communities, that grow on the organic detritus left by the sea along the tidal limit of the beaches. They are formed by halonitrophilous therophytes such as *Cakile maritima* subsp. *integrifolia*, *Salsola kali* and *Euphorbia peplis*. These strandline communities are endangered by the cleaning of beaches and the influx of people. *Euphorbia peplis* and the perennial *Honckenya peploides* are catalogued as vulnerable species by the 'Basque Catalogue of threatened Species of the Wild and Marine Fauna and Flora'. *Arctotheca calendula* is specific to nitrophilous annual communities of disturbed dunes (*Sisymbrietalia*) and *Sporobolus indicus* to trampled fixed dune grasslands formed mainly by *Cynodon dactylon* (*Trifolio–Cynodontion*). In marshes, *Cotula coronopifolia* only grows in open spaces of subhalophilous rush communities (*Glauco–Juncion*) and *Paspalum vaginatum* grasslands, and *Spartina alterniflora* occupies intertidal muddy soils (*Spartinion maritimae*). On cliffs, *Matthiola incana* and *Senecio cineraria* subsp. *bicolor* have preference for those areas nitrified by sea birds.

Other species have wider affinities and can be found in different coastal habitats. The most threatening ones are *Baccharis halimifolia*, *Spartina patens* and *Paspalum vaginatum*, which are widely distributed through most estuaries of the eastern Cantabrian littoral. Finally, there are some ruderal species not exclusive to the littoral fringe that are also abundant in other types of disturbed habitats, such as *Conyza* spp., *Oenothera* spp. or *Aster squamatus*.

Dune plant communities form very dynamic ecosystems, with many open spaces that allow the quick settlement of some xenophytes with high primocolonizing potential. Some of these species have short life-histories and grow very fast, in such a way that they create a significant seed bank that ensures the survival of the population (*Arctotheca*, *Oenothera*). Others grow more slowly by means of rhizomes, stolons, etc., so that with time they succeed in excluding any possible competition (*Carpobrotus*, *Stenotaphrum*, *Spartina*). The continuous human flow in these habitats, especially in summer, ensures the constant arrival of propagules from many different habitats. Strandline communities (*Cakiletalia*), foredune and mobile dune communities (*Ammophiletalia*) are usually very disturbed and their physiognomy and floristic composition change remarkably when invaded by the aforementioned species. Trampling and increased nitrification in dune systems and beach entries favour the spread of *Sisymbrietalia*, *Dauco–Melilotion* and *Trifolio–Cynodontion* ruderal communities. These communities have their own xenophyte flora: *Arctotheca calendula*, *Sporobolus indicus*, *Conyza* spp., *Solanum chenopodioides*, *Oenothera* spp., etc.

Some of the most abundant holoagrophytes (xenophytes established in natural communities) find their optimum habitat in the territory in subhalophilous communities: rush communities of *Juncus maritimus* (*Juncetalia maritimi*), helophytic communities of *Scirpus maritimus* (*Scirpetalia compacti*) and halonitrophilous communities of *Elymus athericus* (*Elytrygion athericae*). In these communities, the invasive plants reach the highest densities, and sometimes they constitute monospecific formations that seriously menace the conservation of the native communities and even the balance of the marsh ecosystem. Environmental conditions in marshes (daily flooding with brackish water and sedimentation/erosion dynamics) limit the colonization of these ecosystems to well-adapted species such as *Baccharis halimifolia*, *Paspalum vaginatum*, *Stenotaphrum secundatum*, *Spartina alterniflora* and *Spartina patens* that occupy similar habitats in their native countries.

The North American nanophanerophyte *Baccharis halimifolia* constitutes the biggest problem in the area (Meaza and Cadiñanos 2000). The development of monospecific *Baccharis halimifolia* communities prevents the growth of the heliophilous species typical of saltmarshes and provokes a marked change in the structure, physiognomy and diversity of the community invaded (transformer species, *sensu* Richardson et al. *op. cit*.). After invading abandoned areas in moist grasslands reclaimed from the marsh, it colonizes *Juncus maritimus* rush communities, *Elymus athericus* grasslands and helophytic vegetation with *Phragmites australis* or *Scirpus maritimus*. In the last years the advance of this shrub has reduced the populations of species growing in these habitats such as *Glaux* *maritima*, *Cochlearia aestuaria* and *Matricaria maritima*. The latter one is included within the category 'danger of extinction' in the 'Basque Catalogue of Threatened Species of the Wild and Marine Fauna and Flora'.

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Appendix

Syntaxonomical scheme. The plant communities marked with an asterisk (*) belong to the category of 'priority habitat' (Annex I of Habitats Directive 92/43/EEC).

