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**Spatial patterns and drivers of three
invasive alien plant species on coastal
dunes of the North Adriatic coast**

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Abstract

Invasion of alien species is considered one of the most important causes of biodiversity loss. Alien species are often unintentionally transported by human towards new habitats, where they establish and reproduce, adapting to local environmental conditions. This study aimed at analyzing factors that influence the spatial distribution of *Oenothera stucchii*, *Ambrosia psilostachya* and *Erigeron canadensis*, three invasive alien plant species in coastal dune ecosystems of the North Adriatic coast. We placed nine linear transects, parallel to the coast line and perpendicular to beach accesses, collecting data on plant species presence and abundance in correspondence with the vegetation belt of xerophilous grasslands of semi-fixed dunes. We took into account biotic factors (coverage of native species), abiotic factors (site geomorphology, i.e. the height of foredunes, the height above sea level) and anthropogenic factors (distance from beach accesses). Results of a zero-inflated Poisson regression model showed that spatial patterns of target species are influenced by, depending on the species, the height of foredunes, the height above sea level, the distance from the paths and the coverage of some specific growth forms of native species. We suggest improving protection and management of coastal dune communities by reinforcing anti-trampling barriers or fencing coastal communities, and promoting restoration of coastal dunes.

1. INTRODUCTION

The presence of an alien plant species in a given area can be the result of two processes: deliberate or unintentional human-driven introduction (Vitousek et al. 1997), or natural spread towards an area where they are non-native (Galasso et al. 2018).

The introduction of invasive alien species (hereafter also IAS) into natural environments is one of the most dangerous components of global environmental change (Vitousek et al. 1997; Jiang et al. 2011).

“Biological invasion” is a term used to identify the human-driven process of transport, dispersal, and spread of alien species from their natural areas to new habitats where they establish, survive and reproduce (Richardson et al. 2012). The invasion process is made of three fundamental stages representing a continuum (Jiang et al. 2011): it starts from the ‘introduction’ stage; then, when the introduced species are able to produce fertile offspring for several life cycles they reach the ‘naturalization’ phase; lastly, a species reaches the ‘invasion’ stage if, after naturalization, it overcomes environmental barriers and becomes able to produce fertile offspring, reproduce, and spread at large distances into new habitats. Reaching the last stage of invasion depends on the capability of a plant species of overcoming human, ecological and abiotic barriers (i.e., species invasiveness), resistance of native species to competition, climate conditions and resistance of introduced species to human pressure (i.e., habitat invasibility; Richardson et al. 2012).

During last decades, the phenomenon of plant invasion has become of primary importance in many countries (Defeo et al. 2008), mostly in urbanized and disturbed areas (Vitousek et al. 1997; Fuselier et al. 2017), where the human presence has so far favored the spread of alien species.

In their studies, Kühn et al. (2003) and Stohlgren et al. (2005) have demonstrated that alien species are more commonly invasive in landscapes rich of native species than landscapes poor of them (Chytrý et al. 2008). At a smaller scale, Dimitrakopoulos et al. (2017) obtained comparable results, suggesting that habitat heterogeneity influences the abundance of alien species, leading to a positive relationship between native and alien species’ richness. Moreover, Thomas et al. (2018) suggested that invasion is facilitated by previous invaders that create a fitting environment, exploitable for new invaders; nevertheless, not all habitat types show the same susceptibility to invasion events (Chytrý et al. 2008; Celesti-Grapow et al. 2016). Habitat invasibility is related to several environmental conditions, nutrients

availability and anthropogenic activities (Paudel and Battaglia 2015). Gaps in native species cover increases alien species colonization and establishment (Mavimbela et al. 2018). IAS often establish better in habitat edges, where environmental parameters differ from those at the core of the habitat. Indeed, at the edge of habitat the major human presence generally makes environmental conditions adverse for indigenous and specialist species while creating suitable conditions for alien and generalist species (Mavimbela et al. 2018).

Indeed, IAS can generally spread because they show phenotypic plasticity, high adaptability to environmental changeable conditions and they produce large amounts of long-living seeds (Vicente et al. 2019). Furthermore, alien species often show life history traits (e.g. the growth form) that permit them to have an optimal performance under human disturbance (Castro-Díez et al. 2016; Silan et al. 2017).

Given their ecological characteristics, alien species can be found in many situations, in which they can perform better than native species due to particular combinations of biotic (i.e., native species richness/cover), abiotic (i.e., climate, topography, landscape heterogeneity) and anthropogenic (i.e., human population density, roads network, habitat fragmentation) conditions (Dyderski and Jagodziński 2016; Stešević et al. 2017). IAS can substitute native species, compete with them by subtracting vital space, nutrients from the soil or light, ultimately modifying community composition and diversity (Castro-Díez et al. 2016; Lee et al. 2018). Invasive alien species cause several irreversible ecological impacts on ecosystems (Dyderski and Jagodziński 2016; Stešević et al. 2017) and they are considered among direct drivers of biodiversity loss (Convention on Biological Diversity 1992). Alien species may affect nutrients cycle and productivity of ecosystems and damage, as a consequence, ecosystems services and human well-being (Vilà et al. 2011; Fuselier et al. 2017).

This fact is especially evident in habitats of coastal sand dune ecosystems (Thomas et al. 2018) which are subjected to intense human pressure and disturbances (Buffa et al. 2012; Thomas et al. 2018) and have been recognized among the most vulnerable habitats of the world to biological invasion (Chytrý et al. 2008; Jørgensen and Kollman 2009; Santoro et al. 2012; Paudel and Battaglia 2015). The main causes of alien plant invasion in these environments are tourism and recreational activities, urban “sprawl”, agriculture intensification and transports industry (Vitousek et al. 1997; Defeo et al. 2008).

