



Using fine-scale field data modelling for planning the management of invasions of *Oenothera stucchii* in coastal dune systems

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ABSTRACT

Invasive alien species risk assessment and adaptive management are often hindered by a lack of information for most species. This work aims at predicting the probability of successful establishment and invasion of *Oenothera stucchii* Soldano, a neophyte invasive species belonging to the sect. *Oenothera* subsect. *Oenothera*, in xerophilous grasslands of grey dunes. Based on fine-scale field data, we modelled *O. stucchii* presence/absence and abundance as a function of environmental factors, human disturbance, and attributes of the recipient community through a zero-inflated Poisson model. The invasion success of *O. stucchii* depended on a combination of factors which differed when considering either the patterns of occurrence (species presence/absence) or those of species abundance. While human-driven disturbance strongly influenced the probability of presence/absence of *O. stucchii*, patterns of abundance were mostly driven by a combination of environmental and biotic features. Attributes of the recipient community remarkably influenced both *O. stucchii* presence and abundance. Based on fine-scale field data, we determined the mechanisms which drive the spatial patterns of presence and abundance of *O. stucchii* in xerophilous grasslands and provided quantitative thresholds to identify the most susceptible areas of grey dune habitats prone to invasion, which combine human disturbance (distance from the nearest beach access), attributes of the resident community (resident vegetation cover and structure), and environmental disturbance (foredune ridge height). These results provide useful insights to be used to plan cost-effective measures to prevent *O. stucchii* establishment and spread in sandy coastal systems. Our model may also be applied to closely related congener species included in the subsect. *Oenothera*, sharing similar biological and ecological traits.

1. Introduction

Invasive alien plant species (IAPs) are considered one of the main causes of global biodiversity loss, especially when interacting with other drivers of global change such as habitat loss and climate change (Bellard et al., 2013; Gentili et al., 2017). Alien plant species negatively impact many ecological variables in several ways (Mason et al., 2008). Many invasive plants are known to cause species extinctions thereby reducing local plant species diversity, alter fire regimes, hydrology, geomorphological and soil nutrient cycling processes, eventually impacting ecosystem services and human well-being (e.g., Ehrenfeld, 2003; Pejchar and Mooney, 2009).

The spread of IAPs and the consequences on biodiversity and ecosystem functioning elicit numerous issues regarding their management and control (Barbet-Massin et al., 2018). Recently, the European Union adopted a new Regulation on Invasive Alien Species (European

Regulation No 1143/2014) which aims at preventing invasions; minimizing and/or mitigating the detrimental impact of invasive alien species on biodiversity and ecosystem services, economy, and human health; and finally, at establishing early warning and possibly rapid eradication procedures (Genovesi et al., 2015).

The Regulation recognises the prevention of invasive species' establishment and further spread as a more efficient and cost-effective management strategy compared to eradication, containment and control that are required when the species has fully established. However, forecasting the risk that an introduced species will establish, increase in abundance, spread, and cause impacts to biodiversity and ecosystem services is challenged by a lack of information for most species (Leung et al., 2012), thereby limiting the effectiveness of risk assessments and adaptive management (Uden et al., 2015). Thus, early warning and rapid eradication procedures could largely profit from research aiming at understanding those factors that influence the spatiotemporal

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patterns in plant invasions (Simberloff et al., 2005). This is particularly true for rapidly spreading species that potentially have a great impact on native biodiversity (Skálová et al., 2017).

Many drivers, acting at various spatial scales, have been recognized to influence the invasion success, such as propagule pressure, residence time, and chance events (Richardson and Pyšek, 2006), dispersal by humans (Kowarik, 2003; Smith and Kraaij, 2020), and disturbance, either natural or anthropogenic (Carboni et al., 2010). Moreover, the invasion potential is assumed to be closely related to the invader identity (invasiveness; Alpert et al., 2000) and to the local environmental context (habitat invasibility; Alpert et al., 2000), which may filter alien species based on their ecological requirements and physiological adaptations (environmental or habitat filtering; Gallien and Carboni, 2017). The recipient community may further control alien species colonisation and encroachment through such inherent properties as native species richness and coverage (Sun et al., 2015), which may become even more important than other factors (Santoro et al., 2011).

Sandy coastal dunes are a representative example of an ecosystem in which all kinds of determinants of IAPs invasion are particularly intense (Gallego-Fernández et al., 2019; Jørgensen and Kollmann, 2009; Lazzaro et al., 2020). Sandy coastal systems are characterized by high levels of natural disturbance with strong gradients in environmental factors and biotic features. The complex coast-to-inland environmental gradient is recognisable by differences in the intensity of factors such as wind, salt spray and salinity, and sand burial (Hesp and Martínez, 2007) which decreases with increasing distance from the sea. Thus, all those dune dynamic environmental factors, like the distance from the sea, wind intensity, geomorphology (e.g., the height and width of foredunes), and soil properties, can regulate the invasion process by either hampering or limiting alien plant establishment and spread depending on their ecological requirements and physiological adaptations (e.g., Gallego-Fernández et al., 2019; Lechuga-Lago et al., 2017). Paralleling this environmental gradient is a biotic gradient, evidenced by the typical coastal vegetation zonation, where habitats are progressively exposed to lower environmental stress with increasing distance from the sea (Forey et al., 2009). The coastal vegetation zonation entails a unique habitat diversity, ranging from the upper beach and foredunes close to the sea, to the more stable inland fixed dunes, with habitats shaped and defined by distinct processes (Jiménez-Alfaro et al., 2015) and showing different diversity patterns (Torca et al., 2019). According to the biotic resistance hypothesis (Elton, 1958; Sun et al., 2015), this, in turn, makes different dune habitats differentially sensitive to alien invasion (Konlechner et al., 2015; Marcantonio et al., 2014). Other than natural disturbance, coastal areas are also strongly affected by direct human disturbance (e.g., trampling, levelling of dunes). Being preferred environments for leisure, coastal dune systems have a crucial role for recreation and tourism (Everard et al., 2010). Notably, the Mediterranean coasts are among the preferred destinations for international tourists (Carranza et al., 2020) and tourism continuous growth is exerting huge pressures, leading to dune reshaping or flattening, loss of habitat and fragmentation, destruction of protective vegetation, increased erosion during storms, reduced biodiversity, and alien invasion (Defeo et al., 2009; Fantinato, 2019; Hilton, 2006).

