

Habitat type and community age as barriers to alien plant invasions in coastal species-habitat networks

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ABSTRACT

Sand shore ecosystems are extremely vulnerable to alien plant invasions. While most of the abiotic drivers of alien success have been identified, less is known on the role of biological processes driving the invasion. Studying the interactions between alien and native plant communities across different habitats and along the ecological succession (i.e. community maturity) can elucidate the dynamics of alien invasions in dune systems.

In this study, we sampled alien and native plant communities in 100 patches across 10 natural coastal landscapes in NE Italy. The patches represented three main habitat types (foredune, backdune and salt marsh, which differ in terms of sea storm-related disturbance and soil salinity) distributed along a gradient of community maturity (i.e. number of years since the plant community was completely eroded by a sea storm). We analysed the effects of alien/native status, habitat type and maturity on species richness and colonization potential of plant species pools. Colonization potential was estimated by applying for the first time on plant data a species-habitat network approach, which allowed us to assess in detail the effect of each plant community on the others.

In backdune habitats, alien plant species richness was negatively related with community maturity, which in turn had a positive effect on native species richness. Colonization potential was positively influenced by age for native communities and negatively for alien communities in salt marshes. Among habitat types, backdune patches were also particularly prone to alien invasions and very efficient donors of alien plants to other patches. Salt marshes were in general very resistant to invasion but potentially acting as secondary reservoirs for some backdune alien species.

This study identified backdune habitats as key nodes for alien plant introduction and spread in coastal ecosystems, underlining the importance of maintaining mature undisturbed patches as a barrier to alien invasions. This information could prove pivotal in optimizing monitoring and management efforts of alien plant species in these ecosystems, as well as in conservation prioritization.

1. Introduction

Sand shores ecosystems are notable for their unique biodiversity and related ecosystem services, which are increasingly threatened by human activities (Barbier et al., 2011; Brown and McLachlan, 2010, 2002; Defeo et al., 2009; Paprotny et al., 2021; Schlacher et al., 2007). Among the most severe pressures are alien species invasions, which have been demonstrated to be a major threat to ecosystem integrity and

biodiversity (Heywood and Iriondo, 2003; Simberloff et al., 2013; Vilà et al., 2010). Coastal zones are indeed considered one of the ecosystems most prone to invasion by alien plant species (Defeo et al., 2009; Giulio et al., 2020; Lonsdale, 1999; Tordoni et al., 2021). Such invasions may cause severe alterations on coastal ecosystems by modifying their physical processes (Gordon, 1998; Gritti et al., 2006; Macdonald et al., 1989) and their species composition and diversity (Alvarez and Cushman, 2002; Crooks, 2002; Vitti et al., 2020). It thus becomes imperative

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to elucidate the mechanisms that facilitate alien plant invasions, in order to better manage and preserve native biodiversity.

Local factors such as habitat type and disturbance represent the most effective ecological filters that determine the invasion success of alien species. This is especially true in harsh environments such as coastal habitats, where the effects of soil salinity and natural disturbance events can shape plant communities (Marcantonio et al., 2014; Vitti et al., 2020). Besides abiotic factors, plant-plant competition is a key mechanism to regulate plant community assembly during biological invasions (Boscutti et al., 2017; Dillon et al., 2018; Fargione et al., 2003; McLane et al., 2012; Pearson et al., 2018). Both biotic and abiotic factors exert their effect (potentially interactively) on the seed banks and propagules dispersed by alien and native plants in their own habitat patch or spilling over to other habitats (Meiners et al., 2015; Turnbull et al., 2000). The range of propagule dispersal varies according to environmental conditions and plant species traits (Boscutti et al., 2018; Rejmánek et al., 2005; Tamme et al., 2014; Thomas and Moloney, 2015).

A potential solution to elucidate these complex spatial relationships is represented by species-habitat networks, a method recently proposed to study the interactions between entire biotic communities and multiple habitat patches (Marini et al., 2019). This method can describe the whole network structure and the level of habitat specialization of each species (Lami et al., 2021), but it can also elucidate the contribution of individual habitat patches to network structure and function (Nardi et al., 2019), including their role in the network and their ability to influence the biotic communities of other patches through colonization events. This latter information would allow to investigate the relationships between patch features (e.g. habitat type, maturity of the resident plant community) and the ability of the community to resist/trigger new colonization events from or to other communities. Using this tool to compare alien and native species assemblages we would be able to

depict the interplay between susceptibility and resistance to alien invasion.

In this study, we examined plant communities sampled in patches along a gradient of community maturity (i.e. patch age) in the main habitat types of dune systems in Northern Adriatic Sea (Italy). Invasive alien species are in most cases highly successful in disturbed or degraded habitats with empty niches (Marvier et al., 2004; Pellegrini et al., 2021) but are bound to be particularly susceptible to strong environmental barriers that would require specific adaptations to compete with specialized native species (Burns and Winn 2006; Del Vecchio et al. 2015). For this reason, we studied three habitat types (foredune, backdune and salt marshes) that greatly differ in terms of abiotic conditions, mainly due to disturbance regime and soil salinity. Foredune is a highly dynamic habitat strongly shaped by recurrent winter storms that can either disturb or erase the resident plant communities, with a moderate soil salt content. Backdune is more stable and less subjected to extreme weather events, with moderate salinity. Finally, salt marshes exhibit high salinity, high percentage of clay and an absence of seasonal soil disturbance due to sea storms. In general, we expected frequent colonization events (including alien invasions) between patches belonging to the same habitat type, owing to specific biological adaptations to said habitats (Fig. 1). We also expected relatively frequent exchanges between habitats with comparable soil salinity (i.e. foredune and backdune), with salt marshes being more isolated in terms of colonization events, due their extreme salinity conditions (Flowers and Colmer, 2008; Vitti et al., 2020).