As urbanization and human activities increase, introduced species can rapidly modify and strongly influence the relative abundance of native species and the balance between native and alien species (O’Shea and Kirkpatrick 2000; Wang and Xu 2016).

Highly urbanized coastal areas are sources of invasive species propagation to surrounding zones (Lechuga-Lago et al. 2017).

Humans are a dynamic dispersal vector for invasive species and they facilitate their transportation, extending the invasion area (Campos et al. 2004; Maun 2009; Dimitrakopoulos et al. 2017). Roadside verges, usually rich of non-native species, are known to be potential drivers of dispersion of individuals and seeds by vehicles, bikes, and walkers (Gelbard and Belnap 2003). In other words, roadsides (or tracks, avenues, paths) are migration corridors for alien colonization (von der Lippe and Kowarik 2006). In a 2003 study, Gelbard and Belnap showed that roadside verges areas are richer in alien species than inland habitats.

Tourism is the main factor of disturbance and coastal habitats degradation (Buffa et al. 2007). This is because it mostly increases trampling pressure on sand dunes, altering pedogenetic processes (like intensification of soil compaction, that becomes a limit for sand transportation and dunes development) and communities' composition; habitat modifications can, in turn, imply alterations of species distribution (Del Vecchio et al. 2014; Silan et al. 2017). Human trampling enhances habitat fragmentation and increases non-vegetated areas by creating paths and tracks that help alien species to establish (Buffa et al. 2007; Del Vecchio et al. 2014; Silan et al. 2017). To reach the seashore, tourists walk on sand dunes and they forge "braiding" of tracks reducing dune vegetation cover. Sandy soils show low resistance to penetration and they are more susceptible to trampling than other types of soil (Davenport and Davenport 2006). Secondly, tourism on coasts feeds a large industry that disrupts dunes and their habitats to make room for ever-larger bathing beaches and to maintain them "clear" by sand removing and smoothing works.

Dune ecosystems provide several ecological services of fundamental importance for coastal society such as erosion control, storms and sea-level rise buffering, biological linkage between marine and terrestrial environments and habitats for a wide variety of organisms (Buffa et al. 2012; Barbier et al. 2008; Defeo et al. 2009; Schlacher et al. 2008).

Despite their ecological interest, at present, very few studies concerning the small-scale distribution of alien species in these areas have been carried out, especially along the Mediterranean coast (Carboni et al. 2010). Moreover, little is known about the magnitude of human activities on alien species distribution, when compared with natural factors (Gelbard and Belnap 2003).

This study aims at identifying the local drivers and patterns of distribution of three alien species along the North Adriatic coast.

The increasing tourist presence along the North Adriatic coast since the second half of the last century, has led alien species' cover and frequency to increase at the expense of natives (ISPRA 2008). Native coastal vegetation is very sensitive and vulnerable to introduced species and human impacts (Del Vecchio et al. 2014; O'Shea and Kirkpatrick 2000).

Specifically, we studied whether there are some ecological relationships between natural and human factors and invasive plants distribution considering a global-scale phenomenon, but using a local scale approach.

In addition to data on vegetation, we have also taken into account physical and anthropogenic parameters such as the height of foredune, distance from the sea and from the paths, all related to species coverage. It is not clear which parameter best describes species distribution (Fois et al. 2018).

Our testing hypothesis is that IAS abundance is expected to be denser near the path sides, decreasing towards hinterland (Gelbard and Belnap 2003; Sharma and Raghubanshi 2009).

2. MATERIALS AND METHODS

2.1 Study area

We collected data in three different sites across the North Adriatic coast (Fig. 1), which is the most urbanized coastal site of the Mediterranean Sea (WWF 2014).



Fig. 1. Study area with three yellow rectangles indicating the three sampling sites (Google Maps).

The North Adriatic coast was originally characterized by an almost uninterrupted line of sand dunes and seashores; however, after the '50s more and more dunes were destroyed or modified (Bondesan et al. 2008; ISPRA 2008). Specifically, foredunes are especially important for coastal protection and the most vulnerable to human disturbance because they are the nearest dunes to the beach, where tourist presence reaches its maximum (Fontolan et al. 2013). As a consequence, touristic activities have lowered dune ridges, creating gaps, paths and other negative modifications for dunes' morphology. One of the first direct effects of sand dunes disruption is the loss of plant communities' structure and biodiversity (Schlacher et al. 2008), and the increasing presence of alien species.

The study area is characterized by a temperate steppe-oceanic climate different to that of the other Mediterranean coastal areas which have a Mediterranean climate (Rivas-Martinez 2004). The North Adriatic coast is located into the continental Eurosiberian biogeographic region (Rivas-Martinez 2004) and featured by windy hot summers (30-35°C commonly reached between June and August) and cold winters, with an average of 800 mm of annual rainfall (Hidore 1993).

The Adriatic Sea is a depositional basin, part of the bigger Mediterranean basin. It presents Quaternary origins, influenced by some rivers that flow into it and transport sediment from Alps and Apennines (Fontana et al. 2008). The three sites of the study case receive sediments by rivers Piave, Sile, Livenza and Tagliamento and they are sandy-silty beaches with terrigenous (about 75%) and low-calcareous soils. They are composed of dolomitic calcium carbonates deposited together with calcite, quartz, feldspars, granite, and apatite of marine origin (Emelyanov and Shimkus 1986; Fontana et al. 2008).

Along the Adriatic Sea, coastal sand dunes occur only in the north-western coasts. There are ancient dunes (Pleistocene), now covered by forests, villages or cultivated lands, and few recent dunes (Holocene) where it is still possible to see the typical morphology of sand dunes and the vegetation zonation and distribution strictly related to the environmental disturbance gradient (Muñoz-Vallès and Cambrollè 2015).