The quantification of the relative importance of these different factors in influencing the plant invasion process, and the identification of the contexts in which they operate and gain importance, still remains a challenge (Akin-Fajiyé and Gurevitch, 2018). Approaches used to describe the successful establishment and spread of invasive species are generally large in extent and grain and based on presence-only data (Brummer et al., 2013). However, the invasion process and its effects are scale-dependent (e.g., Sun et al., 2015), with effects significantly increasing with decreasing unit size (Del Vecchio et al., 2015); therefore, if we aim at informing sustainable management plans and developing spatially differentiated IAPs management strategies at local scale, we need knowledge on spatiotemporal patterns of plant invasions at a fine scale (Brummer et al., 2013). Moreover, we need to integrate presence

and abundance data to understand whether these two population parameters are influenced by similar factors.

In light of these considerations, in the present study we aim at examining the influence of human disturbance (in the form of trampling), environmental factors, and biotic resistance of native communities in determining the presence and abundance of *Oenothera stucchii* Soldano in the xerophilous grasslands of grey dunes along the North Adriatic coast (Italy). *O. stucchii* is an herbaceous neophyte invasive species (Galasso et al., 2018) belonging to the sect. *Oenothera* subsect. *Oenothera*, the most complex group of species in the Onagraceae (Dietrich et al., 1997; Mihulka et al., 2006). This genus is native to the temperate areas of the North America (Dietrich et al., 1997) and its numerous representatives were introduced into Europe where they grow with varying success, from casual to invasive (Mihulka and Pyšek, 2001). *Oenothera* representatives have been intensively studied to investigate fecundity, growth rate of seedlings, competitive ability and how these characteristics contribute to their invasion potential (Mihulka et al., 2006; Greiner and Köhl, 2014). However, though the high invasiveness of *Oenothera* representatives is well acknowledged, the factors controlling their establishment (i.e., presence/absence) and spread (i.e., abundance) are still poorly understood.

2. Methods

2.1. Target species

Oenothera stucchii Soldano is an herbaceous plant that belongs to the sect. *Oenothera* subsect. *Oenothera* (Fig. A1; Rostański, 1977; Soldano, 1993). According to Dietrich et al. (1997), *O. stucchii* is a stabilized hybrid between *O. jamesii* Torrey & A. Gray, and one of the European phenotypes of *O. biennis* L. It is supposed to have evolved very recently, in northern Italy, where it was collected for the first time in 1952 (Soldano, 1980).

O. stucchii has a vigorous biennial life cycle, which, in case of adverse environmental conditions, allows it to persist in the rosette stage for several years. Rosettes can vary between 10 and 40 cm and give the plant a high tolerance to trampling (Cole, 1995). *O. stucchii* is the biggest among the congeners, with an average flowering stalk height of 120–200 cm (Soldano, 1993), and up to 300 cm during the anthesis which normally occurs from mid-July to October. *O. stucchii* is predominantly autogamous, thereby not suffering pollinator limitation (Fantinato, 2019). The capsules are approximately 2 cm long with a cylindrical shape and contain several tiny brown seeds of spherical shape (Del Vecchio et al., 2020b). The number of capsules per plant, the number of seeds per capsule and the number of seeds per plant are very changeable. On average individual plants of *O. stucchii* produce 24–98 capsules containing 89–185 seeds each, with a seed production ranging from 2500 to 14,400 seeds per plant (authors' personal observation). Seeds are long-lived (Del Vecchio et al., 2020b), thereby ensuring the persistence of the species in the soil seed bank and its chance to sprout over long periods. Germination occurs in the light (Del Vecchio et al., 2020b). Seeds lack specialised morphological adaptation for dispersal and this, alongside the capability of germinating in the light, led to hypothesise that the spread of *Oenothera* species is mainly due to human-mediated transport rather than to natural dispersal agents (Frean et al., 1997). Based on these features, *O. stucchii* is classified as a neophyte invasive species (Galasso et al., 2018). Besides open habitats such as fallow fields, road and stream sides, *O. stucchii* colonizes sand dune habitats. Although present since the 1950s, it now seems to have been entering the 'increase-phase', as it is testified by the outstanding spread and increase in occurrence (Del Vecchio et al., 2015). However, its spatiotemporal invasion dynamics differs across sand dune habitats, with xerophilous grasslands of grey dunes (category B1.4; European Nature Information System EUNIS; Davies et al., 2004; Fig. A2), hosting the most abundant populations (Del Vecchio et al., 2015).

Xerophilous grasslands of grey dunes represent one of the most

valuable and diversified habitats of the semi-fixed or fixed dune sector (Doing, 1985). Grey dunes are found along much of the European coast (Houston, 2008) and they mainly occupy the transition zone along the sea–inland vegetation zonation, developing between the herbaceous vegetation of the foredune and the scrub and woodland of the fixed dune. Grey dunes are typically located inland from the shore and benefit from the protection action exerted by foredune ridges against wind erosion, salt deposition, and sand burial. Being less exposed to the severe coastal environmental conditions, they are colonised by perennial grasslands, normally with a higher vegetation cover and higher species richness compared to other early successional dune habitats (Del Vecchio et al., 2018; Houston, 2008). In addition to herbaceous species, plant communities comprise a dense carpet of mosses and lichens, and woody species, mostly dwarf shrubs. They host a large variety of species, often rare, endemic, or endangered, and a very high number of different plant communities (Martínez et al., 2004; Provoost et al., 2004), which, alongside serious anthropogenic threats, make them habitats of major conservation concern (Bakker et al., 2016; Janssen et al., 2016). Grey dunes are highly susceptible to change from both natural and human-induced events (Lemauiel and Rozé, 2003). While in Northern Europe grey dune ecosystems are declining from the encroachment of grass and shrub species due to sand dune over-stabilization, high nitrogen deposition, and a decline in rabbit populations (Houston, 2008; Isermann et al., 2010), touristic development and recreational activities (trampling, infrastructure) are the most severe threats in the Mediterranean coast (e.g., Malavasi et al., 2014).