Additionally, we expected for mature communities, which have been undisturbed for a long time, to represent a barrier to new colonization events in comparison with younger communities establishing themselves after major disturbances (Lake and Leishman, 2004). Periodic soil disturbances (such as winter storms), even when they do not completely

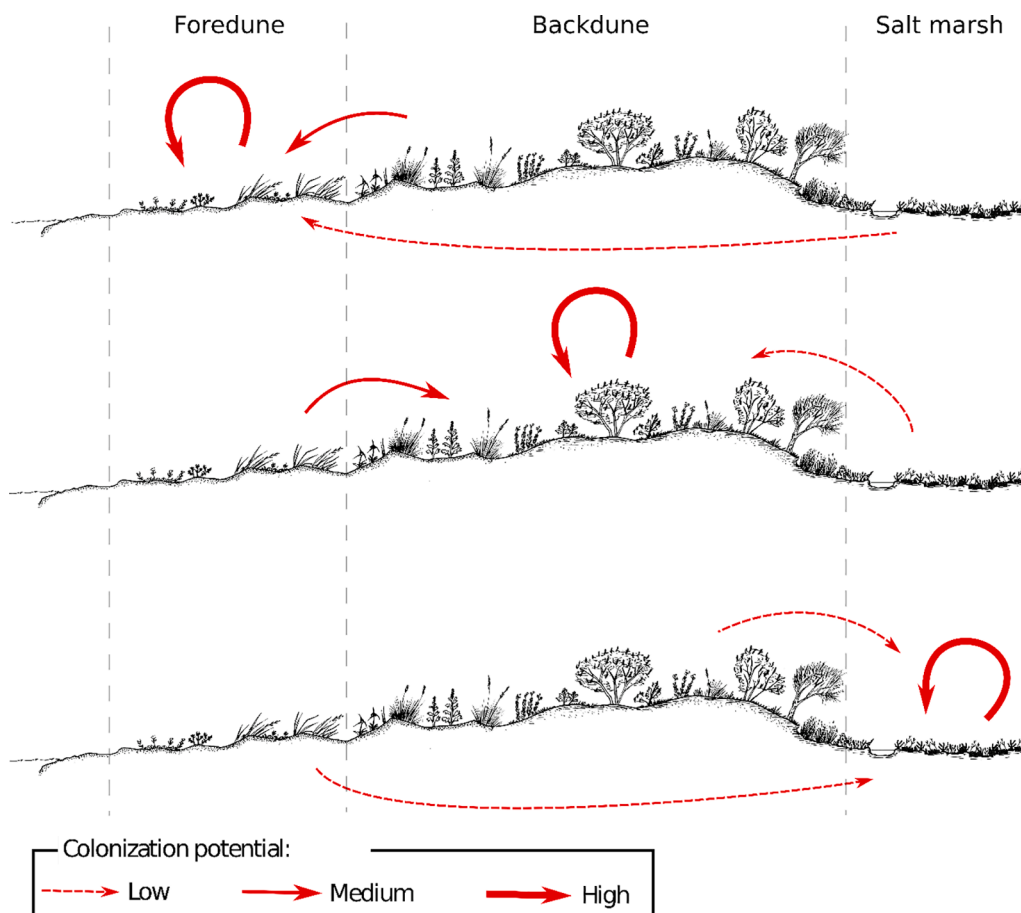


Fig. 1. Hypotheses about the influence that habitat patches (i.e. plant communities) can have on each other in terms of community composition depending on habitat type. Based on plant adaptations to specific ecological conditions, species exchanges are expected to be particularly strong between patches of the same habitat type, and relatively strong between different habitats which share some ecological conditions – for instance, foredune and backdune have relatively similar levels of soil salinity. Exchanges are expected to be very low between habitats that differ in key ecological parameters – for instance, salt marsh soil salinity is significantly higher than in the other two habitats, and this should hinder between-habitat species exchanges.

wipe out the community, are bound to free niches that can be colonized by opportunistic generalists, such as most alien species (Bhattarai and Cronin, 2014; D'Antonio, 1993; Hobbs, 2021; Kotanen, 1997), potentially allowing a more frequent species exchange even between different habitat types. From this point of view, the highly weather-disturbed foredune habitats could be expected to be particularly prone to invasions.

We estimated species diversity and colonization potential separately

for alien and native plant species pools, focusing on the role that each habitat patch had in influencing and being influenced by the plant community of other patches of the species-habitat network. We parsed the effect of the interactions of habitat type and community maturity with plant community status (native or alien). The resulting information could find application in improving the management of invasive species for these fragile ecosystems.

