Disentangling native and alien plant diversity in coastal sand dune ecosystems worldwide

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Abstract

Aims i) To disentangle the global patterns of native and alien plant diversity on coastal sand dune ecosystems across habitats and floristic kingdoms, ii) to determine the main drivers of variation in species richness in native and alien species in these endangered ecosystems, and iii) to test for an interaction between spatial scale and native-alien richness patterns, as predicted by the invasion paradox.

Location Global.

Methods We collated a dataset of 14,841 vegetation plots in coastal sand dune ecosystems from around the world. Generalized Linear Models (GLMs) and Generalized Linear Mixed Models (GLMMs) were used to assess the patterns and main ecological determinants underlying native and alien species richness. Variation partitioning revealed the relative importance of environmental and anthropogenic variables.

Results GLMs revealed strong differences among both habitats and floristic kingdoms in the number of native and alien species. Specifically, native species richness increased along the sea-inland gradient and was higher in the Cape and Paleotropical kingdoms. In contrast, alien species richness was relatively similar across habitats and kingdoms, though some differences were detected. There were strong differences between the drivers of native and alien richness; anthropogenic factors such as Gross Domestic Product were positively associated with alien richness whereas native richness was more strongly related to environmental factors. Furthermore, we found a weak support for an invasion paradox effect.

Conclusions Our results revealed the complexity of causal processes underpinning coastal sand dune plant biodiversity and highlight the importance of considering native and alien species separately. Recognition of these differences while researching variation in biodiversity patterns and processes at multiple spatial scales will lead to a better mechanistic understanding of the causes of
invasion worldwide, and in coastal ecosystems in particular, allowing the development of more focused control and management measures.

**Keywords:** Alien species, Biodiversity, Biogeography, Coastal dune habitats, Diversity patterns, Invasion paradox, Macroecology, Species richness.
Introduction

The coastlines of our planet extend to approximately 1.5 million km of which about 31% are sandy beaches (World Resources Institute, 2005; Luijendijk et al., 2018). Along these coastlines, sand dune ecosystems are widespread and occur from the polar regions to the tropics, encompassing a wide range of climates, biomes and habitats (van der Maarel, 1993; Maun, 2009). Vegetation plays a primary role in sand dune formation and consolidation due to its ability to stabilize the substrate and to enhance sand deposition (Maun, 2009). Regardless of differences in species composition, all sand dune species and habitats worldwide share the same limiting factors, such as sand burial, sand blasting, marine aerosol, water deficiency and lack of nutrients (Acosta et al., 2009; Monserrat et al., 2012; Pardini et al., 2015; Mahdavi and Bergmeier, 2016), and exhibit a characteristic sea-inland gradient (‘zonation’; Wilson and Sykes, 1999; Acosta et al., 2009; Miller et al., 2010; Tordoni et al., 2018).

An estimated 41% of the human population lives within 100 km of the shoreline (World Resource Institute, 2005), and the number of people living or vacationing in coastal areas is steadily increasing (Brown et al., 2013). This has already caused loss, alteration, degradation and/or habitat simplification of many sand dune environments, with severe consequences for biodiversity and associated ecosystems services (Dolan and Walker, 2006; Janssen et al., 2016). Human encroachment, including tourism and urbanization, along with increased shoreline erosion, have led to the so called ‘coastal squeeze’ effect (Defeo et al., 2009), leaving coastal ecosystems ‘trapped’ between erosion on the coastline and human settlements inland. Another source of concern stems from biological invasions, which are deemed a severe threat to biodiversity (second only to habitat loss and fragmentation; DAISIE, 2009; Vilà et al., 2011; EEA, 2012). Coastal areas are often reported to host many alien species (Von Holle and Motzkin, 2007; Chytrý et al., 2008; Giulio et al., 2020) and are considered as one of the most invaded ecosystems worldwide (Dawson et al., 2017). Especially in sand dune habitats, alien species can exert strong ecological impacts (e.g. Carboni et
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...al., 2010a; Novoa et al., 2013), which may lead to the extinction of native taxa of conservation concern, including endemic and keystone species (Acosta et al., 2009; Pardini et al., 2015).

