Contrasting responses of native and alien plant species to soil properties shed new light on the invasion of dune systems

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Abstract

Aims

Among terrestrial ecosystems, coastal sandy dunes are particularly prone to alien plant invasion. Many studies related the invasion of dune habitats to anthropic causes, but less is known about the role of soil properties and plant traits in plant invasion. In this study we tested the relationships between soil features and alien plant invasion in dune systems, focusing on the interplay between soil nutrients, soil salinity and plant functional traits.

Methods

Study sites were sandy barrier islands of the Marano and Grado lagoon (northern Adriatic Sea). One hundred plots (4x4 m) were selected within 10 areas according to the main habitats occurring along the ecological gradient of dune system (foredune, backdune and saltmarsh). In each plot we recorded all plant species occurrence and abundance and we collected a soil core. For each soil sample, soil texture, conductivity (as proxy of soil salinity), organic carbon and nitrogen content were analyzed and related to the species number and cover of native and alien plants. Variation of main reproductive and vegetative functional traits among habitats was also analyzed for both alien and native species.

Important Findings

Soil properties were strongly related to overall plant diversity, by differently affecting alien and native species pools. In backdune, the most invaded habitat, a high soil conductivity limited the number of alien species, whereas the content of soil organic carbon increased along with alien plant abundance, suggesting also the occurrence of potential feedback processes between plant invasion and soil. We found a significant convergence between native and alien plant functional trait spectra only in backdune habitat, where environmental conditions ameliorate and plant competition increases. Our findings suggest that in harsh conditions only native specialized plants can thrive while at intermediate conditions, soil properties gradient acts in synergy with plant traits to curb/facilitate alien plant richness.

Keywords: invasive alien species, functional traits, soil nutrients, plant communities, dune system

Introduction

Coastal areas are globally considered among the most valuable but endangered habitats due to their susceptibility to global changes (Defeo *et al.*, 2009). Among coastal systems, dune has been already proved to be particularly prone to biological invasion (Campos *et al.*, 2004; Giulio *et al.*, 2020), which leads to major shifts in biodiversity, ecosystem integrity, functions and services (Vilà *et al.*, 2010; Simberloff *et al.*, 2013).

In dune systems, many studies focused on the relationships between invasive plants and regional environmental variables (Marcantonio *et al.*, 2014; Malavasi *et al.*, 2014; Tordoni *et al.*, 2018; Marzialetti *et al.*, 2019). However, while land-use and climate are considered pivotal at large-scale (i.e. landscape), variations of soil and stand structure might prevail when considering the local spread of alien species in semi-natural habitat (Ohlemüller *et al.*, 2006). Soil features are supposed to directly affect the success of exotic plants in introduced habitats (Carvalho *et al.*, 2010). Among soil properties, nutrient content and organic matter are known as important determinants of plant community diversity (Chapin III *et al.*, 1986). For instance, high levels of soil nitrogen increase the abundance of invasive alien plants and decrease plant diversity (Vitousek *et al.*, 1997). On the other hand, some invaders can trigger cascading effects on ecosystem proprieties by altering nutrient cycles (Boscutti *et al.*, 2020). In coastal systems, soil salinity is the major driver of species distribution (Donnelly and Pammenter, 1983; Gorham, 1992; Lortie and Cushman, 2007). Nonetheless, the effect of salinity on the distribution of invasive species was studied only for few specific alien taxa, focusing on their phenotypic response to salt stress (Ishikawa *et al.*, 1991; Caño *et al.*, 2016).

Abiotic site conditions can influence ecosystem processes both directly, by determining environmental stress conditions, and indirectly, through the functional response of plants (Boscutti *et al.*, 2018a; Pellegrini *et al.*, 2018; Bu *et al.*, 2019). In turn, the range of functions provided by a plant community is thought to largely depend on the diversity of functional traits (Díaz and Cabido, 2001), expressed as global variability of functional traits (functional spectrum). For these reasons, plant functional traits have been proved to be pivotal in elucidating plant invasion success (Rejmanek and Richardson, 1996; Boscutti *et al.*, 2018b). In particular, plasticity of plant traits are supposed to affect the success of alien plants (Davidson *et al.*, 2011) by producing a divergence/convergence of plant traits in response to the invaded habitat conditions (e.g. Marchini et al. 2019). In fact, invasive species are supposed to be more tolerant to environmental stresses (Alpert *et al.*, 2000; Antunes *et al.*, 2018), showing a general higher phenotypic plasticity than native species (Feng *et al.*, 2007; Raizada *et al.*, 2009).

In this observational study, we aimed at parsing the relationships between native and alien plants and soil properties (i.e. soil conductivity, soil nutrients) in three main habitats of coastal dune systems, i.e. foredune, backdune and saltmarsh. In addition, the variation of important reproductive and vegetative functional traits for both alien and native species were considered. In particular, we hypothesized that:

(i) low soil conductivity (i.e. less salt content) favours the abundance and richness of alien species in each considered habitat;

(ii) soil nutrients increase along with alien species abundance;

(iii) alien and native species functional spectra differ according to the considered habitat and its level of invasion.

Materials and methods

Study site and plant communities

The study sites were the barrier islands of the Marano and Grado lagoon (from 45°42’10.5’’N 13°9’17.8’’ E to 45°40’49.8’’N 13°21’31.2’’ E), located in the northern part of the Adriatic Sea (Friuli Venezia Giulia region, Italy) (Fig. 1a-b). The lagoon is included in the Natura 2000 network, recognized both as Special Area of Conservation (SAC) and Special Protection Area (SPA). The mean annual rainfall is 974 mm. The driest month is July. The mean lowest temperature is in January; with a value of 3.1°C; the mean highest temperature is in July, with a value of 29.0°C. Wind average speed ranges from 7.8 to 10.4 km/h.