2.2. Study area and data collection

The study took place on the xerophilous grasslands of grey dunes of the North Adriatic coast (Italy; Fig. 1), the northernmost part of the Mediterranean basin. The most abundant populations of *O. stucchi* are mainly found in xerophilous grasslands of grey dunes which currently result the most impacted communities of the coastal zonation (Del Vecchio et al., 2015).

The North Adriatic coast shows a Temperate Oceanic bioclimate (Del Vecchio et al., 2018). The annual average temperature is about 13 °C and the annual average precipitation is 831.5 mm (Fantinato et al., 2018). Until the 1950s, the North Adriatic coast was almost entirely fronted by sandy dunes up to 10 m in height (Bezzi and Fontolan, 2003). 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), with summer beach tourism representing one of the main incomes of the region (Bezzi and Fontolan, 2003). Despite the intense tourism, remaining natural sites are biodiversity hotspots as they host many endemic species and habitats (Buffa et al., 2007; Gamper et al., 2008; Sburlino et al., 2008, 2013).

In the study area we chose three sampling sites: Vallevecchia (45.619982 N, 12.945629 E), Mort Lagoon (45.532188 N, 12.735531 E) and Cavallino Peninsula (45.439669 N, 12.453017 E). In the sampling sites, xerophilous grasslands of grey dunes develop inland of the foredunes and occupy the portion of the coastal zonation approximately ranging from 20 m to 80 m from the sea. They vary in structure and species composition depending on the level of disturbance (Buffa et al., 2005; Del Vecchio et al., 2015, 2016). Under low anthropogenic

