Received: 10 July 2019 | Revised: 30 October 2019 | Accepted: 19 February 2020
DOI: 10.1111/avsc.12490

RESEARCH ARTICLE

Applied Vegetation Science
IAVS

Alien flora across European coastal dunes

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Funding information
ATRA was supported by the Grant of Excellence Departments, MIUR Italy (article 1, *subsection* 314–337, law 232/2016), MCar by a Rita Levi Montalcini Grant, MIUR Italy, JAC, JL and CorMar were funded by the Basque Government (IT936-16), MCh and CorMar by grant no. 19-28491X of the Czech Science Foundation, and JP and PP by grant no. 19-28807X of the Czech Science Foundation and long-term research development project RVO 67985939 (The Czech Academy of Sciences).

Co-ordinating Editor: Ingolf Kühn

Abstract

Questions: The spread of alien plant species is one of the main threats to the biodiversity of different natural habitats, and coastal dune habitats are among the most affected. There is a considerable local and regional variation in the level of alien plant invasion on coastal dunes. We asked what are the patterns of invasion across European coastal dunes and how they depend on habitat types and coastal regions.

Location: Atlantic, Baltic, Black Sea and Mediterranean coasts of Europe.

Methods: We used vegetation-plot records from shifting dunes and stable dune grasslands extracted from the European Vegetation Archive (EVA). We quantified richness, frequency and distribution of alien plant (neophyte) species across dune habitats and coastal regions. We also explored the donor habitats and invasion trajectories of these species.

Results: In the flora of European coastal dunes, 7% of species were neophytes, for two-thirds originating from outside of Europe and mostly naturalised and ruderal. Shifting and stable dunes were similar in neophyte species composition, but there were more individual occurrences of neophytes in shifting dunes. The neophyte flora composition differed considerably between the Atlantic, Baltic, Black Sea and Mediterranean regions. The highest number of neophyte species was observed on the Atlantic dunes, while the highest number of neophyte occurrences was on the Black Sea dunes. Most of the neophytes originated from North America and the Mediterranean-Turanian region. *Erigeron canadensis*, *Xanthium orientale*, *Oenothera biennis* and *Oenothera oakesiana* were the most common neophytes.

Conclusions: We provided a comprehensive assessment of alien plant invasions in the coastal dunes across Europe and highlighted that coastal dunes should be in the focus of European invasion management strategies.

KEYWORDS
alien flora, Atlantic, Baltic, Black Sea, coastal dune habitats, Mediterranean, neophyte, non-native, plant invasion, vegetation-plot data

1 | INTRODUCTION

The homogenising force of globalisation has triggered a massive spread of species to areas outside of their native ranges (van Kleunen *et al*., 2015). Many plant species have become naturalised in new areas, overcoming local abiotic and reproductive barriers to establish self-sustained populations. A subset of these species have become invasive, spreading across considerable distances (Richardson *et al*., 2000) and causing impacts on wildlife, plant biodiversity, and ecosystem functioning (Vilà *et al*., 2011; Blackburn *et al*., 2019). Plant invasions are known to be promoted by humans both directly through species introductions and indirectly through anthropogenic alterations of the environment (Thuiller *et al*., 2006; Rodríguez-Labajos *et al*., 2009; Pyšek *et al*., 2010). In Europe, the rapid increase in human settlements and activities in coastal areas has thus caused not only habitat loss (Heslenfeld *et al*., 2008) but also the introduction of many alien plants (Campos *et al*., 2004; Carboni *et al*., 2010). As a consequence, sandy shores are now among the most invaded European terrestrial environments (Chytrý *et al*., 2008, 2009). Thus, the highly specialised flora of coastal dunes, which in Europe includes many narrow-niched endemics (van der Maarel and van der Maarel-Versluys, 1996), is currently under serious threat. In light of this, several European countries are expressing the need for a European dune network in the context of the Natura 2000 system of protected areas (European Commission, 2018), including an early warning system for invasive alien species. However, little is still known about the current patterns of diversity and distribution of alien flora on the European coasts at a broad geographical scale.

Coastal dunes are characterised by a strong sea–inland environmental and biotic gradient and by disturbances, which occur at a variety of scales and potentially affect habitat vulnerability to invasions. Different habitat types (further also "habitats") that occur in the coastal zone are shaped and defined by distinct processes (Jiménez-Alfaro *et al*., 2015) and display contrasting diversity patterns (Torca *et al*., 2019). The effects of marine aerosol and winds decrease from the sea to the back-dune habitats, while other factors, such as grazing pressure from wild herbivores and livestock, arable cultivation, afforestation, settlement and tourism, can increase towards the back-dunes. Furthermore, because the coastal vegetation is strongly influenced by the sea–inland gradient and less so by climate ("azonal" vegetation; Del Vecchio *et al*., 2018), it is largely homogenous and comparable across Europe and neighbouring areas. Still, differences in macroclimate, history and socio-economic background between regions influence the floristic composition (Del Vecchio *et al*., 2018; Marcenò *et al*., 2018) and invasion patterns (Chytrý *et al*., 2009). All these conditions provide a unique research framework to study invasion phenomena in the same ecosystem type but across different characteristic habitats and coastal regions.

Alien species are in some cases intentionally planted on dunes for ornamental purposes, but more commonly they are unintentionally dispersed by human visitors (Carboni *et al*., 2011; Weeda, 2010). These plants may come from other parts of the world, as well as from inland habitats of the same continent (Nielsen *et al*., 2011; Prisco *et al*., 2016; Remke *et al*., 2009; Valcheva *et al*., 2019). Intercontinental trade is considered the main global driver of invasions (Seebens *et al*., 2015; Westphal *et al*., 2008), but geographic invasion trajectories are not known for specific dune habitats. Identifying the most successful invasion trajectories of alien species in European coastal dunes is important because by understanding the mechanisms that drive plant invasions, we might be able to apply more targeted control measures in these systems.

Thus, in this study we analyse, for the first time, the composition of the alien flora of the coastal dunes all around Europe, using data from the European Vegetation Archive (EVA), a large repository of multiple vegetation-plot databases (Chytrý *et al*., 2016). We addressed the following questions: (a) what is the pattern in the level of invasion across the coastal dunes surrounding Europe? (b) are European coastal dunes invaded mainly by coastal specialists or by plants that are also found in inland habitats in their native ranges? (c) what geographic invasion trajectories do these species follow from donor areas to recipient dunes? and (d) what is the degree of overlap in alien species across different dune habitats and European regions?

To answer these questions, we first considered the patterns of (a) the dune systems of all the European coastal zones as a whole. Then we inspected how each pattern varied across (b) coastal dune habitat types, i.e. shifting dunes and stable dune grasslands; and (c) the main European coastal regions.

Based on previous knowledge, we postulated specific expectations for each of our four questions. First, because of the ecological variability of coastal dune habitats and climatic regions of Europe, we should observe different levels of invasion in different European coastal dune habitat types and in different biogeographical regions. Second, considering the peculiar and harsh conditions that strongly shape the native flora of these habitats, we expect the invading species to be specifically adapted to coastal environments. Third, because on the European continent the alien species originating from outside of the region outnumber those with European origin (van Kleunen *et al*., 2015, but see also Lambdon *et al*., 2008), we expect that European coastal dunes are more likely colonised by alien plants originating from outside of Europe as well (sampling hypothesis; Wagner *et al*., 2017). Finally, based on the previous assumptions, we also expect different groups of alien species to be specific to each habitat and coastal region combination, resulting in little overlap across habitats and regions.

