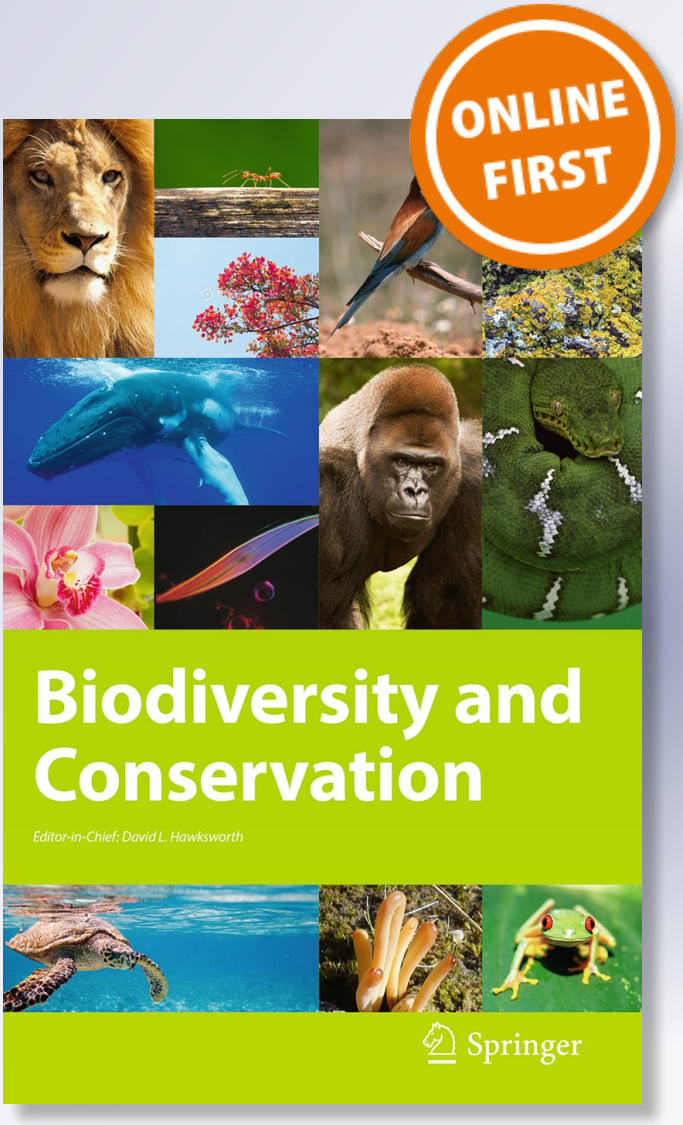
The response of plant community diversity to alien invasion: evidence from a sand dune time series

Silvia Del Vecchio, Leonardo Pizzo & Gabriella Buffa

Biodiversity and Conservation

ISSN 0960-3115

Biodivers Conserv
DOI 10.1007/s10531-014-0814-3



Springer

Your article is protected by copyright and all rights are held exclusively by Springer Science +Business Media Dordrecht. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Author's personal copy

Biodivers Conserv
DOI 10.1007/s10531-014-0814-3

ORIGINAL PAPER

The response of plant community diversity to alien invasion: evidence from a sand dune time series

Silvia Del Vecchio · Leonardo Pizzo · Gabriella Buffa

Received: 1 October 2013 / Revised: 22 September 2014 / Accepted: 3 October 2014
© Springer Science+Business Media Dordrecht 2014

Abstract This study examines the process of invasion of coastal dunes in north-eastern Italy along a 60-year time series considering alien attributes (origin, residence time, invasive status, and growth form strategy) and habitat properties (species richness, diversity and evenness, proportion of aliens, and proportion of focal species). Vegetation changes through time were investigated in four sandy coastal habitats, using a fine-scale diachronic approach that compared vegetation data collected by use of the same procedure, in four time periods, from the 1950s to 2011. Our analysis revealed an overall significant decline of species richness over the last six decades. Further, both the average number of species per plot and the mean focal species proportion were proved to be negatively affected by the increasing proportion of alien species at plot level. The severity of the impact, however, was found to be determined by a combination of species attributes, habitat properties, and human disturbance suggesting that alien species should be referred to as "passengers" and not as "drivers" of ecosystem change. Passenger alien species are those which take advantage of disturbances or other changes to which they are adapted but that lead to a decline in native biodiversity. Their spread is facilitated by widespread anthropogenic environmental alterations, which create new, suitable habitats, and ensure human-assisted dispersal, reducing the distinctiveness of plant communities and inducing a process of biotic homogenization.

Keywords Alien species · Anthropogenic pressure · Biotic homogenization · Coastal sand dune · Habitat properties · Time series

Communicated by Eckehard G. Brockerhoff.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-014-0814-3) contains supplementary material, which is available to authorized users.

S. D. Vecchio · L. Pizzo · G. Buffa (✉)
Centre for Estuarine and Marine Studies, DAIS, University Ca' Foscari of Venice, Castello 2737b, 30122 Venice, Italy
e-mail: gabriella.buffa@unive.it

Published online: 21 October 2014

Author's personal copy

Introduction

Coastal ecosystems are regarded as threatened by alien invasion worldwide (McLachlan and Brown 2006; Santoro et al. 2012). Their high sensitivity to alien establishment seems to be related to natural and anthropogenic factors such as habitat heterogeneity, intensive propagule pressure from ancient times, and frequent and diverse disturbances (Acosta et al. 2007, 2008). In recent years, coastal dune ecosystems have been extensively transformed as a result of urban expansion, agricultural and forestation spread, and industrial and harbour development (Schlacher et al. 2007). Population increase and the growing demand for recreation opportunities are the ultimate drivers of escalating pressure on sandy beaches (Dugan and Hubbard 2010). In fact, urbanization and other human pressures are estimated to be responsible for approximately 70 % of dune system loss in Europe during last century (McLachlan and Brown 2006).

The problem is not negligible given that coastal dune systems make up 20 % of the area occupied by the world's coastal landscapes (van der Maarel 2003). Dunes offer unique ecological services, for example filtration of seawater, nutrient recycling, flood control, and storm protection (McLachlan and Brown 2006; Millennium Ecosystem Assessment 2005) which are closely associated with well preserved ecosystems (Barbier et al. 2011). Moreover, by occupying a transition zone between terrestrial and marine ecosystems, dune environments constitute one of the most dynamic landscapes on earth (Van der Meulen and Udo de Haes 1996) and host a particularly specialized flora and fauna with high coenological biodiversity (van der Maarel 2003). According to the latest European Commission Report (European Commission 2008) most EU dune habitats are currently characterised by inadequate or very bad conservation status; even in those that are still well preserved, biodiversity is highly endangered (Prisco et al. 2012).

Efforts to explain the ecological effects of invader species have primarily focussed on their functional attributes (and how they differ from those of the resident species) and their abundance (Lloret et al. 2005; Stanisci et al. 2010; Vitousek 1990) or, on the habitat properties responsible for inherent vulnerability to invasion, i.e. invasibility (Chytrý et al. 2008b; Davis et al. 2000; Rejmánek et al. 2005). Both approaches basically treat species and "recipient communities" as static entities with fixed sets of traits (Whitney and Gabler 2008). However, increasing evidence shows that evolutionary or ecological processes can change the behaviour of invader species or modulate their effects (Strayer et al. 2006). The invasion process itself has been found to approximately follow a sequence of stages, irrespective of the taxonomic identity of the invader (Theoharides and Dukes 2007). Invasive species can also drive both natural selection and evolutionary response in the recipient communities (Callaway et al. 2005). As a result, the effect of invasion changes constantly, because of temporal changes to the invader, the invaded community, and the abiotic environment (Mooney and Cleland 2001; Lee 2002; Lambrinos 2004; Barrett et al. 2008; Suarez and Tsutsui 2008). Evolutionary or ecological processes can thus have a significant effect on the magnitude of the invasion process, making invasions and their consequences very changeable over time. Effect size is also affected by spatial scale dependency (Pyšek and Hulme 2005). Traditionally, the proportional representation of alien species has been assessed in large areas such as countries, cities, or grid squares of floristic maps, but much less has been done at smaller scale, e.g. vegetation plots. In general, the shift to a finer scale strongly affects the representation of alien species, and effects on native species significantly increase with decreasing unit size (Gaertner et al. 2009; Pyšek and Hulme 2005). In particular, plot size commonly used in phytosociological studies has been proved to be suitable as they capture a reasonably high proportion of

Author's personal copy

species present in the habitat, and the scale enables precise assessment of the effects of environmental variables, not possible on larger scales (Pyšek et al. 2010).