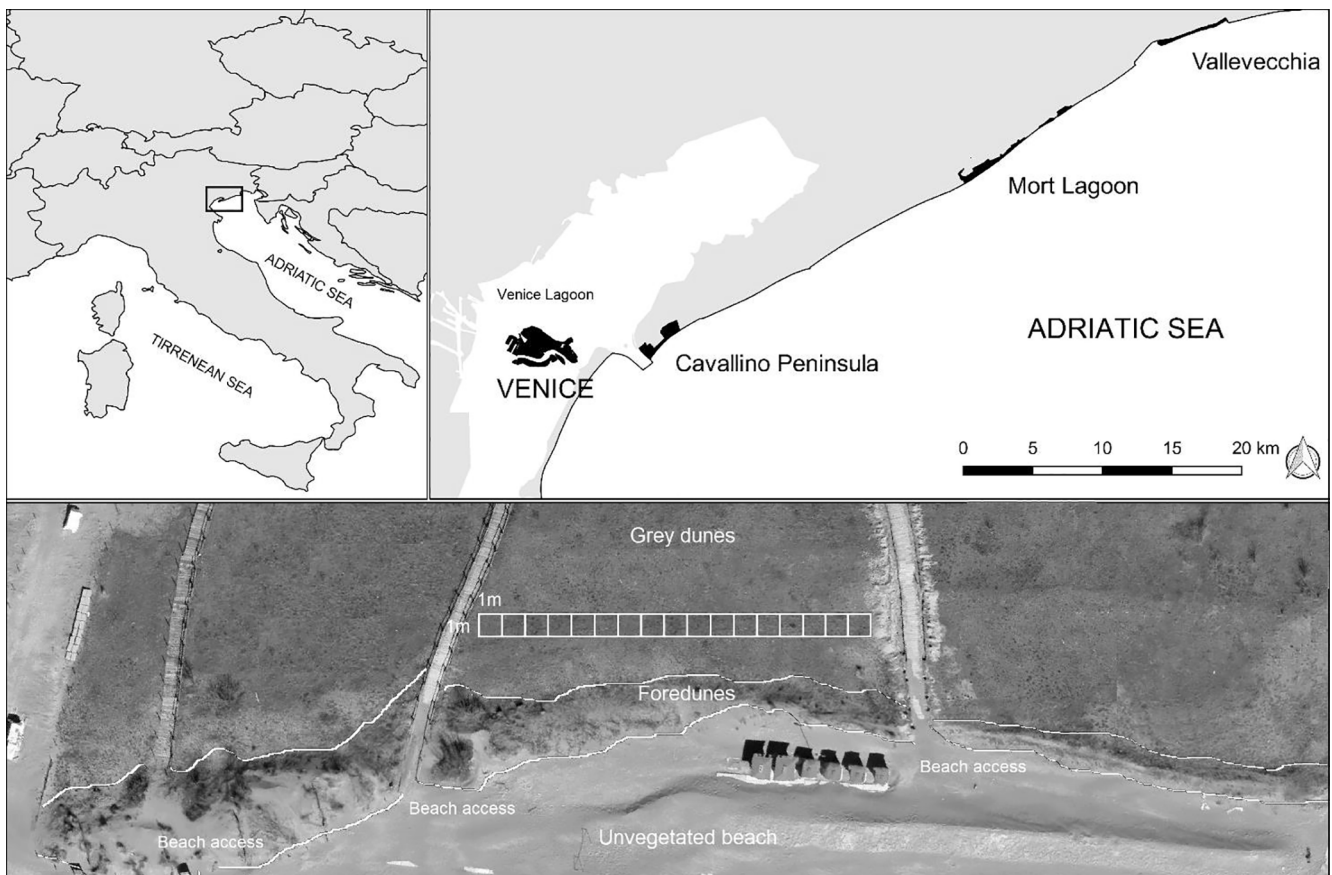


Fig. 1. Map of the study area and belt transect sampling design. The broad geographical location of the study area is shown at the upper left corner. Sampling sites (in black) are shown at the upper right corner. An example of a belt transect sampling design is shown below. Belt transects consisted of adjacent plots of 1 m × 1 m and were laid down parallel to the shoreline. Transects were placed in correspondence of xerophilous grasslands of grey dunes and stood between the edge of two consecutive beach accesses, either formal or informal. The position of the 9 belt transects sampled in the study sites was randomly selected using xerophilous grasslands of grey dunes as strata. In the figure, the drawn belt transect is out of scale.

disturbance (i.e., low path percentage cover in each plot surroundings; Silan et al., 2017), and inland of high and wide foredune systems, which exert a protection function from natural disturbance factors (e.g., wind, aerosol, and sand burial; Drius et al., 2019), xerophilous grasslands are dominated by perennial plant species, both woody (dwarf shrubs such as e.g., *Fumana procumbens* (Dunal) Gren. & Godr., *Teucrium polium* L., *Thymus pulegioides* L.) and herbaceous (e.g., *Koeleria splendens* C. Presl). The vascular species cover is high, on average higher than 90% (Silan et al., 2017). Under disturbed conditions, namely under intense human trampling (i.e., high path percentage cover in each plot surroundings; Silan et al., 2017), and/or behind relatively narrow and low foredune ridges, the average cover of vascular plants decreases to around 60% (Silan et al., 2017) and perennial plants are replaced by annual species such as *Cerastium semidecandrum* L., *Phleum arenarium* L. and *Silene conica* L. The moss-lichen stratum also changes under disturbed conditions; specifically, lichens (mostly *Cladonia* spp.) totally disappear, while the moss layer (i.e., *Syntrichia ruraliformis* (Besch.) Cardot and *Pleurochaete squarrosa* (Brid.) Lindb.) increases forming a dense crust with percentage cover up to 100%.

At the end of April 2018, we placed a total of 9 belt transects (Fig. 1). The number of transects per sampling site varied according to the overall extent of xerophilous grasslands per site based on the habitat map of the Veneto region (<https://www.regione.veneto.it/web/agricoltura-e-foreste/siti-m2000>; scale 1:10,000; consulted 20.04.2018). Accordingly, we placed 3 belt transects at Vallevicchia, 1 at the Mort Lagoon and 5 at the Cavallino Peninsula. Using xerophilous grasslands as strata, we selected belt transects position using a stratified random sampling design (Random points inside polygons; Quantum GIS Development Team, 2020). Belt transects consisted of adjacent plots of 1 m × 1 m (Del Vecchio et al., 2019), and were laid down parallel to the shoreline, standing between the edge of two consecutive beach accesses, either formal or informal. The mean number of plots per belt transect (which is equal to the overall transect length) was of 35.6 ± 20.8 (mean \pm SD); overall, we recorded 321 plots. We chose to lay transects between the edge of two consecutive beach accesses to account for the contribution of human disturbance, in the form of trampling, to the occurrence and spread of *O. stucchii* (Fig. 1). Trampling has been proved to be one of the most critical threats to Mediterranean coastal dune systems, exerting both direct (reducing individual plant fitness) and indirect (increasing erosion and sand movements) impacts (Gallet and Rozé, 2001; Santoro et al., 2012). Trampling has also been suggested as a key factor in alien plant invasion, spreading propagules, creating or prolonging disturbance (Rose and Hermanutz, 2004), and possibly influencing germination patterns (Del Vecchio et al., 2020a). To describe the spatial pattern of the influence of the human trampling in determining *O. stucchii* establishment and spread, we recorded the distance of each plot from the closest beach access (m) by means of a tape measure. To detect the influence of the environmental factors in determining *O. stucchii* establishment and spread, as proxies of wind intensity, salt spray and sand burial, we recorded the plot height above sea level (m), the distance from the sea, and the correspondent height and width of foredunes (m). The latter were derived from the 15-cm resolution digital spatial model (DSM) of the sites (deliverable of the European LIFE project LIFE16 IT/NAT/000589 REDUNE; <http://www.liferedune.it/>; consulted 22.05.2019). Lastly, we described the biotic features of the invaded communities by recording in each plot vascular plants presence and coverage (%), the total coverage (%) of mosses, and the number of individuals of *O. stucchii*. The total coverage of mosses has been included since in the study area it can be used as an indicator of disturbance (Silan et al., 2017). Moreover, we classified each vascular plant species according to its life cycle by distinguishing annual plant species from perennials. Sand parameters such as pH, moisture, organic matter, size and sorting of sand grains, were not considered because highly uniform within and between the sampling sites (Silan et al., 2017).

2.3. Data analysis

The distribution of counts of *O. stucchii* showed an excess of zero count. For this reason, fitting a generalized model with Poisson marginal distribution would lead to a bias in the conclusions. To deal with this distribution, we opted for a zero-inflated Poisson model (Zuur et al., 2009). Zero inflated Poisson model is the result of a mixture of two stochastic models. The first model generates zero values of counts of *O. stucchii* in a plot with a probability π . These zeros are called structural zeros. The second model generates counts with a probability $1-\pi$ according to a Poisson distribution with mean λ . Note that in this case there is a non-zero probability to generate zeros. The resulting expected number of individuals of *O. stucchii* is given by $(1-\pi)\lambda$. Higher values of π foster the absence of individuals, instead larger values of λ foster the abundance. In our modelling framework, parameters π and λ are function of some covariates and are estimated jointly.