2 | METHODS

2.1 | Study area

The study area includes all the European coastal dune systems, depending on data availability (Figure 1). In addition, we also considered the non-European coasts of the sea basins that border Europe. The area can be divided into four coastal regions: Atlantic, Baltic, Black Sea and Mediterranean (the latter including the coasts of North Africa and the Middle East). We focussed specifically on the two most

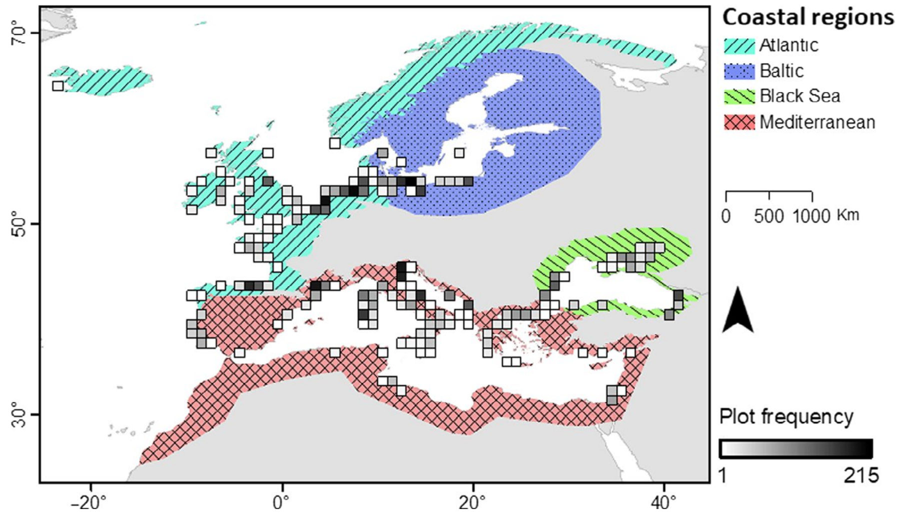

FIGURE 1 Plot distribution in resampled dataset across the four coastal regions. Plot frequency shown in a one-degree resolution grid [Colour figure can be viewed at wileyonlinelibrary.com]

characteristic and dynamic habitat types in the coastal dune vegetation zonation (Marcenò *et al.*, 2018): B1.3. *Shifting coastal dunes* and B1.4. *Coastal stable dune grasslands* (*grey dunes*), according to the habitat classification of the European Nature Information System (EUNIS; Janssen *et al.*, 2016; see also Feola *et al.*, 2011). Shifting coastal dunes (B1.3) are partly covered by open grasslands, modelled by wind and occasionally subjected to inundation by tides and waves. Stable dune grasslands (B1.4) are covered mainly by perennial grasses, forbs, low shrubs and succulent plants. The degree of disturbance and extent of these habitats vary across Europe. On the Atlantic and Baltic coasts, strong winds have favoured the formation of dunes that may stretch many kilometres inland (Doody, 1991), and a wet climate coupled with their use for livestock grazing has helped create rich grasslands. In the Western Mediterranean, dunes are narrower and were mostly destroyed by recreational and other pressures, while on the coasts of the Eastern Mediterranean and the Black Sea dunes often cannot develop because of rocky shorelines, but they do form close to river mouths, in places as parts of delta systems.

2.2 | Data extraction and classification

An initial dataset of 23,446 georeferenced vegetation plots (relevés) containing 2,035 vascular plant species was extracted from EVA (Chytrý *et al.*, 2016). We selected all plots corresponding to the phytosociological classes (vegetation types) of coastal dune vegetation, i.e., *Ammophiletea*, *Honckenyo-Elymetea arenarii* and *Koelerio-Corynephoretea canescentis pro parte* (compare Marcenò *et al.*, 2018). Each plot was classified at the alliance level (Appendix S1) using the Expert System for automatic classification of European and Mediterranean coastal dune vegetation (Marcenò *et al.*, 2018) run in the JUICE software (Tichý, 2002). Subsequently, the plots were assigned to the corresponding habitat types based on the information about their alliance membership. Using the geographic information system ArcGIS 10.3.1 (ESRI, Redlands, CA, USA), we assigned the plots to one of the four coastal regions (Figure 1). Coastal regions were identified according to the main sea basins, while to trace the boundaries between adjacent regions we followed the map of the European biogeographical regions (European Environment Agency, 2016).

2.3 | Species attributes

First, to characterise the alien species pool, we identified the alien species in relation to the country where each plot was located. The data on the alien/native status of the species were taken from the DAISIE (2009) European Invasive Alien Species Gateway, and verified and corrected using the sources listed in Appendix S2: Table S2.1. Then, the taxa were grouped in categories of biogeographic status (Essl *et al.*, 2018), based on the origin and species residence time: neophyte (alien plant introduced after 1,500; Pyšek and Jarošík, 2005) from outside of Europe, neophyte from within Europe (including the regions bordering the Mediterranean Basin, i.e., North Africa and the Middle East), and other species beside neophytes, including natives, archaeophytes (i.e., introduced before 1,500) and species of unclear origin (cryptogenic). We concentrated our further analyses on neophytes only, as in some regions there is often no clear distinction between archaeophytes and native plants. Some species were both native in some plot records and neophyte from within Europe in other records and were considered accordingly in the calculations. In order to trace geographic invasion trajectories, neophytes from outside of Europe were further grouped into six categories, according to their geographic origin (Central/Southern African, North American, Central American, South American, East Asian, and Oceanian species; Appendix S2: Table S2.2 and Figure S2.1), and neophytes from within Europe into four categories (Atlantic, Euro-Siberian, Balkan-Pontic, and Mediterranean-Turanian species; sources listed in Appendix S2). When a taxon was known to be associated with more than one region of origin, all possible regions were considered. Although we focused our analysis on the entire pool of neophytes, we also split the neophyte species according to their invasion status: casual (species whose occurrence in the wild is limited to human intervention; we considered as casual also the species for which the literature reported insufficient information), naturalised (i.e., able to sustain their populations in the new range without human intervention, based on sources listed in Appendix S3: Table S3.1), and invasive species for which we found documented impacts in coastal dunes ecosystems of Europe (sources listed in Appendix S3: Table S3.2). Finally, to determine if alien species were specifically adapted to sandy coastal habitats, we classified the neophyte species according to the habitat of origin in their native range (donor habitats; based on sources listed in Appendix S3: Table S3.3) into coastal specialists (plants typical of sandy coastal habitats in their native range) and generalists (plants that are commonly found in other habitats besides dunes in their native range).

2.4 | Data filtering

To compare the level of invasion between habitats and regions, we considered only invaded plots, i.e., those that reported the presence of at least one alien plant (2,942 plots; *n* species = 1,283). This was done to correct for potential biases in the comparisons, as most of the EVA data originated from phytosociological surveys (Braun-Blanquet, 1932). Such surveys were mostly focussed on describing native vegetation and thus often followed a preferential sampling, avoiding sites with alien plants, especially in older surveys (Michalcová *et al.*, 2011). The Atlantic shifting dunes, the Atlantic stable dune grasslands, and the Mediterranean shifting dunes were over-sampled compared to the other coastal regions. We partially overcame this bias using the heterogeneity-constrained random (HCR) resampling (Lengyel *et al.*, 2011), stratified across each of these three region–habitat combinations. We set the number of plots for each of these combinations to 300 (a number close to the number of plots in most of the under-sampled region–habitat combinations; Appendix S4: Table S4.1). In this way, we obtained a resampled dataset of 1,727 plots (Figure 1) and 1,200 species. Dataset resampling was carried out through the package "vegclust" (De Cáceres *et al.*, 2010) in the R software (R Core Team, 2018). Plots in the resampled dataset were collected between 1935 and 2015 (mostly after the 1960s in all the coastal regions, Appendix S4: Figure S4.1). Plot size varied, but mostly ranged between 3 and 100 m (Appendix S4: Figure S4.2). Note that our metrics to quantify invasion were not dependent on plot size and were not aimed at assessing trends across time. However, results for the most recent relevés are shown in Appendix S5: Table S5.1.