The impacts of biological invasions are strongly scale-dependent (e.g. Levine and D’Antonio, 1999; Vellend et al., 2017). One of the most frequently discussed impacts of alien species is the reduction in species richness of the invaded community (Vilà et al., 2015), but the relationship between native and alien species diversity is still a matter of discussion in plant ecology (Fridley et al., 2007), with different interpretations of the phenomenon often reflecting different spatial scales of observation or study design (e.g. Muthukrishnan et al., 2018; Tomasetto et al., 2019). Generally, more negative relationships have been described at finer scales (experimental or small-scale studies), whereas the opposite trend is usually observed at larger observation scales (from large plot to landscape or biome). In response to this scale-related inconsistency, scientists coined the term ‘invasion paradox’ to describe the scale dependency of native-alien richness patterns (Fridley et al., 2007).

In coastal sand dunes, integration of scale of observation is particularly important for understanding native plant community assemblage and richness (Carboni et al., 2013). At finer scales (few m²), biotic interactions usually predominate (Forey et al., 2010; de Toledo Castanho et al., 2015). At regional scales, several studies (e.g. Forey et al., 2008; Brunbjerg et al., 2012) have shown that a suite of stressors (e.g. water and nutrient stress) and disturbance factors (e.g. sand burial) interact in shaping plant communities and their species richness. At even larger spatial extents, environmental and biogeographical factors become predominant (Jiménez-Alfaro et al., 2015).

Recently, great efforts have been made to disentangle broad-scale patterns of species richness (e.g. Kreft and Jetz, 2007; Bruelheide et al., 2019) and several theories have been proposed to explain mechanisms responsible for species richness worldwide. Most of them rely on how water-energy dynamics drive species richness gradients (Francis and Currie, 2003; Currie et al., 2004; Kreft and...
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Jetz, 2007), along with the sensitivity of plants to frost and drought (Wiens and Donoghue, 2004). Other hypotheses consider environmental heterogeneity (Stein et al., 2014) or historical and evolutionary processes (e.g. Médail and Diadema, 2009; Kerkhoff et al., 2014).

To our knowledge, no study has comprehensively investigated the patterns of native and alien plant species diversity in sand dune ecosystems in the context of spatial scale, either across habitats or across floristic kingdoms. Here, we use a large dataset of vegetation plots we have compiled from five continents (see Supplementary material Fig. S1.1 in Appendix S1) to fill this gap and to present a global analysis of vascular plant diversity of coastal sand dune ecosystems. At a global scale, we hypothesized that native species richness would show a similar pattern to that of vascular plants (i.e. a decrease of species richness from the equator towards the poles; Kreft and Jetz, 2007). In contrast, we expected to find an uneven level of invasion, suggesting the presence of hotspots of invasion across the globe (Pyšek et al., 2017) whose occurrence may be more influenced by anthropogenic factors (e.g. GDP) than natural ones. At a local scale, whereas several studies have reported a strong gradient of species richness moving from the drift line to the landward part of the beach, especially for native species (e.g. Acosta et al., 2009), the global pattern of alien species richness has not yet been investigated. Nevertheless, some evidence coming from local and regional scale studies located in the Mediterranean Basin (e.g. Carboni et al., 2010a) suggests that higher values of alien richness are often observed at intermediate levels of the sea-inland gradient.

Thus, our aims were: i) to disentangle the global patterns of native and alien plant diversity on coastal sand dune ecosystems across habitats and floristic kingdoms, ii) to determine the main drivers of variation in species richness in native and alien species in these endangered ecosystems, and iii) to test for an interaction between spatial scale and native-alien richness patterns, as predicted by the invasion paradox.
163 **Methods**

164 **Study sites and species data**

165 We compiled a database consisting of 14,841 vegetation plots sampled in coastal sand dune communities distributed across Europe, North America, South America, Africa (Cape and Paleotropical kingdoms) and Oceania (except Australia). Species richness per sampling unit was obtained from plots and phytosociological relevés (hereafter plots) derived from literature and plant databases both public and private such as the European Coastal Vegetation Database (http://www.givd.info/ID/EU-00-017) or KRITI database (http://www.givd.info/ID/EU-GR-001).