On continental or regional scales, invasion processes have been reconstructed by use of herbarium records (Comin et al. 2011; Fuentes et al. 2008; Mihulka and Pyšek 2001), but few studies of long-term patterns of local spread (Damgaard et al. 2011) are available. To analyse vegetation changes through time on a local scale, several direct, though very demanding, methods are usually adopted, for example repeated surveys, permanent plots, and field experiments. Yet, having received support from studies indicating close correspondence of synchronic and diachronic data (Foster and Tilman 2000; Walker et al. 2010), the most frequent indirect approach for monitoring temporal dynamics involves the use of chronosequences and associated space-for-time substitution (Pickett 1989; Walker et al. 2010).

Within this framework, this paper reports analysis of the temporal dynamics of alien plant invasion along a 60 year chronosequence to determine their effect on coastal plant communities in terms of loss of biodiversity and changes in community structure. This paper addresses, in detail, the questions:

- Have any changes in species richness and evenness occurred over the last 60 years?
- What are the temporal trends in alien species versus native focal species over the study period?
- Do these changes differ among vegetation types?

Materials and methods

Study area

The study area corresponds to the Venetian portion of the North Adriatic coast (north-eastern Italy), delimited by the estuaries of the Adige and Tagliamento rivers (Fig. 1).

Sites consist of narrow, recent dunes (Holocene), bordered by river mouths and tidal inlets, mostly fixed by docks. Recent dunes are in contact with ancient dunes (Pleistocene), alluvial or lacustrine deposits, or run bordering the Venice Lagoon.

Until the 1950s, the Venetian coast was almost entirely fronted by dunes up to 10 m in height (Bezzi and Fontolan 2003; Pignatti 2009). Few of these still survive and the coastline suffers from increasing erosion, reduction in sand supply, alteration of geomorphic processes and heavy human use (Nordstrom et al. 2009). From the 1950s onward, large stretches of coastal dunes have been fragmented by housing and resort development and by road construction. To defend shorefront buildings and to provide space for leisure use, large beach sectors have been protected by groynes, jetties, and revetments. Most sites are managed by private corporations, and land lying behind the beaches has been mostly developed as campsites, resorts, towns, and villages. In the 2011 summer season (from May to September) the number of visitors to beaches in the Veneto region numbered more than 25 million; tourist arrivals and night-stays in Cavallino, a 15 km long stretch of beach near Venice, increased from approximately 250,000 in the 1950s to almost eight million in 2011. As a matter of fact, summer beach tourism is one of the main resources of the region (Bezzi and Fontolan 2003); the average density of facilities for accommodating people is approximately 76.3/100 km^2.

Despite this intense tourism, the Venetian coastline is a regional and national biodiversity hotspot hosting many habitats, most of which are endemic communities (Buffa

Author's personal copy

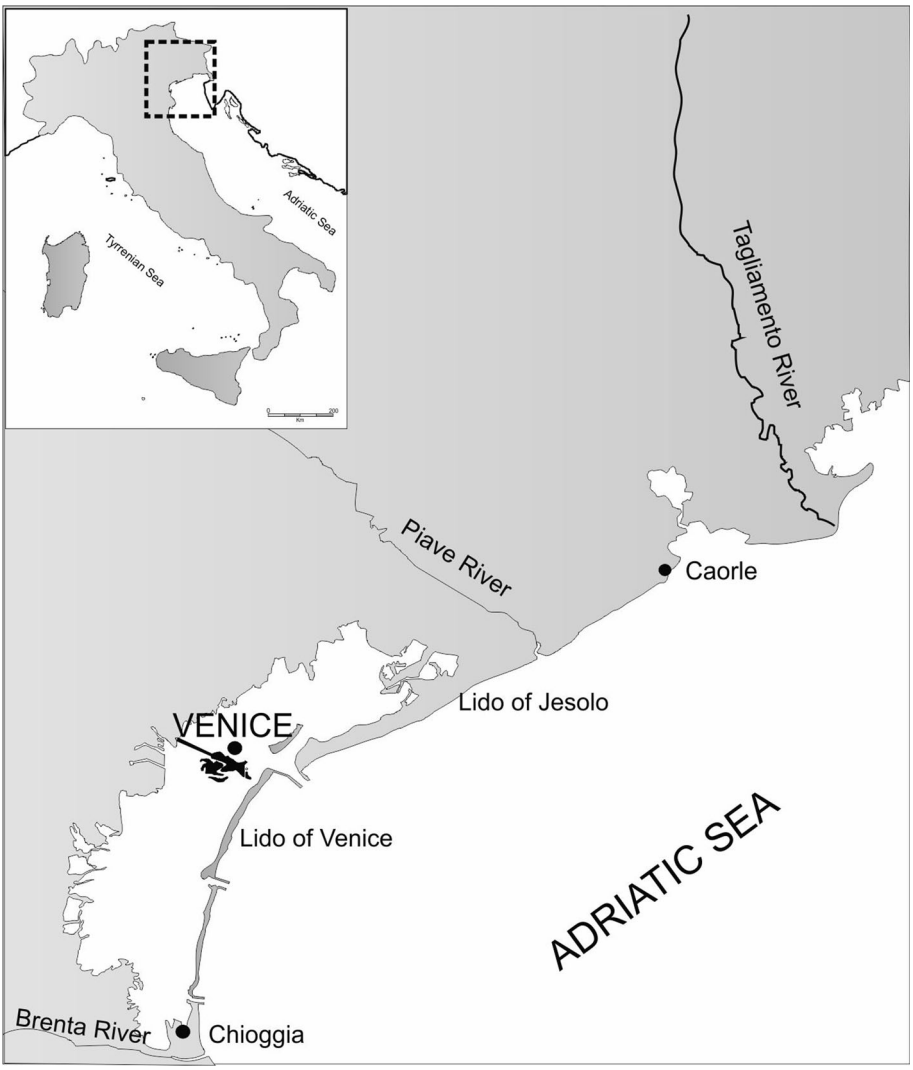


Fig. 1 Map of the study area

et al. 2012; Sburlino et al. 2008, 2013), included as "Natural habitats of European Community interest" in Annex I of the EU Habitat Directive (CE 43/92). Three of these, "Fixed coastal dunes with herbaceous vegetation (grey dunes)", "Coastal dunes with *Juniperus* spp." and "Wooded dunes with *Pinus pinea* and/or *Pinus pinaster*", are included in the category "priority habitats" (Buffa and Lasen 2010).

Data collection

The investigation focalised on the four distinct plant communities listed in Table 1.

Table 1 List and short description of the plant communities found in the study areas along the sea–inland gradient

Position along the dune profile	Upper beach	Foredune	Mobile dune	Transition dune and/or semi-fixed dunes
Habitat 92/43/ECC	1210—Annual vegetation of drift lines	2110—Embryonic shifting dunes	2120—Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes)	2130—* Fixed coastal dunes with herbaceous vegetation (grey dunes)
Phytosociological reference	*Salsolo kali–Cakiletum maritimae*	*Sporobolo arenarii–Agropyretum juncei*	*Echinophoro spinosae–Ammophiletum australis*	*Tortulo ruralis–Scabiosetum gramuntiae*
Focal species	*Cakile maritima*, *Chamaesyce peplis*, *Salsola kali*	*Elymus farctus* ssp. *farctus*, *Cyperus capitatus*, *Eryngium maritimum*, *Medicago marina*	*Ammophila arenaria* ssp. *australis*, *Cyperus capitatus*, *Eryngium maritimum*, *Echinophora spinosa*, *Euphorbia paralias*, *Medicago marina*	*Silene otites*, *Phleum arenarium*, many chamaephytes (*Fumana procumbens*, *Teucrium* sp.pl) and abundant carpets of lichens (*Cladonia* sp. pl.) and mosses (*Tortula ruraliformis*)

The nomenclature used follows Conti et al. (2005). Phytosociological references are those of Prisco et al. (2012). Focal species were selected in accordance with the Italian Interpretation Manual of EU Habitats, Biondi et al. (2009) and Prisco et al. (2012)

* Priority habitats (EU Habitat Directive)

Author's personal copy

Author's personal copy

Although spatially closed, the plant communities investigated have several distinctive features in terms of composition, structure, and spatial occupancy pattern. *Salsolo–Cakiletum* is an annual, nitrophilous community of the upper zone of the beach, near the shoreline. Being exposed to wave inundation, salt spray, and wind stress, the community is often patchy and naturally fragmented. Because of the extremely stressful environment, the total percentage of vegetation cover is low (Prisco et al. 2012) and the community is normally dominated by a few ephemeral species, for example *Cakile maritima* and *Salsola kali*. *Sporobolo arenarii–Agropyretum juncei* is a pioneer community found on the low embryo-dunes dominated by perennial dune-forming plants, for example *Elymus farctus* subsp. *farctus*, and such other perennial herbaceous species as *Cyperus capitatus*, *Eryngium maritimum*, and *Medicago marina*. It develops on poor sandy substrata, with low organic matter and of high salinity. Sand movement on a local scale causes vegetation burial and sand blasting and the community is characterised by low total cover. *Echinophoro spinosae–Ammophiletum australis* is a perennial herb community growing on a more stabilized sandy substrate and inner coastal dunes, where salinity and salt spray are usually lower than in the preceding community. It is dominated by *Ammophila arenaria* subsp. *australis*, which builds the dune by capturing blown sand and binding it together with its tough, fibrous rhizome system. Because of the less harsh environmental conditions, vegetation cover can reach 50–70 % of the total surface and the community is semi-permanent (Prisco et al. 2012). Finally, *Tortulo ruralis–Scabiosetum* is a perennial dry microprairie dominated by dwarf shrubs (in particular, *Fumana procumbens*, *Teucrium chamaedrys*, *T. montanum*, and *T. polium*), perennial herbaceous species, mosses, and lichens that cover semi-fixed dunes (Sburlino et al. 2013). Being less exposed to severe coastal conditions, the community has higher cover value, which can reach 100 %, and greater species richness than the other communities.

