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► To cite this version:

Enrico Tordoni, Giovanni Bacaro, Patrick Weigelt, Michela Cameletti, John A.M. Janssen, et al.. Disentangling native and alien plant diversity in coastal sand dune ecosystems worldwide. *Journal of Vegetation Science*, 2021, 32 (1), 10.1111/jvs.12961 . hal-03727604

HAL Id: hal-03727604

<https://hal.science/hal-03727604>

Submitted on 5 Feb 2024

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

3

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42 **Abstract**

43

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

49 **Location** Global.

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

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

63 **Conclusions** Our results revealed the complexity of causal processes underpinning coastal sand
64 dune plant biodiversity and highlight the importance of considering native and alien species
65 separately. Recognition of these differences while researching variation in biodiversity patterns and
66 processes at multiple spatial scales will lead to a better mechanistic understanding of the causes of

67 invasion worldwide, and in coastal ecosystems in particular, allowing the development of more
68 focused control and management measures.

69
70 **Keywords:** Alien species, Biodiversity, Biogeography, Coastal dune habitats, Diversity patterns,
71 Invasion paradox, Macroecology, Species richness.

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88 **Introduction**

89 The coastlines of our planet extend to approximately 1.5 million km of which about 31 % are sandy
90 beaches (World Resources Institute, 2005; Luijendijk *et al.*, 2018). Along these coastlines, sand dune
91 ecosystems are widespread and occur from the polar regions to the tropics, encompassing a wide
92 range of climates, biomes and habitats (van der Maarel, 1993; Maun, 2009). Vegetation plays a
93 primary role in sand dune formation and consolidation due to its ability to stabilize the substrate and
94 to enhance sand deposition (Maun, 2009). Regardless of differences in species composition, all sand
95 dune species and habitats worldwide share the same limiting factors, such as sand burial, sand
96 blasting, marine aerosol, water deficiency and lack of nutrients (Acosta *et al.*, 2009; Monserrat *et al.*,
97 2012; Pardini *et al.*, 2015; Mahdavi and Bergmeier, 2016), and exhibit a characteristic sea-inland
98 gradient ('zonation'; Wilson and Sykes, 1999; Acosta *et al.*, 2009; Miller *et al.*, 2010; Tordoni *et al.*,
99 2018).

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

113 *al.*, 2010a; Novoa *et al.*, 2013), which may lead to the extinction of native taxa of conservation
114 concern, including endemic and keystone species (Acosta *et al.*, 2009; Pardini *et al.*, 2015).

115 The impacts of biological invasions are strongly scale-dependent (e.g. Levine and D'Antonio,
116 1999; Vellend *et al.*, 2017). One of the most frequently discussed impacts of alien species is the
117 reduction in species richness of the invaded community (Vilà *et al.*, 2015), but the relationship
118 between native and alien species diversity is still a matter of discussion in plant ecology (Fridley *et*
119 *al.*, 2007), with different interpretations of the phenomenon often reflecting different spatial scales of
120 observation or study design (e.g. Muthukrishnan *et al.*, 2018; Tomasetto *et al.*, 2019). Generally,
121 more negative relationships have been described at finer scales (experimental or small-scale studies),
122 whereas the opposite trend is usually observed at larger observation scales (from large plot to
123 landscape or biome). In response to this scale-related inconsistency, scientists coined the term
124 'invasion paradox' to describe the scale dependency of native-alien richness patterns (Fridley *et al.*,
125 2007).

126 In coastal sand dunes, integration of scale of observation is particularly important for
127 understanding native plant community assemblage and richness (Carboni *et al.*, 2013). At finer scales
128 (few m²), biotic interactions usually predominate (Forey *et al.*, 2010; de Toledo Castanho *et al.*,
129 2015). At regional scales, several studies (e.g. Forey *et al.*, 2008; Brunbjerg *et al.*, 2012) have shown
130 that a suite of stressors (e.g. water and nutrient stress) and disturbance factors (e.g. sand burial)
131 interact in shaping plant communities and their species richness. At even larger spatial extents,
132 environmental and biogeographical factors become predominant (Jiménez-Alfaro *et al.*, 2015).