2.5 | Data analysis

We assessed (a) the levels of invasion; (b) donor habitat types; (c) geographic origins; and (d) distribution of neophytes, always considering the study area from three perspectives: (i) the entire sand dune system; (ii) a comparison of the two dune habitats; and (iii) a comparison of the four coastal regions (Figure 1). To avoid bias in comparisons between habitats and regions, in the first step, we used both the initial and final dataset while in the others, only the final dataset. To quantify the level of invasion, we focused on two main metrics (Catford *et al.*, 2012): percentage in the total species pool in a group (% species) and frequency of occurrence across plots (% occurrences), counting each species record in a plot as one species occurrence (Wagner *et al.*, 2017). To quantify the levels of invasion for the entire study area, we calculated the proportion of neophytes in the species pool, and further decomposed this into casual, naturalised and neophytes with known impacts. To compare the levels of invasion between habitats and regions, we plotted rarefaction curves of absolute richness (interpolated accumulation curves, where the sample is randomised iteratively with increasing number of plots; Colwell *et al.*, 2004) for neophytes and native species for each habitat and region. To understand if donor habitat type was important, we compared the proportion of neophytes that were sandy coast-restricted vs generalists in their native range. To trace the geographic invasion trajectories from donor areas to the recipient dunes, we counted the total number of donated neophytes for (a) each region of origin from (i) outside and (ii) within Europe; and for (b) each recipient coastal region. To quantify the degree of overlap in alien species across habitats and regions, we inspected the distribution of the alien flora through the percentage overlap in neophyte species composition between (a) habitat types in each coastal region; and (b) pairs of coastal regions for each habitat. In each step, we used a two-sided exact binomial test of goodness-of-fit (for small numbers; McDonald, 2014) at $\alpha = 0.05$, to identify significant differences between groups.

3 | RESULTS

3.1 | Invasion levels

All vegetation plots (initial dataset) included 133 neophytes (Figure 2), which represented 7% of all species. The subset of invaded plots was 13% of the total one. The final data set included 125 neophytes, comprising 11% of all species in invaded plots (Appendix S5: Figure S5.1). Most of the neophytes were recorded as naturalised in at least one country (Figure 2a), and 7% of them had documented impacts on biodiversity or ecosystem functions of European coastal dunes. Furthermore, most of them were not restricted to sandy coastal habitats but instead occurred also in other habitat types besides coastal dunes in their native ranges (Figure 2b), and most were from outside of Europe (Figure 2c). In terms of occurrences, neophytes represented 2% of the occurrences of all species (9% of occurrences in the invaded plots; Appendix S5: Figure S5.2), and neophytes from outside of Europe occurred more often than those from within Europe. *Erigeron canadensis* and *Xanthium orientale* were the most common neophytes (Appendix S6). These two species, together with *Oenothera biennis* and *Oenothera oakesiana*, all of American origin, accounted for 44% of all neophyte occurrences.

Species rarefaction curves for the two habitat types (Figure 3) showed that neophyte species' absolute richness was higher in

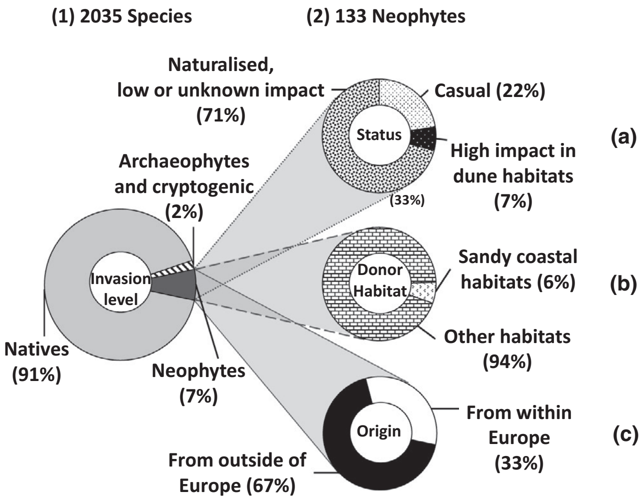

FIGURE 2 Percentages, in (1) entire species pool, of species categories in relation to their origin and residence time; and among (2) neophytes only, of alien species categories in relation to (a) invasion status, (b) habitat in the area of origin, and (c) geographic origin

stable dune grasslands (B1.4) than in shifting dunes (B1.3). In the case of species from outside of Europe, this difference was marginally greater than expected by chance (two-sided exact binomial test of goodness-of-fit: $p = 0.05$; Figure 3a). With increasing sample size, stable dune grasslands also accumulated native species faster than shifting dunes (Figure 3c). However, the percentage of neophyte species (Figure 3d) was similar between the two habitats, and their frequency of occurrence (Figure 3e) was even higher on shifting dunes (B1.3; though the difference in frequency was not greater than expected by chance according to an exact binomial test). The two habitat types also differed in the species composition of neophytes. *Erigeron canadensis* was much more common in stable dune grasslands than in shifting dunes (Appendix S6), while *Xanthium orientale* was the commonest species in shifting dunes, though little represented in stable dune grasslands.

The comparisons of coastal regions showed that the Atlantic region was the richest in neophytes (Figure 4), while the Mediterranean harboured the greatest number of natives. However, in terms of frequencies of occurrence (Figure 4e), Black Sea dunes had the highest invasion level (though again not significantly different from the other regions), indicating that although they hosted fewer neophytes, these species were more widespread. This is especially true for *Xanthium orientale* (Appendix S6), which occurred also on the Mediterranean dunes but was nearly absent elsewhere. The second commonest neophyte on the Black Sea dunes, *Ambrosia artemisiifolia*, did not reach one-third of the frequency of *X. orientale* there. *Erigeron canadensis*, well represented everywhere, was especially common on the Baltic dunes, together with *Senecio leucanthemifolius* and *Lactuca tatarica* (two neophytes from within Europe), while *Oenothera oakesiana* was the most common neophyte on the Atlantic dunes but was not found in the other coastal regions. Among the species of the neophyte genus *Oenothera*, *O. biennis* was the most common in general, mainly found on the Mediterranean dunes but also distributed on the Atlantic and Baltic dunes. *Carpobrotus edulis* was another common neophyte, mainly on the Mediterranean dunes.

3.2 | Habitat specificity

Only 6% of neophytes were specific of sandy coastal habitats (Figure 2b), growing mainly on coastal dunes in their native regions. Instead, most of the neophytes were generalist species, typical of ruderal, disturbed and human-made habitats of coastal and inland regions. This pattern was similar in shifting and stable dune habitats and in all coastal regions.