We specified a zero-inflated model for the number of individuals of *O. stucchii* by including (i) the distance from the beach access, (ii) the plot height above sea level, (iii) the height of foredunes, (iv) the richness of annual plants, (v) the richness of perennial plants, (vi) the total coverage of vascular plants (without *O. stucchii* cover) and (vii) the total cover of mosses as covariate variables. Since foredune width and height were collinear ($r > 0.7$), we included in the model only the height of foredunes. Indeed, according to Durán and Moore (2013) the height of foredunes represents a critical feature of coastal dunes, which deeply influences coastal dune vulnerability. Moreover, since belt transects were parallel to the shoreline, the distance from the sea only differed among transects resulting in too low variability of the covariate which therefore was not included in the model. The zero inflated Poisson models were fitted the function *zeroinfl* using the R package *pscl* (Jackman, 2017; R version 3.4.3) and simplified by backward elimination of non-significant covariates.

3. Results

Overall, *O. stucchii* occurred in 198 plots (64% of plots), with an average number of 7.43 ± 6.63 (mean \pm SD) individuals per plot. The minimum number of individuals of *O. stucchii* found in a plot was 0, while the maximum was 76 (Fig. 2).

Environmental and biotic features of the xerophilous grasslands of grey dunes widely differed among sampling plots. Specifically, the plot height above the sea level ranged from 2 m to 4.5 m, with an average height of 2.4 ± 0.4 m, while the correspondent height of foredunes ranged from 3 m to 5.5 m, with an average height of 3.8 ± 0.5 m. The richness of annual plants per plot ranged from 0 to 10, with an average number of 4.9 ± 2.6 annual plants per plot; while that of perennials ranged from 1 to 11, with an average number of 4.5 ± 1.6 perennial plants per plot. The total coverage of vascular plants per plot ranged from 1% to 56%, with an average coverage of $11.4 \pm 8.1\%$; while that of mosses from 0% to 100%, with an average coverage of $45.1 \pm 37.2\%$.

According to the zero-inflated model, the probability of absence of *O. stucchii* (π) (Table 1) was strongly related to the proximity of the beach access, and to the environmentally disturbed portions of grey dunes. Specifically, the probability of absence of *O. stucchii* increased with the distance from the beach access (see Fig. 3A for an example). Moreover, the height of foredunes influenced the absence of *O. stucchii*, with the probability of absence increasing with increasing height of the foredune ridges (Fig. 3B). Besides human disturbance and environmental factors, also biotic features of invaded communities significantly influenced the probability of absence of *O. stucchii*. Specifically, the probability of absence of *O. stucchii* decreased with increasing richness of annual plant species (Fig. 3C) and with increasing coverage of mosses (Fig. 3E), while it increased with the total coverage of vascular plants (Fig. 3D).

For each covariate, our model allowed to evidence the probability of absence estimated as function of the selected covariate, setting the other

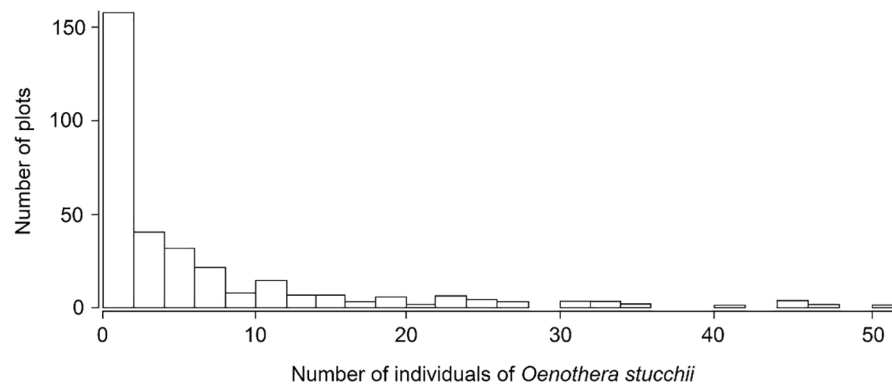


Fig. 2. Histogram showing the frequency of the observed number of individuals of *O. stucchii* in the sampled plots.

Table 1

Results of the zero-inflated Poisson model. Here π is the probability of not observing any individual of *O. stucchii* in a plot, while λ is the expected number of individuals of *O. stucchii* in a plot. Positive values of β^π indicate positive associations between covariates and the absence of *O. stucchii*, while β^λ indicate positive associations between covariates and the expected number of individuals of *O. stucchii*. Only coefficients of significant covariates were included.

Covariate variable	Estimate β^π	Standard Error β^π	P-value β^π	Estimate β^λ	Standard Error β^λ	P-value β^λ
Distance from the beach access	0.054	0.012	<0.001	.	.	.
Height above sea level
Height of foredunes	1.144	0.288	<0.001	-0.676	0.055	<0.001
Richness of annual plants	-0.493	0.084	<0.001	.	.	.
Richness of perennial plants	.	.	.	-0.061	0.021	0.003
Total coverage of vascular plants	0.130	0.036	<0.001	-0.073	0.006	<0.001
Total coverage of mosses	-0.012	0.005	0.018	0.010	0.000	<0.001

covariates equal to a fixed value. For example, by using the mean value as fixed value, the estimated probability of absence of *O. stucchii* is almost 70% at 56 m from the beach access (Fig. 3A), i.e., the probability of presence of *O. stucchii* is almost 30% at 56 m from the beach access. Moreover, the probability of absence tends to 100% at foredune height of almost 5.5 m (Fig. 3B) and at vascular plant coverage of 40% (Fig. 3D). On the other hand, the probability of absence of *O. stucchii* decreased with increasing richness of annual species, tending to 0% at the presence in a plot of 10 annual plant species (Fig. 3C).