The four main barrier islands of the Lagoon considered for the present study were: (from W to E) Martignano (length 1.8 km, maximum width 0.8 km), Sant’Andrea (length 5.3 km, maximum width 0.7 km), Bocca d’Anfora (length 3.1 km, maximum width 0.7 km) and Banco d’Orio (length 4.9 km, maximum width 0.2 km). Each barrier island represents a dynamic system produced by the interaction between tidal movements and alongshore sediment transport, where both dune and halophile systems coexist. In this study, three main habitats were surveyed, namely: foredune, backdune and saltmarsh, which reflect the zonation of the vegetation along the environmental sea–inland gradient (Fig. 1c). Foredune, the nearest habitat to the shoreline, represent the first colonized part of the sandy shore, encompassing highly dynamic communities, strongly shaped by winter wash over events. Backdune is more stable, less subjected to winter storms and shows a greater ecological complexity when compared to foredune. On the lagoon side, the influence of tide produces the establishment of saltmarsh habitats. Saltmarsh are a major, widely distributed, intertidal habitat which differs from dunes for soil salinity and soil texture (larger presence of clay), and consequently on soil nutrient availability. Despite many saltmarshes are estuarine, they can also be found associated with barrier islands, usually due to wash over events that brake the sand barrier and leads to the deposit of fine soil particles just behind dunes (Fontolan *et al.*, 2012).

Sampling design

Along the islands shore we identified a total of 10 areas (ca. 5 ha each). Each area represented the described ecological gradient including the 3 main habitats of our interest (i.e. foredune, backdune and saltmarsh). Ten points were randomly selected within each of the 10 previously selected areas (see Fig. 1c as example), giving overall 100 points: 32 points for foredune, 40 for backdune and 28 for saltmarsh. In each point, plant communities and soil were surveyed.

Data collection

Plant community

At each point, a sample area (plot) of 16 m^2 (4x4 m) was established. Within each plot we recorded the occurrence and abundance (cover percentage) of the vascular plant species. Species nomenclature follows Bartolucci et al. (2018) and Galasso et al. (2018) for natives and aliens, respectively. Native and alien status of the species were assigned according to Buccheri et al. (2018). Out of the considered literature, we selected 5 functional traits supposed to be highly sensitive to the analyzed environmental gradient and putatively related to the success of invasive species in the studied area. The selected functional traits were specific leaf area (SLA), seeds mass, mean length of flowering period, mean flowering month and root depth. Data were derived from Landolt et al. (2010) and Kleyer et al. (2008).

Soil

Within each plot, a soil sample was collected using a cylindrical tube (height: 12 cm, width: 3.5 cm, volume: 115.5 cm^3), transported to the lab and stored at 4°C. Soil samples (n=100) were afterwards homogenized and divided into two aliquots. The first aliquot was air-dried, sieved at 2 mm and ball-milled for the further chemical analysis of soil organic carbon (C) and nitrogen (N), while the second aliquot was stored at 4°C in plastic bags for the analyses of conductivity and granulometry.

Soil organic carbon and nitrogen content were measured on a set of subsamples using a CHNS Elemental Analyser (Vario Microcube © Elementar). Before analysis, all soil samples were treated with HCl to remove the carbonate fraction.

Conductivity was measured in 5:1 extract using about 10 g of dry soil and 50 mL of water. The solution was shacked for 2 hours and filtered using a Whatman n°42 filter paper. Conductivity was measured in the filtered solution using the CM35+ portable conductivity meter (Crison).

The Bouyoucos method was applied to determine granulometry. A small amount of soil was used to determine soil humidity. About 50 g of corresponding dry soil was treated with 100 ml of sodium hexametaphosphate (SHMP). The extract (1:2) was shacked for 2 hours and then pour in a Bouyoucos' cylinder, where density was measured with the hydrometer ASTM 152H after 4 minutes and 2 hours (silt plus clay and only clay, respectively).

Data analysis

All statistical analyses were performed with the statistical software R 3.4.4 (R Team, 2019).

For each plot, we calculated species richness (number of species) and abundance (sum of species cover) of the overall, native and alien pools of species, respectively. Since the ranges of native and alien species richness and abundance were very different, we standardized species richness and abundance (z-scores) within each status level.

Differences between habitat in terms of overall and status-pooled species richness were tested using linear mixed-effects models (LMMs), considering the id of the 5 ha surveyed area (i.e. area id) and sub replicates for the status (i.e. plot id) as random effects. A Tukey pairwise test was then applied to detect significant differences between habitat and status (native or alien) interaction ($p<0.05$). LMMs were applied with the "nlme" package (Pinheiro *et al.,* 2019), pairwise comparisons were performed with the 'multcomp' R package (Hothorn *et al.*, 2008).

We used Multi-Model Inference (Barton, 2015) to evaluate the influence of soil on standardized species richness and abundance of aliens and natives, respectively, within the different habitats (Burnham and Andreson 2002). Preliminarily, we analyzed the correlation (Pearson test) between all the soil features measured (see online Supplementary Material, Fig. S1). As the correlation between all soil granulometry term (i.e. sand, silt and clay content %) and soils conductivity was high ($r > |0.75|$, $p < 0.001$), we used only soil conductivity in further analyses to avoid collinearity issues (Dormann *et al.*, 2013). We used LMMs to estimate model parameters as model residuals did not violated any linear model assumption. We further tested the performance of Generalized Mixed-Effects Models with Poisson distribution but models residuals were worst. Models included standardized species richness or abundance as response variable and species status (i.e. aliens or natives), habitat type, and main soil features (i.e. soil carbon and nitrogen content, soil conductivity) and their interaction with habitat and status as fixed effects. The random effects of the

5 ha surveyed area (i.e. area id) and sub replicates for the status (i.e. plot id) were included. Given the non-linear relationship between independent variable and dependent variables, the models were linearized by logarithmic transformation as best solution after considering the inclusion of a quadratic term. Multi-model inference compared the fit of all possible models obtained by the combination of the variables. We used Akaike's information criterion (AIC) to choose the best fitting model. The best fit is indicated by the lowest AIC value (AIC MIN). In a set of models each model *i* can be ranked using its difference in AIC score to the best-fitting model (Δ AIC*i* = AIC*i*- AIC*i* MIN). A model in the set can be considered plausible if its Δ AIC is below 2 (Burnham and Anderson 2002).The multi-model inference based on AIC was executed using the 'MuMIn' package (Barton, 2015). The LMMs were applied using the "nlme" package (Pinheiro *et al.,* 2019).