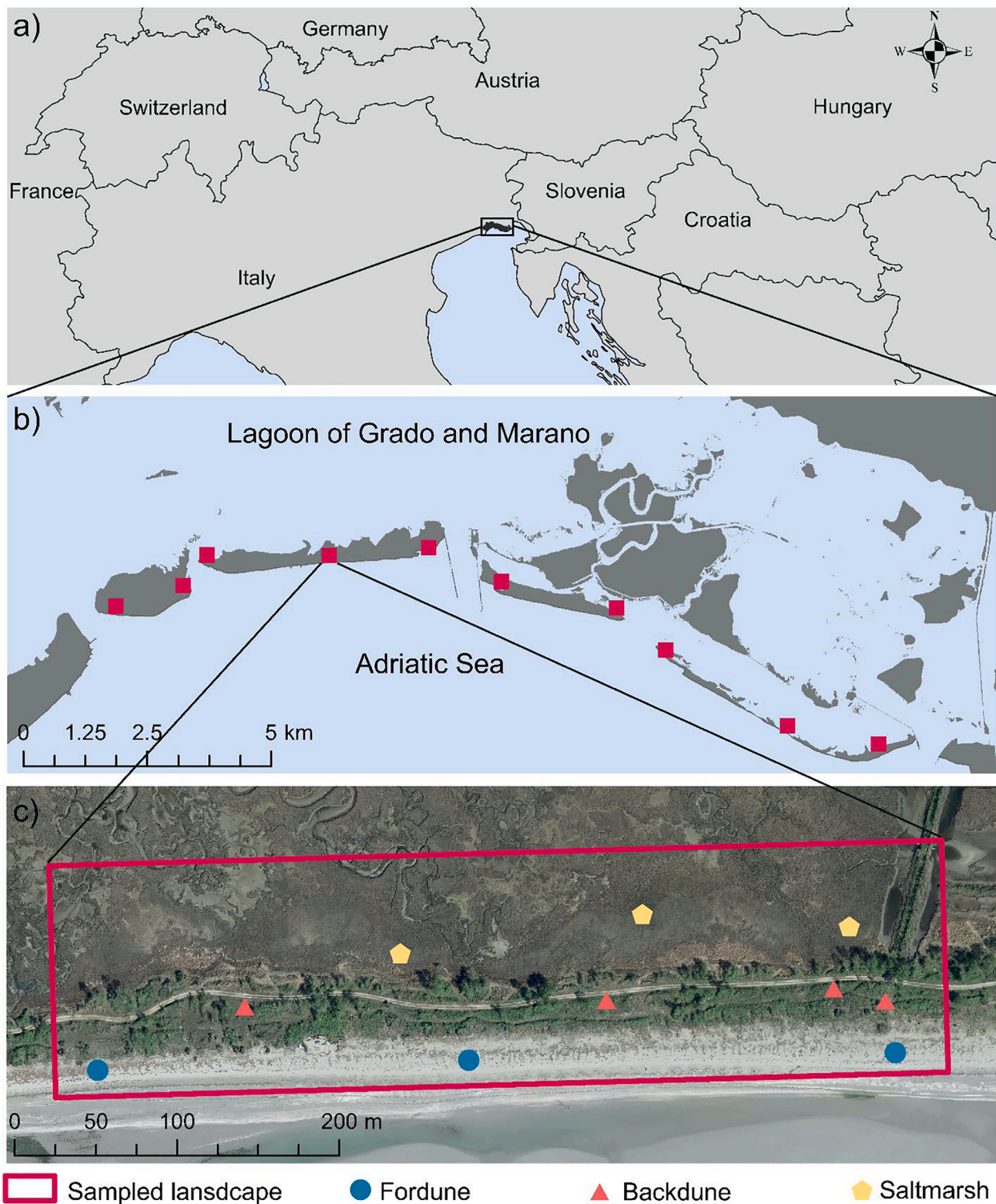


Fig. 2. The study area in the lagoon of Marano and Grado in the northern Adriatic Sea (a), the 10 sampled landscapes spread across 4 of the islands (b) and the 10 sampling plots in one of the sampled landscapes on San Andrea island (c).

2. Materials and methods

2.1. Study area

The study took place on four barrier islands of the Marano and Grado lagoon (from 45°42'10.5"N 13°9'17.8" E to 45°40'49.8"N 13°21'31.2" E) in the Northern Adriatic Sea (Friuli Venezia Giulia, Italy) (Fig. 2). The site is designated as both a Special Area of Conservation (SAC) and a Special Protection Area (SPA) in the Natura 2000 network. The mean annual rainfall is 974 mm, with an average temperature ranging from 3.1 °C in January to 29.0 °C in July.

Tidal movements and alongshore sediment transport interact to make these islands highly dynamic natural systems where both dune and halophile systems coexist. The zonation of the vegetation along the environmental sea–inland gradient can be broadly divided into three main habitats: (i) foredune, including upper-beach, embryo-dunes and mobile dunes (EU Habitat Code 1210, 2110 and 2120), (ii) backdune, fixed dune encompassing those environments dominated by perennial communities of the inland side (EU Habitat Code 2130 and 6420), and (iii) salt marsh (EU Habitat Code 1403 and 7210). These three main habitat types greatly differ in abiotic conditions, mainly due to disturbance regime and soil salinity. These factors are expected to influence plant communities, with the highly disturbed foredune favouring alien generalists, the salt marshes mostly inhabited by extreme soil condition specialists, and backdune (with lower disturbance than foredune but also lower salinity than salt marshes) representing an intermediate scenario. In the study area, the average soil conductivity (used as a proxy of soil salinity) for foredune, backdune and salt marsh habitats was 114.4 $\mu\text{S cm}^{-1}$ (SE = 8.0), 224.8 $\mu\text{S cm}^{-1}$ (SE = 45.9) and 7189.3 $\mu\text{S cm}^{-1}$ (SE = 835.9), respectively. Conductivity was measured by a CM35 + portable conductivity meter (Crison) in soil samples taken from each site (5:1 extracts using 10 g of dry soil and 50 mL of water per sample).

2.2. Sampling design

The sampling was performed during summer 2018 in 10 landscapes (ca. 5 ha each) placed across the shore of the four islands (Fig. 2b). Ten sampling plots (4x4 m) were randomly selected within each landscape (Fig. 2c), for a total of 100 sampling plots. Within each landscape, sampling plots included the three main habitats (foredune, backdune and salt marsh), with the number of plots per habitat reflecting the abundance of each habitat in each landscape, and resulting in a total of 32 plots for foredune, 40 for backdune and 28 for salt marsh.