Data analysis

The temporal dynamics of plant communities were analysed by use of a fine-scale diachronic approach, by comparing vegetation data collected, at plot level, by use of the same procedure. Up-to-date and past phytosociological data for the study area enabled the identification of a chronosequence which started in the 1950s and ended in 2011. Each chronosequence was composed of four time steps. All recent vegetation surveys (2011) were recorded by using the Braun–Blanquet seven-degree scale of abundance and dominance (Westhoff and van der Maarel 1978), adopting the same method as used by previous authors. Surveys were recorded at the same localities as specified by previous authors, although not exactly in the same plots, because of lack of detailed information.

The analysis is based on a dataset of 171 phytosociological surveys as follows (Table 2):

Vegetation plot data were selected from a large database of 824 surveys comprising all the phytosociological relevés conducted over time within the study area and relative to the sand dune landscape. Survey areas (Table 3) are scattered along a coastline 100 km long but are concentrated in those sites which historically include natural coastal dunes and have been recently incorporated in the Natura 2000 European network as Sites of Community Importance (SCI) and/or Special Protection Areas (SPAs) (Buffa and Lasen 2010).

Vegetation surveys had an even spatial distribution but were unevenly distributed in time. The 1980s, in particular, were numerically under-represented. Because plot size has been recognized as a possible bias affecting estimation of species richness within each community, only vegetation samples of comparable size were selected, in accordance with

Table 2 List and number of phytosociological relevés used in the analysis

	First step (1950s)	Second step (1980s)	Third step (2000s)	Fourth step (2011)
Salsolo–Cakiletum	13	7	9	10
	(Pignatti 1959)	(Gèhu et al. 1984)	(unpublished)	(unpublished)
Sporobolo–Agropyretum	15	4	10	7
	(Pignatti 1959)	(Gèhu et al. 1984)	(unpublished)	(unpublished)
Echinophoro–Ammophiletum	18	4	10	14
	(Pignatti 1959)	(Gèhu et al. 1984)	7 rel. (unpublished); 3 rel. (Poldini et al. 1999)	(unpublished)
Tortulo–Scabiosetum	12	10	18	10
	(Pignatti 1959)	(Caniglia 1978)	(unpublished)	(unpublished)

Author's personal copy

Author's personal copy

Table 3 Individual survey sites

	Site surface (ha)	Latitude	Longitude
Chioggia	40.30	44°47′49.80″N	12°16′11.53″E
Lido di Venezia	178.34	45°24′36.06″N	12°22′27.20″E
Lido di Jesolo	27.14	45°26′44.22″N	12°28′8.49″E
Caorle	117.27	45°39′18.23″N	13°6′11.82″E

Site surface refers to the total area covered by the plant communities studied. Latitude and longitude (degrees, minutes, and seconds) are the geographic coordinates of the central point

the standardised procedure proposed by Haveman and Janssen (2008); this led to exclusion of all surveys of extreme or anomalous size. We overlooked the procedure only for surveys of *Tortulo–Scabiosetum* recorded in the 1980s for which, on average, areas were larger than for those of other time steps. Because they were the only available data and our work was conducted retrospectively on historical data collected at different times, we chose to retain them to avoid loss of precision because of the lack of intermediate observations. However, to eschew possible plot size effects, we chose not to use absolute species number in the subsequent data analysis.

The information considered was:

1 Year of the record, converted to one of the four time steps (referred to as 1950s, 1980s, 2000s, and 2011 hereafter);
2 Cumulative species pool and level of invasion; the cumulative species pool was calculated as the total number of species, both native and alien, recorded within each vegetation type in each time step, whereas the level of invasion corresponds to the percentage of alien species compared with the cumulative species pool (Chytrý et al. 2005);
3 Average number of species and mean proportion of alien and native focal species per plot; alien species were classified in accordance with Celesti-Grapow et al. (2009, 2010a) and Prieto et al. (2011) for the genus *Spartina*; definitions of "casual", "naturalized", or "invasive" are in accordance with Rejmánek et al. (2005); native focal species, that is the key species pivotal to habitat structure and function, were chosen in accordance with the "Italian Interpretation Manual of the 92/43/EEC Directive Habitats" (Biondi et al. 2009; Prisco et al. (2012);
4 Mean Shannon Diversity Index (H') and mean Evenness Index (J) per plot; the Evenness index J was calculated as $H'/\ln S$, where H' is the Shannon diversity index and S the number of species; for calculation of H' (Magurran 1988), the Braun–Blanquet scale values were previously transformed to percentage cover as follows: $r = 0.1$ %; $+ = 1.0$ %; $1 = 2.5$ %; $2 = 15.0$ %; $3 = 37.5$ %; $4 = 62.5$ %; $5 = 87.5$ %.

We also considered such qualitative species attributes as origin, residence time, invasive status, and growth form strategy, collected from available bibliographic sources and on-line archives (Banfi and Galasso 2010; Celesti-Grapow et al. 2010b; Maniero 2000; Pignatti 1982; Ruchinger 1818; Vignolo-Lutati 1935).

Author's personal copy

Statistical analysis

To determine the effect of the invasion process over time in terms of loss of biodiversity and changes in community structure, we applied a General Linear Model or a Generalized Linear Model (depending on data distribution). The proportion of alien species was included in the models as a continuous predictor variable. Time steps and vegetation types were used as grouping (categorical) variables (factors with four levels each). Habitat properties, i.e. Shannon Diversity Index H', Evenness Index J, average number of species per plot, and proportion of focal species per plot were incorporated as response (dependent) variables. Chi-squared tests were used to test the null hypothesis of an even invasion level distribution and of alien and focal species species-specific frequencies along the time series (the Yates correction was applied for one degree of freedom).

Results

The alien species pool

Ten alien species were found along the time series. These are listed in Table 4, which summarizes their different features. Only those alien species sampled within the plots are documented and, as such, the entire pool of alien species present in the Venetian coastal sand system is not included.

Most of the species are from temperate areas of the New World, where they usually occupy primary or secondary open disturbed habitats, for example grasslands, street sides, riverbanks, and dunes. The precise native range of two species is uncertain; *Oenothera stucchii* is assumed to have recently originated in Italy from American populations of *O. biennis* (Soldano 1993; Dietrich et al. 1997). The origin of the genus *Xanthium* is also unclear. Only *Xanthium strumarium* s.str. is usually claimed to be an Old World species, other members of the genus being native to the New World (Strother 2006). According to Piva and Scortegagna (1993), the subspecies *italicum* is probably a new entity which has evolved in southern Europe.

The recorded alien species pool is entirely represented by neophytes, i.e. species which immigrated after 1500. Most species are referred to as invasive at the national level; four are classified as naturalized or established plants, that is, plants capable of independent growth but that do not necessarily invade natural or semi-natural ecosystems. Only one species (*E. angustifolia*) has been classified as casual, i.e. species that rely on repeated introduction for their persistence.

Most of the species are represented by either annual or perennial herbaceous species, particularly, therophytes (four species), rhizomatous geophytes (two), and biennial hemicryptophytes (one). Only three species are woody perennials or partially woody shrubs (e.g. *Senecio inaequidens*).

Table 5 shows the species' temporal and spatial pattern of occupancy and their trend in frequency along the time series.

Only four species (*X. orientale* ssp. *italicum*, *O. stucchii*, *E. canadensis* and *C. longispinus*) were already present in the 1950s; all the others, for example *S. inaequidens*, *A. fruticosa*, were first recorded in the 1980s or, for *A. psilostachya* and *S. versicolor*, even more recently.