166 For more details about the data sources see Table S1.1 in Appendix S1. In order to be considered in the study, all plots had to comply with the following inclusion criteria: 1) a georeferenced location, 2) a defined sampling unit size, and 3) a defined habitat or coastal plant community (see below for the adopted classification).

167 Species names were standardized with the Taxonomic Name Resolution Service (Boyle et al., 2013; http://tnrs.iplantcollaborative.org/). Furthermore, doubtful species and records not identified to the species level were omitted. The status of the species (native or alien), if not provided by the author of the data, was assigned using online databases or national alien species checklists (see Table S1.2 in Appendix S1). For each plot, we obtained two response variables: a) native species richness and b) alien species richness. Plots with size smaller than 0.25 m$^2$ or with missing data for any of the variables described below were excluded leaving 11,988 plots for analysis. Even though the majority of the plots ranged in size from 0.25 to 100 m$^2$ (see Fig. S1.2 in Appendix S1), plot size has been directly added in the models as a covariate to control for its effect on species richness (Arrhenius, 1921).

186 **Environmental variables**
Each plot was classified as representing one of three main macrohabitat types: (1) forédunes, including drift line, upper beach, embryo dunes and mobile dunes dominated by pioneer annual and dune-forming perennial plants tolerant to salt spray, strong winds, and sand burial; (2) fixed dunes, encompassing communities dominated mainly by perennial plants (generally herbs and shrubs) and occurring in the inner part of the coastline, or more developed communities such as coastal forests and woodlands; and, (3) interdunes, comprised of interdunal swales, slacks and humid depressions. This coarse classification based on dune dynamics was necessary to standardize habitat types, owing to the great heterogeneity present across the globe (Doing, 1985).

We tested the following environmental variables related to the growth and distribution of vascular plants as possible predictors of native and alien species richness: mean annual precipitation (mm/year), precipitation seasonality (percentage variation in monthly precipitation totals over the course of the year; larger values indicate greater variability), mean annual temperature (°C), and temperature seasonality (percentage measure of temperature change over the course of the year). Climatic data were obtained from the CHELSA database (Karger et al., 2017, accessed June 2017), a high-resolution climatology resource (30 arc seconds, ~1 km) spanning the years 1973 to 2013. Values were assigned to each plot with nearest neighbor algorithm using QGIS 3.10 with GRASS 7.8.3 (Quantum GIS Development Team, 2020). We also included insularity (mainland vs island) and floristic kingdom according to the floristic divisions of Takhtajan (1986) to control for the generally lower diversity of island communities and the effect of unquantified historical or evolutionary processes.

**Anthropogenic variables**

Based on previous research (e.g. Bellard et al., 2016; Chapman et al., 2016), we considered a set of anthropogenic variables as predictors of alien species diversity that are surrogates for propagule pressure and/or potential introduction pathways. Among these, human population density has been identified as one of the main determinants of alien species richness at the continental scale (Pyšek et
al., 2010). Thus, we employed adjusted human population density (people / km²) based on the Gridded Population of the World at a resolution of 30 arc seconds (GPWv4; CIESIN, 2015), which provides gridded human population density estimated for the year 2015 adjusted to match United Nations (UN) estimated national-level population counts. As a proxy for trade volume, we used Gross Domestic Product per capita (standardized to international dollars, int$), (http://data.worldbank.org) based on Gross Domestic Product (GDP) constructed from purchasing-power-parity (PPP) per capita GDP (year 2015). Among human-related variables, proximity of airports, sea ports and cities also have been recognized as facilitators of biological invasions for several taxa (e.g. Seebens et al., 2013; Bellard et al., 2016). For this reason, we included the following predictors: Distance to nearest city with more than 50,000 inhabitants (Nelson, 2008); Distance to nearest airport (Pope and Sietinsone, 2017) and Distance to nearest port (GISCO Ports, 2013). Year of sampling was also included to assess whether there is an effect of time of the surveys. All datasets were accessed on September 2017. Distances were calculated through proximity analyses using QGIS 3.10 with GRASS 7.8.3.