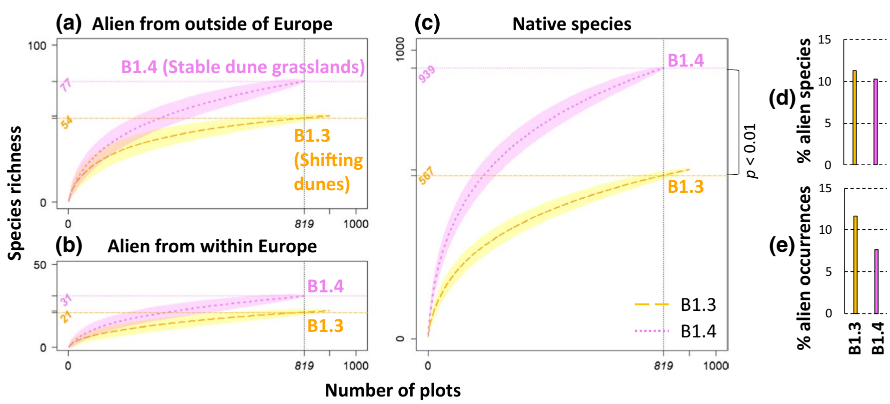

FIGURE 3 Rarefaction curves (with confidence intervals representing twice the standard deviation across randomizations) showing the number of plant species depending on the number of plots for (a) neophytes from outside of Europe, (b) neophytes from within Europe, and (c) natives, with interpolated values of accumulated richness shown for each curve along the y-axis, and the maximum number of plots used to compare the habitats along the x-axis; and bar plots showing (d) the percentage of neophyte species and (e) the percentage of occurrences of neophytes in shifting dunes (B1.3) and in stable dune grasslands (B1.4). When the difference in richness between habitats is significant according to an exact binomial test, significance level is shown [Colour figure can be viewed at wileyonlinelibrary.com]

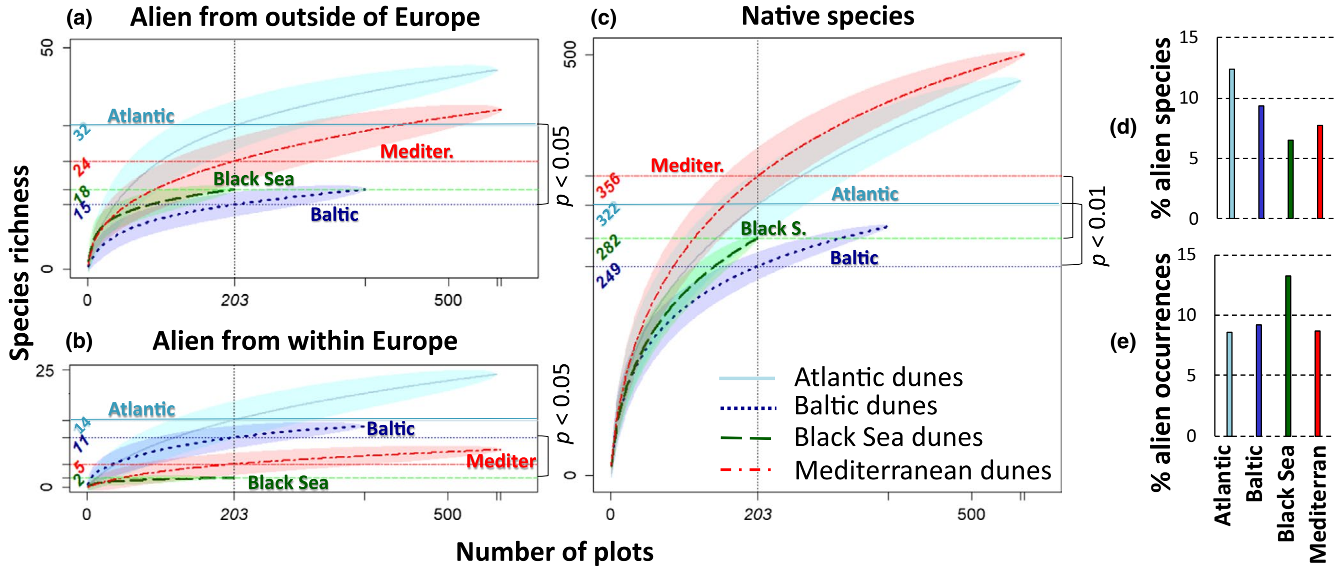

FIGURE 4 Species rarefaction curves (with confidence intervals, representing twice the standard deviation across randomizations) for the neophyte plant species from outside of Europe (a), from within Europe (b) and for natives (c), with interpolated values of accumulated richness shown for each curve along the *y*-axis, and the maximum number of plots used to compare the regions along the *x*-axis; and percentage of neophyte species (d) and frequency of occurrences (e), on the Atlantic, Baltic, Black Sea and Mediterranean coasts. When the difference between regions is significant according to an exact binomial test, significance level is shown [Colour figure can be viewed at wileyonlinelibrary.com]

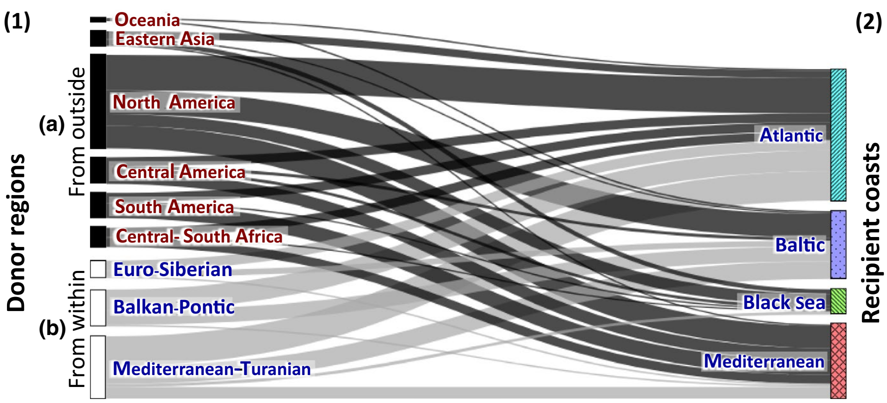

FIGURE 5 Number of neophytes from each (1) donor region (a) outside and (b) within Europe, donated to each (2) recipient coastal region (Sankey diagram) [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Geographic invasion trajectories

Neophytes originating from outside of Europe were significantly more represented than neophytes from within Europe (87 vs 38 species; Figure 2c). The main donor of species was North America (Figure 5), providing 46 neophytes. The second donor was the Mediterranean-Turanian region (34 neophytes). Both these regions donated species to all the coastal regions of the study area, but mostly to the Atlantic one. Then, Central America, South America, South-Central Africa, Eastern Asia (outside of Europe), and the Balkan-Pontic region (within Europe) contributed about a dozen species each. North American species dominated in the neophyte species pools of the Baltic and the Black Sea dunes, South American species reached mainly the Mediterranean dunes, and East Asian and Mediterranean-Turanian species mainly occurred on the Atlantic dunes. Some Mediterranean-Turanian neophytes also occurred in the Mediterranean region itself, as plants from northern Africa colonising southern Europe.

3.4 | Distribution of the alien flora

Many neophytes were shared between the shifting and stable dune habitats, especially in the Black Sea region. Shifting dunes always hosted a lower number of exclusive neophytes (those occurring only in one of the two habitats; Figure 6), but this difference was significant only for the Atlantic and Baltic dunes. In contrast, very few neophytes were shared between pairs of coastal regions (in all cases <19%). These patterns were similar to those of native flora, but in the Black Sea region shifting dunes did not host fewer natives than stable dune grasslands, while Baltic and Atlantic dunes shared a larger percentage of native flora (35%).

4 | DISCUSSION

We compared the levels of plant invasion (question 1) in the most characteristic open coastal dune habitat types (shifting dunes and stable dune grasslands), across the whole of Europe for the first time. Overall, the percentage of neophytes in these environments (7%) can be considered high, and similar values were obtained by Wagner *et al.* (2017) for European woodlands. Not only the percentage of neophytes was high, but also most of the neophytes were naturalised at the country level, and 7% of these had documented negative impacts on European coastal dunes.

We found no significant difference in the level of invasion of the two habitat types (shifting coastal dunes vs stable dune grasslands), neither in terms of percentage of neophytes in the species pool nor in percentage of neophyte occurrences. A similar result was also observed in the Basque section of the Spanish Atlantic coast (Campos *et al.*, 2013). However, we found a marginally significantly higher number of neophytes from outside of Europe in stable dune grasslands, along with significantly higher native species richness. Different studies (Acosta *et al.*, 2009; Bauer and Sherman, 1999; Isermann, 2005; Torca *et al.*, 2019) have previously shown that this is related to the positive correlation between plant species richness and the environmental sea–inland gradient. Indeed, stable dune grasslands hosted more species exclusive of this habitat and not occurring in shifting dunes (for both neophytes and natives).