2.3. Plant community and patch age characterization

In each 4x4 m sampling plot, we recorded the occurrence and cover percentage of all vascular plant species. Species nomenclature follows the most recent checklists for Italian Flora (Bartolucci et al., 2018; Galasso et al., 2018). The status of alien or native was assigned to each species according to Buccheri et al. (2019). For each plot, plant species richness of both native and alien species was calculated (Gotelli and Colwell, 2011).

Plant community maturity in each sampled patch (plot) was considered equivalent to patch age, itself defined as the number of years passed since the last time that the vegetation and the organic soil were completely destroyed by a sea storm, assumed as the start of a new ecological succession. Age of each plot was retrieved by interpretation of historical aerial photos spanning from 1954 to 2018 (available years: 1954, 1970, 1988, 1990, 1994, 2003, 2006, 2011, 2014, 2015, 2017, and 2018). The average age for foredune, backdune and salt marsh sites was respectively 8.4 years (SE = 1.5), 27.7 years (SE = 3.1) and 25.9 years (SE = 3.6).

2.4. Statistical analysis

2.4.1. Network analysis: The colonization potential

Network analyses were performed with the package “bipartite” v2.15 (Dormann et al., 2008) in R 3.6.2 (R Core Team, 2016). For each of the 10 landscapes, a species-habitat network was built using species and sampled habitat patches as nodes, with the strength of the link between a species and a patch represented by the species cover. In order to avoid biases when estimating habitat use for very rare species (Dorado et al., 2011), for this analysis we removed all singletons and doubletons from each network (i.e. species which appeared in only one or two plots in the network, covering less than 1% of their plot).

In order to quantify the influence that the community of each patch had on the others, we used the Potential for Apparent Competition metric (PAC) (Holt, 1977; Muller et al., 1999). PAC was originally developed to study the apparent competition between herbivores that is actually mediated by shared parasitoids in host-parasitoid networks (Morris et al., 2005, 2004). The idea is that host species can influence each other not only through direct competition, but also by acting as a breeding resource for parasitoid species that can then attack other hosts. The concept has also been applied to the study of mutualistic plant-pollinator networks, showing how plants can influence each other (in this case beneficially) through shared pollinators (Carvalho et al., 2014). PAC has been applied successfully to animal species-habitat networks (Nardi and Marini, 2021), and here we suggest to use it to investigate how each habitat patch influences the other patches in terms of plant community composition. In this context, PAC could be considered a measure of colonization potential, as its values are dependent on the species shared by each possible pair of interacting patches. The index formula is identical to the one described by Muller et al. (1999) as implemented in the bipartite v2.14 package in R. The colonization potential of the community in habitat patch j on the community of habitat patch i thus follows the formula:

$$\text{Colonization Potential of } j \text{ on } i = \sum_k \left[\frac{\alpha_{ik} \alpha_{jk}}{\sum_l \alpha_{il} \sum_m \alpha_{mk}} \right]$$

Here, α_{ik} represents the abundance (plant cover) of plant species k in patch i , $\sum_l \alpha_{il}$ represents the total abundance of all plant species in patch i , α_{jk} represents the abundance of plant species k in patch j and $\sum_m \alpha_{mk}$ represents the total abundance of plant species k in the network.

In the case of animals, abundance is generally quantified as the number of individuals (Carvalho et al., 2014; Nardi and Marini, 2021); for plants, quantifying individuals is usually problematic and it is replaced by the use of percentage cover of each plant species (Floyd and Anderson, 1987; van der Maarel and Franklin, 2012). For each plot and each plant species, we therefore had integer numerical values ranging from 0 to 100. In spite of this difference, the interpretation of the metric is similar between plant and animal species-habitat networks, as a higher abundance of a certain species is likely to increase its colonization potential. In plants, the colonization potential is linked with the number of propagules that the species can produce (i.e. propagule pressure) and its dispersal ability, which have been proved to be proportional to the species abundance (i.e. plant cover) (Donnelly et al., 2017; Eschtruth and Battles, 2009; Leishman and Murray, 2001; Rouget and Richardson, 2003; Warren et al., 2013).

Colonization potential values can range between 0 (there is no species exchange, and patches do not influence each other in terms of community composition) to a theoretical maximum of 1, with higher values corresponding to a higher influence in terms of community composition – i.e. the influence of patch j on patch i increases if plant species of i are abundant in j . Each value of colonization potential refers to a couple of patches: one donor and one target. A higher colonization potential therefore corresponds to a higher colonization ability of the donor patch community and a higher colonization susceptibility of the target patch community. The influence between patches is directional, e.

g. some patches might exert an influence (high colonization ability) on other patches and be very weakly influenced in return (low colonization susceptibility). This means that in most cases the colonization potential corresponding to a patch pair where patch *i* is the donor and patch *j* is the target (colonization ability of *i* and colonization susceptibility of *j*) will be different from the colonization potential corresponding to patch pair where *j* is the donor and *i* is the target (colonization ability of *j* and colonization susceptibility of *i*).

We were particularly interested in quantifying alien community colonization patterns in contrast to native communities. For this reason, the index was calculated for alien and native plant communities, separately. This is a common practice in alien species ecology studies focusing on a variety of community features, including taxonomic and functional diversity, abundance and distribution (Arévalo et al., 2005; Boscutti et al., 2018; Geppert et al., 2021; Marini et al., 2009; Okimura and Mori, 2018; Pellegrini et al., 2021).