Species richness patterns across floristic kingdoms and habitats

We first tested for differences in species richness across floristic kingdoms and habitat types using generalized linear modeling (GLM). Due to the presence of severe overdispersion in the data (variance >> mean), we used a negative binomial error distribution (Zuur et al., 2007). The explanatory power of each predictor was evaluated through likelihood ratio tests in the R package ‘car’ (Fox and Weisberg, 2011) and effects were estimated using the package ‘effect’ (Fox and Weisberg, 2018). As a measure of model fit, we reported the amount of deviance explained by each GLM (D² adjusted; Barbosa et al., 2014). To quantitatively test for the invasion paradox, we fitted a negative binomial GLM to describe alien species richness as a function of native species richness, sampling unit area and their first-order interaction. This analysis was also repeated for the Holarctic
kingdom alone to test for consistency of the results, since most of the data (including larger plots) belonged to this kingdom.

**Ecological drivers**

The ecological drivers of native and alien species richness were evaluated by means of Generalized Linear Mixed Models (GLMMs), with random intercept to account for possible bias deriving from having data from different sources nested within floristic kingdoms. In order to linearize the relationship with species richness, some predictors were transformed as follows: population density and GDP were $\log_{10}(x+1)$ transformed, whereas plot size was $\log_{10}$ transformed. Furthermore, all continuous variables were standardized (zero mean, unit variance) in order to obtain comparable coefficients.

GLMMs were estimated using the R package ‘glmmTMB’ (Brooks *et al.*, 2017) and $R^2$ values developed by Nakagawa and Schielzeth were also computed (Nakagawa and Schielzeth 2013). To isolate the effect of each group variable, four models were fitted (two for native and two for alien species), considering environmental and anthropogenic variables separately (see Table S1.3 in Appendix S1 for descriptive statistics of fixed effects). The response families were the same as for the GLMs (negative binomial). Furthermore, the possible occurrence of spatial autocorrelation of residuals in each model was assessed by means of spline-correlograms using the R package ‘ncf’ (Bjørnstad, 2020). Specifically, 95% pointwise bootstrap confidence intervals were calculated from 1000 bootstrap samples of Pearson residuals after accounting for the level of spatial autocorrelation explained by the explanatory variables in each model. To further explore the role of ecological drivers on species richness, a variation partitioning approach through partial linear regressions was used to assign the total variation in native and alien species richness into purely environmental, purely anthropogenic, shared and unexplained fractions (Borcard *et al.*, 1992; Legendre, 2008) using the ‘vegan’ package (Oksanen *et al.*, 2019). All analyses were performed using R 4.0.2 (R Core Team,
Results

Global patterns of native and alien richness in sand dunes

Overall, fitted values of native and alien species richness varied strongly among habitats and floristic kingdoms (Fig. 1; Table S1.4, S1.5 in Appendix S1 of Supplementary material). There was a significant interaction between habitat and floristic kingdom, both for native and alien species (Likelihood Ratio Test $\chi^2 (6) = 326.6, P < 0.001$, $D^2_{\text{adjusted}} = 0.45$; $\chi^2 (6) = 132.9, P < 0.001$, $D^2_{\text{adjusted}} = 0.19$; respectively). These explanatory variables were strong predictors of global variation of species richness for natives whereas they were relatively weak predictors for alien species (there was a difference in deviance explained of 26% between the two models). For native species, fixed dunes tended to have higher species richness compared to foredunes and interdunes in all the floristic kingdoms (Fig. 1a) showing highest species richness in Cape and Paleotropical kingdoms. In contrast, Holantarctic kingdom was the poorest one. Surprisingly, in some kingdoms, such as the Cape and Holantarctic, alien species displayed a different pattern with respect to habitat compared to that of native species (Fig. 1b) showing greater variation among habitats along the sea-inland gradient with respect to native species. Specifically, foredunes showed higher levels of alien plants relative to fixed dunes in the Cape and Holantarctic kingdoms, whereas the opposite was observed in the Holarctic and Paleotropical kingdoms. On average, interdunes tended to have the lower levels of invasion (Fig. 1b). As hypothesized, higher values of alien species richness were clustered in specific regions, such as New Zealand, North America or some European countries (Fig. 2).