Patterns in the levels of invasion across coastal regions showed that the Atlantic dunes hosted more neophytes than the other regions, from outside as well as from within Europe. A possible explanation could be related to the Atlantic climatic conditions which might be more favourable for colonising species, such as more constant rainfall supply and lower temperature oscillations throughout the year compared to the other regions. The pronounced urban and socio-economic development of northwestern European regions could be another factor potentially related to high propagule pressure (Vilà and Pujadas, 2001). However, many plants are still expanding their range northwards since the last glacial maximum (Hewitt, 2000). Similarly, the ongoing climate change is expected to exacerbate the northward expansion of species ranges (Lososová *et al.*, 2018). Finally, though the Atlantic dunes were most invaded, the Mediterranean Basin also had a high richness of neophytes on dunes, but mainly from northern Africa and other continents and not from other European regions.

Contrary to our expectation on donor habitat specificity (question 2), most of the neophytes were not restricted to sandy coastal habitats in their native range; rather they were generalist species, often ruderal (sensu Grime, 1979), or more typical of disturbed semi-natural or human-made donor habitats. In fact, the spread of ruderal plants from inland habitats is an increasing phenomenon in the coastal dunes of the northern Atlantic (Nielsen *et al.*, 2011), Baltic (Remke *et al.*, 2009), Black Sea (Valcheva *et al.*, 2019) and Mediterranean regions (Prisco *et al.*, 2016). This process leads to floristic homogenisation and simplification which is probably related to human activities that increase soil nutrient availability (Nielsen *et al.*, 2011; Remke *et al.*, 2009; Valcheva *et al.*, 2019). The most frequent neophytes and the most invasive ones also had wide niche breadths.

Our observations on geographic invasion trajectories (question 3) confirmed the predominance of neophytes from outside of Europe over those from within Europe, as already observed for the whole neophyte flora of the continent (Pyšek *et al.*, 2017; van Kleunen *et al.*, 2015). The azonal nature of the European dune and sandy coastal habitats, which include many species that are native across all the European coastal regions, together with the cosmopolitan or

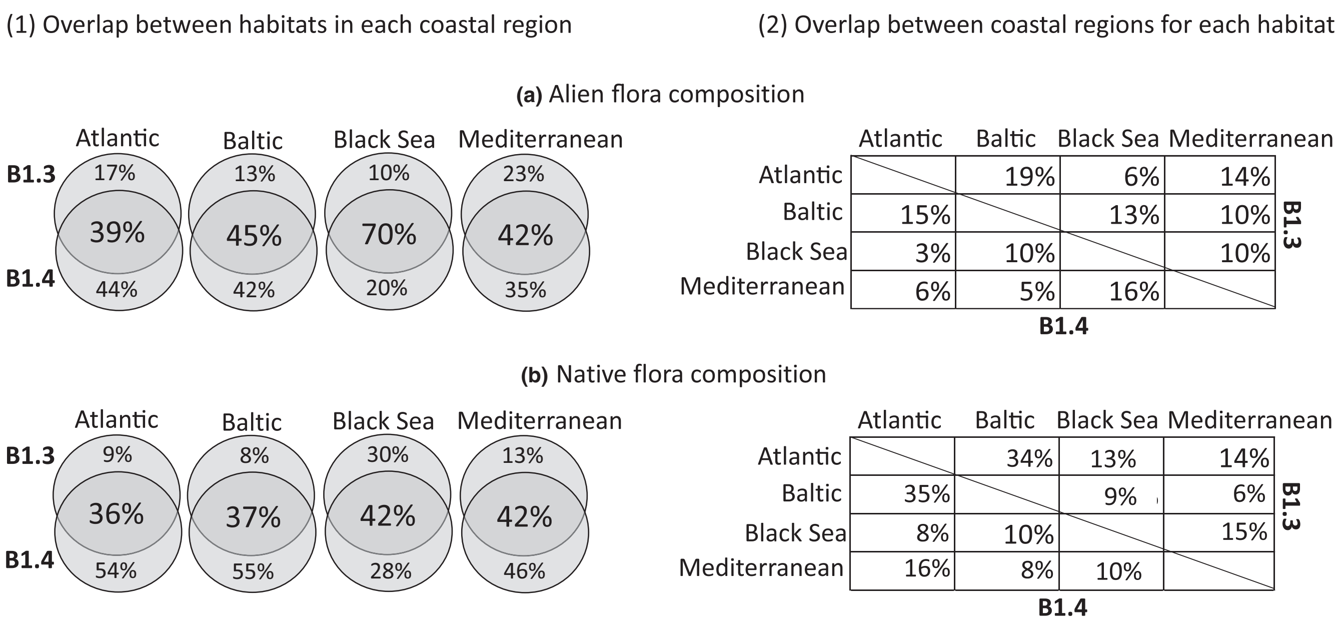

FIGURE 6 Overlap in (a) alien plant species composition and (b) native flora between (1) shifting (B1.3) and stable dune grassland (B1.4) habitats, and between (2) coastal regions, considering the species found in each pair of (1) habitats in each region and then (2) regions in each habitat

subcosmopolitan distribution of many ruderal plants that are considered native across most of Europe, implies that few European plants could be potentially considered alien in some parts of the European coast. Most neophytes came from North America, as previously shown in different European coastal areas (Sobrino *et al.*, 2002; Campos *et al.*, 2004; Acosta *et al.*, 2008). Proximity and climatic similarities between the donor and recipient regions might help understand some geographic invasion trajectories of incoming neophytes. Indeed, relative geographical proximity can explain the high percentage of species from North America on the Atlantic dunes and of the Balkan-Pontic neophytes on the Baltic dunes. A relative similarity in climatic conditions could partially reflect the high percentage of species from North America on Baltic dunes, and the high percentage of species from Central and South America on Mediterranean dunes. However, many Mediterranean neophytes from northern Africa and many others from central or southern Africa also colonised the Atlantic and Baltic dunes, pointing to the involvement of more complex, additional factors in determining invasion trajectories. In particular, socio-economic relationships between human populations are an important introduction pathway worldwide (Vilà and Pujadas, 2001).

Our analysis of the degree of overlap in the alien flora (question 4) revealed strong differences in alien species composition between the four studied regions, but a very similar composition in different types of dune habitats in all the regions. This suggests that habitat conditions are likely to have a stronger effect on the level of invasion than the alien species identity (Chytrý *et al.*, 2008; Kalusová *et al.*, 2015). Indeed, human impacts, especially in southern European coastal regions, but also disturbance by livestock and wildlife such as rabbits and invertebrates, especially in northern regions, are important in plant species dispersal, and might also result in gaps suitable for alien plant establishment (Houston, 2008; Maun, 2009). *Erigeron canadensis* could be highlighted as an exception because, in addition to being the most widespread, it occurs in all the coastal regions. Furthermore, Black Sea dunes stand out in their alien species composition and invasion level, mainly driven by a high relative frequency of *Xanthium orientale* (5% of the occurrence of all the flora in this region; Appendix S6). The distribution of this plant has been shown to be on the rise in the Black Sea shifting dunes (Tzonev *et al.*, 2005; Valcheva *et al.*, 2019). Moreover, more than two-thirds of the neophytes occurring here colonised both shifting and stable dune grassland habitats (Figure 6, 1a).