Functional traits variation was assessed using a multivariate approach testing the differences between habitat, species status and their interaction in terms of traits homogeneity. Homogeneity of traits was tested calculating the distance between centroids ('variation' of beta diversity) and testing for homogeneity of multivariate dispersion between habitats and species status (i.e. alien vs native). This method produces an independent dissimilarity value for each sample, distance to group centroid (Anderson *et al.*, 2006). Differences in mean trait distances were tested using PERMANOVA on the distance matrices ran with 999 permutations. Analyses of traits variation was performed using the "vegan" R package (Oksanen *et al.*, 2019), considering the Euclidean distance applied to standardized traits values (z-scores) as distance metric.

Results

Plant diversity, habitat and alien plant invasion

The total number of species within the 100 surveyed plots was 97 (73 native and 24 alien) (Supplementary Table S1). The most common native species were *Cakile maritima* Scop., occurring in 38% of the overall number of plots, *Elymus acutus* (DC.) M.A. Thiébaud (29 %), *Limonium narbonense* Mill. (28 %) and *Limbarda crithmoides* (L.) Dumort. (28%). Among the alien species, the most frequent were *Sporobolus pumilus* (Roth) P.M. Peterson & Saarela (50 %), *Xanthium italicum* Moretti (35 %), *Ambrosia psilostachya* DC. (34%) and *Oenothera biennis* L. aggr. (30 %).

The average species number found in each plot was 7.8 ± 3.1 (mean ± standard deviation). Species richness was significantly different among habitats ($F_{2-88} = 8.34$, $p < 0.001$), where foredune (7.7 ± 3.23) and backdune (9.2 ± 2.7) had significant higher values than saltmarsh (5.7 ± 2.3) ($p < 0.05$). A significant interaction was found between habitat and status (i.e. alien vs native) ($F_{2-97} = 18.7$, $p < 0.001$). Differences between native and alien standardized species richness (hereafter species richness) were significant in saltmarsh and backdune where native species showed higher values (Fig. 2).

Relationships between plant invasion and soil features

Multi-Model Inference analysis showed that species richness of alien and native plants were related to soil features by only one plausible model (Δ AIC < 2), which included soil conductivity, soil nitrogen content and the interactions with species status and habitat for the conductivity, and with habitat, for the soil nitrogen (Table 1; R^2=0.51).

Soil conductivity affected alien and native species number in relation to the habitat (Fig. 3a-f). In foredune, plant species number was positively related with soil conductivity, native species showed a stronger increase respect to aliens (Fig. 3a). In backdune, native species number increased when conductivity increased, whereas alien species number decreased (Fig. 3b). In saltmarsh, the number of specie was not correlated with soil conductivity (Fig. 3c).

High values of nitrogen content in the soil increased the overall number of species in foredune, while decreasing it in saltmarsh (Fig. 3d). Finally, in backdune, the number of both native and alien species was not affected by soil nitrogen (Fig. 3e).

We also analyzed the effect of conductivity, soil organic carbon and total nitrogen on the abundance of species (species overall cover) in relation to each status and habitat. Multi-model inference analysis showed that only one model was plausible (Δ AIC < 2) and it included all considered interactions (Table 2), explaining the 48% of the total variation in species abundance.

High soil conductivity favored native species abundance in both foredune and backdune (Fig. 4a, b), whereas plant cover was not related to soil conductivity in saltmarsh (Fig. 4c).

Soil organic carbon content was positively related to alien overall cover in both foredune and backdune, whereas native plant abundance decreased with increasing content of soil organic carbon, but only in backdune (Fig. 4e). In saltmarsh, species abundance was not affected by soil organic carbon content (Fig. 4f).

Soil nitrogen showed negligible effects on species cover in foredune and saltmarsh (Fig. 4g, i). In backdune there was a considerable increase of native species cover, whereas alien cover slightly decreased in nitrogen rich-soils (Fig. 4h).

Functional convergence

We found a significant difference between native and alien plant functional trait spectrum (distance) (PERMANOVA: $r^2 = 0.09$, $p = 0.001$), in different habitats ($r^2 = 0.14$, $p = 0.001$) and their interaction was significant as well ($r^2 = 0.06$, $p = 0.001$). Interestingly, we found a functional convergence (similarity) between alien and native species pool only in backdune habitat, which was also the most invaded. On the other hand, functional traits variation (dispersion) did not differ between species status, habitat and their interactions ($p > 0.05$) (see online Supplementary Material, Fig. S2).

Discussion

Our findings suggest that plant invasion of dune systems is related to soil properties, whose nutrients and conductivity (i.e. salinity) showed contrasting relationships with plant diversity and abundance in the studied habitats across the sea-inland gradient. Most invaded habitat was backdune, where its highest overall biodiversity was also sustained by the high level of invasion. In backdune, abundance and richness of alien species were more affected by soil features than in the other habitats, also probably due to a less intensive disturbance regime (weaker wash over influence). In general, soil conductivity determined the species richness of both alien and native species, while soil organic carbon and nitrogen were related to their abundance. In backdune, a significant functional convergence was also found, which is probably consistent to a greater habitat stability which also contributed to ameliorate the general ecological conditions of these communities. Here, in less salty soil, the overlap of studied traits (reproductive and growth traits) between native and alien species suggests that competition of aliens consist in substituting native species rather than filling the empty ecological space (niche differentiation).

Plant diversity, habitat and alien plant invasion

Alien species represented the 25% of the total species richness in the studied dune system, much higher than the frequency of alien taxa at regional (16%) and national (12%) scale (Galasso *et al.*, 2018); hence confirming that coastal dunes are one of the most invaded habitat by neophytes at the European level (Chytrý *et al.*, 2008).

Saltmarsh showed an overall low plant diversity, similar to what found by Kunza and Pennings (2008), but also harbored a low number of alien species. In this habitat, flooding, sediment anoxia and salt create extremely harsh conditions (Redelstein *et al.*, 2018), difficult to cope for generalist plants. Only few adapted species thrive in this habitat and their response to the environment can indirectly ameliorate pant community condition and overall plant diversity (Redelstein *et al.*, 2018; Pellegrini *et al.*, 2018).