In all, the area has experienced an increase in the level of invasion, i.e. the percentage of alien species compared with the cumulative species pool, from the 1950s to 2011. The

Table 4 Geographical and biological features of alien species recorded within the plots, arranged in alphabetical order

Taxa	Growth form	First record	Manner of introduction	Native habitat	Origin	Status
Ambrosia psilostachya	G rhz	1927	Accid.	Meadows; disturbed habitats	N-America	N
Amorpha fruticosa	NP scap	1818	Cult. Orn.	River banks	N-America	I
Cenchrus longispinus	T scap	1933	Accid.	Disturbed habitats	N-America	I
Cuscuta cesattiana	T par	1876	Accid.	–	N-America	N
Elaeagnus angustifolia	NP scap	1600 (?)	Cult. Orn.	Disturbed habitats; river banks	CW Asia	C
Erigeron canadensis	T scap	1644	Cult. Orn.	Disturbed habitats; river banks; dunes	N-America	N
Oenothera stucchii	H bi	1952	–	Disturbed habitats; river banks	Uncertain	N
Senecio inaequidens	Ch sufr	1960	Accid.	Disturbed habitats	S-Africa	I
Spartina versicolor	G rhz	?	–	Wetlands; salt marshes	N-America	I
Xanthium orientale ssp. *italicum*	T scap	1745	Accid.	Disturbed habitats	Uncertain	I

Explanation of abbreviations: growth forms: *T* therophyte, *H* hemicryptophyte, *G* geophyte, *Ch* chamaephyte, *NP* nanophanerophyte, *bi* biennial, *par* parasite, *rhz* rhizomatous, *scap* scapose plant, *sufr* suffruticose. First record refers to the first report along the Venetian coast or, when unknown, to the first record in Northern Italy; *?* time of introduction unknown or uncertain. Status: *N* naturalized, *I* invasive, *C* casual (status according to Celesti-Grapow et al. 2009, 2010a, b). Definitions of "casual", "naturalized", and "invasive" are in accordance with Rejmánek et al. (2005). Manner of introduction: *Accid.* accidental, *Cult. Orn.* cultivated as ornamental plants

Author's personal copy

Author's personal copy

Table 5 Temporal and spatial pattern of alien species occupancy within the target communities

	Ist step 1950s				IInd step 1980s				IIIrd step 2000s				IVth step 2011			
	SC	SA	EA	TS	SC	SA	EA	TS	SC	SA	EA	TS	SC	SA	EA	TS
Cumulative species pool	75				108				89				58			
Level of invasion	0.05				0.09				0.10				0.16			
Ambrosia psilostachya									0-25	0-25	75-100		0-25	25-50	0-25	75-100
Amorpha fruticosa								0-25			0-25					
Cenchrus longispinus			0-25					25-50	0-25	25-50	0-25			25-50	25-50	0-25
Cuscuta cesattiana							0-25	25-50			0-25					0-25
Elaeagnus angustifolia								25-50				0-25				0-25
Erigeron canadensis			0-25	0-25				25-50		0-25	0-25	0-25			0-25	0-25
Oenothera stucchii		0-25	50-75	0-25		25-50	25-50	75-100		25-50	25-50	75-100		50-75	25-50	0-25
Senecio inaequidens							0-25					0-25				0-25
Spartina versicolor																25-50
Xanthium orientale ssp. italicum	75-100	75-100	75-100	0-25	75-100	75-100	75-100	0-25	75-100	75-100	50-75		75-100	75-100	75-100	0-25

Cumulative species pool represents the sum of both native and alien species recorded at each time step; the level of invasion refers to the proportion of alien species to the cumulative species pool. Different shades of grey refer to four classes of increasing frequency in plots, from light grey (frequency < 25 % of plots) to dark grey (frequency > 75 % of plots), as indicated by numbers. SC, *Salsolo–Cakiletum*; SA, *Sporobolo–Agropyretum*; EA, *Echinophoro–Ammophiletum*; TS, *Tortulo–Scabiosetum*

change has been gradual, however, and significant differences have been detected only by comparing the two extremes of the chronosequence (χ^2 1950s/2011 with 1 $df = 4.76$, $p < 0.05$).

Overall trends in species diversity and evenness

A significant effect of the invasion process on community composition was detected by our models (Online Resource 1).

In fact, both the average number of species per plot and the proportion of native focal species per plot turned out to be significantly affected by the proportion of alien species and an overall negative trend over time was observed. Conversely, neither the mean Shannon Diversity Index (H') nor the mean Evenness Index (J) per plot provided evidence of a relationship with the proportion of alien species. All habitat properties were closely related to vegetation type, i.e. vegetation type significantly affected the response to the invasion process, and changes as a result of the time steps (variable "year") were always significant in the interaction with vegetation type.

Trends in each community are summarized in Fig. 2. Additional data are given in Online Resource 2.

H', J, species number, focal species, and representation of aliens in the vegetation types

Salsolo kali–Cakiletum maritimae

Excluding alien species, the recorded cumulative native species pool consisted of 13 vascular plant species, three of which were focal species representing approximately 23 % of these. The ratio of alien species to the cumulative species pool, i.e. the level of invasion, increased only slightly over time, with no significant differences along the time series (χ^2 never significant) (Online Resource 2).

Author's personal copy

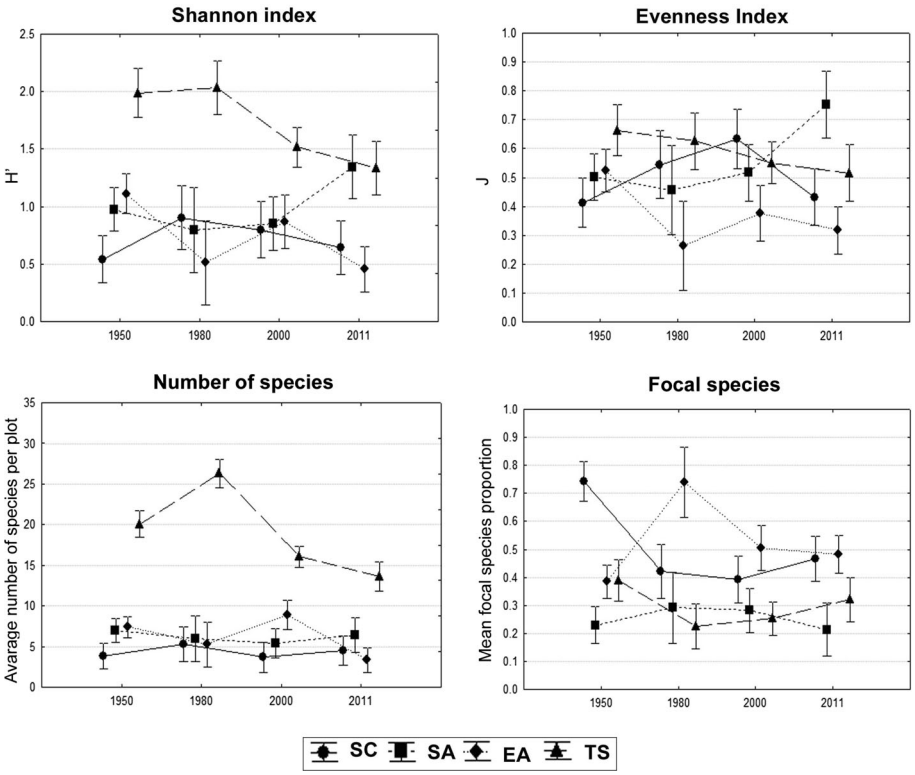


Fig. 2 Means (±SE) of Shannon Diversity Index H', Evenness Index J, average number of species per plot, and mean focal species proportion in the different vegetation types over time. *SC*, *Salsolo–Cakiletum*; *SA*, *Sporobolo–Agropyretum*; *EA*, *Echinophoro–Ammophiletum*; *TS*, *Tortulo–Scabiosetum*

As summarised in Online Resource 2 and graphically represented in Fig. 2, both Shannon index H' and evenness J underwent some fluctuations over time but, on the whole, their current values were comparable with those in the 1950s. A similar trend was apparent for the average number of species per plot.

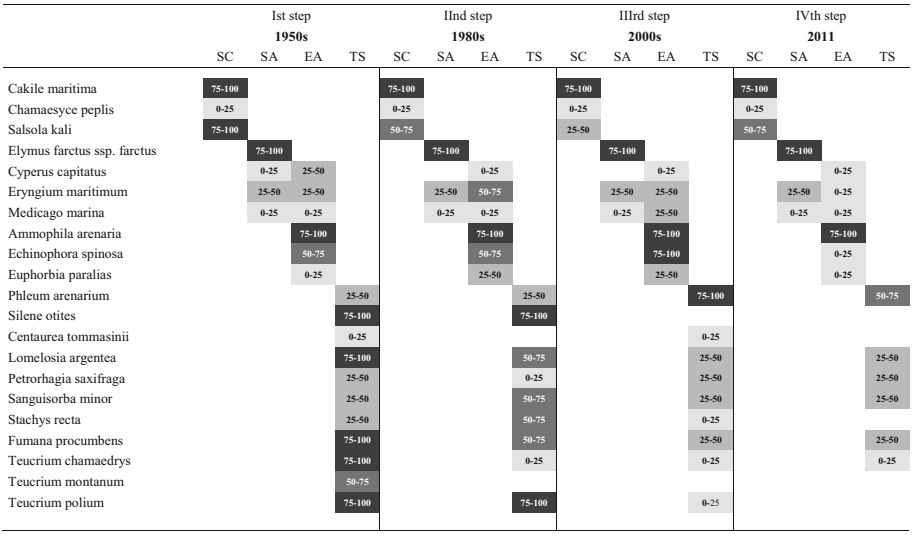
After a drop between the two first time steps, the mean proportion of focal species remained constant. The integrity of the focal species pool was ensured by steady frequencies of *Cakile maritima* and *Chamaesyce peplis*, whereas *Salsola kali* underwent a significant change in frequency from 100 % in the 1950s to 60 % in 2011 (χ^2 1950s/2011 with 1 $df = 9.51$, $p < 0.01$) (Table 6).