2.4.2. Effect of spatial distance on community composition

The dissimilarity between communities (i.e. β -diversity) was calculated separately for alien and native plants by using the Bray-Curtis dissimilarity index (Bloom, 1981). To test for spatial autocorrelation in species composition for both alien and native communities, we used a Multiple Regression Matrices (MRM) analysis (Lichstein, 2007) for each network, with the response matrix being the β -diversity matrix and the explanatory matrix being the matrix of geographic distances (in meters) between patches. The analysis was run for both the entire dataset (used for the species richness) and for the dataset with removed singletons and doubletons (used for the colonization potential), and was carried out with the ecodist v2.0.7 package (Goslee and Urban, 2007) in R 3.6.2.

2.4.3. Effects of habitat type and community age on plant diversity and colonization

The effects of patch age and plant community status (alien vs. native) and their interaction on species richness in each habitat type were tested with generalized linear mixed-effects models assuming a Poisson distribution (Models 1–3), with landscape and patch identity being included as nested random factors. Habitat types were tested in separate models due to the lower mean patch age for foredune in contrast to the other habitats, inducing possible age-dependent bias for the model including the interaction of habitat factor. Model assumptions were checked using the DHARMA package (Hartig, 2021) in R 3.6.2. We checked for spatial autocorrelation in the residuals using Moran's I test (Legendre and Legendre, 2012) and found no evidence for spatial autocorrelation (p -value > 0.05) for models 1 and 3 (foredune and salt marsh). As model 2 (backdune) showed significant spatial autocorrelation (p -value = 0.002), we additionally re-ran it including also latitude and longitude as explanatory variables; the results were comparable with the original model, and latitude and longitude did not have significant effects (Table A.1).

As for colonization potential, we focused on the effects of donor patch habitat type and target patch age, and thus fitted three linear mixed-effects models, one for each possible target habitat type (Models 4–6). Before proceeding, we excluded from the datasets all colonization potential values for which the donor patch hosted no plant species. In all models we tested the effects of the interaction between plant community status and target patch age, as well as the effects of the interaction between community status and donor patch habitat type. Consistently with previous models, landscape and target patch identity were included as nested random factors. In all 3 models, the response variable was log-transformed to meet model assumptions. We further conducted post-hoc tests for significant interactions between community status and donor habitat type, by calculating pairwise comparisons with a Tukey adjustment in the package emmeans v1.4.4 (Lenth, 2021) in R 3.6.2.

All models were analysed using the packages nmlme v3.1.142 and lme4 v1.1.21 (Pinheiro et al., 2021) in R 3.6.2.

3. Results

3.1. Species richness and β -diversity

We recorded 97 plant species (73 native and 24 alien) across the 100 surveyed plots. Species richness in foredune (average \pm standard deviation: 7.7 ± 3.2) and backdune habitats (9.2 ± 2.7) was significantly higher than in salt marshes (5.7 ± 2.3) ($p < 0.05$). For a more detailed report and a full inventory of plant diversity in the studied areas see Vitti et al., 2020.

Results of MRM analysis were comparable between the complete dataset and the dataset without singletons and doubletons (Table A.2). In both cases, community similarity was significantly influenced by spatial distance for 4 out of 10 landscapes in the case of native communities, and only in 1 out of 10 landscapes in the case of alien communities.

3.2. Effect of patch age on species richness

We detected a significant interaction between plant status (i.e. alien vs. native) and patch age on backdune species richness (Table 1, Fig. 3). In this habitat, native species richness increased and alien species richness decreased with patch age. This interaction was not significant in neither foredune nor salt marsh habitats, although there was a significant effect of age and status on species richness in salt marsh when the interaction was removed ($p < 0.01$), with an overall decrease in species number with increasing patch age and native communities being overall more species-rich than aliens.

3.3. Colonization potential

Colonization potential values, indicating the ability of plant communities to shape other communities through colonization, ranged from 0 to 0.7, with roughly 78% of the data points showing values lower than 0.1.

The interaction between plant community status and target patch age had significant effects on the colonization potential only for salt marsh habitats (Table 2), in which colonization potential tended to increase for native communities and decrease for alien communities in old stands (Fig. 4c).

There were significant interactive effects of community species status and donor patch habitat on the colonization potential directed at all three possible target habitat types (Table 2, Fig. 4d-f). The alien and native communities of target foredune patches were mostly influenced by other foredune patches, with a lower influence from backdune and from salt marshes (Fig. 4d). In the case of donor backdune patches the colonization potential of alien communities was significantly higher than the colonization potential of native communities.

Backdune communities were also mainly influenced by other patches

Table 1

Results of the generalized linear mixed-effects models testing the effects of plant community status (alien/native) and community maturity (patch age) on plant species richness in the three habitat types.

		Estimate	Std. Error	z value	Pr(> z)
Foredune	<i>Model 1</i>				
	Status	0.218	0.183	1.189	0.235
	Patch Age	0.004	0.014	0.280	0.780
	Status X Patch Age	0.009	0.015	0.616	0.538
Backdune	<i>Model 2</i>				
	Status	-0.157	0.189	-0.832	0.406
	Patch Age	-0.010	0.005	-1.984	0.047
	Status X Patch Age	0.020	0.006	3.433	<0.001
Salt marsh	<i>Model 3</i>				
	Status	2.332	0.644	3.623	<0.001
	Patch Age	-0.043	0.032	-1.374	0.169
	Status X Patch Age	0.032	0.032	1.001	0.317