An overall negative relationship between native and alien species richness was observed without considering plot size (Fig. 3a). However, when grain size was specifically considered in the model, the slope of the relationship shifted from negative to positive with increasing plot size, in agreement...
with the pattern suggested by the invasion paradox (Fig. 3b). The GLM with alien species richness as response variable showed a significant interaction between native richness and plot size ($\chi^2 (1) = 63.90, P < 0.001$), even though a poor predictive power was detected ($D^2_{\text{adjusted}} = 0.02$). However, the overall relationship between native and alien species richness became positive when considering only the data coming from the Holarctic kingdom, no longer supporting the invasion paradox effect (Fig. S1.3, $\chi^2 (1) = 4.22, P < 0.05, D^2_{\text{adjusted}} = 0.01$).

Global ecological determinants of native and alien richness

GLMMs revealed large differences between the responses of alien and native species richness to environmental and socio-economic variables. Native species richness was strongly associated with global environmental gradients and only marginally with anthropogenic variables. Alien species richness, in contrast, was more strongly associated with anthropogenic variables (Fig. 4, Table S1.6 in Appendix S1). These outcomes were further corroborated by the variation partitioning approach where native species were mainly driven by environmental variables, whereas for alien species anthropogenic variables accounted for a greatest percentage of explained variation (Fig. 5).

Specifically, native species richness significantly differed among habitats and, furthermore, was positively related to mean annual temperature ($b = 0.06 \pm 0.02$ SE, Table S1.6 in Appendix S1), and mean annual precipitation ($0.03 \pm 0.01$). A negative coefficient was observed for precipitation seasonality ($-0.07 \pm 0.02$), meaning that higher seasonality was associated with lower species richness. Insularity, in contrast, did not have a pronounced effect on local coastal dune diversity of native plants. The only anthropogenic variables with a positive effect on native species richness was population density ($0.09 \pm 0.01$) whereas a negative relationship with the distance of the closest city was detected ($-0.026 \pm 0.01$).

For alien species, some strikingly different results were obtained. In contrast to the results for native species, insularity had a strongly negative effect on alien species richness ($-0.44 \pm 0.20$, Table S1.6 in Appendix S1). Negative effects on alien richness were also observed for mean annual
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temperature (-0.22 ± 0.06), precipitation amount (-0.11 ± 0.01) and precipitation seasonality (-0.18 ±
0.06). Almost all of the anthropogenic predictors tested were highly informative (confidence intervals
did not overlap zero). Notably, a positive association was observed with GDP (0.70 ± 0.10),
population density (0.04 ± 0.02) and year of sampling (0.010 ± 0.002), as expected. Accordingly, a
negative estimate was observed considering the distance to the closest city (-0.21 ± 0.02), whereas a
positive effect of the distance to the closest airport was found (0.11 ± 0.02).

All four spline correlograms (Fig. S1.4 in Appendix S1 of Supplementary material) failed to reveal
any evidence of spatial autocorrelation in the residuals, thereby allowing us to exclude its influence
on model parameter estimates.

Discussion

Diversity patterns across habitats and floristic kingdoms

We explored the relationships between native and alien species, and the main environmental and
anthropogenic factors associated with their distribution. Overall, some contrasting patterns and
relationships between species diversity and its drivers emerged among habitats and floristic
kingdoms. Among floristic kingdoms, higher native species richness was detected in Cape and
Paleotropical kingdoms whereas the Holarctic and Holantarctic were significantly poorer (Fig. 1, 2).
This result is consistent with well-known global trends for vascular plants (i.e. higher richness in
Cape region; Kier et al., 2005; Kreft and Jetz, 2007), even though these results might be partially
influenced by the spatial configuration of our database.