Four ruderal species of American origin (*Erigeron canadensis*, *Xanthium strumarium*, *Oenothera biennis* and *Oenothera oakesiana*), already considered as invasive locally (Stanisci *et al.*, 2014; Weeda, 2010), accounted for almost half of all the neophyte occurrences. It is worth highlighting that these species can be found both in coastal and in inland habitats as well as in natural and human-made habitats. All four species are short-lived (annual or biennial), and share combinations of other key traits potentially favouring their spread, including the ability to tolerate drought, production of many small seeds, rapid growth, earlier access to resources than potential competitors (Hall *et al.*, 1988; Weaver, 2001), or potential phytotoxic or allelopathic effects (Shao *et al.*, 2012). However, in coastal dunes, these species are also often associated with human disturbance. For example, *Erigeron canadensis*, *Oenothera biennis* and *Xanthium strumarium* are widespread in coastal tracts heavily impacted by trampling, flattening and waste deposits (Stanisci *et al.*, 2010, 2014). A relationship between the presence of *Erigeron canadensis* and a decrease in plant diversity was already observed (Wu *et al.*, 2019). However, effects of these species on the European coastal dune biodiversity were not fully explored and further studies are needed to plan effective invasion management strategies at European level.

We reported other 7% of neophyte species which are known to have high impacts on European sand dune habitats. Among these, *Baccharis halimifolia* is the only one that is currently listed in the Consolidated List of Invasive Alien Species of Union concern (European Commission, 2019), due to its dense thickets that choke native dune vegetation in Atlantic coastal dunes. Moreover, other neophytes affect European coastal dunes at local scales. In particular, on the Atlantic and Mediterranean dunes, *Carpobrotus edulis* and *Carpobrotus acinaciformis* are considered a serious threat to endangered native plants and to species diversity (Campoy *et al.*, 2018), and *Senecio inaequidens* is known to induce changes in the floristic composition of dune vegetation (Heger and Böhmer, 2006). On the Atlantic and Baltic coastal dune grasslands, *Rosa rugosa* forms dense stands with high impact on the native vegetation (Isermann, 2008; Kelager *et al.*, 2013). In some cases, neophytes have also been shown to affect the invertebrate fauna (e.g., *Solidago canadensis* on Baltic dunes; De Groot *et al.* 2007; Zhang *et al.* 2009) or the breeding of endangered coastal birds associated to coastal dunes (e.g., *Carpobrotus* sp., Campoy *et al.*, 2018). For some of these neophytes there is not agreement among experts on their level of invasivity, and consequently there are not management strategies yet. Moreover, some neophytes have not shown any evidence of threatening native vegetation yet, but are spreading quickly (e.g., *Lactuca tatarica* on Baltic shifting dunes; Kowalski *et al.*, 2015), and consequently they require monitoring.

Finally, while the results of our study appear robust to our methodological choices (Appendix S5: Table S5.1, Figures S5.2 and S5.4), some main limitations should be highlighted. First of all, to avoid biases introduced by the potential preferential sampling of non-invaded sites, especially by older surveys, we based most of our evaluations on a subset of invaded plots, which represents only 13% of the initial dataset. Nevertheless, the percentage of neophyte species in our final dataset (based on invaded plots only) did not differ much from the percentage in the initial dataset. This means that the resampling protocol produced a subsample representative of the overall species pool. Second, even after resampling, there was still some unbalance in the number of plots between regions, but it was not possible to further control for factors affecting this unbalance, such as the extent of the target habitats vs the sampling effort. Indeed, high-quality maps of dune extent were not available for all regions of our study area (e.g., for northern Africa and the southern Black Sea coast). Third, the boundaries we assigned between donor regions were broad, because subjected to the availability of information on the native ranges of neophytes. Many species from North America, in particular, could be introduced from different North American climatic regions. However, our results on invasion trajectories are only meant to represent general overall patterns and should not be interpreted in terms of specific pathways.

5 | CONCLUSION

Our study is the most comprehensive, to date, providing a robust assessment of alien plant invasions on the dunes of the European coastal regions. We showed that dunes are colonised by many neophyte species, mostly with broad niches but at the same time with preferences for specific dune habitats and regions, and we found that four neophytes are particularly common. The levels of invasion do not differ considerably between shifting and stable dunes, but vary between the regions, with the highest number of alien species found on the Atlantic dunes. North America is shown as the leading donor of alien plants to the European coastal dunes, and the Mediterranean Basin as both an important donor and recipient. Overall, our results highlight that the dune habitats should be in the focus of invasion management strategies at the European level.

ACKNOWLEDGEMENTS

We thank the EVA database managers Stephan Hennekens and Ilona Knollová, as well as all the EVA data contributors, for making this study possible.

AUTHOR CONTRIBUTIONS

SG, AA, JL and CorMar conceived the research idea; all authors collected data; SG performed analyses and led the writing; all authors discussed the results and critically commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data used in this paper are stored in the European Vegetation Archive, project reference no. 66 (http://euroveg.org/eva-database-eva-projects).

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REFERENCES

Acosta, A., Carranza, M.L., Di Martino, L., Frattaroli, A., Izzi, C.F. and Stanisci, A. (2008) Patterns of native and alien plant species occurrence on coastal dunes in Central Italy. In: Tokarska-Guzik, B., Brock, J.H., Brundu, G., Child, L., Daehler, C.C. and Pyšek, P. (Eds.) *Plant Invasions: Human Perception, Ecological Impacts and Management*. Leiden, NL: Backhuys Publishers, pp. 235–248.

Acosta, A., Carranza, M.L. and Izzi, C.F. (2009) Are there habitats that contribute best to plant species diversity in coastal dunes? *Biodiversity and Conservation*, *18*(4), 1087–1098. https://doi.org/10.1007/s10531-008-9454-9.

Bauer, B.O. and Sherman, D.J. (1999) Coastal dune dynamics: problems and prospects. In: Goudie, A.S., Livingstone, I. and Stokes, S. (Eds.) *Aeolian Environments, Sediments and Landforms*. Chichester, UK: Wiley, pp. 71–104.

Blackburn, T.M., Bellard, C. and Ricciardi, A. (2019) Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and Evolution*, *17*(4), 203–207. https://doi.org/10.1002/fee.2020.

Braun-Blanquet, J. (1932) *Plant Sociology. The Study of Plant Communities*. New York, NY and London, UK: Mcgraw-Hill Book Company Inc.

Campos, J.A., Herrera, M., Biurrun, I. and Loidi, J. (2004) The role of alien plants in the natural coastal vegetation in central-northern Spain. *Biodiversity & Conservation*, *13*(12), 2275–2293. https://doi.org/10.1023/B:BIOC.0000047902.27442.92.

Campos, J.A., Biurrun, I., García-Mijangos, I., Loidi, J. and Herrera, M. (2013) Assessing the level of plant invasion: a multi-scale approach based on vegetation plots. *Plant Biosystems*, *147*(4), 1148–1162. https://doi.org/10.1080/11263504.2013.861538.

Campoy, J.G., Acosta, A.T., Affre, L., Barreiro, R., Brundu, G., Buisson, E. *et al*. (2018) Monographs of invasive plants in Europe: *Carpobrotus*. *Botany Letters*, *165*(3–4), 440–475. https://doi.org/10.1080/23818107.2018.1487884.

Carboni, M., Thuiller, W., Izzi, F. and Acosta, A. (2010) Disentangling the relative effects of environmental versus human factors on the abundance of native and alien plant species in Mediterranean sandy shores. *Diversity and Distributions*, *16*(4), 537–546. https://doi.org/10.1111/j.1472-4642.2010.00677.x.

Carboni, M., Santoro, R. and Acosta, A.T. (2011) Dealing with scarce data to understand how environmental gradients and propagule pressure shape fine-scale alien distribution patterns on coastal dunes. *Journal of Vegetation Science*, *22*(5), 751–765. https://doi.org/10.1111/j.1654-1103.2011.01303.x.