The previous setting also allowed us to consider the effect of human disturbance, environmental factors, and biotic features of invaded communities on the abundance of *O. stucchii*. When assessing the effects of human disturbance and environmental factors on the abundance of *O. stucchii* (Table 1), only the height of foredunes showed a significantly negative association with the expected number of individuals of *O. stucchii* ($(1 - \pi)\lambda$; Fig. 4A). On the other hand, biotic features of invaded communities were significantly related to the expected number of individuals of *O. stucchii*. Specifically, the expected number of individuals of *O. stucchii* showed a negative association with the richness of perennial plants (Fig. 4B) and the total coverage of vascular plants (Fig. 4C); while it showed a positive association with the coverage of mosses (Fig. 4D).

4. Discussion

Predicting the probability of successful establishment and invasion of alien species, identifying factors responsible for the spatiotemporal patterns of invasions, and quantifying their relative importance are priority tasks for the risk assessment and adaptive IAPs management.

Consistent with other recent studies (e.g., Bazzichetto et al., 2018), our research confirms that the invasion success depends on a combination of conditions, factors, and mechanisms, which, however, may change when considering either the patterns of occurrence (i.e., presence/absence) or those of species spread (i.e., abundance). Patterns of occurrence of *O. stucchii* were positively related to the proximity of

beach accesses and foredune morphology, with the probability of absence increasing with the distance from the nearest beach access and with the height of the foredune. The occurrence of *O. stucchii* was also fostered by some attributes of the resident community, such as the richness of annual species and the cover of the moss layer, while at increasing total coverage of vascular plants the probability of *O. stucchii* presence decreased.

The link between alien plant occurrence and beach accesses has been already reported for other alien plants (e.g., Bazzichetto et al., 2018) and explained with increasing propagule pressure as adjacency with human structures increases (Malavasi et al., 2014). Indeed, several studies revealed that tourists can unintentionally act as vectors for seed dispersal carrying high seed loads on their clothing and footwear (Pickering and Mount, 2010; Smith and Kraaij, 2020), thereby fostering dispersal of alien plant species (Ansong and Pickering, 2014). Our results also evidenced a spatial gradient in the influence of beach accesses, with effects on *O. stucchii* occurrence decreasing with increasing distance from the access edge. This result is consistent with previous research which found that the distance from trail edge explained both the variation in plant community attributes (Purvis et al., 2015; Rowe et al., 2018) and the total number of alien species (Ballantyne and Pickering, 2015; Bella, 2011). Bella (2011) also found a significant reduction in alien species presence beyond a 500 m distance from a trail edge.

The overwhelming importance of propagule pressure (Lockwood et al., 2005) in promoting IAPs invasion has been highlighted in many different ecosystems; as for example steppes (Bangert and Huntly, 2010), old fields (Marco et al., 2010), temperate forests (Buffa et al., 2018), or oceanic islands (Arteaga et al., 2009). The strong influence of propagule pressure on IAPs invasion was also emphasized by Shmida and Wilson (1985) who suggested that a continuous propagule pressure (i.e., mass effect) may assure the permanence of an introduced species despite environmental unsuitability. However, consistent with other studies (e.g., Britton-Simmons and Abbott, 2008), our model suggests that in this system the interaction between propagule input and the