We found harsh condition of saltmarsh to limit plant invasion. In contrast, backdune had concurrently a high number of alien and native plants. In this habitat, the interplay between stability and disturbance of habitat (wash over events) might explain the high values of invasion. In fact, when dune habitats are subject to naturally induced disturbance (e.g. winter storms) they harbor a large number of alien species (Del Vecchio *et al.*, 2015). On the other hand, the particularly extreme conditions given by natural events (e.g. seashore nearness, high wind speed, sand storm, shore erosion) occurring in foredune (Perumal and Maun, 2006; Ciccarelli, 2014) allow only few characteristic native species to colonize the habitat, e.g. *Cakile maritima* and *Salsola kali* (Debez *et al.*, 2004). Backdune showed concurrently high richness of both native and alien species. This could be related to a weaker influence of direct stressors (distance from the sea) which ameliorate the environment conditions, becoming adequate also for generalist species coming from other habitats such as inland agricultural land-use and semi-natural grasslands (Marcantonio *et al.*, 2014).

Relationships between plant invasion and soil features

Among the analyzed soil features, soil conductivity (i.e. salinity), organic carbon and nitrogen content showed significant relationships with plant species abundance and diversity, with contrasting trends between alien and native plants, especially in backdune habitat. Soil conductivity have been proved to affect plant distribution in coastal dunes (Ishikawa *et al.*, 1995) and altering the interactions between native and alien species (Wang *et al.*, 2006). Moreover, many alien species are supposed to be less competitive than native species in relation to salt stress (Mesléard *et al.*, 1993; Borgnis and Boyer, 2016). Salt content create harsh condition principally by reducing water availability and increasing osmotic stress. On sandy soils, this is exacerbated by the high soil porosity and thus water drainage. In these conditions, native adapted species thrive better than alien (Antunes *et al.*, 2018). In contrast, a previous study showed that alien species richness increased in sites with high rainfall, as a consequence of a higher soil water availability and salt leaching.

Soil nitrogen content increased along with the overall number of species found in foredune, whereas it was not influent in the other habitats. Despite several studies linked a reduction of plant diversity to nutrient concentration and hence ecosystem productivity a consistent pattern among terrestrial ecosystem is lacking (Tilman *et al.*, 1997; Fridley, 2001). In foredune, the average nitrogen content was very low. In such conditions, it is plausible that an increase of nutrients availability allow to a higher number of species to colonize the bare soil, whose occurrence can also indirectly increase the soil organic matter (positive feedback).

We found that nitrogen and organic carbon soil content (i.e. overall representing also organic matter content) were mainly involved in explaining plant abundance of alien and native species. The relationships between nitrogen and carbon soil content and species abundance were stronger in backdune, while in the harsher environments the other drivers (e.g. waterlogging, salinity, wave action, storms disturbance) seem to overrule on such effects. In backdune, a high content of nitrogen increased along with the abundance of native species, but not with the abundance of alien species. It is thought that plant invasion is favored by high content of nitrogen, triggering positive feedback between plant invasion and carbon and nitrogen cycles in invaded ecosystems (Liao *et al.*, 2008). Our findings, instead, support the idea that in very poor soils native rather than alien species can intercept such nutrient resources and increase their abundance.

However, we cannot exclude the aftereffect of the overall plant abundance (biomass) accumulating in a more stable habitat less subjected to wash over events.

In contrast, soil organic carbon was positively related to the increase of alien species abundance in backdune. The content of organic carbon had a great effect on other soil properties and structure, altering microbial activity (Sparling, 1992) and water cycle. Our study suggests that a high content of soil organic carbon might ameliorate soil structure and nutrients-water availability (the more organic matter is present in the soil, the more water is kept and nutrients less leached) thus favoring the growth of generalist alien species. Nonetheless it is also true that a higher abundance of plants, and in particular of some invasive alien species might be the cause of the increase in soil organic carbon (Boscutti *et al.*, 2020), which can accumulate in backdune, less subjected to wash over. In the light of the observational nature of the study it was not possible to definitely define a cause-effects mechanism between soil and plants, opening future experimental perspectives.

Functional convergence

Plant trait analysis is a methodological approach to better understand the processes linked to alien species invasion (Richardson *et al.*, 2000; Richardson and Pyšek, 2006). Stressed plant communities are mainly ruled by habitat filtering, whereas functional convergence is mainly related to this ecological process (Cornwell *et al.*, 2006). When different plant species are co-existing in the same community, it is usual for species to show some morphological and functional similarities (Grime, 2006; de Bello *et al.*, 2009). Environmental filtering can contribute to communities similarity and the result of this process is functional redundancy for species traits inside a community (Cornwell *et al.*, 2006). Our findings suggest the presence of an overlap of niche between native and alien species and a potential substitution of native species in the most invaded habitat, namely the backdune. Kowarik (2008) explains that changes in environmental factors can generate a more efficient niche invasion by alien species, rather than favor native species. In fact, this mechanism is known to be more effective where environmental conditions are not extremely harsh (Carboni *et al.*, 2010). In these conditions, we can hypothesize that less specialized alien species are favored to invade dune ecosystem due to ecosystem characteristic which present a higher similarity to human-disturbed habitats (e.g. urban sites or agricultural) where the alien species commonly thrive (Kowarik, 2008).

In foredune and saltmarsh, instead, the analyses of trait variability suggest that alien and native species have separated functional spectra, suggesting that here alien species are filling empty ecological niches rather that replace native ones. Given the uniqueness of the environmental niches, plant species evolved to specialized species and only few alien species are suitable to colonize these areas (Marcantonio *et al.*, 2014).

Conclusions

Our findings suggest that main soil properties and plant functional traits are related to the plant invasion across the shore-saltmarsh gradient in barrier islands. The initial hypotheses were supported by our results, showing that soil conductivity curb both abundance and specific richness of alien species, favoring the presence of native species. Moreover, nitrogen and organic carbon in soil were related to plant with particular regard to plant abundance, underpinning plausible feedback mechanisms between plant and soil which understanding would need specific experimental approach. The magnitude of the effect is habitat specific: while backdune are the most sensitive habitat, foredune and saltmarsh were mostly unaffected by plant invasion and regardless to soil feature gradients. Finally, the higher invasion of backdune was consistent with a functional convergence between alien and native species pool.