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134 Recently, great efforts have been made to disentangle broad-scale patterns of species richness (e.g.
135 Kreft and Jetz, 2007; Bruelheide *et al.*, 2019) and several theories have been proposed to explain
136 mechanisms responsible for species richness worldwide. Most of them rely on how water-energy
137 dynamics drive species richness gradients (Francis and Currie, 2003; Currie *et al.*, 2004; Kreft and

138 Jetz, 2007), along with the sensitivity of plants to frost and drought (Wiens and Donoghue, 2004).
139 Other hypotheses consider environmental heterogeneity (Stein *et al.*, 2014) or historical and
140 evolutionary processes (e.g. Médail and Diadema, 2009; Kerkhoff *et al.*, 2014).

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

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

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162

163 **Methods**

164 *Study sites and species data*

165 We compiled a database consisting of 14,841 vegetation plots sampled in coastal sand dune
166 communities distributed across Europe, North America, South America, Africa (Cape and
167 Paleotropical kingdoms) and Oceania (except Australia). Species richness per sampling unit was
168 obtained from plots and phytosociological relevés (hereafter plots) derived from literature and plant
169 databases both public and private such as the European Coastal Vegetation Database
170 (<http://www.givd.info/ID/EU-00-017>) or KRITI database (<http://www.givd.info/ID/EU-GR-001>).
171 For more details about the data sources see Table S1.1 in Appendix S1. In order to be considered in
172 the study, all plots had to comply with the following inclusion criteria: 1) a georeferenced location,
173 2) a defined sampling unit size, and 3) a defined habitat or coastal plant community (see below for
174 the adopted classification).

175 Species names were standardized with the Taxonomic Name Resolution Service (Boyle *et al.*, 2013;
176 <http://tnrs.iplantcollaborative.org/>). Furthermore, doubtful species and records not identified to the
177 species level were omitted. The status of the species (native or alien), if not provided by the author
178 of the data, was assigned using online databases or national alien species checklists (see Table S1.2
179 in Appendix S1). For each plot, we obtained two response variables: a) native species richness and
180 b) alien species richness. Plots with size smaller than 0.25 m² or with missing data for any of the
181 variables described below were excluded leaving 11,988 plots for analysis. Even though the majority
182 of the plots ranged in size from 0.25 to 100 m² (see Fig. S1.2 in Appendix S1), plot size has been
183 directly added in the models as a covariate to control for its effect on species richness (Arrhenius,
184 1921).

185
186 *Environmental variables*

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

195 We tested the following environmental variables related to the growth and distribution of vascular
196 plants as possible predictors of native and alien species richness: *mean annual precipitation*
197 (mm/year), *precipitation seasonality* (percentage variation in monthly precipitation totals over the
198 course of the year; larger values indicate greater variability), *mean annual temperature* (°C), and
199 *temperature seasonality* (percentage measure of temperature change over the course of the year).
200 Climatic data were obtained from the CHELSA database (Karger *et al.*, 2017, accessed June 2017),
201 a high-resolution climatology resource (30 arc seconds, ~1 km) spanning the years 1973 to 2013.
202 Values were assigned to each plot with nearest neighbor algorithm using QGIS 3.10 with GRASS
203 7.8.3 (Quantum GIS Development Team, 2020). We also included *insularity* (mainland vs island) and
204 floristic *kingdom* according to the floristic divisions of Takhtajan (1986) to control for the generally
205 lower diversity of island communities and the effect of unquantified historical or evolutionary
206 processes.