Coastal dunes are transitional ecosystems with crucial ecological functions, diversity, and importance (Muñoz-Vallès and Cambrollè 2015). Coastal dunes are shaped by an environmental gradient from the seashore inlands. Environmental conditions such as salt spray, wind intensity, and other abiotic parameters change, diminishing from the seashore inlands, while sediment humidity and nutrients availability increase (Della Croce et al. 1997). This ecological gradient generates a precise sequence of plant communities, the so-called “coastal zonation” (Doing 1985).

Along the North Adriatic coast, looking at one perpendicular-to-coast section of the area, the first geomorphological element present near the coastline is represented by embryonic dunes. This is a belt of low dunes built on pioneer nitrophilous, psammophilous species (such as *Cakile maritima*) that is subjected to the worst environmental conditions: high salt spray and wind disturbance, low humidity, low nutrients availability and low substrate cohesion (Buffa and Lasen 2010). Proceeding towards inland white dunes (or mobile dunes) can be found, high and dynamic ridges of sand with the plant community of the dune builders such as *Elymus farctus* and *Ammophila arenaria* (Fantinato et al. 2018). Specifically, the epigeal part of *A. arenaria* traps major quantity of sand particles transported by wind and it grows up covered by sand, developing a huge hypogeal rhizomes system and forming the so-called “foredunes” (Bird 2008; Del Vecchio et al. 2014; 2016).

After mobile dunes, on which the whole coastal system ecologically and morphologically depends, there are lower grey dunes (or transition dunes, or semi-fixed dunes) with

sometimes interdunal wetlands. They are characterized by partially or totally stabilized sandy or sandy-gravelly sediment. Habitats of grey dunes are protected from wind and salty aerosols by higher foredunes. Accordingly, these areas show a higher edaphic (underlined by the presence of bryophytes) and higher organic matter content (Maun 2009; Della Croce et al. 1997). As a consequence, species diversity increases forming wide xerophilous grasslands with mosses, lichens, grass, and dwarf shrubs (Del Vecchio et al. 2016).

On grey dunes, a mosaic of more structured herbaceous communities develops, with some endemic associations such as the perennial *Tortulo-Scabiosetum* Pignatti 1952 dominated by a carpet of mosses (i.e., *Syntrichia ruraliformis*), sometimes lichens (*Cladonia* sp. pl.) and phanerogams (i.e., *Lomelosia argentea*, *Fumana procumbens*, *Sanguisorba minor*), and the annual community of *Silene conica* and *Cerastium semidecandrum* ('Habitat' Directive 2013; Sburlino et al. 2013).

At the end of the coastal zonation, fixed stabilized dunes can be observed, where sediment has almost real soil properties and wind disturbance is negligible. Xerophilous plant communities of the fixed dunes are more complex, with natural or artificial pine forests, and shrubs (i.e., *Erica carnea*; Sburlino et al. 2013; Fantinato et al. 2018).

Sampling sites were located in Vallevicchia (municipality of Caorle, VE), Laguna del Mort (municipality of Eraclea, VE) and Ca' Savio (municipality of Cavallino-Treporti, VE). They belong to the Natura 2000 Network. Sampling sites have also been included in the European LIFE *Redune* Project (LIFE16 NAT/IT/000589).

These locations, where semi-natural dune systems are still present, have different geomorphological origins, conservational statuses, and touristic pressure, but all have been invaded by alien species.

Ca' Savio (VE). It is situated in the peninsula of Cavallino. It is a 15 km long peninsula in NE of Venice lagoon between Punta Sabbioni and the mouth of river Sile.

The Cavallino peninsula is a popular touristic destination in summer and dune habitats are constantly pressured by human presence (Fig. 3). In Ca' Savio, the complete coastal dune vegetation zonation of the North Adriatic coast can be observed (Fig. 2), starting from the annual vegetation of the drift line to the pine wood of the fixed dunes.



Fig. 2. Transitional dunes, Ca' Savio, VE.

(Ph. Piccoli Stefano)



Fig. 3. Path used by tourists to reach the

seashore, Ca' Savio, VE. (Ph. Piccoli Stefano)

Laguna del Mort (VE). This is a narrow strip of land that encloses a small lagoon, located at east of the estuary of Piave River. It hosts a pine forest (Fig. 4) and a relict dune system in which the landscape is almost completely natural, showing a wide biodiversity of habitats and animals, especially sea birds. The site is characterized by the presence of mobile dunes, a wide area of grey dunes with endemic plant communities and endemic species, and stabilized dunes (Bondesan et al. 2008). Though, man has created some paths to reach the sandy beach altering habitats and has constructed a seawall and groins defense system for beach management.



Fig. 4. Pine forest of fixed dunes in Laguna de Mort, VE (Ph. Piccoli Stefano).

Vallevecchia (VE). This is a recently reclaimed coastal area 5 km long, which is located between the mouths of Livenza and Tagliamento rivers. Vallevecchia is an almost natural place, but dune habitats, beach, and short interdunal lowlands have been threatened by agriculture, tourism, and alien species after restoration works. The coastal zone is featured by

a broad stabilized backdune system with an artificial pine forest, where it is sometimes possible to sight wild roes (Bondesan et al. 2008). Towards the sea, there is a psammophilous gradient of plant communities (Buffa and Lasen 2010; Fig. 5).

This strip of land is the longest free beach of Veneto Region, with high tourist pressure in summer. The area is entirely controlled by “Veneto Agricoltura” regional agency for natural management.



Fig. 5. Coastal gradient of plant communities in Vallev ecchia, VE. (Ph. Piccoli Stefano)

2.2 Target species

We focused on three different alien species that are commonly present on Venetian coasts: *Oenothera stucchii*, *Ambrosia psilostachya* and *Erigeron canadensis*.