Our results highlight that even though coastal systems are reported to be among the most invaded habitats by neophytes (Chytrý *et al.*, 2008), some plant communities may be much more affected by invasion than others, representing real conservation priorities. In these habitats, further experiments concerning the changes/manipulation of soil conductivity and soil nutrients could shed new perspectives in limit ecosystem deterioration in terms of overall biodiversity and invasiveness.

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References

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol Evol Syst* **3**:52–66.

Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. *Ecol Lett* **9**:683–693.

Antunes C, Pereira AJ, Fernandes P, *et al.* (2018) Understanding plant drought resistance in a Mediterranean coastal sand dune ecosystem: Differences between native and exotic invasive species. *J Plant Ecol* **11**:26–38.

Bartolucci F, Peruzzi L, Galasso G, *et al.* (2018) An updated checklist of the vascular flora native to Italy. *Plant Biosyst - Int J Deal Asp Plant Biol* **152**:179–303.

Barton K (2015) Package 'MuMIn'. Multi-Model Inference. Ver 1.40.0.In*Cran R-Proj*.

Bello F de, Thuiller W, Lepš J, *et al.* (2009) Partitioning of Functional Diversity Reveals the Scale and Extent of Trait Convergence and Divergence. *J Veg Sci* **20**:475–486.

Borgnis E, Boyer KE (2016) Salinity Tolerance and Competition Drive Distributions of Native and Invasive Submerged Aquatic Vegetation in the Upper San Francisco Estuary. *Estuaries Coasts* **39**:707–717.

Boscutti F, Casolo V, Beraldo P, Braidot E, Zancani M, Rixen C (2018a) Shrub growth and plant diversity along an elevation gradient: Evidence of indirect effects of climate on alpine ecosystems. *PLOS ONE* **13**:e0196653.

Boscutti F, Pellegrini E, Casolo V, Nobili M de, Buccheri M, Alberti G (2020) Cascading effects from plant to soil elucidate how the invasive Amorpha fruticosa L. impacts dry grasslands. *J Veg Sci* **n/a**.

Boscutti F, Sigura M, Simone SD, Marini L (2018b) Exotic plant invasion in agricultural landscapes: A matter of dispersal mode and disturbance intensity. *Appl Veg Sci* **21**:250–257.

Bu W, Huang J, Xu H, *et al.* (2019) Plant Functional Traits Are the Mediators in Regulating Effects of Abiotic Site Conditions on Aboveground Carbon Stock-Evidence From a 30 ha Tropical Forest Plot. *Front Plant Sci* **9**:1958 10.3389/fpls.2018.01958.

Buccheri M, Boscutti F, Pellegrini E, Martini F (2018) La flora aliena nel Friuli Venezia Giulia - Alien flora in Friuli Venezia Giulia. *Gortania* **40**:7–78.

Burnham KP, Anderson DR, Burnham KP (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. New York: Springer.

Campos JA, Herrera M, Biurrun I, Loidi J (2004) The role of alien plants in the natural coastal vegetation in central-northern Spain. *Biodivers Conserv* **13**:2275–2293.

Caño L, Fuertes-Mendizabal T, García-Baquero G, Herrera M, Begoña González-Moro M (2016) Plasticity to salinity and transgenerational effects in the nonnative shrub Baccharis halimifolia: Insights into an estuarine invasion. *Am J Bot* **103**:808–820.

Carboni M, Santoro R, Acosta ATR (2010) Are some communities of the coastal dune zonation more susceptible to alien plant invasion? *J Plant Ecol* **3**:139–147.

Carvalho LM, Antunes PM, Martins-Loução MA, Klironomos JN (2010) Disturbance influences the outcome of plant-soil biota interactions in the invasive Acacia longifolia and in native species. *Oikos* **119**:1172–1180.

Chapin III FS, Vitousek PM, Cleve KV (1986) The Nature of Nutrient Limitation in Plant Communities. *Am Nat* **127**:48–58.

Chytrý M, Maskell LC, Pino J, *et al.* (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *J Appl Ecol* **45**:448–458.

Ciccarelli D (2014) Mediterranean Coastal Sand Dune Vegetation: Influence of Natural and Anthropogenic Factors. *Environ Manage* **54**:194–204.

Cornwell WK, Schwilk DW, Ackerly DD (2006) A TRAIT-BASED TEST FOR HABITAT FILTERING: CONVEX HULL VOLUME. *Ecology* **87**:1465–1471.

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecol Lett* **14**:419–431.

Debez A, Ben Hamed K, Grignon C, Abdelly C (2004) Salinity effects on germination, growth, and seed production of the halophyte Cakile maritima. *Plant Soil* **262**:179–189.

Defeo O, McLachlan A, Schoeman DS, *et al.* (2009) Threats to sandy beach ecosystems: A review. *Estuar Coast Shelf Sci* **81**:1–12.

Del Vecchio S, Pizzo L, Buffa G (2015) The response of plant community diversity to alien invasion: evidence from a sand dune time series. *Biodivers Conserv* **24**:371–392.

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* **16**:646–655.

Donnelly FA, Pammenter NW (1983) Vegetation zonation on a Natal coastal sand-dune system in relation to salt spray and soil salinity. *South Afr J Bot* **2**:46–51.

Dormann CF, Elith J, Bacher S, *et al.* (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**:27–46.

Feng Y, Wang J, Sang W (2007) Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. *Acta Oecologica* **31**:40–47.

Fontolan G, Pillon S, Bezzi A, *et al.* (2012) Human impact and the historical transformation of saltmarshes in the Marano and Grado Lagoon, northern Adriatic Sea. *Estuar Coast Shelf Sci* **113**:41–56 10.1016/j.ecss.2012.02.007.

Fridley JD (2001) The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos* **93**:514–526.

Galasso G, Conti F, Peruzzi L, *et al.* (2018) An updated checklist of the vascular flora alien to Italy. *Plant Biosyst - Int J Deal Asp Plant Biol* **152**:556–592.

Giulio S, Acosta ATR, Carboni M, *et al.* (2020) Alien flora across European coastal dunes. *Appl Veg Sci* 10.1111/avsc.12490.

Gorham J (1992) Salt tolerance of plants. *Sci Prog* **76**:273–285.