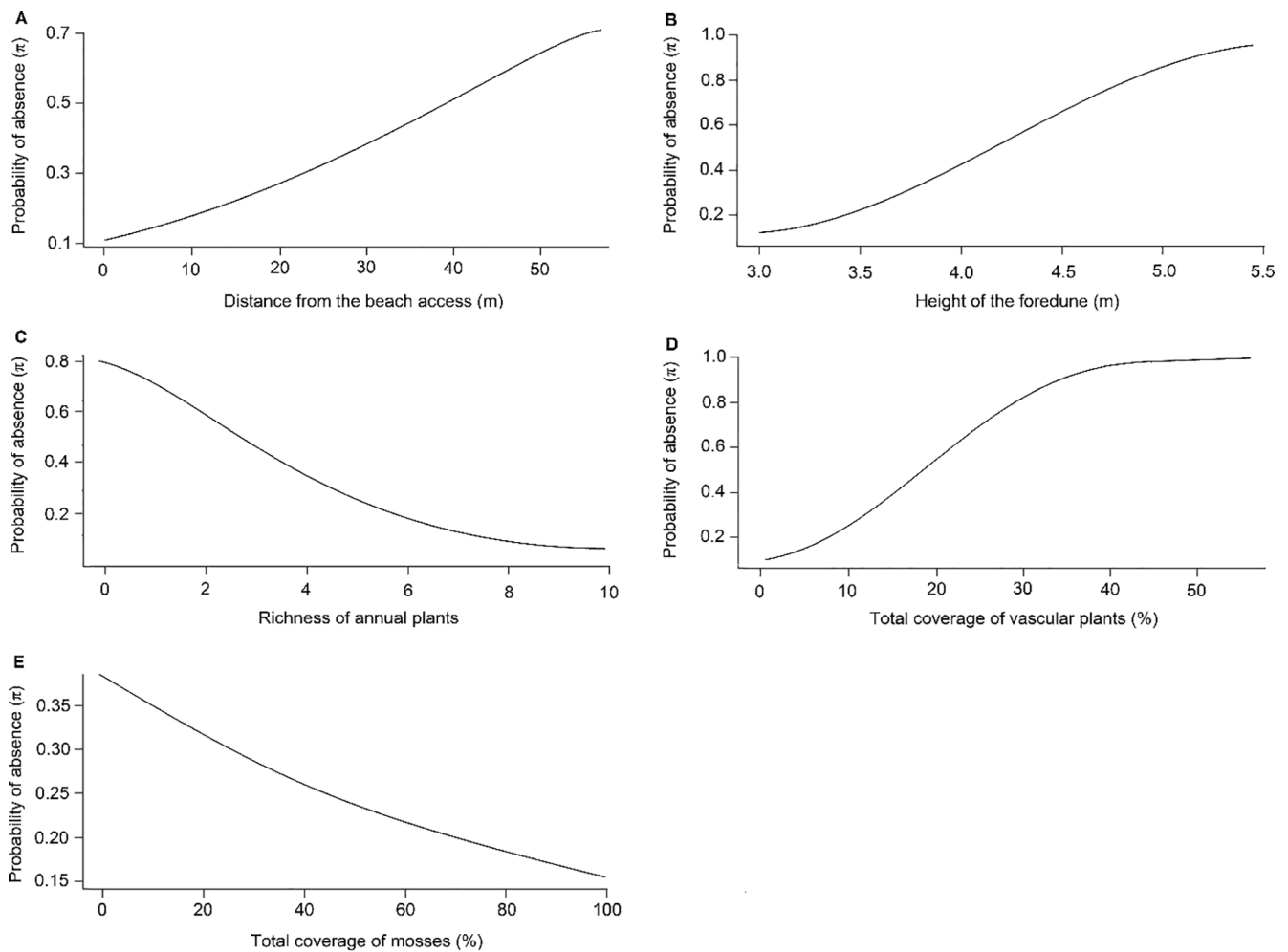


Fig. 3. Association between the probability of absence of *O. stucchii* (π) and the distance from the beach access (A), the height of foredunes (B), the richness of annual plants (C), the total coverage of vascular plants (D), and the total coverage of mosses (E). For each covariate, the probability of absence was estimated as function of the selected covariate, setting the other covariates equal to their mean values.

patterns of disturbance is key to understand the pattern of occurrence.

Foredune morphology, especially crest height, has been proved to directly affect foredune efficiency in protecting inland habitats (Zar-netske et al., 2015) by acting as a natural physical barrier against wind, salt spray and salinity, and sand burial. Lower foredune ridges, or even poorly vegetated gaps in foredunes (Nordstrom et al., 2007), contribute to increased wind disturbance and sand inundation of inland areas, thereby inducing grey dune habitats degradation and instability. Sand movements resulting from wind erosion have an adverse effect on the plants of the grey dunes, which are not adapted to unstable substrata (Lemauiel and Rozé, 2003). Moreover, burial may reduce seed germination, seedling emergence and survival, and growth of seedlings and adult plants, thereby acting as a filter and selectively eliminating less tolerant, susceptible species (Maun, 2009). High natural disturbance acts synergically with human trampling, which has been proved to negatively affect coastal plant communities' structure and species composition, causing death or severe reduction of species fitness (Bernhardt-Römermann et al., 2011; Busch et al., 2019; Cole, 1995). Trampling effects are especially detrimental for the species of grey dune grasslands. The almost flat topography of grey dunes and the presence of woody species give Mediterranean xerophilous grasslands a certain resistance to mechanical disturbance such as trampling (Lemauiel and Rozé, 2003); however, once damaged, the woody stratum can regenerate only very slowly (Cole, 1995; Del Vecchio et al., 2016). Thus, by directly removing or decreasing populations of native competitive

species, human trampling and increased wind and sand burial disturbance synergically act increasing the formation of small gaps (namely new, suitable habitats), thereby facilitating the establishment of alien species into coastal dunes (Campos et al., 2004). This pattern is confirmed by the attributes of the resident community that play a role in governing the pattern of occurrence of the target species. Firstly, the positive effect that the increase in the total coverage of vascular plants (which mirrors a decrease in bare sand) has on the probability of absence of *O. stucchii*. Secondly, the richness of annual species. Annual species are fast-growing species that colonize, and often dominate, periodically or continuously disturbed environments (Symonides, 1988), where they may attain dominance because potential perennial competitors are removed by disturbance (Grime, 2001). In addition, due to their life-history traits and features (e.g., short life-span, capacity for rapid and extensive regeneration, adaptation to exploit environments intermittently favourable for rapid plant growth) annual plants form populations that undergo spatial and temporal fluctuations in size often leaving empty gaps (Grime, 2001). This set of factors and processes perfectly fits the invader identity and in particular the biennial life cycle, well-adapted to the colonization of open, irregularly disturbed habitats (Mihulka et al., 2006) and that allows the species to persist in the rosette stage in case of adverse environmental conditions. Moreover, since *O. stucchii* seeds preferably germinate in the light (Del Vecchio et al., 2020b), sand movements caused by either wind or trampling, can indirectly enhance germination and seedling recruitment by