***Oenothera stucchii* Soldano**

It is an invasive non-native species of northern Italy. This species is a hybrid between two naturalized populations of *Oenothera biennis* L. and *Oenothera jamesii* (Gates 1958; Dietrich et al. 1997). *O. biennis* and *O. jamesii* are two North American species of Onagraceae family introduced as ornamental flowers into Europe in the 17th century (Gates 1958). *O. stucchii* species occurs mostly in the Italian regions of Friuli-Venezia-Giulia, Veneto, Liguria, Piedmont, Lombardy, Tuscany, Molise and Emilia-Romagna (Fig. 6) but it occurs also in some southern coasts of France (Soldano 1993); it prefers roadsides, fallow fields, rivers and riparian zones (Dietrich et al. 1997).

O. stucchii is a biennial hemicryptophyte (Fig. 7) with a 200-300 cm stem tall. During the first year, the plant forms a basal rosette of leaves (15-25 cm long, 2-4 cm wide; Fig. 8) and a deep taproot; thanks to its growth form, *O. stucchii* is very tolerant to human trampling. In the second (or sometimes third) year, a stem elevates with cauline leaves and flowering begins during the second half of July till the first decade of October (Soldano 1993). The stem is green or flushed with red, usually branched obliquely with petiolate cauline leaves 6-15 cm long and 2-3 cm wide. Green leaves are oblanceolate with dentate margins; they have white-pale green veins. The floral tube is the longest among the species of *Oenothera* genus (Soldano 1993): it can reach 7,5 cm long. Sepals are yellow-green (1,7-2,5 cm long, 4-5 mm wide); after flowering they typically bend downwards. Five yellow petals are 2-3,5 cm long and 2-3,4 cm wide (Fig. 7). Pollination is primarily autogamous; 2-3,5 cm capsules contain brown seeds 1-1,8 mm long and they are spread by wind. *Oenothera* spp. prefer wide habitats with light and sandy-gravelly disturbed soils with human presence (Puentes and Johnson 2016; Stešević et al. 2017).

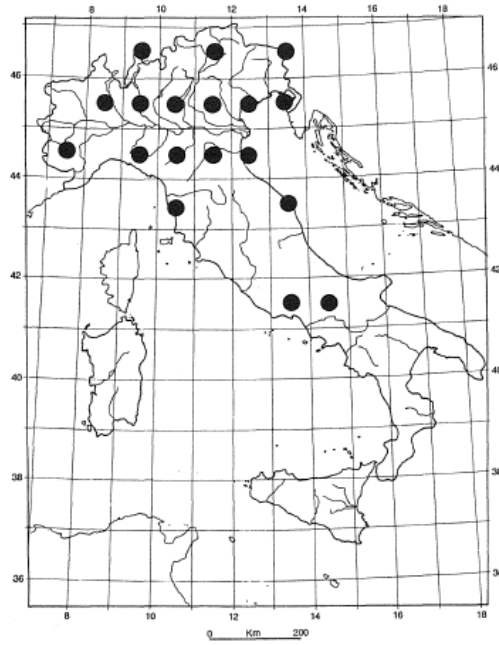


Fig. 6. Geographical distribution of *Oenothera stucchii* (Soldano 1993).



Fig. 7. Inflorescence of *Oenothera stucchii*
(Ph. Piccoli Stefano)



Fig. 8. Basal rosette of *Oenothera stucchii*
(Ph. Piccoli Stefano)

***Ambrosia psilostachya* DC**

It is a perennial herbaceous species of Asteraceae family, with North American origins (Fig. 9), but it is widespread in Europe (seen for the first time in Italy in 1927) and other continents (Montagnani et al. 2017). It has reached Europe unintentionally by cereal seeds transportation from Canada to Russia; *A. psilostachya* occurs along transportation corridors, dunes, croplands, semi-natural grasslands and generally disturbed open habitats with a low density of plants and a high level of human impact (Montagnani et al. 2017).

It is a rhizomatous geophyte, with a vigorous and horizontal underground rhizomes system (Bassett 1975; Montagnani 2017). It spreads by seeds (anemophilous pollination) or mostly by rhizomes (vegetative reproduction; Fig. 11); generally, only a few seeds developed per plant, so rootstocks are the common way of reproduction. A single vegetative clone can cover a 2 m² area (Bassett and Crompton 1975). Erect slightly branched stems reach 90-105 cm; leaves (green to grayish-green) are pinnatifid with dentate margins and short hairs, subsessile and sometimes petiolate with a winged petiole. It is a monoic species (Fig. 10), with male and female flowers in different parts of the same plant: male flowers (till 40 per head/cluster) with 5 petals are arranged in little hairy spikes on the top of stems or on branches terminals; female flowers (single or clustered) are located in the upper axils (Bassett and Crompton 1975). Achenes with only one brown seed 3-6 mm long and 3,5 mm wide, without pappus.