Grime JP (2006) Trait Convergence and Trait Divergence in Herbaceous Plant Communities: Mechanisms and Consequences. *J Veg Sci* **17**:255–260.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. *Biom J* **50**:346–363.

Ishikawa S-I, Furukawa A, Oikawa T (1995) Zonal plant distribution and edaphic and micrometeorological conditions on a coastal sand dune. *Ecol Res* **10**:259–266.

Ishikawa S, Oikawa T, Furukawa A (1991) Responses of photosynthesis, leaf conductance and growth to different salinities in three coastal dune plants. *Ecol Res* **6**:217–226.

Kleyer M, Bekker RM, Knevel IC, *et al.* (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *J Ecol* **96**:1266–1274.

Kowarik I (2008) On the Role of Alien Species in Urban Flora and Vegetation.In Marzluff JM, Shulenberger E, Endlicher W, et al. (eds). *Urban Ecology*. Boston, MA: Springer US, 321–338.

Kunza AE, Pennings SC (2008) Patterns of Plant Diversity in Georgia and Texas Salt Marshes. *Estuaries Coasts* **31**:673–681.

Landolt E, Bäumler B, Erhardt A, *et al.* (2010) *Flora Indicativa - Ecological indicator values and biological attributes of the flora of Switzerland and the alps*. 2nd ed. Haupt.

Liao C, Peng R, Luo Y, *et al.* (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol* **177**:706–714.

Lortie CJ, Cushman JH (2007) Effects of a directional abiotic gradient on plant community dynamics and invasion in a coastal dune system. *J Ecol* **95**:468–481.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) BIOTIC INVASIONS: CAUSES, EPIDEMIOLOGY, GLOBAL CONSEQUENCES, AND CONTROL. *Ecol Appl* **10**:22.

Malavasi M, Carboni M, Cutini M, Carranza ML, Acosta ATR (2014) Landscape fragmentation, land-use legacy and propagule pressure promote plant invasion on coastal dunes: a patch-based approach. *Landsc Ecol* **29**:1541–1550.

Marcantonio M, Rocchini D, Ottaviani G (2014) Impact of alien species on dune systems: a multifaceted approach. *Biodivers Conserv* **23**:2645–2668.

Marchini GL, Maraist CA, Cruzan MB (2019) Trait divergence, not plasticity, determines the success of a newly invasive plant. *Ann Bot* **123**:667–679.

Marzialetti F, Bazzichetto M, Giulio S, *et al.* (2019) Modelling Acacia saligna invasion on the Adriatic coastal landscape:An integrative approach using LTER data. *Nat Conserv* **34**:127–144 10.3897/natureconservation.34.29575.

Mesléard F, Tan Ham L, Boy V, Wijck C van, Grillas P (1993) Competition between an introduced and an indigenous species: the case of Paspalum paspalodes (Michx) Schribner and Aeluropus littoralis (Gouan) in the Camargue (southern France). *Oecologia* **94**:204–209.

Ohlemüller R, Walker S, Bastow Wilson J (2006) Local vs regional factors as determinants of the invasibility of indigenous forest fragments by alien plant species. *Oikos* **112**:493–501.

Oksanen J, Guillaume Blanchet F, Friendly M, *et al.* (2019) Community Ecology Package. 1–296.

Pellegrini E, Boscutti F, De Nobili M, Casolo V (2018) Plant traits shape the effects of tidal flooding on soil and plant communities in saltmarshes. *Plant Ecol* **219**:823–835.

Perumal VJ, Maun MA (2006) Ecophysiological response of dune species to experimental burial under field and controlled conditions. *Plant Ecol* **184**:89–104.

Pinheiro J, Bates D, DebRoy S, Sarkar D (2019) *nlme: Linear and Nonlinear Mixed Effects Models*.

R Team C (2019) *R: A Language and Environment for Statistical Computing*.

Raizada P, Singh A, Raghubanshi AS (2009) Comparative response of seedlings of selected native dry tropical and alien invasive species to CO2 enrichment. *J Plant Ecol* **2**:69–75.

Redelstein R, Dinter T, Hertel D, Leuschner C (2018) Effects of Inundation, Nutrient Availability and Plant Species Diversity on Fine Root Mass and Morphology Across a Saltmarsh Flooding Gradient. *Front Plant Sci* **9**:98 10.3389/fpls.2018.00098.

Rejmanek M, Richardson DM (1996) What Attributes Make Some Plant Species More Invasive? *Ecology* **77**:1655–1661.

Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Prog Phys Geogr Earth Environ* **30**:409–431.

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* **6**:93–107.

Simberloff D, Martin J-L, Genovesi P, *et al.* (2013) Impacts of biological invasions: what's what and the way forward. *Trends Ecol Evol* **28**:58–66.

Sparling GP (1992) Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. *Soil Res* **30**:195–207.

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: Theoretical considerations. *Proc Natl Acad Sci* **94**:1857–1861.

Tordoni E, Petruzzellis F, Nardini A, Savi T, Bacaro G (2019) Make it simpler: Alien species decrease functional diversity of coastal plant communities. (Z Botta-Dukát, Ed.). *J Veg Sci* 10.1111/jvs.12734.

Vilà M, Basnou C, Pyšek P, *et al.* (2010) How well do we understand the impacts of alien species on ecosystem services? A pan- European, cross-taxa assessment. *Front Ecol Environ* **8**:135–144.

Vitousek PM, Aber JD, Howarth RW, *et al.* (1997) HUMAN ALTERATION OF THE GLOBAL NITROGEN CYCLE: SOURCES AND CONSEQUENCES. *Ecol Appl* **7**:737–750.

Wang Q, Wang CH, Zhao B, *et al.* (2006) Effects of growing conditions on the growth of and interactions between salt marsh plants: implications for invasibility of habitats. *Biol Invasions* **8**:1547–1560.

Tables

Table 1: Results of the linear mixed-effects models relating standardized species richness with habitat (i.e. foredune, backdune and saltmarsh), species status (i.e. alien and native), soil conductivity (cond), soil nitrogen content (N) and the interactions between species status, habitat and soil conductivity, nitrogen content and habitat type. Degrees of freedom (DF), F-value and p-value are reported. In bold are indicated the significant outcomes (p<0.05).