Catford, J.A., Vesk, P.A., Richardson, D.M. and Pyšek, P. (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. *Global Change Biology*, *18*(1), 44–62. https://doi.org/10.1111/j.1365-2486.2011.02549.x.

Chytrý, M., Maskell, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X. and *et al*. (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, *45*(2), 448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x.

Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L.C. and Vilà, M. (2009) European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions*, *15*(1), 98–107. https://doi.org/10.1111/j.1472-4642.2008.00515.x.

Chytrý, M., Hennekens, S.M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F. *et al*. (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. *Applied Vegetation Science*, *19*(1), 173–180. https://doi.org/10.1111/avsc.12191.

Colwell, R.K., Mao, C.X. and Chang, J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, *85*(10), 2717–2727. https://doi.org/10.1890/03-0557.

DAISIE (2009) *Handbook of Alien Species in Europe*. Berlin, Germany: Springer.

De Cáceres, M., Font, X. and Oliva, F. (2010) The management of vegetation classifications with fuzzy clustering. *Journal of Vegetation Science*, *21*(6), 1138–1151. https://doi.org/10.1111/j.1654-1103.2010.01211.x.

De Groot, M., Kleijn, D., & Jogan, N. (2007). Species groups occupying different trophic levels respond differently to the invasion of semi-natural vegetation by Solidago canadensis. *Biological Conservation*, *136*(4), 612-617. https://doi.org/10.1016/j.biocon.2007.01.005

Del Vecchio, S., Fantinato, E., Janssen, J.A.M., Bioret, F., Acosta, A., Prisco, I. *et al*. (2018) Biogeographic variability of coastal perennial grasslands at the European scale. *Applied Vegetation Science*, *21*(2), 312–321. https://doi.org/10.1111/avsc.12356.

Doody, J.P. (Ed.) (1991) *Sand Dune Inventory of Europe*. Peterborough, UK: Joint Nature Conservation Committee, European Union for Coastal Conservation.

Essl, F., Bacher, S., Genovesi, P., Hulme, P.E., Jeschke, J.M., Katsanevakis, S. *et al*. (2018) Which taxa are alien? Criteria, applications, and uncertainties. *BioScience*, *68*(7), 496–509. https://doi.org/10.1093/biosci/biy057.

European Commission. (2018) Conservation of dune habitats in the Atlantic Biogeographic Region. Version 2. Available at: http://ec.europa.eu/environment/nature/natura2000/platform/documents/Roadmap%20for%20dunes%20of%20the%20Atlantic%20Region-%20V2-%20LIFE%20FLANDRE%20Conference.pdf

European Commission. (2019). Commission Implementing Regulation (EU) 2019/1262 of 25 July 2019 amending Implementing Regulation (EU) 2016/1141 to update the list of invasive alien species of Union concern C/2019/5360. Published on 26–07-2019. *Official Journal of the European Union*, L 199.

European Environment Agency (2016) *Biogeographical Regions*. Available at: https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3

Feola, S., Carranza, M.L., Schaminée, J.H.J., Janssen, J.A.M. and Acosta, A.T.R. (2011) EU habitats of interest: an insight into Atlantic and Mediterranean beach and foredunes. *Biodiversity and Conservation*, *20*, 1457–1468. https://doi.org/10.1007/s10531-011-0037-9.

Grime, J.P. (Ed.) (1979) *Plant Strategies and Vegetation Processes*. Chichester, UK: John Wiley & Sons.

Hall, I., Steiner, E., Threadgill, P. and Jones, R.W. (1988) The biology of Canadian weeds. 84. *Oenothera biennis* L. *Canadian Journal of Plant Science*, *68*, 163–173. https://doi.org/10.4141/cjps88-016.

Heger, T. and Böhmer, H.J. (2006) *Nobanis*, *Invasive Alien Species Fact Sheet*. *Senecio inaequidens*. From Online Database of the European Network on Invasive Alien Species. Available at: www.nobanis.org [Accessed 21 October 2019].

Heslenfeld, P., Jungerius, P.D. and Klijn, J.A. (2008) European coastal dunes: ecological values, threats, opportunities and policy development. In: Martínez, M.S. and Psuty, N.P. (Eds.) *Coastal Dunes*. *Ecology and Conservation*. Berlin, Heidelberg: Springer, pp. 335–351.

Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, *405*, 907–913. https://doi.org/10.1038/35016000

Houston, J. (2008) *Management of Natura 2000 habitats. 2130 *Fixed coastal dunes with herbaceous vegetation ('grey dunes')*. European Commission. Technical Report 04/24. Available at: http://ec.europa.eu/environment/nature/natura2000/management/habitats/models_en.htm

Isermann, M. (2005) Soil pH and species diversity in coastal dunes. *Plant Ecology*, *178*(1), 111–120. https://doi.org/10.1007/s11258-004-2558-8.

Isermann, M. (2008) Expansion of *Rosa rugosa* and *Hippophae rhamnoides* in coastal grey dunes: effects at different spatial scales. *Flora*, *203*(4), 273–280. https://doi.org/10.1007/s10530-012-0356-0.

Janssen, J.A.M., Rodwell, J.S., García Criado, M., Gubbay, S., Haynes, T., Nieto, A., *et al*. (2016). *European Red List of Habitats. Part 2. Terrestrial and Freshwater Habitats*. Luxembourg: Publications Office of the European Union. https://doi.org/10.2779/091372

Jiménez-Alfaro, B., Marcenò, C., Guarino, R., & Chytrý, M. (2015). Regional metacommunities in two coastal systems: spatial structure and drivers of plant assemblages. *Journal of Biogeography*, *42*(3), 452-462. https://doi.org/10.1111/jbi.12437

Kalusová, V., Chytrý, M., Peet, R.K. and Wentworth, T.R. (2015) Intercontinental comparison of habitat levels of invasion between temperate North America and Europe. *Ecology*, *96*(12), 3363–3373. https://doi.org/10.1890/15-0021.1.

Kelager, A., Pedersen, J.S. and Bruun, H.H. (2013). Multiple introductions and no loss of genetic diversity: invasion history of Japanese Rose, *Rosa rugosa*, in Europe. *Biological Invasions*, *15*, 1125–1141. https://doi.org/10.1007/s10530-012-0356-0

Kowalski, W.A.W., Łysko, A. and Popiela, A. (2015) *Lactuca tatarica* (*Asteraceae*) in embryonic dunes on Wolin Island (NW Poland). *Biodiversity Research and Conservation*, *39*, 61–66. https://doi.org/10.1515/biorc-2015-0023.

Lambdon, P.W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F. *et al*. (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia*, *80*(2), 101–149.

Lengyel, A., Chytrý, M. and Tichý, L. (2011) Heterogeneity-constrained random resampling of phytosociological databases. *Journal of Vegetation Science*, *22*(1), 175–183. https://doi.org/10.1111/j.1654-1103.2010.01225.x.

Lososová, Z., Tichý, L., Divíšek, J., Čeplová, N., Danihelka, J., Dřevojan, P. *et al*. (2018) Projecting potential future shifts in species composition of European urban plant communities. *Diversity and Distributions*, *24*(6), 765–775. https://doi.org/10.1111/ddi.12725.

Marcenò, C., Guarino, R., Loidi, J., Herrera, M., Isermann, M., Knollová, I. *et al*. (2018) Classification of European and Mediterranean coastal dune vegetation. *Applied Vegetation Science*, *21*(3), 533–559. https://doi.org/10.1111/avsc.12379.

Maun, M.A. (2009) Seed dispersal (Chapter 3). In: Maun, M.A. (Ed.) *The Biology of Coastal sand Dunes*. Oxford, UK: Oxford University Press, pp. 40–52.