Three alien species were found along the time-series (Table 5). Two were annual species, *X. italicum* and *C. longispinus*, whereas the third, *A. psilostachya*, was a rhizomatous geophyte. *X. italicum* was the only alien recorded since the 1950s whose frequency over time remained relatively steady (χ^2 never significant). *Cenchrus longispinus* was first recorded in the 2000s and *A. psilostachya* in 2011. In both cases, their frequency (11 and 10 % respectively) was low.

Overall, although changeable over time, the *Cakile maritima* community has remained rather constant during the last 60 years; the only attribute changing markedly between the two extremes of the chronosequence was the mean proportion of focal species.

Author's personal copy

Table 6 Temporal pattern of occupancy of focal species within the target communities



Different shades of grey refer to four classes of increasing frequency in plots, from light grey (frequency < 25 % of plots) to dark grey (frequency > 75 % of plots), as indicated by numbers. SC, *Salsolo–Cakiletum*; SA, *Sporobolo–Agropyretum*; EA, *Echinophoro–Ammophiletum*; TS, *Tortulo–Scabiosetum*

Sporobolo arenarii–Agropyretum juncei

The cumulative native species pool amounted to 21 species, four of which were focal species (19 %). The level of invasion (proportion of aliens to the cumulative species pool) increased from 0.11 in the 1950s to 0.31 in the 2000s and 2011 (χ^2 1950s/2011 with 1 $df = 9.76$, $p < 0.01$) (Online Resource 2).

In the *Elymus farctus* community, both H' and J increased over time (Online Resource 2 and Fig. 2). Conversely, the average number of species per plot and the mean focal species ratio remained rather stable, as did the focal species-specific frequency, except for *Cyperus capitatus*, which has not been recorded in this community since the 1950s (Table 6).

Different from the previous community, two other alien species were found: the annual *E. canadensis* and the biennial *O. stucchii* (Table 5). Both *X. italicum* and *O. stucchii* have been present since the 1950s. Whereas the frequency of the former has been relatively stable (χ^2 never significant), *O. stucchii* has increased gradually and significantly (χ^2 1950s/2011 with 1 $df = 37.52$, $p < 0.001$). *Ambrosia psilostachya* and *C. longispinus* only emerged in large numbers in the 2000s, with the increase in frequency of *Ambrosia* being outstanding (χ^2 2000s/2011 with 1 $df = 19.32$, $p < 0.001$).

Echinophoro spinosae–Ammophiletum australis

The cumulative native species pool comprised 47 species, six of which (approx. 13 %) were focal. The level of invasion has grown over time from 0.13 to 0.33 (χ^2 1950s/2011 with 1 $df = 7.85$, $p < 0.01$) (Online Resource 2). As for the *Elymus farctus* community,

Author's personal copy

the process developed gradually but significantly, and the community is nowadays experiencing its highest levels of invasion to date.

Over the years, the community experienced a modification in its structure with a loss of both diversity H' and evenness J. In contrast with what occurred in *Salsolo–Cakiletum* and *Sporobolo–Agropyretum*, the chronosequence revealed an undeniable drop in the average number of species per plot. Apart from an increase between the two first time steps, the mean proportion of focal species remained essentially constant (Online Resource 2 and Fig. 2).

Among the focal species pool (Table 6), only *Echinophora spinosa* (χ^2 1950s/2011 with 1 $df = 37.779$, $p < 0.001$) and *Eryngium maritimum* (χ^2 1950s/2011 with 1 $df = 48.020$, $p < 0.001$) significantly decreased in frequency. For all other species, particularly *Ammophila arenaria*, frequency values were consistent over time.

On the whole, the community hosted eight alien species (Table 5) most of which are shared with the former communities. Three species were new: the annual *C. cesattiana* and two woody species *A. fruticosa* and *S. inaequidens*. Therophytes still dominated, however. The frequency of annual species (recorded since the 1950s) was stable (*X. orientale*) or increasing (particularly significantly for *C. longispinus*; χ^2 1950s/2011 with 1 $df = 12.255$, $p < 0.001$). Behaviour of perennial species was discordant, with frequency stable (*A. psilostachya*) or decreasing (*O. stucchii*); woody species appeared only occasionally and sporadically.

Many habitat attributes had undergone apparent changes in the comparison between the first and the last step of the chronosequence: level of invasion, the average number of species per plot, H', and J.

Tortulo ruralis–Scabiosetum gramuntiae

The cumulative native species pool totalled 93 species, which included 11 focal species (12 %). Compared with the other communities, the level of invasion of the microprairie was lowest (although with a significant increase; χ^2 1950s/2011 = 7.04, $p < 0.01$) but alien diversity was highest, amounting to 10 species (Table 5).

Both H' and J decreased along the chronosequence. The average number of species per plot changed over time, dropping from approximately 20 in the 1950s to approximately 13 in 2011 (Online Resource 2). The peak registered in the 1980s could have been because of the larger plot surface used in that period; solid confirmation of the temporal trend is, however, given by the outstanding difference between the first and the last time step. Likewise, the number of focal species per plot decreased along the chronosequence. In particular, the dwarf shrub component of the focal species pool decreased dramatically in frequency over time (Table 6). *Fumana procumbens* and *Teucrium chamaedrys* dropped from 92 to 30 and 20 %, respectively (χ^2 1950s/2011 = 30.50, and = 45,009 respectively, both $p < 0.001$), and *Teucrium montanum* and *T. polium* have not been recorded in any vegetation plot since the 1980s.

In the alien species pool, the number of annual species diminished slightly in favour of herbaceous (*A. psilostachya O. stucchii* and *S. versicolor*) or woody (*A. fruticosa*, *E. angustifolia* and *S. inaequidens*) perennials.

The temporal pattern was quite dissimilar among species. After a peak in the 1980s, some of them (*E. canadensis* and *X. orientale* or *O. stucchii*), slowly returned to frequencies comparable with those of the 1950s (comparison significant for *E. canadensis* only, $\chi^2 = 4.321$, $p < 0.05$). Such species as *C. longispinus* and *C. cesattiana* had fluctuating patterns, quite typical of those of annual populations, alternately appearing and

Author's personal copy

disappearing, but, when present, maintaining high frequency. Recorded for the first time only in the 2000s at high frequency, occurrence of *A. psilostachya* further increased to 90 % of the surveyed plots in 2011 (χ^2 2000s/2011 = 18.050, $p < 0.001$). A similar pattern was observed for *S. inaequidens*, although at less critical frequencies (χ^2 2000s/2011 = 0.563 ns).

Discussion

The alien species pool

Our analysis revealed a level of invasion similar to those observed in other regional and habitat-specific studies (Campos et al. 2004; Chytrý et al. 2008b; Vilà et al. 2007). In other words, when coastal, littoral, and riverine habitats are subject to high human and/or naturally induced disturbance and high propagule pressure, they also harbour a large number and proportion of alien species.