	DF	F-value	p-value
habitat	**2-76**	**13.372**	**<.0001**
status	1-87	0.001	0.984
log(cond)	1-76	0.619	0.433
log(N + 0.1)	1-76	0.293	0.589
habitat:status	**2-87**	**27.200**	**<.0001**
habitat:log(cond)	**2-76**	**4.820**	**0.011**
status:log(cond)	**1-87**	**4.950**	**0.029**
habitat:log(N + 0.1)	**2-76**	**3.712**	**0.029**
habitat:status:log(cond)	**2-87**	**3.535**	**0.033**

Table 2: Results of the linear mixed-effects models relating the standardized species abundance with habitat (i.e. foredune, backdune and saltmarsh), species status (i.e. alien and native), soil conductivity (cond), soil nitrogen content (N), soil organic carbon (C) and the interactions between species status, habitat and soil conductivity, nitrogen content, organic carbon content and habitat type. Degrees of freedom (DF), F-value and p-value are reported. In bold are indicated the significant outcomes (p<0.05).

	DF	F-value	p-value
log(cond)	1-73	0.743	0.391
Habitat	**2-73**	**6.833**	**0.002**
Status	1-81	0.001	0.981
C	1-73	0.003	0.955
log(N + 0.1)	1-73	0.498	0.482
log(cond):habitat	2-73	0.384	0.682
log(cond):status	**1-81**	**92.082**	**<.0001**
habitat:status	**2-81**	**8.792**	**0.001**
habitat:C	2-73	1.552	0.219
status:C	1-81	1.968	0.164
habitat:log(N + 0.1)	2-73	0.866	0.425
status:log(N + 0.1)	1-81	3.564	0.062
log(cond):habitat:status	2-81	0.550	0.579
habitat:status:C	2-81	1.313	0.274
habitat:status:log(N + 0.1)	2-81	2.389	0.098

Figures and figure legends

Figure 1: location of the study area in the lagoon of Marano and Grado in the northern Adriatic Sea (a), the barrier islands and 10 sampling areas (b), and an example of 10 points distribution inside each sampling area (San Andrea island) (c).

Figure 2: differences in standardized species richness between status (native=solid line, alien=dashed line) within the considered habitats. Confidence intervals (95 %) are also shown (shaded).

Figure 3: effects of soil conductivity (a, b, c) and soil nitrogen (d, e, f) on standardized plant species richness of native (solid line) and alien (dashed line) status within habitats (vertical columns). Confidence intervals (95 %) are also shown (shaded).

Figure 4: effects of soil conductivity (a, b, c), organic carbon content in soil (d, e, f) and nitrogen content in soil (g, h, i) on standardized species cover (abundance) between status (native=solid line, alien=dashed line) and within habitats (vertical columns). Confidence intervals (95 %) are also shown (shaded).

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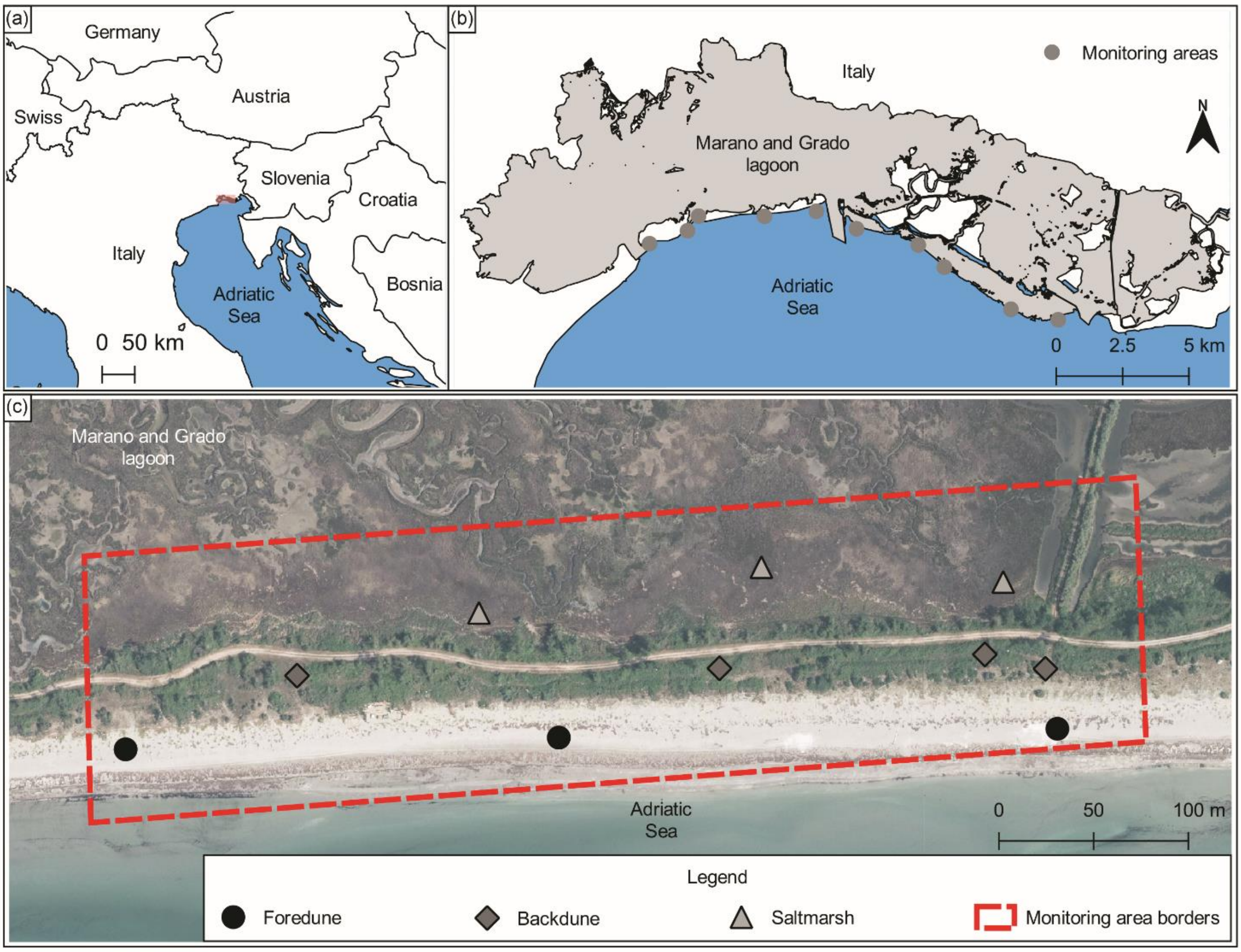