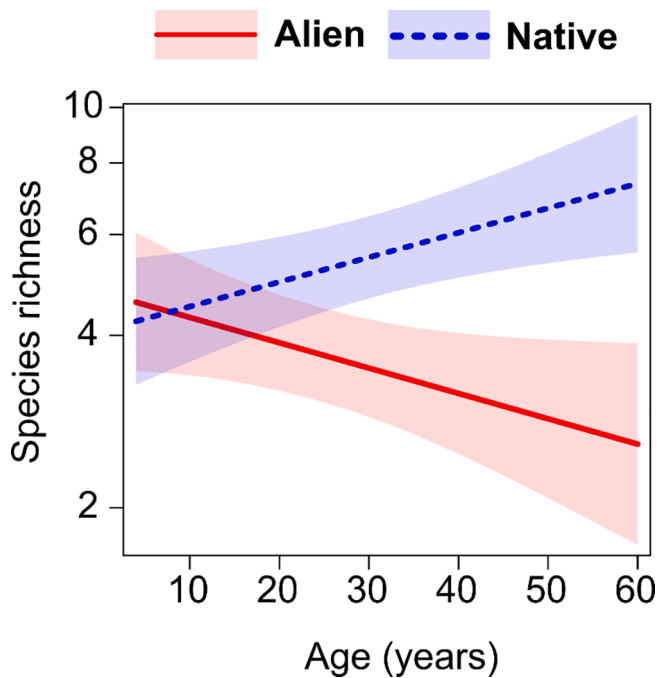


Fig. 3. Effect plot showing the influence of community maturity (patch age) on alien and native plant species richness in backdune habitats.

Table 2

Results of the linear mixed-effects models testing the effects of plant community status (alien/native), donor habitat type and target community maturity (patch age) on colonization potential towards the three habitat types. Colonization potential was log-transformed to meet model assumptions, according to the formula $\log(X + 0.01)$.

		df	F-value	p-value
Foredune target	<i>Model 4</i>			
	Target age	1, 21	0.391	0.538
	Status	1, 470	0.086	0.769
	Donor habitat	2, 470	46.123	0.000
	Target age X Status	1, 470	0.083	0.773
	Status X donor Habitat	2, 470	4.365	0.013
Backdune target	<i>Model 5</i>			
	Target age	1, 29	3.296	0.080
	Status	1, 595	7.032	0.008
	Donor habitat	2, 595	40.709	0.000
	Target age X Status	1, 595	1.308	0.253
	Status X donor Habitat	2, 595	6.597	0.002
Salt marsh target	<i>Model 6</i>			
	Target age	1, 17	3.432	0.081
	Status	1, 428	9.373	0.002
	Donor habitat	2, 428	10.126	0.000
	Target age X Status	1, 428	16.545	0.000
	Status X donor Habitat	2, 428	89.371	0.000

of backdune communities, and only secondarily influenced by salt marsh and foredune communities (Fig. 4e). In cases pertaining to target backdune habitats, the colonization potential of alien communities was significantly higher than the colonization potential of native communities for salt marsh and backdune donor patches (Fig. 4e, Fig. 5).

The most glaring difference in patterns of colonization potential between alien and native communities was detected for salt marsh target patches. On the one hand, the native plant community of salt marshes was almost exclusively influenced by other salt marsh patches, with the contribution of foredune and backdune patches being negligible. On the other hand, the colonization potential of all three habitat types on salt marsh alien communities was relatively low, but was significantly higher than native communities for backdune patches (Fig. 4f, Fig. 5).

4. Discussion

Our study found significant effects of habitat type and community maturity (patch age) on the richness and colonization abilities of coastal plant communities, with the effects often being different between native and alien species communities. Habitats along the sea-inland gradient differently contributed to alien plant invasion, in relation to their species assembly, with backdune playing a pivotal role in colonization processes of the whole dune system. Species richness of this key habitat was further modulated by patch age, suggesting an increasing resistance to alien invasion along the ecological succession generally associated with an increase of native species diversity.

4.1. β -diversity and species richness dynamics

Native community composition was significantly influenced by spatial distance between patches more frequently than alien communities. This could be explained by differences in dispersal limitation, as alien species tend to have higher dispersal abilities than native species (Boscutti et al., 2018; Lake and Leishman, 2004). In fact, dispersal ability is often a defining factor for an alien species to successfully become invasive (Nathan et al., 2008; Wang et al., 2011), and our results suggest that coastal ecosystem invaders are no different in that regard.

As for species richness, community maturity in backdune patches generally favoured native plant species, as expected based on evidence from other ecological successions (Boscutti et al., 2017; Bruelheide et al., 2011; Purschke et al., 2013). Species richness, in fact, increased with patch age for native plants and decreased for alien plants. At the early stages, the soil disturbance triggering the succession creates new available niches and subsequently a rapid increase of generalist species, such as annual and alien plants, as observed in many disturbance experiments (Debussche et al., 1996; Della Longa et al., 2020; Geppert et al., 2021; Lososová et al., 2004; Oshima and Takahashi, 2020). The bare soil favours the germination of the seed bank that, in invaded ecosystems, is known to be dominated by alien plant seeds rather than native ones (Borokini et al., 2020), also on sand dunes (Gioria et al., 2014; Marchante et al., 2011). In the late successional stages, however, native species with specialized traits prevail over generalist alien colonizers, less adapted to the environmental stability (Fargione et al., 2003).

No significant interaction between community status and patch age was detected on the species richness of foredune and salt marsh habitats. In the case of foredune this might be related with the high frequency of weather-related disturbances, which led to a much lower average community age when compared to the other habitats. This means that foredune communities are frequently destroyed and recolonized by generalist alien and native species, and rarely reach a more mature and stable stage of the succession, in which native species outcompete alien species.