Striking similarities were also found for growth forms. Most of the alien species recorded within the vegetation plots were therophytes and, secondarily, geophytes or hemicryptophytes, which have been proved to be well suited to changing environments such as those of coastal dunes (Acosta et al. 2008; Campos et al. 2004). Species with a short life-history (e.g. *C. longispinus*, *E. canadensis*, *X. orientale* or *O. stucchii*, a biennial hemicryptophyte) grow very quickly and create a significant seed bank that ensures survival of the population. Among perennials, geophytes such as *A. psilostachya* and *S. versicolor* grow more slowly and propagate mostly by way of below-ground organs. Although vegetative propagation does not guarantee long-distance spread, it ensures rapid establishment and maintenance within suitable habitats, and successful exclusion of any possible competition (Lloret et al. 2005). Numerical supremacy and the frequency of herbaceous aliens, both within the plots and along the time series, testify to their successful strategy which, on the other hand, is that of native species. Conversely, woody species are small in number and, although referred to as "invasive species" (e.g. *S. inaequidens* or *A. fruticosa*) at the national level (Celesti-Grapow et al. 2009, 2010a), they do not seem to have a particular adaptive strategy which enables them to establish a stable population in sand dune habitats. Thus, the study confirms that species-identity, in particular growth forms, and the strategy they use substantially affect invasion outcome. Even so, species traits that match opportunities provided by resident habitats are likely to be more significant during the primary phase (i.e. naturalization) than during invasion. Indeed, the time series reveal different species' performances, i.e. a different pattern of spatial occupancy and a different rate of population increase, which seem at least partially independent of the growth form. Further, growth forms can account for the spatial pattern of occupancy. In fact, if such woody perennials or partially woody shrubs as *S. inaequidens* and *E. angustifolia* seem to be very specific to some habitats, particularly those of more sheltered areas (semi-fixed dunes), both annual and perennial herbaceous species, for example *A. psilostachya*, *O. stucchii*, and such annuals as *X. orientale* and *C. longispinus* have greater affinity for different habitats from the beach to the semi-fixed dunes, thus proving, once again, to be best suited form to this environment. However, while in the herbaceous form, some species (e.g. *X. orientale*) maintained stable frequencies over time whereas a rapid increase in occupancy was observed for others (*A. psilostachya* and *C. longispinus*) irrespective of their growth form and life span. This different trend may be explained in relation to the spatio-temporal dynamics of alien invasion. Plant invasions are usually

Author's personal copy

described as a three-phase process, with a first period of slow initial spread (lag-phase) in which species occupy only few, isolated localities, followed by a phase of rapid expansion (exponential phase). A final third phase follows in which aliens have no or only little further areal expansion (Pyšek and Hulme 2005). Thus, alien populations can persist in relatively low numbers for decades before exploding, after various ecological and evolutionary processes have come into play, and then enter a chronic phase (Arim et al. 2006; Strayer et al. 2006) in which the probability of invasion increases with time after their introduction (residence time). All of the recorded species were introduced, either accidentally or voluntarily, after 1500 and can, accordingly, be classified as neophytes (Celesti-Grapow et al. 2009, 2010b; Pyšek et al. 2004). Nevertheless, steady frequencies over time of such species as *X. orientale* and *E. canadensis*, introduced many centuries ago and, therefore, with a long history of coexistence with biologically-similar natives, could imply they have reached the third phase, which entails no or irrelevant further spread. With reference to this issue, it is worth mentioning that, given its long-standing presence in Italy, the alien status of *Xanthium orientale* has been questioned by some authors (Baldoni et al. 2000; Poldini et al. 2001) who refer to the species as an archeophyte. In contrast, *A. psilostachya*, *C. longispinus*, and *O. stucchii* have been introduced much more recently, since 1900, and seem to have been entering the "increase-phase" as testified by their outstanding spread and increase in occurrence. With regard to this, *S. inaequidens*, first recorded along the Venetian coast in the 1960s, still might be in the lag-phase and it could be that the pattern we observe today will change in the coming decades.

Other extrinsic factors might enable species to cross barriers and favour their transit between stages. Changes in soil disturbance, nutrient enrichment, climate, dispersal, of which there are many examples, may result in increasing population growth and dispersal (Pyšek and Hulme 2005). The lack of particular adjustments for long-distance dispersal, in conjunction with the capability of germinating in the light, led Frean et al. (1997) to hypothesize that the spread and the pattern of occurrence of *Oenothera* species was highly dependent on human activity rather than on natural dispersal agents. Similarly, the spines on the burs of *C. longispinus,* which facilitate attachment to almost anything, including machinery, tyres, shoes, and garments have, believably, sped up the spread of the species. Thus, besides species' identity, that is, their life history traits and residence time, the strong intensification of human activity and the continuous human flow along the coast, with trampling, gap creation, and sand movement, could be involved in alien plant spread while, at the same time, ensuring the constant arrival of new propagules.

H', J, species number, focal species and representation of aliens in the vegetation types

It is often hard to demonstrate a cause–effect relationship between the establishment and spread of alien species and the extinction of native species. Even so, our analysis revealed, that despite different patterns among communities, there has been an overall significant decline of species richness, in particular of focal species richness, over the last six decades.

Many studies proved that habitats differ substantially in the numbers and/or proportions of alien species (Chytrý et al. 2005; Pyšek et al. 2002; Rejmánek et al. 2005). Recently, Pyšek et al. (2010) postulated that habitat properties are a much more important predictor of the level of invasion than such other factors as climate or propagule pressure.

Also, among habitat properties, the diversity of native or resident species has been assumed to be important in regulating the extent of invasion, according to the "Diversity Resistance Hypothesis" or the "Biotic Resistance Hypothesis" (Elton 1958). Indeed, since Elton, many studies (Kennedy et al. 2002; Levine et al. 2004; Mitchell et al. 2006; Tilman

Author's personal copy

1999) agree that diverse communities are highly competitive and readily resist invasion, and both the establishment (number of invaders) and success (proportion of invaders) of invading plants are, thus, reduced.

In accordance with data reported for other European coastal dunes (Acosta et al. 2008; Campos et al. 2004), our analysis confirmed that the mean proportion of aliens was negatively related to plot species richness. In the 1950s, the proportion of invaders was highest in the *Cakile maritima* community, resulting in the lowest value in the *Tortulo–Scabiosetum* community, thereby actually following the sea–inland typical zonation with increasing richness from the upper beach to the semi-fixed dunes. In habitats such as those of the upper beach, embryo dunes and mobile dunes, in which species encounter extreme environmental conditions, it is difficult for an incomer to establish and survive. However, given low species richness and scarce vegetation cover, biotic resistance is limited. And, when a suitable genotype arrives or generates (e.g. *X. orientale* or *O. stucchii*), it can successfully establish and form stable populations.

However, communities conformed to the "Diversity Resistance Hypothesis" in the 1950s only. From the 1980s onwards the model changed, and in 2011 the highest level of invasion was found in the *Ammophila* community and the highest alien species richness was in the *Tortulo–Scabiosetum* community. Over time, the proportion of aliens increased in each community, but with differing patterns. In fact, while the level of invasion increased slightly, with no significant differences over time in the *Cakile maritima* community, the number of aliens differed markedly in all other communities, at least between the two extremes of the time series.

As stated in several studies, the occurrence of many alien species has been found to be indicative of land-use change (Maskell et al. 2006) and most habitats ranked as highly invasible are usually associated with human disturbance or alteration of the typical disturbance regime (Alpert et al. 2000; Chytrý et al. 2008a). Several proxy variables are normally used to infer the impact of human disturbance, for example the proportional area of urban and/or agricultural land in the surrounding areas, the density of buildings, or the human population density (Carboni et al. 2010; Chytrý et al. 2008a). The lack of precise information on the geographic location of past phytosociological relevés prevented us from ascertaining the exact extent of past disturbance or its change over time. Nevertheless, the coastal ecosystems of the study area have undoubtedly suffered from escalating human pressure in the form of coast-bound tourism, which has become, in the twentieth Century, one of the main economic resources of the region. Mass tourism has been proved to widely affect vegetation, both directly and indirectly (Andersen 1995; Davenport and Davenport 2006; Rickard et al. 1994). Specifically, excessive visitor pressure and consequent trampling has been proved to damage dune morphology and lead to the degradation of vegetation, even if the impact varies in severity according to species' morphological characteristics and local habitat properties. Overall, tolerance to trampling, i.e. the ability of vegetation to withstand a cycle of disturbance and recover, seems primarily a function of stature, erectness, and growth form (Cole 1995; Sun and Liddle 1993). The most tolerant plants are annuals, caespitose graminoids, rosette hemicryptophytes, and geophytes, whereas the least tolerant plants are the chamaephytes. According to Cole (1995), tolerance is explained more by plant morphological traits than by site characteristics, even though relatively flat sites are less affected than sloped sites (Weaver and Dale 1978).

Referring to this last issue, tolerance to trampling could help explain the different temporal trend of the focal species in the four communities. Indeed, focal species of the first three types of coastal zonation are either annuals (*Cakile* community) or caespitose

Author's personal copy

graminoids and geophytes (*Elymus* and *Ammophila* communities), capable of both resisting trampling and recovering, as demonstrated by their steady frequencies.

Conversely, there was evidence of an substantial decrease of the focal species pool of semi-fixed dunes. Semi-fixed dunes occupy relatively flat sites on stable soils (Bini et al. 2002). In addition to herbaceous species, a dense carpet of mosses, lichens, and chamaephytic species forms a short prairie with high total cover (*Tortulo–Scabiosetum*). The flat topography and the presence of many chamaephytic species enhance resistance to mechanical disturbance such as trampling but, as characteristics that support the ability to resist trampling damage differ from those that allow plants to recover quickly (Cole 1995), once damaged, the woody stratum can regenerate only very slowly. Therefore, because of trampling, tolerant herbaceous species can replace sensitive dwarf shrubs. In fact, the most widespread aliens recorded in *Tortulo–Scabiosetum* are short annuals (i.e. *C. longispinus*), rosette hemicryptophytes (*O. stucchii*), and geophytes with below-ground perennating tissues (*A. psilostachya*), all growth forms resistant to trampling. With the alteration of natural disturbance or the introduction of new disturbances, resident species have become, thus, increasingly less adapted to the local environment whereas newcomers are better fitted and more competitive under the new conditions. With reference to this, alien species should then be regarded to as "passengers", not as "drivers" of ecosystem change, namely species which take advantage of altered disturbance regimes or other changes to which they are pre-adapted but that lead to declines in native biodiversity (Bauer 2012; MacDougall and Turkington 2005).