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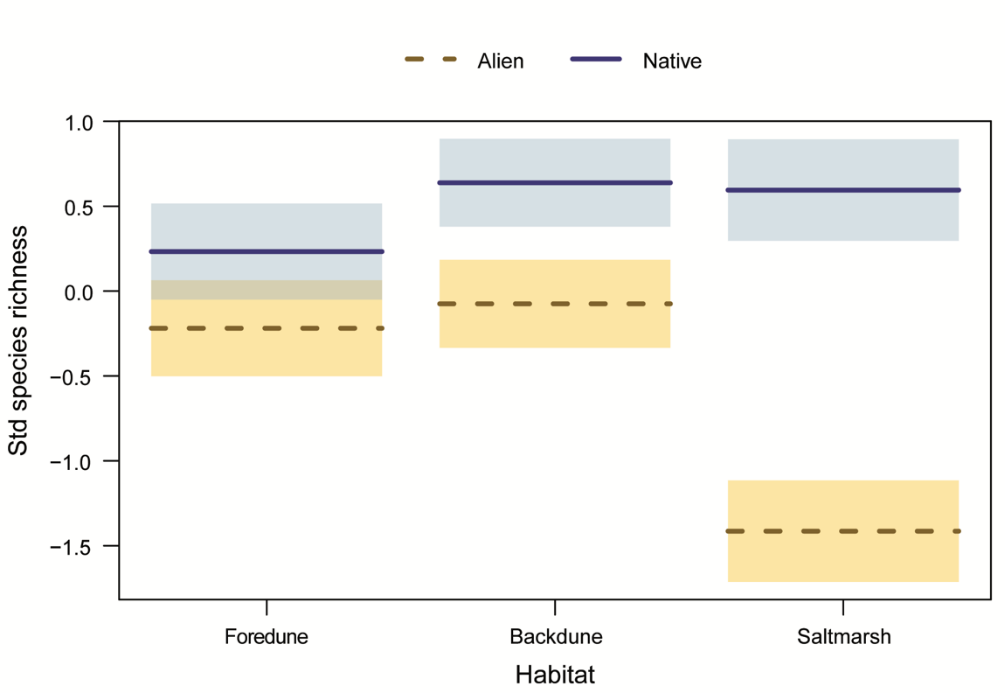

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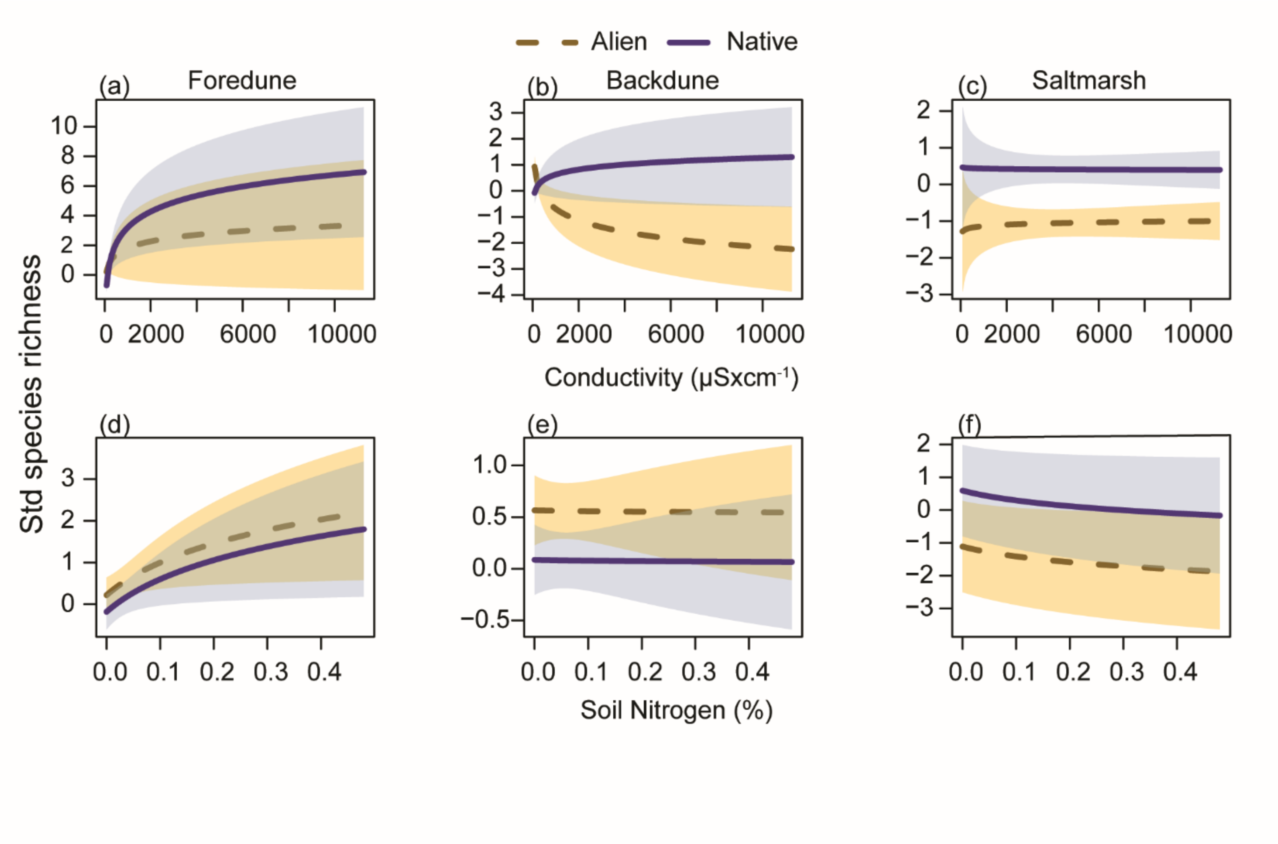

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