207 *Anthropogenic variables*

208 Based on previous research (e.g. Bellard *et al.*, 2016; Chapman *et al.*, 2016), we considered a set of
209 anthropogenic variables as predictors of alien species diversity that are surrogates for propagule
210 pressure and/or potential introduction pathways. Among these, human population density has been
211 identified as one of the main determinants of alien species richness at the continental scale (Pyšek *et*

212 *al.*, 2010). Thus, we employed *adjusted human population density* (people / km²) based on the
213 Gridded Population of the World at a resolution of 30 arc seconds (GPWv4; CIESIN, 2015), which
214 provides gridded human population density estimated for the year 2015 adjusted to match United
215 Nations (UN) estimated national-level population counts. As a proxy for trade volume, we used *Gross*
216 *Domestic Product per capita* (standardized to international dollars, int\$), (<http://data.worldbank.org>)
217 based on Gross Domestic Product (GDP) constructed from purchasing-power-parity (PPP) per capita
218 GDP (year 2015). Among human-related variables, proximity of airports, sea ports and cities also
219 have been recognized as facilitators of biological invasions for several taxa (e.g. Seebens *et al.*, 2013;
220 Bellard *et al.*, 2016). For this reason, we included the following predictors: *Distance to nearest city*
221 with more than 50,000 inhabitants (Nelson, 2008); *Distance to nearest airport* (Pope and Sietinsone,
222 2017) and *Distance to nearest port* (GISCO Ports, 2013). *Year* of sampling was also included to
223 assess whether there is an effect of time of the surveys. All datasets were accessed on September
224 2017. Distances were calculated through proximity analyses using QGIS 3.10 with GRASS 7.8.3.

225
226 *Species richness patterns across floristic kingdoms and habitats*
227

228 We first tested for differences in species richness across floristic kingdoms and habitat types using
229 generalized linear modeling (GLM). Due to the presence of severe overdispersion in the data
230 (variance \gg mean), we used a negative binomial error distribution (Zuur *et al.*, 2007). The
231 explanatory power of each predictor was evaluated through likelihood ratio tests in the R package
232 ‘car’ (Fox and Weisberg, 2011) and effects were estimated using the package ‘effect’ (Fox and
233 Weisberg, 2018). As a measure of model fit, we reported the amount of deviance explained by each
234 GLM (D^2_{adjusted} ; Barbosa *et al.*, 2014). To quantitatively test for the invasion paradox, we fitted a
235 negative binomial GLM to describe alien species richness as a function of native species richness,
236 sampling unit area and their first-order interaction. This analysis was also repeated for the Holarctic

237 kingdom alone to test for consistency of the results, since most of the data (including larger plots)
238 belonged to this kingdom.

239

240 *Ecological drivers*

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

248 GLMMs were estimated using the R package ‘glmmTMB’ (Brooks *et al.*, 2017) and R^2 values
249 developed by Nakagawa and Schielzeth were also computed (Nakagawa and Schielzeth 2013). To
250 isolate the effect of each group variable, four models were fitted (two for native and two for alien
251 species), considering environmental and anthropogenic variables separately (see Table S1.3 in
252 Appendix S1 for descriptive statistics of fixed effects). The response families were the same as for
253 the GLMs (negative binomial). Furthermore, the possible occurrence of spatial autocorrelation of
254 residuals in each model was assessed by means of spline-correlograms using the R package ‘ncf’
255 (Bjørnstad, 2020). Specifically, 95% pointwise bootstrap confidence intervals were calculated from
256 1000 bootstrap samples of Pearson residuals after accounting for the level of spatial autocorrelation
257 explained by the explanatory variables in each model. To further explore the role of ecological drivers
258 on species richness, a variation partitioning approach through partial linear regressions was used to
259 assign the total variation in native and alien species richness into purely environmental, purely
260 anthropogenic, shared and unexplained fractions (Borcard *et al.*, 1992; Legendre, 2008) using the
261 ‘vegan’ package (Oksanen *et al.*, 2019). All analyses were performed using R 4.0.2 (R Core Team,

262 2020); detailed model formulas and specifications are available in Supplementary material (Appendix
263 S2).