Our study confirmed that habitat properties are an important predictor of invasion levels. They can modulate the severity of impact which is related to the structural and functional complexity of the habitat of reference, suggesting that coastal communities function differently, even though they are spatially close. In habitats such as those of the upper beach or fore dunes, native species, and particularly those of the focal species pool, have morphological characteristics that enable them to withstand such disturbances as trampling, and then recover. Indeed, local habitat properties, for example the average number of species per plot and, to some extent, the proportion of focal species, did not substantially change along the time series. Conversely, semi-fixed dunes were profoundly modified. In *Tortulo–Scabiosetum*, native species, particularly dwarf shrubs, seem to have lost their competitive power because of high human pressure, leaving gaps for alien species. Thus, in both cases, alien species seem not to directly compete with native focal species but enter the communities by occupying unexploited gaps.

Accordingly, although different mechanisms may contribute to the invasion of different species, widespread anthropogenic environmental alterations, which create new suitable habitats, and human-assisted dispersal, are undoubtedly facilitating the spread of alien species in the study area.

An alarming aspect apparent from this study is a notable process of biotic homogenization. As stated, whereas some alien species are restricted to a particular habitat, others have spread both within and among communities, contributing to reducing the distinctiveness of plant communities. Homogenization is assumed to lead to simplification that reduces communities' resistance and resilience to environmental disturbance and can further increase the speed at which alien species spread (García-Ramos and Rodríguez 2002; Olden et al. 2004). In this regard, the severe loss of focal species and the structural simplification which occurred in *Tortulo–Scabiosetum* could hasten community degradation and lead to the crossing of irreversibility thresholds (Aronson et al. 1993).

Finally, a noteworthy perspective substantiated in this study is that changes may occur very slowly and gradually, taking many years to unfold, which points out the crucial

Author's personal copy

importance of temporal scale in detecting processes at a community level. As a consequence of the life-history traits of the resident species (Von Holle et al. 2003), plant communities in particular have been proved to have "biological inertia" (Gorham 1957), i.e., the capacity to continue to occupy a site well after environmental conditions become unfavourable. Resident plant community inertia can thus mask both deterioration in ecosystem conditions and unstable behaviour resulting from anthropogenic or environmental stressors. Indeed, the magnitude of the effect changed markedly over time in our study; in most cases, tangible changes in structural characteristics, for example species composition, became evident only as a result of examining the time series in its entirety. Therefore, although a direct approach is the ideal way to determine how invasion effects change temporally, time series, enabling the perception of long-term ecological processes, can truly provide an appealing alternative to long-term studies.

Invading species are not the only agent controlling the ecosystems they invade. Factors such as disturbance, geomorphology, hydrology, and weather (e.g. precipitation or temperature) are important because they interact strongly with both native and invading alien species. Accordingly, only a long-term perspective of the system enables the ultimate causes of species decline to be discerned and both short-term effects, immediately after invasion, and long-term ones, when the chronic phase has set in (Strayer et al. 2006), to be understood.

References

Acosta A, Carranza ML, Izzi CF (2007) Community types and alien species distribution in Italian coastal dunes. Neobiota 7:96–104

Acosta A, Carranza ML, Di Martino L, Frattaroli A, Izzi CF, Stanisci A (2008) Patterns of native and alien plant species occurrence on coastal dunes in Central Italy. In: Tokarska-Guzik B, Brock JH, Brundu G, Child L, Daehler CC, Pysek P (eds) Plant invasions: human perception, ecological impacts and management. Backhuys Publishers, Leiden, pp 235–248

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect Plant Ecol Evolut Syst 3:52–66

Andersen UV (1995) Resistance of Danish coastal vegetation types to human trampling. Biol Conserv 71:223–230

Arim M, Abades SR, Neill PE, Lima M, Marquet PA (2006) Spread dynamics of invasive species. Proc Natl Acad Sci USA 103:374–378

Aronson J, Floret C, Le Floc'h E, Ovalle C, Pontanier R (1993) Restoration and rehabilitation of degraded ecosystems in arid and semiarid regions. I. A view from the south. Restor Ecol 1:8–17

Baldoni G, Viggiani P, Bonetti A, Dinelli P, Catizone P (2000) Classification of Italian *Xanthium orientale* complex based on biological traits, electrophoretic analysis and response to maize interference. Weed Res 40:191–204

Banfi E, Galasso G (eds) (2010) La flora esotica lombarda. Regione Lombardia e Museo Storia Naturale di Milano, Milano

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81(2):169–193

Barrett SCH, Colautti RI, Eckert CG (2008) Plant reproductive systems and evolution during biological invasion. Mol Ecol 17:373–383

Bauer JT (2012) Invasive species: ''back-seat drivers'' of ecosystem change? Biol Invasions 14:1295–1304

Bezzi A, Fontolan G (2003) Foredunes classification and morphodynamic processes along the Veneto coasts (northern Adriatic, Italy). In: Ozhan E (ed) Proceedings of the 6th international conference on the mediterranean coastal environment, MEDCOAST'03, Ravenna, pp 1425–1434

Bini C, Buffa G, Gamper U, Sburlino G, Zilocchi L (2002) Soil and vegetation of coastal and wetland areas in Northern Adriatic (NE Italy). In: Zdruli P (ed) 7th IMSMTC. Options mediterraneennes, series A, vol 50, pp 31–36

Biondi E, Blasi C, Burrascano S, Casavecchia S, Copiz R, Del Vico E et al (2009) Italian interpretation manual of the 92/43/EEC directive habitats. MATTM. http://vnr.unipg.it/habitat/

Author's personal copy

Buffa G, Lasen C (2010) Atlas of natura 2000 sites in Veneto region. Regione del Veneto—Direzione Pianificazione Territoriale e Parchi, Venezia (in Italian)
Buffa G, Fantinato E, Pizzo L (2012) Effects of disturbance on sandy coastal ecosystems of N-Adriatic coasts (Italy). In: Lameed GA (ed) Biodiversity enrichment in a diverse world. InTech, Rijeka, pp 339–372
Callaway RM, Ridenour WM, Laboski T, Weir T, Vivanco JM (2005) Natural selection for resistance to the allelopathic effects of invasive plants. J Ecol 93:576–583
Campos JA, Herrera M, Biurrun I, Loidi J (2004) The role of alien plants in the natural coastal vegetation in central-northern Spain. Biodivers Conserv 13:2275–2293
Caniglia G (1978) Tracce di vegetazione spontanea in un settore del litorale del Cavallino (VE). Boll Mus Civ St Nat Venezia 29:169–192
Carboni M, Thuiller W, Izzi F, Acosta A (2010) Disentangling the relative effects of environmental versus human factors on the abundance of native and alien plant 1 species in Mediterranean sandy shores. Divers Distrib 16:537–546
Celesti-Grapow L, Alessandrini A, Arrigoni PV, Banfi E, Bernardo L, Bovio M et al (2009) Inventory of the non-native flora of Italy. Plant Biosyst 143:386–430
Celesti-Grapow L, Alessandrini A, Arrigoni PV, Assini S, Banfi E, Barni E et al (2010a) Non-native flora of Italy: species distribution and threats. Plant Biosyst 144:12–28
Celesti-Grapow L, Pretto F, Carli E, Blasi C (eds) (2010b) Flora vascolare alloctona e invasiva nelle regioni d'Italia. Università La Sapienza Ed, Roma
Chytrý M, Pyšek P, Tichý L, Knollová I, Danihelka J (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. Preslia 77:339–354
Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008a) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89(6):1541–1553
Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008b) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J Appl Ecol 45:448–458
Cole DN (1995) Experimental trampling of vegetation. II. Predictors of resistance and resilience. J Appl Ecol 32:215–224
Comin S, Ganis P, Poldini L, Vidali M (2011) A diachronic approach to assess alien plant invasion: the case study of Friuli Venezia Giulia (NE Italy). Plant Biosyst 145:50–59
Conti F, Abbate G, Alessandrini A, Blasi C (eds) (2005) An annotated checklist of the Italian vascular flora. Palombi Editori, Roma
Damgaard C, Nygaard B, Ejrnæs R, Kollmann J (2011) State-space modeling indicates rapid invasion of an alien shrub in coastal dunes. J Coastal Res 27(3):595–599
Davenport J, Davenport JL (2006) The impact of tourism and personal leisure transport on coastal environments: a review. Estuar Coast Shelf Sci 67:280–292
Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534
Dietrich W, Wagner WL, Raven PH (1997) Systematics of *Oenothera* section *Oenothera* subsection *Oenothera* (Onagraceae). Syst Bot Monogr 50:1–234
Dugan JE, Hubbard DM (2010) Loss of coastal strand habitat in southern California: the role of beach grooming. Estuar Coasts 33:67–77
Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London
European Commission DG Environment (2008) Article 17 Technical Report 2001–2006 (http://biodiversity.eionet.europa.eu/article17). European Topic Centre on Biological Diversity
Foster BL, Tilman D (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecol 146:1–10
Frean M, Balkwill K, Gold (née Anderson) C, Burt S (1997) The expanding distributions and invasiveness of *Oenothera* in southern Africa. South Afr J Bot 63:449–458
Fuentes N, Ugarte E, Kühn I, Klotz S (2008) Alien plants in Chile: inferring invasion periods from herbarium records. Biol Invasions 10(5):649–657
Gaertner M, Den Bree A, Hui C, Richardson DM (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Prog Phys Geogr 33:319–338
García-Ramos G, Rodríguez D (2002) Evolutionary speed of species invasions. Evolution 56:661–668
Gèhu J-M, Scoppola A, Caniglia G, Marchiori S, Gèhu-Franck J (1984) Les systèmes végétaux de la côte nord-adriatique italienne. Leur originalité à l'échelle européenne. Doc Phytosoc n.s. 8: 486–558
Gorham E (1957) Development of peatlands. Quart Rev Biol 32:145–166
Haveman R, Janssen JAM (2008) The analysis of long-term changes in plant communities using large databases: the effect of stratified resampling. J Veg Sci 19(3):355–362