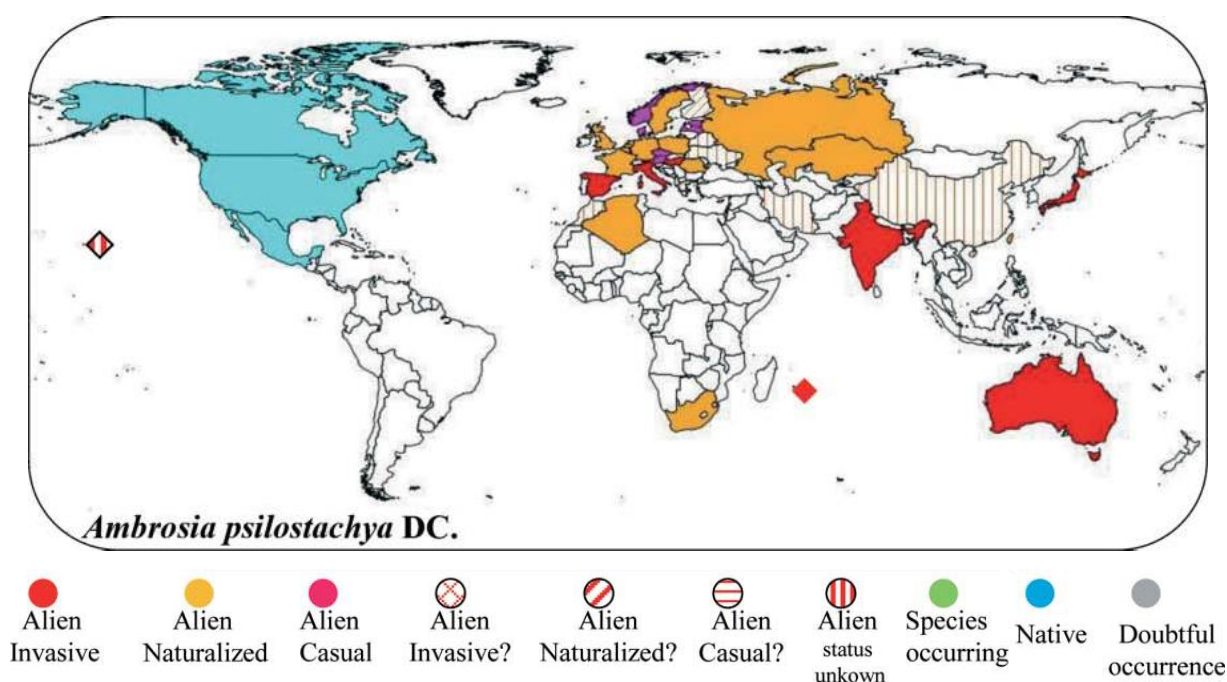


Fig. 9. Geographical distribution of *Ambrosia psilostachya* (Montagnani et al. 2017).



Fig. 10. Erect stem of *Ambrosia psilostachya* (Acta Plantarum).



Fig. 11. Underground rhizome of *Ambrosia psilostachya* (Bassett and Crompton 1975).

***Erigeron canadensis* L**

This species of Asteraceae family is native of North America, but it is a cosmopolitan weed (Fig. 14), widespread especially in southern Europe (Weaver 2001), in which it is an invasive species. The first reports of the presence of this species in Europe date back to 17th century (Michael 1977). It lives in all Italian regions. This species can be commonly observed in abandoned yields, railways and other habitats disturbed by human activities (Weaver 2001). *E. canadensis* is an annual erect leafy therophyte with a taproot and a branched erect stem 10-180 cm high (Weaver 2001) that develops after a starter basal rosette of leaves (30-100 mm long, 10-12 mm wide). The stem is characterized by dark green leaves (30 mm long, 2-5 mm wide) and short hairs all stem long. Flowering heads (Fig. 12), named “capitula” (the typically Asteraceae inflorescence), are composed of a lot of central yellow florets and white ray florets; entomophilous pollination. Every capitulum can develop 60-70 seeds 1-2 mm long with a 3-5 mm pappus (Fig. 13); they spread by wind (Weaver 2001).



Fig. 12. Erect stem of *Erigeron canadensis* with flowering heads (SEINet)

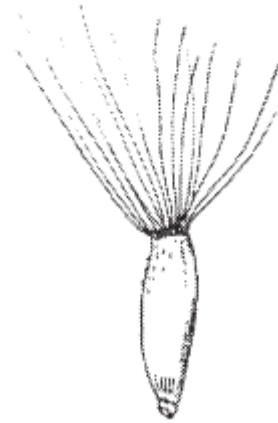


Fig. 13. Seed with attached pappus (Weaver 2001).