Ammophiletea Br.-Bl. and Tüxen ex Westhoff, Dijk and Passchier 1946 (vegetation of coastal sand dunes).
- *Ammophiletalia* Br.-Bl. 1933 (mobile and semi-fixed dune communities).
- **Crucianelletalia maritimae* Sissingh 1974 (fixed coastal dunes with herbaceous vegetation: grey dunes).

Cakiletea maritimae Tüxen and Preising ex Br.-Bl. and Tüxen 1952 (halonitrophilous therophytic communities of beaches).
- *Cakiletalia integrifoliae* Tüxen ex Oberdorfer 1949 corr. Rivas-Martínez, Costa and Loidi 1992.

Molinio–Arrhenatheretea Tüxen 1937 (meadow and grassland vegetation).
- *Holoschoenetalia vulgaris* Br.-Bl. ex Tchou 1948.
  - *Molinio–Holoschoenion vulgaris* Br.-Bl. ex Tchou 1948 (Mediterranean rush formations).
- *Crypsio-Paspaletalia distichi* Br.-Bl. in Br.-Bl., Roussine and Négre 1952.
  - *Paspalo–Agrostion verticillati* Br.-Bl. in Br.-Bl., Roussine and Nègre 1952 (Mediterranean grasslands of humid and nitrified soils).
- *Plantaginetalia majoris* Tüxen and Preising in Tüxen 1950.
  - *Trifolio fragiferi–Cynodontion* Br.-Bl. and O. Bolòs 1958 (Mediterranean intensively grazed and trampled communities on humid soils).

Calluno–Ulicetea Br.-Bl. and Tüxen ex Klika and Hadac 1944 (heathland vegetation).
- *Ulicetalia minoris* Quantin 1935.
  - **Dactylido maritimae–Ulicion maritimi* Géhu 1975 (dry atlantic coastal heaths with *Erica vagans*).

Polygono–Poetea annuae Rivas-Martínez 1975 (synanthropic trampled vegetation).

Polygono arenastri–Poetalia annuae Tüxen in Géhu, Richard and Tüxen 1972 corr. Rivas-Martínez, Báscones, Díaz, T.E., Fernández-González and Loidi 1991.

Artemisietea vulgaris Lohmeyer, Preising and Tüxen ex von Rochow 1951 (synanthropic perennial vegetation).

Artemisietalia vulgaris Lohmeyer in Tüxen 1947.

Dauco–Melilotion Görs 1966 (nitrophilous biennial communities).

Elytrigietalia repentis Oberdorfer, Müller and Görs in Oberdorfer, Görs, Korneck, Lohmeyer, Müller, Philippi and Seibert 1967.

Elytrigion athericae Géhu 1968 (halonitrophilous perennial communities).

Stellarietea mediae Tüxen, Lohmeyer and Preising ex von Rochow 1951 (synanthropic annual vegetation).

Sisymbrietalia officinalis J. Tüxen in Lohmeyer et al. 1962 em. Rivas-Martínez, Báscones, T.E. Díaz, Fernández-González and Loidi 1991 (ruderal communities with summer phenology).

Salicornietea fruticosae Br.-Bl. and Tüxen ex A. and O. Bolòs 1950 (saltmarsh perennial vegetation).

Salicornietalia fruticosae Br.-Bl. 1933.

Salicornion fruticosae Br.-Bl. 1933.

Phragmito–Magnocaricetea Klika in Klika and V. Novák 1941 (helophytic vegetation).

Scirpetalia compacti Dahl and Hadac 1941 corr. Rivas-Martínez, Costa, Castroviejo and E. Valdés 1980.

Scirpion compacti Dahl and Hadac 1941 corr. Rivas-Martínez, Costa, Castroviejo and E. Valdés 1980 (helophytic communities on brackish soils).

Spartinetea maritimae Tüxen in Beeftink and Géhu 1973 (halophilous communities of *Spartina maritima*).

Spartinetalia maritimae Conard ex Beeftink and Géhu 1973.

Spartinion maritimae Conard ex Beeftink and Géhu 1973.

Juncetea maritimi Br.-Bl. in Br.-Bl., Roussine and Nègre 1952 (halophilous and subhalophilous rush communities).

Glauco–Puccinellietalia Beeftink and Westhoff in Beeftink 1962.

Glauco maritimae–Juncion maritimi Géhu and Géhu-Franck 1984 (Cantabrian-Atlantic rush communities on brackish soils).

Limonio ovalifolii–Frankenion laevis Arbesú, Bueno and F. Prieto 2002 (perennial communities of dune–saltmarsh contact).

Crithmo–Armerietalia Géhu 1964.

Crithmo–Armerion maritimae Géhu 1968 (halophilous cliff communities).

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