264

265 **Results**

266 *Global patterns of native and alien richness in sand dunes*

267 Overall, fitted values of native and alien species richness varied strongly among habitats and floristic
268 kingdoms (Fig. 1; Table S1.4, S1.5 in Appendix S1 of Supplementary material). There was a
269 significant interaction between habitat and floristic kingdom, both for native and alien species
270 (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_{adjusted}
271 $= 0.19$; respectively). These explanatory variables were strong predictors of global variation of species
272 richness for natives whereas they were relatively weak predictors for alien species (there was a
273 difference in deviance explained of 26% between the two models). For native species, fixed dunes
274 tended to have higher species richness compared to foredunes and interdunes in all the floristic
275 kingdoms (Fig. 1a) showing highest species richness in Cape and Paleotropical kingdoms. In contrast,
276 Holantarctic kingdom was the poorest one. Surprisingly, in some kingdoms, such as the Cape and
277 Holantarctic, alien species displayed a different pattern with respect to habitat compared to that of
278 native species (Fig. 1b) showing greater variation among habitats along the sea-inland gradient with
279 respect to native species. Specifically, foredunes showed higher levels of alien plants relative to fixed
280 dunes in the Cape and Holantarctic kingdoms, whereas the opposite was observed in the Holarctic
281 and Paleotropical kingdoms. On average, interdunes tended to have the lower levels of invasion (Fig.
282 1b). As hypothesized, higher values of alien species richness were clustered in specific regions, such
283 as New Zealand, North America or some European countries (Fig. 2).

284 An overall negative relationship between native and alien species richness was observed without
285 considering plot size (Fig. 3a). However, when grain size was specifically considered in the model,
286 the slope of the relationship shifted from negative to positive with increasing plot size, in agreement

287 with the pattern suggested by the invasion paradox (Fig. 3b). The GLM with alien species richness
288 as response variable showed a significant interaction between native richness and plot size ($\chi^2(1) =$
289 $63.90, P < 0.001$), even though a poor predictive power was detected ($D^2_{\text{adjusted}} = 0.02$). However, the
290 overall relationship between native and alien species richness became positive when considering only
291 the data coming from the Holarctic kingdom, no longer supporting the invasion paradox effect (Fig.
292 S1.3, $\chi^2(1) = 4.22, P < 0.05, D^2_{\text{adjusted}} = 0.01$).

293 *Global ecological determinants of native and alien richness*

294 GLMMs revealed large differences between the responses of alien and native species richness to
295 environmental and socio-economic variables. Native species richness was strongly associated with
296 global environmental gradients and only marginally with anthropogenic variables. Alien species
297 richness, in contrast, was more strongly associated with anthropogenic variables (Fig. 4, Table S1.6
298 in Appendix S1). These outcomes were further corroborated by the variation partitioning approach
299 where native species were mainly driven by environmental variables, whereas for alien species
300 anthropogenic variables accounted for a greatest percentage of explained variation (Fig. 5).
301 Specifically, native species richness significantly differed among habitats and, furthermore, was
302 positively related to mean annual temperature ($b = 0.06 \pm 0.02$ SE, Table S1.6 in Appendix S1), and
303 mean annual precipitation (0.03 ± 0.01). A negative coefficient was observed for precipitation
304 seasonality (-0.07 ± 0.02), meaning that higher seasonality was associated with lower species
305 richness. Insularity, in contrast, did not have a pronounced effect on local coastal dune diversity of
306 native plants. The only anthropogenic variables with a positive effect on native species richness was
307 population density (0.09 ± 0.01) whereas a negative relationship with the distance of the closest city
308 was detected (-0.026 ± 0.01).

309 For alien species, some strikingly different results were obtained. In contrast to the results for
310 native species, insularity had a strongly negative effect on alien species richness (-0.44 ± 0.20 , Table
311 S1.6 in Appendix S1). Negative effects on alien richness were also observed for mean annual

312 temperature (-0.22 ± 0.06), precipitation amount (-0.11 ± 0.01) and precipitation seasonality ($-0.18 \pm$
313 0.06). Almost all of the anthropogenic predictors tested were highly informative (confidence intervals
314 did not overlap zero). Notably, a positive association was observed with GDP (0.70 ± 0.10),
315 population density (0.04 ± 0.02) and year of sampling (0.010 ± 0.002), as expected. Accordingly, a
316 negative estimate was observed considering the distance to the closest city (-0.21 ± 0.02), whereas a
317 positive effect of the distance to the closest airport was found (0.11 ± 0.02).