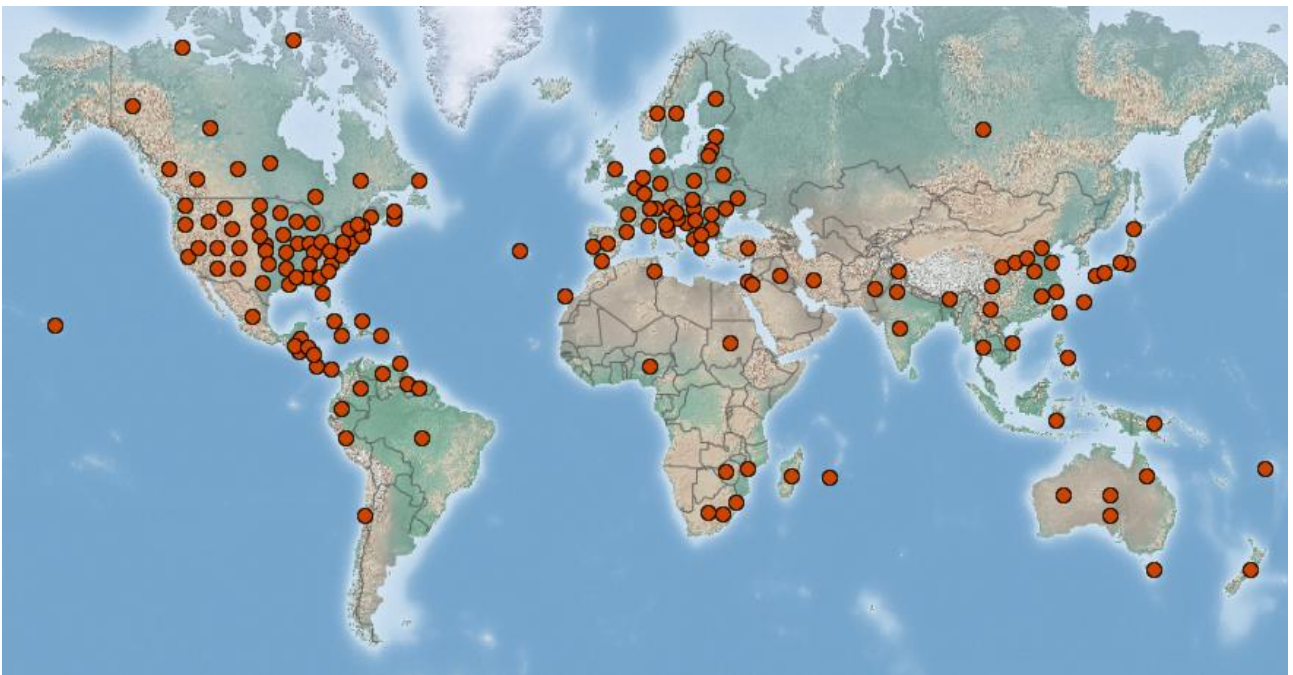


Fig. 14. Geographical distribution of *Erigeron canadensis* (CABI www.cabi.org).

2.3 Data collection

Data were collected in the xerophilous grasslands of semi-fixed dunes in 3 different sites. This particular mosaic of communities (with endemic associations mentioned above) is threatened by human and natural causes and it plays an important functional-ecological role in its ecosystem. Generally, it is spread along the Atlantic and Baltic coasts, with some exceptions like the Black Sea and N-Adriatic Sea. In Italy, it is distributed only among Emilia-Romagna, Veneto and Friuli-Venezia-Giulia regions ('Habitats Directive' 2013; Sburlino et al. 2013; Silan et al. 2017).

Unfortunately, these peculiar communities are disappearing from the North Adriatic coasts, because human trampling disrupts mosses cover and alien plants replace them making this community more vulnerable. These threats are the major causes of the fragmentation of transition dunes, the most invaded habitats by alien species (Carboni et al. 2010; Buffa et al. 2012).

Data collection took place during late spring and early summer 2018, during the period of maximum vegetative growth of target species.

To test our hypothesis that IAS abundance decreases with increasing distance from the paths, we laid 9 linear, perpendicular-to-paths, transects of different lengths by using standard size square plots (1m² area, Fig. 15), laid adjacently in order to use a systematic method of sampling (Del Vecchio et al. 2018).



Fig. 15. Quadrat of 1m² area used to create linear transects (Ph. Piccoli Stefano).

Transects were distributed following a stratified random design within invaded areas and laid in three sites: 5 transects in Ca' Savio, 3 in Vallevicchia and 1 in Laguna del Mort.

For every 1m² georeferenced quadrat, we measured the following biotic parameters: total plant cover, total moss layer cover, total phanerogamic layer cover and mean height. Abiotic parameters measured were the distance from the sea, distance from the nearest path, height above sea level, aspect, slope, and the correspondent height of foredune.

The height of foredunes could be a sign of human pressure because it is indirectly related to the trampling of sand dunes: if there is a large utilization of the beach by tourists, trampling increases and the morphological structure of dunes pulls down. The distance from the beach access is directly related to trampling on sand dunes out of the paths. The height above sea level indicates the gap between the dunes and the underground aquifer and, from an ecologically point of view, the distance from the deep water and nutrients reachable by plant roots.

Moreover, for each plot we counted the number of individuals belonging to the three target species, and we estimated their percentage cover within the sampling quadrat. For each native species recorded we estimated only their percentage cover and we attributed its own growth form. Growth forms reveal the space occupation strategy of plant species (Cornelissen et al. 2003), therefore they deeply influence plant community organization and functioning (Del Vecchio et al. 2016). Following Cornelissen et al. (2003), plant species were assigned the following growth forms: creeping (reptant herbaceous species with a prostrate form), dwarf shrub (semi-woody plants up to 0.8m), erect leafy (plant essentially erect, leaves concentrated in middle and/or top parts), short basal (leaves < 0.5m long concentrated very close to the soil surface, e.g. rosette plants), and tussock (many leaves from basal meristem forming prominent tufts) growth.

We collected abiotic parameters, by using GPS instruments (Garmin XXX). Specifically, we quantified distances from paths and sea, aspect and slope, and elevation of foredunes.

2.4 Data analysis

Since target species showed more zero counts than those expected from the Gaussian distribution, fitting a generalized model would have led to a bias in the predictions. To deal with this distribution, we opted for a zero-inflated Poisson (ZIP) model (Lambert 1992). Zero-inflated models predict the probability that an event occurs through a binomial process and,

conditional to event occurrence, the model predicts the event's abundance through a count process. The parameters involved in the binomial and Poisson processes are estimated simultaneously. These parameters are π (probability of having a zero count in a given plot) and λ (expected number of individuals of target species in a given plot). π is the probability of not observing any alien species in the plot, with higher values of π indicating a higher probability of individual absence. Positive values in λ indicate positive relationships with independent variables (Martin et al. 2005; Ledo et al. 2015).

Specifically, we performed a zero-inflated model (package *pscl*; R version 3.4.3) by including (i) the distance from the nearest beach access (DIST), (ii) the height above sea level (HSLMM), (iii) the height of the active foredune (HFORE), (iv) the coverage of dwarf shrub species (SUFF), (v) the coverage of erect leafy species (SCAP), (vi) the coverage of short basal species (ROS), (vii) the coverage of tussock species (CESP) and (viii) the coverage of creeping species (REPT) as independent variables, and the number of individuals of *Oenothera stucchii*, *Ambrosia psilostachya* and *Erigeron canadensis* as dependent.