The lack of significant effects of the interaction between patch age and community status on the species richness of salt marshes, instead, is likely caused by the extreme environmental conditions of this habitat, such as high salinity and soil water logging, which determine the community assembly and species growth responses (Pellegrini et al., 2018; Vittori Antisari et al., 2017). In particular, soil salinity was already observed to curb plant invasion and acting as a filter, and selecting over time only the most specialized species among all possible colonizers (Chaneton et al., 2002; García et al., 1993; Ren et al., 2014; Vitti et al., 2020). This resulted in a very low number of alien species being able to survive, and a higher (but still limited and lowering with age) number of native specialists occupying most of the available niches.

4.2. Effects of donor habitat type and patch age on plant-habitat colonization potentials

Donor patch habitat type significantly influenced colonization

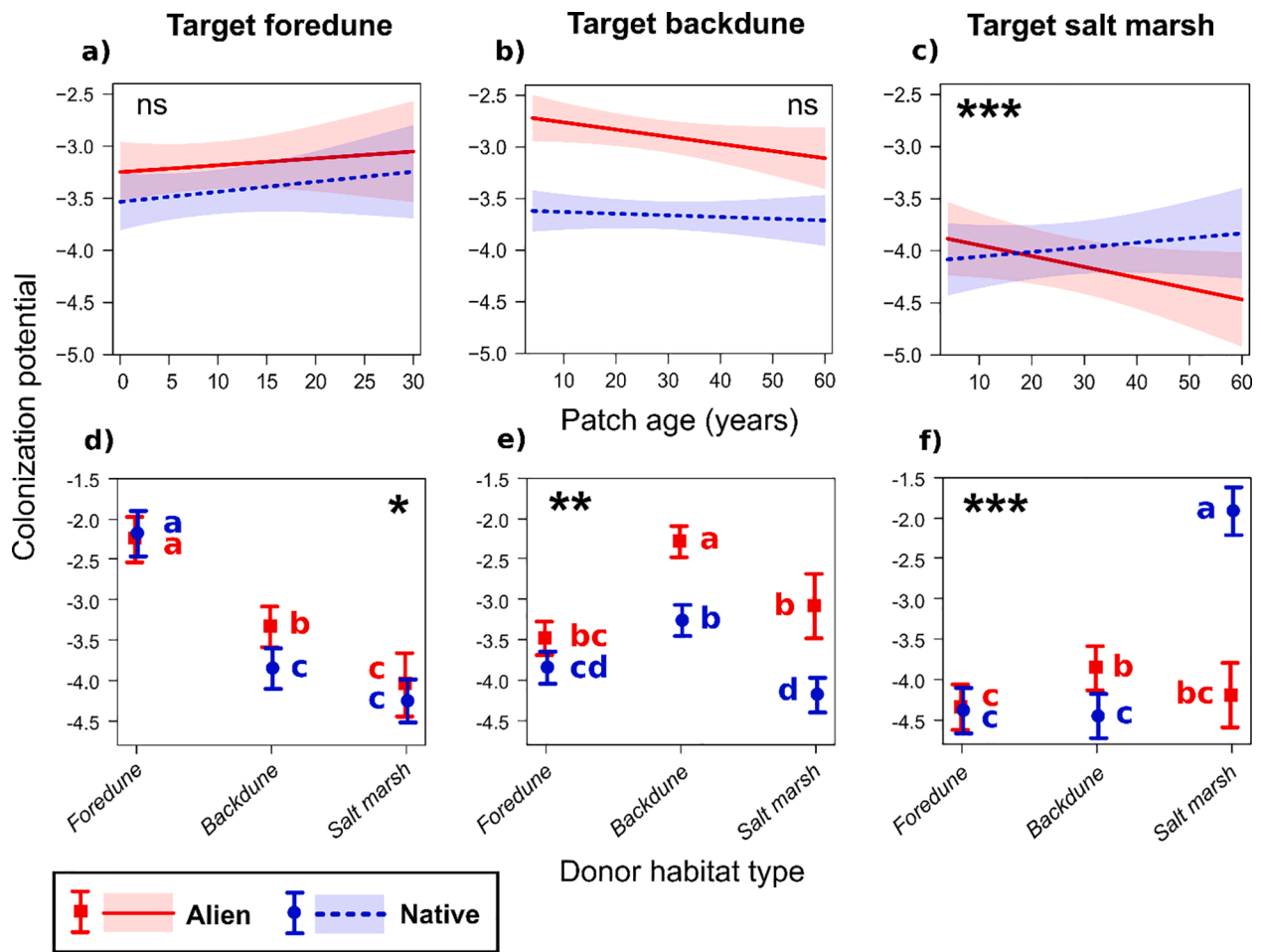


Fig. 4. Effect of donor habitat type on colonization potential of alien and native plant communities in the three possible target habitats according to patch age (a, b, c) and donor habitat type (d, e, f). * = $p < 0.05$; ** $p < 0.01$; *** = $p < 0.001$; ns = Not significant. Colonization potential was log-transformed to meet model assumptions; untransformed colonization potential values ranged from 0 to 0.7. Different letters indicate statistical differences according to the pairwise comparison test with Tukey adjustment ($p < 0.05$).