Author's personal copy

Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638
Lambrinos JG (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. Ecology 85:2061–2070
Lee CE (2002) Evolutionary genetics of invasive species. Trends Ecol Evol 17:386–391
Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989
Lloret F, Médail F, Brundu G, Camarda I, Moragues E, Rita J, Lambdon P, Hulme PE (2005) Species attributes and invasion success by alien plants on Mediterranean islands. J Ecol 93:512–520
MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55
Magurran AE (1988) Ecological diversity and its measurement. Croom Helm, London
Maniero F (2000) Fitocronologia d'Italia. LS Olschki, Firenze
Maskell LC, Bullock JM, Smart SM, Thompson K, Hulme PE (2006) The distribution and habitat associations of non-native plant species in urban riparian habitats. J Veg Sci 17:499–508
McLachlan A, Brown AC (2006) The ecology of sandy shores. Academic Press, Burlington
Mihulka S, Pyšek P (2001) Invasion history of *Oenothera* congeners in Europe: a comparative study of spreading rates in the last 200 years. J Biogeogr 28(5):597–609
Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington
Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA et al (2006) Biotic interactions and plant invasions. Ecol Lett 9:726–740
Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. Proc Nat Acad Sci USA 98:5446–5451
Nordstrom KF, Gamper U, Fontolan G, Bezzi A, Jackson NL (2009) Characteristics of coastal dune topography and vegetation in environments recently modified using beach fill and vegetation plantings, Veneto, Italy. Environ Manage 44:1121–1135
Olden JD, LeRoy Poff N, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. Trends Ecol Evol 19(1):18–24
Pickett STA (1989) Space for time substitution as an alternative to long-term studies. In: Likens GE (ed) Long-term studies in ecology. Wiley, Chichester, pp 71–88
Pignatti S (1959) Ricerche sull'ecologia e sul popolamento delle dune del litorale di Venezia. Il popolamento vegetale. Boll Mus Civ Venezia 12:61–142
Pignatti S (1982) Flora d'Italia. Edagricole, Bologna
Pignatti S (2009) Com'è triste Venezia, soltanto mezzo secolo dopo. Parchi 58:59–70
Piva E, Scortegagna S (1993) Flora e Vegetazione del Delta del Po. Regione Veneto, Tip. Arti Grafiche Padovane, Padova, Le zone litoranee
Poldini L, Vidali M, Fabiani ML (1999) La vegetazione del litorale sedimentario del Friuli-Venezia Giulia (NE Italia) con riferimenti alla regione alto-Adriatica. Stud Geobot 17:3–68
Poldini L, Oriolo G, Vidali M (2001) Vascular flora of Friuli Venezia Giulia: an annotated catalogue and synonimic index. Stud Geobot 21:3–227
Prieto JAF, Cires E, Corominas TS, Vázquez VM (2011) Systematics and management of natural resources: the case of *Spartina* species on European shores. Biologia 66(6):1011–1018
Prisco I, Acosta ATR, Ercole S (2012) An overview of the Italian coastal dune EU habitats. Ann Bot 2:39–48
Pyšek P, Hulme PE (2005) Spatio-temporal dynamics of plant invasions: linking pattern to process. Ecoscience 12(3):302–315
Pyšek P, Jarošík V, Kučera T (2002) Patterns of invasion in temperate nature reserves. Biol Conserv 104:13–24
Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirshner J (2004) Alien plants in checklist and floras: towards better communication between taxonomists and ecologists. Taxon 53:131–143
Pyšek P, Chytrý M, Jarošík V (2010) Habitats and land use as determinants of plant invasions. In: Perrings C, Mooney H, Williamson M (eds) Bioinvasions and globalization. Ecology, economics, management, and policy. Oxford University Press, Oxford, pp 66–79
Rejmánek M, Richardson DM, Pyšek P (2005) Plant invasions and invasibility of plant communities. In: van der Maarel E (ed) Vegetation ecology. Blackwell, Maiden, pp 332–355
Rickard CA, McLachlan A, Kerley GIH (1994) The effects of vehicular and pedestrian traffic on dune vegetation in South Africa. Ocean Coast Manag 23:225–247
Ruchinger G (1818) Flora dei lidi Veneti. Gio. Giacomo Fuchs, Venezia

Author's personal copy

Santoro R, Jucker T, Carboni M, Acosta ATR (2012) Patterns of plant community assembly in invaded and non-invaded communities along a natural environmental gradient. J Veg Sci 23:483–494

Sburlino G, Buffa G, Filesi L, Gamper U (2008) Phytocoenotic originality of the N-Adriatic coastal sand dunes (Northern Italy) in the European context: the *Stipa veneta*-rich communities. Plant Biosystems 142:533–539

Sburlino G, Buffa G, Filesi L, Gamper U, Ghirelli L (2013) Phytocoenotic diversity of the N-Adriatic coastal sand dunes—the herbaceous communities of the fixed dunes and the vegetation of the interdunal wetlands. Plant Sociol 50(2):57–77

Schlacher TA, Dugan J, Schoeman DS, Lastra M, Jones A, Scapini F, McLachlan A, Defeo O (2007) Sandy beaches at the brink. Divers Distrib 13:556–560

Soldano A (1993) Il genere *Oenothera* L., subsect. *Oenothera*, in Italia (Onagraceae). Nat Brescia 28:85–116

Stanisci A, Acosta ATR, Di Iorio A, Vergalito M (2010) Leaf and root trait variability of alien and native species along Adriatic coastal dunes (Italy). Plant Biosyst 144(1):47–52

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends Ecol Evol 21(11):645–651

Strother JL (2006) *Xanthium*. In: Flora of North America Editorial Committee (eds) Flora of North America. Oxford University Press, Oxford, pp 19–20

Suarez AV, Tsutsui ND (2008) The evolutionary consequences of biological invasions. Mol Ecol 17:351–360

Sun D, Liddle MJ (1993) Plant morphological characteristics and resistance to simulated trampling. Environ Manag 17:511–522

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474

van der Maarel E (2003) Some remarks on the functions of European coastal ecosystems. Phytocoenologia 33:187–202

Van der Meulen F, Udo de Haes HA (1996) Nature conservation and integrated coastal zone management in Europe: present and future. Landsc Urban Plan 34:401–410

Vignolo-Lutati F (1935) Il genere *Ambrosia* in Italia (con tav. X-XII). Nuovo Giornale Botanico Italiano n.s. 42(2):364–378

Vilà M, Pino J, Font X (2007) Regional assessment of plant invasions across different habitat types. J Veg Sci 18:35–42

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13

Von Holle B, Delcourt HR, Simberloff D (2003) The importance of biological inertia in plant 650 community resistance to invasion. J Veg Sci 14:425–432

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. J Ecol 98:725–736

Weaver T, Dale D (1978) Trampling effects of hikers, motorcycles and horses in meadows and forests. J Appl Ecol 15:451–457

Westhoff V, van der Maarel E (1978) The Braun–Blanquet approach. In: Whittaker RH (ed) Classification of plant communities. Junk, The Hague, pp 287–399

Whitney KD, Gabler CA (2008) Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. Divers Distrib 14:569–580