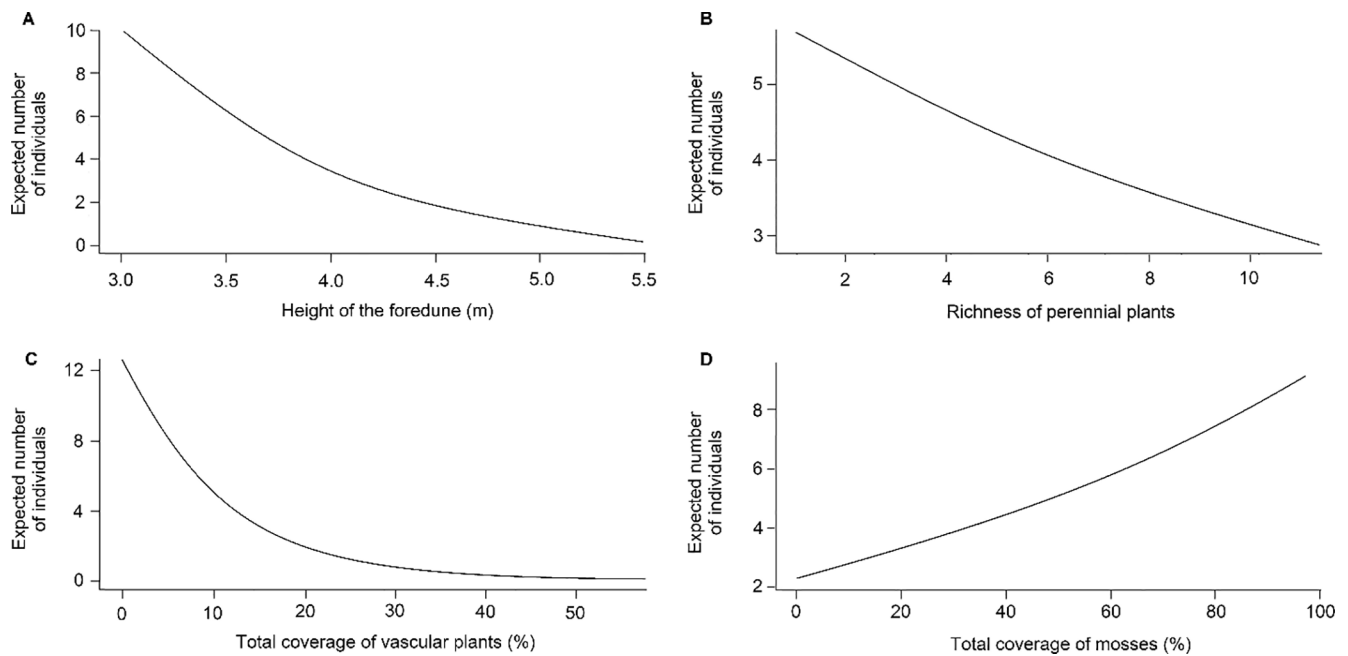


Fig. 4. Association between the expected number of individuals of *O. stucchii* (λ) and the height of foredunes (A), the richness of perennial plants (B), the total coverage of vascular plants (C), and the total coverage of mosses (D). For each covariate, the expected number of individuals was estimated as function of the selected covariate, setting the other covariates equal to their mean values.

resuspending seeds of *O. stucchii*, thus returning buried seeds to depths where germination is favoured (Ensminger and Ikuma, 1987; Hilton et al., 2019). Although we did not track individual germination and survival, the positive effect of moss layer cover on the occurrence of *O. stucchii* could be due to the moss crust that prevents seeds to be buried in the soil, where it may be too dark to germinate.

In the model addressing the pattern of *O. stucchii* abundance, different conditions and factors gained importance. Interestingly, human disturbance in the form of trampling influenced more *O. stucchii* presence than abundance, i.e., human disturbance is an important factor in determining *O. stucchii* establishment, but it does not play any significant role in influencing its abundance. This finding is in accordance with Clark and Johnston (2011) who found contrasting effects of disturbance on invader colonization vs. persistence, with disturbance only facilitating initial invasion.

The properties of the resident community such as structural and functional complexity, namely biotic resistance of native species (Bennett et al., 2016), confirmed their importance as predictors of the invasion level of *O. stucchii*. According to Levine et al. (2004), biotic resistance significantly constrains the abundance of invasive species once they have successfully established. The negative relationship between *O. stucchii* abundance and the total vegetation cover might be due to local competition with native species for space and local resources; or, rather, increase in abundance might be due to a niche gap filling process. Although it is reasonable to assume that both processes are present, the negative relationship with the total vegetation cover provides evidence underpinning the second hypothesis (i.e., gap filling process). Gaps created in the vegetation, together with disturbance-induced sand movements, continuously provide new niches to *O. stucchii*, favouring the formation of abundant populations. Disturbance can thus affect invasion directly, by altering the abiotic environment, or indirectly, by reducing native diversity and by opening and creating available grounds for invasion.

Based on fine-scale field data, we described the mechanisms which determine the spatial patterns of presence and abundance of *O. stucchii* in coastal dunes and provided a quantitative estimate of the most susceptible areas of grey dune habitats prone to *O. stucchii* invasion, which combines proximity to beach accesses (lower than 50 m), low resident

vegetation cover (<40%), high number of annual species (10 species), and low foredune ridges (<5.5 m). These results provide useful hints to be used to plan cost-effective measures to prevent *O. stucchii* establishment and spread in sandy coastal systems. These should include the regulation of beach accesses which should be planned at a distance of at least 200 m from each other, to secure areas sufficiently distant from the beach accesses with a high probability of absence of *O. stucchii*, and the closure of unauthorised trails which jeopardise beach access regulation. Measures that limit human trampling in dune systems need to be supported by stakeholders but have been proven to be effective in allowing plant community recovery even in a short time span. The resilience of xerophilous grasslands of grey dunes could be also enhanced through the filling of vegetation gaps with new plantations of native perennial species to increase biotic resistance. Perennial species permanently occupy the site and form steady communities over time thereby reducing niche vacancy.

By incorporating multicausality, the integrative approach used in this study is a key step for understanding the ecological processes that drive IAPs invasion as well as for mitigating IAPs impacts, predicting invasion vulnerability and finding strategies to anticipate their spread. Given the threats exerted by the increasing number of IAPs, predicting invasion risk represents an unavoidable tool for ecologists, land managers and regulators.

In this regard, although our study specifically focused on *O. stucchii*, it is worth recall that it shares biological and ecological traits with several phylogenetically related species belonging to the sect. *Oenothera* subsect. *Oenothera*; this makes our predictions potentially applicable to functionally similar congeners.

CRediT authorship contribution statement

Gabriella Buffa: Conceptualization, Methodology, Funding acquisition, Writing - original draft, Writing - review & editing. **Carlo Gaetan:** Formal analysis, Writing - review & editing. **Stefano Piccoli:** Investigation. **Silvia Del Vecchio:** Investigation, Writing - original draft. **Edy Fantinato:** Methodology, Investigation, Formal analysis, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107564>.

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Further reading

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