3. RESULTS

Overall, we analyzed 321 sampling plots, and the most prevalent, widespread species on the North Adriatic coastal dunes was *Ambrosia psilostachya*, that was present in 303 plots (94.4%). *Oenothera stucchii* was present in 212 plots (66%), while *Erigeron canadensis* in 205 plots (63.9%). Target species were recorded in all sampling sites, except for *Erigeron canadensis* which was present only in Penisola del Cavallino and Vallevacqua.

3.1 *Oenothera stucchii*

Results of ZIP model analysis applied to abundances of *O. stucchii* showed significant, negative relationships with 4 independent variables (Table 1): height of foredunes ($\lambda=-9.226$; $p=***$), coverage of dwarf shrubs ($\lambda=-6.133$; $p=***$), coverage of erect leafy herbs ($\lambda=-2.046$; $p=*$) and coverage of creeping plants ($\lambda=-3.554$; $p=***$). Despite the significant Poisson relationship observed for erect leafy species and *O. stucchii* number of individuals, coverage of erect leafy species did not show a significant relationship regarding binomial π values. Binomial process of ZIP analysis showed relationships between presence of *O. stucchii* and the height of foredunes ($\pi=3.325$; $p=***$), coverage of dwarf shrubs species ($\pi=5.487$; $p=***$), and coverage of creeping species ($\pi=-2.586$; $p=**$). Our results do not prove our original testing hypothesis: abundance of *O. stucchii* is not dependent on distance from the beach access.

		Poisson		Binomial	
Variables		λ	p	π	p
<i>Oenothera stucchii</i>	DIST	0,081	0,935595	1,062	0,288425
	HSLMM	-1,718	0,08574	-1,618	0,105634
	HFORE	-9,226	< 2E-16	3,325	0,000883
	SUFF	-6,133	8,61E-10	5,487	4,08E-08
	SCAP	-2,046	0,040789	0,199	0,842462
	ROS	-0,664	0,506739	-0,576	0,564518
	CESP	-3,554	0,000379	-2,586	0,009723
	REPT	-0,269	0,787891	-0,921	0,357198

Table 1. Results of ZIP analysis for *Oenothera stucchii*. Grey cells indicate significant relationship.

3.2 *Ambrosia psilostachya*

Values of abundances of *A. psilostachya* showed a significant relationship with all considered independent variables (Table 2). Abundance of *A. psilostachya* was positively related to the height of foredune ($\lambda=32.491$; $p=***$), coverage of tussock species ($\lambda=4.122$; $p=***$), coverage of creeping species ($\lambda=8.256$; $p=***$). Growth of numerous populations of *A. psilostachya* is negatively influenced by the distance from the path ($\lambda=-9.405$; $p=***$), height above sea level ($\lambda=-12.934$; $p=***$), coverage of dwarf shrub species ($\lambda=-23.91$; $p=***$), coverage of erect leafy species ($\lambda=-9.054$; $p=***$), and coverage of short basal species ($\lambda=-9.225$; $p=***$).

Binomial distribution of presence/absence of *A. psilostachya* showed a significant, negative relationship only with the height of foredunes ($\pi=-2.605$; $p=**$) and the coverage of creeping plants ($\pi=-2.293$; $p=*$). These results show that the distribution of individuals of *A. psilostachya* is related with all abiotic, anthropogenic and biotic parameters of the sampling sites.

		Poisson		Binomial	
Variables		λ	p	π	p
<i>Ambrosia psilostachya</i>	DIST	-9,405	< 2E-16	-0,633	0,52678
	HSLMM	-12,934	< 2E-16	1,729	0,8383
	HFORE	32,491	< 2E-16	-2,605	0,00918
	SUFF	-23,91	< 2E-16	-1,199	0,23058
	SCAP	-9,054	< 2E-16	-0,862	0,38887
	ROS	-9,225	< 2E-16	-1,682	0,09259
	CESP	4,122	3,75E-05	-1,257	0,20871
	REPT	8,256	< 2E-16	-2,293	0,02186

Table 2. Results of ZIP analysis for *Ambrosia psilostachya*. Grey cells indicate significant relationship.

3.3 *Erigeron canadensis*

Results of Poisson regression model (Table 3) showed significant relationships with 6 variables: distance from the path ($\lambda=7.494$; $p=***$), height above sea level ($\lambda=-15.238$; $p=***$), height of foredunes ($\lambda=-26.886$; $p=***$), coverage of native dwarf shrubs ($\lambda=-17.137$; $p=***$), coverage of native erect leafy herbs ($\lambda=-4.08$; $p=***$), coverage of native short basal plants ($\lambda=-13.673$; $p=***$). The height of foredunes and the coverage of erect leafy species show only significant relationships with abundances of *E. canadensis*, while they did not influence the presence or absence of the target species in sampled plots. Number of individuals of *Erigeron canadensis* showed to be significantly related to the distance from the path ($\pi=-2.025$; $p=*$), the height above sea level ($\pi=-3.028$; $p=**$), coverage of dwarf shrub species ($\pi=2.387$; $p=*$), coverage of short basal species ($\pi=-2.206$; $p=*$), coverage of tussock species ($\pi=-2.39$; $p=*$), and coverage of creeping species ($\pi=-3.068$; $p=**$).

	Variables	Poisson		Binomial	
		λ	p	π	p
<i>Erigeron canadensis</i>	DIST	7,494	6,68E-14	-2,025	0,04288
	HSLMM	-15,238	< 2E-16	-3,028	0,00246
	HFORE	-26,886	< 2E-16	-1,667	0,09545
	SUFF	-17,137	< 2E-16	2,387	0,01701
	SCAP	-4,08	4,51E-05	-0,233	0,81569
	ROS	-13,673	< 2E-16	-2,206	0,0274
	CESP	-1,049	0,2941	-2,39	0,01686
	REPT	-1,656	0,0976	-3,068	0,00216

Table 3. Results of ZIP analysis for *Erigeron canadensis*. Grey cells indicate significant relationship.