McDonald, J.H. (2014). Exact test of goodness-of-fit. In: *Handbook of Biological Statistics*. Available at: http://www.biostathandbook.com/exactgof.html [Accessed 12 December 2018].

Michalcová, D., Lvončík, S., Chytrý, M. and Hájek, O. (2011) Bias in vegetation databases? A comparison of stratified-random and preferential sampling. *Journal of Vegetation Science*, *22*(2), 281–291. https://doi.org/10.1111/j.1654-1103.2010.01249.x.

Nielsen, K.E., Degn, H.J., Damgaard, C., Bruus, M. and Nygaard, B. (2011) A native species with invasive behaviour in coastal dunes: evidence for progressing decay and homogenization of habitat types. *Ambio*, *40*(7), 819–823. https://doi.org/10.1007/s13280-011-0144-6.

Prisco, I., Stanisci, A. and Acosta, A.T.R. (2016) Mediterranean dunes on the go: evidence from a short term study on coastal herbaceous vegetation. *Estuarine, Coastal and Shelf Science*, *182*, 40–46. https://doi.org/10.1016/j.ecss.2016.09.012

Pyšek, P. and Jarošík, V. (2005) Residence time determines the distribution of alien plants. In: Inderjit, S. (Ed.) *Invasive Plants: Ecological and Agricultural Aspects*. Basel, Switzerland: Birkhäuser, pp. 77–96. https://doi.org/10.1007/3-7643-7380-6.

Pyšek, P., Jarošik, V., Hulme, P.E., Kühn, I., Wild, J., Winter, M. (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)*, *107*(27), 12157–12162. https://doi.org/10.1073/pnas.1002314107.

Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H. *et al*. (2017) Naturalized alien flora of the world: species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia*, *89*, 203–274. https://doi.org/10.23855/preslia.2017.203.

R Core Team. (2018) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Remke, E., Brouwer, E., Kooijman, A., Blindow, I., Esselink, H. and Roelofs, J.G. (2009) Even low to medium nitrogen deposition impacts vegetation of dry, coastal dunes around the Baltic Sea.

Environmental Pollution, *157*(3), 792–800. https://doi.org/10.1016/j.envpol.2008.11.020.
Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. and West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, *6*(2), 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x.
Rodríguez-Labajos, B., Binimelis, R. and Monterroso, I. (2009) Multi-level driving forces of biological invasions. *Ecological Economics*, *69*, 63–75. https://doi.org/10.1016/j.ecolecon.2009.08.022.
Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J. *et al.* (2015) Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology*, *21*, 4128–4140. https://doi.org/10.1111/gcb.13021.
Shao, H., Huang, X., Wei, X. and Zhang, C. (2012) Phytotoxic effects and a Phytotoxin from the invasive plant *Xanthium italicum* Moretti. *Molecules*, *17*, 4037–4046. https://doi.org/10.3390/molecules17044037.
Sobrino, E., Sanz-Elorza, M., Dana, E.D. and González-Moreno, A. (2002) Invasibility of a coastal strip in NE Spain by alien plants. *Journal of Vegetation Science*, *13*(4), 585–594. https://doi.org/10.1111/j.1654-1103.2002.tb02085.x.
Stanisci, A., Acoosta, A.T.R., Di Iorio, A. and Vergalito, M. (2010) Leaf and root trait variability of alien and native species along Adriatic coastal dunes (Italy). *Plant Biosystems*, *144*(1), 47–52. https://doi.org/10.1080/11263500903454252.
Stanisci, A., Acosta, A.T.R., Carranza, M.L., De Chiro, M., Del Vecchio, S., Di Martino, L. *et al.* (2014) EU habitats monitoring along the coastal dunes of the LTER sites of Abruzzo and Molise (Italy). *Plant Sociology*, *51*(1), 51–56. https://doi.org/10.7338/pls2014512S1/07.
Thuiller, W., Richardson, D.M., Rouget, M., Proches, S. and Wilson, J.R.U. (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology*, *87*(7), 1755–1769. https://doi.org/10.1890/0012-9658(2006)87[1755:IBESTA]2.0.CO;2.
Tichý, L. (2002) JUICE, software for vegetation classification. *Journal of Vegetation Science*, *13*(3), 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x.
Torca, M., Campos, J.A. and Herrera, M. (2019) Changes in plant diversity patterns along dune zonation in south Atlantic European coasts. *Estuarine Coastal and Shelf Science*, *218*, 39–47. https://doi.org/10.1016/j.ecss.2018.11.016.
Tzonev, R., Dimitrov, M. and Roussakova, V. (2005) Dune vegetation of the Bulgarian Black Sea coast. *Hacquetia*, *4*(1), 7–32.
Valcheva, M., Sopotlieva, D., Meshinev, T. and Apostolova, I. (2019) Is penetration of non-psammophytes an underestimated threat to sand dunes? A case study from western Pontic coast. *Journal of Coastal Conservation*, *23*, 271–281. https://doi.org/10.1007/s11852-018-0656-3.
van der Maarel, E. and van der Maarel-Versluys, M. (1996) Distribution and conservation status of littoral vascular plant species along the European coasts. *Journal of Coastal Conservation*, *2*(1), 73–92. https://doi.org/10.1007/BF02743039.
van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E. *et al.* (2015) Global exchange and accumulation of non-native plants. *Nature*, *525*(7567), 100–103. https://doi.org/10.1038/nature14910.
Vilà, M. and Pujadas, J. (2001) Land-use and socio-economic correlates of plant invasions in European and North African countries. *Biological Conservation*, *100*, 397–401. https://doi.org/10.1016/S0006-3207(01)00047-7.
Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošik, V., Maron, J.L. *et al.* (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*, 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x.
Wagner, V., Chytrý, M., Jiménez-Alfaro, B., Pergl, J., Hennekens, S., Biurrun, I. *et al.* (2017) Alien plant invasions in European woodlands. *Diversity and Distributions*, *23*(9), 969–981. https://doi.org/10.1111/ddi.12592.
Weaver, S.E. (2001) The biology of Canadian weeds. 115. *Conyza canadensis*. *Canadian Journal of Plant Science*, *81*(4), 867–875. https://doi.org/10.4141/P00-196.
Weeda, E.J. (2010) The role of archaeophytes and neophytes in the Dutch coastal dunes. *Journal of Coastal Conservation*, *14*(2), 75–79. https://doi.org/10.1007/s11852-009-0079-2.
Westphal, M.I., Browne, M., MacKinnon, K. and Noble, I. (2008) The link between international trade and the global distribution of invasive alien species. *Biological Invasions*, *10*(4), 391–398. https://doi.org/10.1007/s10530-007-9138-5.
Wu, B., Zhang, H., Jiang, K., Zhou, J. and Wang, C. (2019) *Erigeron canadensis* affects the taxonomic and functional diversity of plant communities in two climate zones in the North of China. *Ecological Research*, *34*(4), 535–547. https://doi.org/10.1111/1440-1703.12024.
Zhang, S., Jianjun, Y. J., & Chen, X. (2009). The invasive plant Solidago canadensis L. suppresses local soils pathogns through allelopathy. *Applied Soil Ecology*, *41* (2), 215-222. https://doi.org/10.1016/j.apsoil.2008.11.002

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. List of phytosociological alliances and corresponding habitat types assigned to vegetation plots
Appendix S2. Classification of alien species origins
Appendix S3. References for alien species status and donor habitat type
Appendix S4. Resampled dataset summary
Appendix S5. Supporting results
Appendix S6. Ranking of neophytes from the most to the least common

How to cite this article: Giulio S, Acosta ATR, Carboni M, et al. Alien flora across European coastal dunes. *Appl Veg Sci*. 2020;23:317–327. https://doi.org/10.1111/avsc.12490