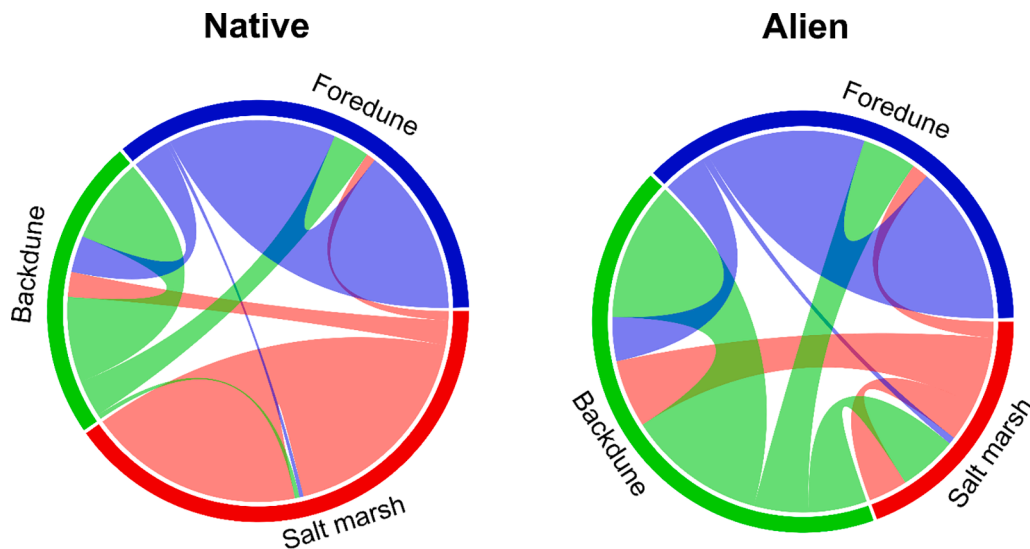


Fig. 5. Chord diagrams representing native and alien colonization potential (averaged between patches) of the three main habitat types. Band color corresponds to donor habitat color, and band size is proportional to average colonization potential value.

potential between patches. Backdune habitats appeared to be the focal nodes for alien plant invasion and diffusion in coastal networks, being an important target and source of alien colonization for other backdune, foredune and even salt marsh patches. This defied our original prediction of foredune habitats being the main focal points for coastal alien invasions owing to the more frequent weather-related disturbances and the mild soil stress conditions (e.g. salt content). On the one hand, foredune receptiveness to alien plant community colonization from other foredune patches is high, but comparable to its receptiveness to native plant community colonization. It is plausible that the higher frequency of disturbance events occurring in foredune might favour not only generalist alien fast colonizers, but also a number of native species specialized for these conditions (Ciccarelli, 2014; Perumal and Maun, 2006). Alien communities of backdune habitats, on the other hand, had a significantly higher ability than native communities to influence the species composition of foredune patches through colonization, remarking the important role of backdune for coastal alien invasions. This is consistent with observations by Polo-Ávila et al. (2019) about the propagule density of backdune habitats (i.e. ecotone between the salt marshes and coastal dunes), suggesting that it acts as a propagule sink habitat. We propose that, rather than remaining mere sinks, in certain contexts these habitats can develop into central crossroads for the spread of alien species in coastal landscapes.

Salt marshes were further confirmed as alien-resistant habitats, with a significant low susceptibility to alien colonization from all habitats. However, a surprising and noteworthy pattern emerged when considering the relationship between salt marshes and backdune: while native salt marsh communities had the potential to almost only colonize other salt marshes, alien salt marsh communities had a relatively high potential for the colonization of backdune and they were influenced at least as much by backdune as by other salt marshes. This suggests that the limited number of alien species hosted by salt marshes mostly comprised backdune colonizers with a certain tolerance to salinity (e.g. *Sporobolus pumilus* (Roth); Casolo et al., 2015). These salt marsh communities thus ended up acting as secondary reservoirs from which the alien species can potentially continuously recolonize backdune patches.

Finally, colonization potential was significantly affected by target patch age only in salt marshes, highlighting the usefulness of preserving mature salt marsh patches to reduce the contribution of this habitat type to alien species spread. As abovementioned, community assembly of mature patches is thought to be less prone to the invasion of new species, favouring competitive species (*sensu* Grime, 1973). The results for foredune and backdune thus contrasted with our expectation for more mature communities to be more resistant to colonization. Even though community maturity did not seem to limit the colonization abilities of existing alien communities in these habitats, it must be remembered that, as explained in section 4.1, it was negatively linked with the number of alien species hosted by backdune habitats. With the colonization potential analysis highlighting the critical role of backdune habitats in coastal alien invasions, it can be concluded that mature backdune communities can indeed play an important role in limiting invasions.

4.3. Conclusions

The novel information provided by this study through the species-habitat network approach could be applied to the management of invasive alien species and coastal ecosystem conservation in general. Even though the strongest species exchanges tended to occur between habitats of the same type, backdune habitats were identified as key nodes for alien plant invasions and diffusion to other habitats, with salt marshes potentially acting as secondary reservoirs for certain alien backdune species, but becoming more resistant to invasions with community maturity. Additionally, plant community maturity was confirmed to influence alien and native species richness in the key backdune habitats, with younger communities hosting more alien

invasive species. This knowledge will help to prioritize habitat patches for monitoring actions or alien eradication efforts depending on their habitat type or age, also revealing the necessity to preserve mature integer backdune and salt marsh habitats as a barrier to novel invasions.

CRediT authorship contribution statement

Francesco Lami: Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft. **Stefano Vitti:** Conceptualization, Methodology, Investigation, Data curation. **Lorenzo Marini:** Methodology, Writing – review & editing. **Elisa Pellegrini:** Investigation, Data curation. **Valentino Casolo:** Supervision, Funding acquisition. **Giacomo Trotta:** Investigation, Data curation. **Maurizia Sigura:** Supervision, Funding acquisition. **Francesco Boscutti:** Conceptualization, Methodology, Investigation, Data curation, Funding acquisition, Supervision, Visualization, Writing – review & editing.

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.2021.108450>.

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