4. DISCUSSION

Our study allowed us to understand patterns of alien species distribution along the North Adriatic coast.

Results showed that abundances of *Oenothera stucchii*, *Ambrosia psilostachya* and *Erigeron canadensis* was negatively related to the coverage of erect leafy and dwarf shrub species.

Dwarf shrubs and erect leafy species are, however, the two most common growth forms among transitional dunes' native species in N-Adriatic sand dune ecosystems (Del Vecchio et al. 2016). This could explain the first results: dwarf shrubs like semi-woody *Fumana procumbens* and a huge percentage cover of erect leafy herbs may limit space occupancy of herbaceous alien species by competition for space, soil, nutrients, ect. Consequently, preserving endemic communities such as *Tortulo-scabiosetum* under a favorable conservation status, can help the safeguard of local biodiversity and reduce alien species' spreading and colonization.

Regarding *Oenothera stucchii*, results showed that species' abundance decreases when the height of foredunes increases. With this result, it can be assumed that *O. stucchii* dispersion is affected by trampling of humans that reach the seashore and, hence, by anthropogenic disturbance. Reaching the seaside could be easier when foredunes are lower because it is possible to cross diagonally the paths, enhancing trampling among dune habitats. *O. stucchii* could enter in competition with some native species: it decreases when coverage of native erect leafy herbs, dwarf shrubs and tussocks increase. Moreover, a low foredune height might not be effective in limiting environmental disturbance, which can favor the spread of *Oenothera stucchii* by resuspending seeds on the top of the sand and limiting the growth of native species.

The abundance of *Ambrosia psilostachya*, the most common invasive species on Venetian coast, showed to be significantly related with all considered independent variables. The abundance of this alien species decreased with the distance from the nearest path; it is a matter of fact that *A. psilostachya* grows mainly in habitats disturbed by human pressure and near the roadsides (Montagnani et al. 2017). This ecological feature of the species has already been mentioned many times by some authors in recent reviews (Del Vecchio et al. 2014;

Montagnani et al. 2017). Our results suggest that the development of huge populations of *Ambrosia psilostachya* is favored by human trampling.

Individuals of *A. psilostachya* showed a positive relationship with the height of the foredune. Moreover, results revealed a negative relationship between species' abundance and the height above sea level. These two results could be explained by the ecology of the studied species: it does not show deep roots but only a horizontal rhizome system, so it is more susceptible to wind disturb; higher foredunes act as anti-wind barriers for transition dunes (Bird 2008; Maun 2009), ultimately favoring *A. psilostachya*. Furthermore, the higher abundance in areas with low height-above-sea-level suggests that it probably cannot reach deep sources because of its shallow roots system.

Horizontally developed, this species could enter competition with dwarf shrub, erect leafy and short basal native species. When there are high percentages in the coverage of these growth forms *A. psilostachya* decreases, while it seems to increase in areas where also tussock and creeping species prevail. Especially, when creeping species are present there are higher probabilities of *A. psilostachya* presence.

Unlike *Ambrosia psilostachya*, results evidenced that *Erigeron canadensis* was more abundant at higher distances from the paths; we can hypothesize that this alien species might be more sensitive to trampling than other species.

With regard to the height of foredune, a negative relationship with the abundance of *E. canadensis* arose. When the height of foredunes increases, number of individuals decreases; this might be explained by the dispersal ecology of *E. canadensis*. The main spreading driver of this species is wind (Weaver 2001): if there are low foredunes, wind might be more intense, ultimately favoring the spreading of this species in coastal habitats.

Another negative relationship has been observed between abundance of individuals and height above sea level; this result may highlight the incapability of this species in exploiting deep resources/water.

When dwarf shrub, erect leafy and short basal native species' coverage increases (as seen for *Ambrosia psilostachya*), *Erigeron canadensis*'s abundance decreases. This could suggest that, as for the other target species, competition with native species for soil/space resources might exist between *E. canadensis* and natives.

In this study, a series of ecological relationships between alien, native species and human factors emerged. As suggested by Paudel and Battaglia (2015), in this study the distribution of alien species in coastal habitats was affected by both biotic and human factors. Especially, human disturbance arose as a major driver in determining alien species distribution along coastal habitats of the North Adriatic coast.

A solution to the problem could be the restoration of sand dunes, in particular the morphology of foredunes. The restoration of the integrity of foredunes might limit the spread of alien species in transitional dunes, as showed for *Erigeron canadensis*.

Acting on paths and beach accesses, by installing placing fences would limit the growth and dispersion of alien species on grey dunes. Especially, this solution could reduce the presence of *Ambrosia psilostachya* near the paths and, consequently towards the core of habitat patches. Fences are methods to forbid trampling and to enforce dunes' structure, preventing damages to communities. The reduction of trampling impact may help to thicken edges of habitats, and increase cores' defense from edge effects (such as preservation of biodiversity richness and low presence of alien species).

Oenothera stucchii did not seem to be directly affected by trampling. We can propose and suggest actions of habitat management and restoration. Since the abundance of this species was significantly related with the coverage of some specific growth forms of native species (especially dwarf shrubs), it may be helpful to protect and maintain plant communities showing a high presence of dwarf shrub species.

European programs, as LIFE Projects, have already been working on endemic communities and species protection, and they aim at eliminating alien species from natural habitats on European coastal ecosystems (Silva et al. 2017). However, environmental education remains among the best ways to protect the environment and reduce its destruction by incorrect human activities. It could be helpful to continue to spread information about recognizing alien species, as well as biodiversity and habitat importance, by explaining ecosystem services derived from them. This last solution would not work only for coastal environments but can be extended to other areas with natural habitats under threat by human activities.

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