Native species richness showed a general increase along the sea-inland gradient from the species-
poor foredunes to more diverse communities on fixed dunes. This trend was consistent across floristic
kingdoms and confirms numerous local and regional case studies from around the world (e.g. Acosta
et al., 2009; Miller et al., 2010; Monserrat et al., 2012; Ciccarelli et al., 2012; Jiménez-Alfaro et al.,
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The increase in species richness along the dune gradient is attributable to the variable effect of limiting factors acting in these environments: low levels of nutrients and moisture, salt spray, sand burial and soil features (see Forey et al., 2008; Houle, 2008; Acosta et al., 2009; Ciccarelli and Bacaro, 2016; Angiolini et al., 2017). Thus, the more extreme conditions in foredunes cause them to be, on average, more species-poor compared to the other habitats, even though a strong biogeographical signal is evident across floristic kingdoms. This signal may be partially explained by the climate (even though this effect is stronger in stable dunes, Jiménez-Alfaro et al., 2015) and by dispersal processes occurring along the coastline that might be favored by sea currents (Clausing et al., 2000). Fixed-dune communities, in contrast, displayed higher species richness due to less dynamic habitats and to the more mature, diverse and deeper soils; at increasing distance from the coastline, vegetation is progressively less exposed to extreme conditions allowing for the establishment of perennial plants and forest vegetation (Wiedemann and Pickart, 2004; Maun, 2009). Thus, our analysis showed that, irrespective of the floristic kingdom considered, there is a strong gradient of native species richness moving from the foredunes to the landward part of the beach.

Regarding alien species, we detected some hotspots of invasion, mainly located in North America and New Zealand. Our results are consistent with those of other researchers (Pyšek et al., 2017; Dawson et al., 2017) who have found higher richness of naturalized aliens in New Zealand and United Kingdom among islands, and in several North American regions (e.g. California) for mainland. The effect of habitat on alien species richness was a bit less pronounced with respect to native species and this pattern was not consistent across floristic kingdoms. Specifically, landward beach areas (i.e. fixed dunes and interdunes) were more invaded than foredunes, which may be explained mostly by the overall less stressful conditions in these environments. Invasiveness of alien species have been mostly explained by their higher phenotypic plasticity coupled with their ability in the use of resources (Davidson et al., 2011; Tordoni et al., 2019). Other factors to consider include the capability of alien plants to spread their propagules across habitats (see Simberloff, 2009 for a review on the role of
propagule pressure in biological invasions) associated with trampling in touristic beaches and proximity to artificial surfaces (Carboni et al., 2010a; Malavasi et al., 2014). Interestingly, higher values of alien species richness were observed in the foredunes of the Holantarctic and Cape kingdoms. Previous studies (e.g. Hertling and Lubke, 1999; Hilton et al., 2006) have reported that foredunes are heavily invaded by alien species, for example by the west Holarctic marram grass (Ammophila arenaria) that was widely planted during the 1900s to construct or re-establish foredunes and stabilize shifting dune systems in New Zealand and South Africa (Johnson, 1992; Lubke et al., 1995).

Scale-dependency of diversity patterns

Several authors have described the scale-dependence of the relationship between native and alien species richness (see Levine and D’Antonio, 1999; Davies et al., 2005, among others). In our study, we observed a general negative linear relation between native and alien species richness, i.e. more species-rich sites were less invaded (Fig. 3). However, when accounting for plot size, we detected the invasion paradox pattern as proposed by Fridley et al. (2007). Accordingly, even though at very fine spatial grain a clear negative trend exists between native and alien richness (e.g. Levine, 2000), the opposite holds true at larger spatial grains (Fig. 3b, Stohlgren et al., 2003, among others). Similar results have also been observed in a meta-analysis of Mediterranean-type ecosystems including sand dune vegetation (Gaertner et al., 2009). Fridley et al. (2007) did not provide a single interpretation to this phenomenon, but rather a suite of possible explanations. At a fine scale, environmental and disturbance-based features predominate and shape community composition. Sampling effects may arise in the sense that communities may include particularly invasion-resistant or competitive species; another possible explanation relies on the concept that in stressful, regularly-disturbed environments such as sand dune ecosystems, facilitative interactions may ease the establishment and colonization of alien species across functional groups (Von Holle, 2013). In contrast, at a larger spatial scale, native and alien species richness increased in concert. The biotic processes are superseded by
historical, environmental, or biogeographic factors, among which probably spatial and environmental heterogeneity play a crucial role (Gaertner et al., 2009; Stein et al., 2014). In addition, communities experiencing high species dispersal or in highly disturbed ecosystems (e.g. roadside and riparian habitats) often exhibit these positive relationships (Brown and Peet, 2003). Nevertheless, it is worth noting that when considering only the plots located in the Holarctic kingdom the relationship between native and alien species remained steadily positive across all scales considered (see Fig. S1.3). This in agreement with recent studies (Peng et al., 2019; Tomasetto et al., 2019) suggesting that an explanation for this effect could rely on the sampling design used by different authors, the nature of the data (observational vs experimental) coupled with a strong bias towards particular study systems such as grassland habitats. Although we found a highly significant interaction between plot size and richness values, the poor performance of the models coupled with the inconsistency of the invasion paradox effect when downscaling the data seem to lend support to these recent findings. Additionally, despite the fact that macrohabitat classes are quite evenly represented in the dataset within each kingdom (except for Neotropical), we cannot exclude that the pattern observed may be influenced by the spatial clustering of the data in terms of plot location relative to plot size (the largest plots are only in Europe and North America). Second, alien species richness may be biased downward in the oldest phytosociological relevés, which are largely European, due to preferential sampling (Chytrý, 2001).

Ecological drivers of plant species richness

GLMMs and variance partitioning revealed that environmental and anthropogenic factors (Fig. 4, 5) acted differently on native and alien species. Climatic and ecological variables predict worldwide patterns of native species richness. Usually, water-energy interactions exert strong effects on plant species richness (Francis and Currie, 2003; Kreft and Jetz, 2007) and global diversity gradients in general (Hawkins et al., 2003). At a global scale, the distribution and the strong geographical differentiation in the floristic composition of plant communities have been classically attributed to
climatic differences and regional-scale processes of speciation, extinction and dispersal (Ricklefs, 1987). Even though foredunes are deemed an azonal habitat, local climate seems to influence the species present in the inner part of the beach (Mahdavi and Bergmeier, 2016; Del Vecchio et al., 2018). The relationships between native species richness and anthropogenic factors such as population density (proxy for urbanization) has been previously described in literature (Kühn et al., 2004; Luck, 2007; Lucrezi et al., 2014) suggesting a key role of nutrient enrichment and abundance of resources. Regarding the year of sampling, a very weak positive relationship was observed meaning that there was an increase of native species richness according to time of the survey. However, due to the small value of the coefficient (< 0.001), this effect could be considered as relatively weak.

Coastal dune habitats have been reported previously to be highly invaded by alien plant species, with a general consensus that propagule pressure is among the most important causes of greater invasion success (Carboni et al., 2010a; Malavasi et al., 2014; Basnou et al., 2015). Generally, highly disturbed sites that were close to human activities and/or had been heavily transformed by humans had greater chance to host more alien species (see Fig. 4), regardless of the biodiversity present in the area (Basnou et al., 2015; Dawson et al., 2017). Nevertheless, climatic factors influence alien species richness (Carboni et al., 2010b), as reported also in other global-scale studies in terrestrial ecosystems (e.g. Pyšek et al., 2017) and even considering different taxa such as birds (e.g. Dyer et al., 2017). In contrast to Carboni et al. (2010b), we observed a negative relationship of alien species richness with precipitation amount, precipitation seasonality and mean annual temperature suggesting that more successful invaders were found in mildest climates, as observed in other environments across the world (Gassó et al., 2009).

It is generally accepted that islands are more invaded than mainland sites (Lonsdale, 1999; Pyšek et al., 2017; Moser et al., 2018). In this study, we observed an opposite pattern with higher alien species richness in coastal sand dunes in mainland areas than on islands (Fig. 4). This is consistent
with observations by Vilà et al. (2010), who compared Spanish coastal plant communities. The smaller exotic species pool which is present on islands compared to mainland locations could result from the lower human population density on islands compared to mainland in our dataset (average density of 201.15 vs 515.52, respectively) which likely translates into lower propagule pressure. Nonetheless, this pattern might just arise as a sampling effect due to the spatial distribution of our data, being only few of our plots located on small islands, and even fewer on oceanic islands.

Socio-economic factors such as per-capita GDP (which is directly related to a country's volume of trade as well as the disposable income of its population) and population density (proxy for urbanization) played a key role in explaining alien species richness, which is consistent with other studies (McKinney, 2006; Carboni et al., 2010ab; Pyšek et al., 2010). Nonetheless, it has been suggested that the full consequences of biological invasions often realize only decades after their introduction (so called “invasion debt”, Essl et al. 2011). The positive relationship between alien richness and year of the study can be explained by the effect of the so-called “residence time” (the period since the introduction of a taxon to a new area occurred) and might therefore reflect a real temporal accumulation of alien species, even though this pattern might be influenced by the fact that older plots mainly belonged to the Holarctic kingdom and more than half of them were collected in only the last twenty years (Fig. S1.5 in Appendix S1). Other possible explanations might rely on increased global trade network along with the relatively recent interest in this topic which caused an increase in research intensity (Hulme et al., 2013). Cities are often the introduction epicenter of alien species (Pyšek, 1998; Tordoni et al., 2017) due to synergic effects of human activities and transports, which ensure a high dispersion rate of the propagules through a road network (Bacaro et al., 2015). The distances to the closest city may be easily related to the concept of the pathways of introduction and spread and they can be considered as major drivers of invasion throughout the world (Bellard et al., 2016). More generally, especially across coastal areas, alien plant introductions into new areas have happened both unintentionally (through major trade routes, Tatem and Hay, 2007; Tatem, 2009;
Chapman et al., 2016; Bellard et al., 2016) and intentionally (for instance by preventing sand drift or by establishing ornamental plants). Thus, anthropogenic factors were primarily involved as drivers of alien species richness patterns of coastal sand dune ecosystems worldwide.

Conclusions

This study provides a global view on patterns and drivers of native and alien plant species richness in coastal sand dune ecosystems. A key finding from our study is that native and alien species richness in coastal sand dune environments differs across habitats and floristic kingdoms. Our study reveals a consistent sea-inland gradient in native species richness with fixed dunes being the richest, whereas the richness of alien species tended to be more similar across habitats. Overall, global trends of vascular plant diversity were also confirmed. We found some support for a scale-dependent change in the direction of the native-alien relationship consistent with the invasion paradox effect, even though with a relatively weak predictive power and consistency across floristic kingdoms. Species richness of coastland habitats is differentially related to ecological and anthropogenic factors. Even though there was a strong imprint of environmental factors such as climate variables for both native and alien species richness, the effect of anthropogenic impacts on the latter was much more pronounced. More detailed and more mechanistic understanding of the causes of invasion should allow more focused control and management measures and might lead to similar explorations among other ecosystem types across the globe.

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Author contributions

ET., HK conceived the idea and designed the study. PW provided help in compiling the database. GB and MC provided support in statistical analyses. ET led the writing with inputs from HK, PW, GB, RKP, ATRA, HLB, JAMJ, EB and EF. All the authors except HK, PW, MC collected the data. All authors agreed with the final version of the manuscript.

Data availability statement

Appendix S1 in Supporting Information contains information on the sources of the data used. Data were collected from published papers and vegetation database and are available from each author on request.

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**Supporting Information**

**Appendix S1.** Additional information regarding the database and the results

**Appendix S1.** Model specifications
Figures

Figure 1. Bar charts displaying the effect of habitat across floristic kingdoms on a) Native species, b) Alien species. Values reported are estimated species richness per plot ± 95% confidence intervals.
Figure 2. Global map showing the distribution of the vegetation plots according to Takhtajan floristic kingdoms (Takhtajan, 1986). Please note that the size of the symbol is proportional to the absolute number of alien species; lower inset represents a detail of Cape and Paleotropical kingdoms.
Figure 3. a) Scatterplot illustrating the relationship between alien and native species richness. Solid line represents the overall regression trend. b) Effect plot displaying the dynamic pattern between alien species richness and native species richness according to plot size. Shaded areas represent 95% confidence intervals. Plots were grouped in three classes according to their size (0.25-100, 101-500, 501-10000 m²) for ease of interpretation.
Figure 4. Summary of GLMMs. x-axis reports the estimate ± 95% Wald confidence interval, y-axis the model’s predictors.
Figure 5. Variation partitioning reporting the proportion of variance explained expressed as percentage by environmental variables and anthropogenic variables for native and alien species richness.