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

321

322 **Discussion**

323 *Diversity patterns across habitats and floristic kingdoms*

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

332 Native species richness showed a general increase along the sea-inland gradient from the species-
333 poor foredunes to more diverse communities on fixed dunes. This trend was consistent across floristic
334 kingdoms and confirms numerous local and regional case studies from around the world (e.g. Acosta
335 *et al.*, 2009; Miller *et al.*, 2010; Monserrat *et al.*, 2012; Ciccarelli *et al.*, 2012; Jiménez-Alfaro *et al.*,

2015). 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

361 propagule pressure in biological invasions) associated with trampling in touristic beaches and
362 proximity to artificial surfaces (Carboni *et al.*, 2010a; Malavasi *et al.*, 2014). Interestingly, higher
363 values of alien species richness were observed in the foredunes of the Holantarctic and Cape
364 kingdoms. Previous studies (e.g. Hertling and Lubke, 1999; Hilton *et al.*, 2006) have reported that
365 foredunes are heavily invaded by alien species, for example by the west Holarctic marram grass
366 (*Ammophila arenaria*) that was widely planted during the 1900s to construct or re-establish foredunes
367 and stabilize shifting dune systems in New Zealand and South Africa (Johnson, 1992; Lubke *et al.*,
368 1995).

369 *Scale-dependency of diversity patterns*

370 Several authors have described the scale-dependence of the relationship between native and alien
371 species richness (see Levine and D'Antonio, 1999; Davies *et al.*, 2005, among others). In our study,
372 we observed a general negative linear relation between native and alien species richness, i.e. more
373 species-rich sites were less invaded (Fig. 3). However, when accounting for plot size, we detected the
374 invasion paradox pattern as proposed by Fridley *et al.* (2007). Accordingly, even though at very fine
375 spatial grain a clear negative trend exists between native and alien richness (e.g. Levine, 2000), the
376 opposite holds true at larger spatial grains (Fig. 3b, Stohlgren *et al.*, 2003, among others). Similar
377 results have also been observed in a meta-analysis of Mediterranean-type ecosystems including sand
378 dune vegetation (Gaertner *et al.*, 2009). Fridley *et al.* (2007) did not provide a single interpretation to
379 this phenomenon, but rather a suite of possible explanations. At a fine scale, environmental and
380 disturbance-based features predominate and shape community composition. Sampling effects may
381 arise in the sense that communities may include particularly invasion-resistant or competitive species;
382 another possible explanation relies on the concept that in stressful, regularly-disturbed environments
383 such as sand dune ecosystems, facilitative interactions may ease the establishment and colonization
384 of alien species across functional groups (Von Holle, 2013). In contrast, at a larger spatial scale,
385 native and alien species richness increased in concert. The biotic processes are superseded by

386 historical, environmental, or biogeographic factors, among which probably spatial and environmental
387 heterogeneity play a crucial role (Gaertner *et al.*, 2009; Stein *et al.*, 2014). In addition, communities
388 experiencing high species dispersal or in highly disturbed ecosystems (e.g. roadside and riparian
389 habitats) often exhibit these positive relationships (Brown and Peet, 2003). Nevertheless, it is worth
390 noting that when considering only the plots located in the Holarctic kingdom the relationship between
391 native and alien species remained steadily positive across all scales considered (see Fig. S1.3). This
392 is in agreement with recent studies (Peng *et al.*, 2019; Tomasetto *et al.*, 2019) suggesting that an
393 explanation for this effect could rely on the sampling design used by different authors, the nature of
394 the data (observational *vs* experimental) coupled with a strong bias towards particular study systems
395 such as grassland habitats. Although we found a highly significant interaction between plot size and
396 richness values, the poor performance of the models coupled with the inconsistency of the invasion
397 paradox effect when downscaling the data seem to lend support to these recent findings. Additionally,
398 despite the fact that macrohabitat classes are quite evenly represented in the dataset within each
399 kingdom (except for Neotropical), we cannot exclude that the pattern observed may be influenced by
400 the spatial clustering of the data in terms of plot location relative to plot size (the largest plots are
401 only in Europe and North America). Second, alien species richness may be biased downward in the
402 oldest phytosociological relevés, which are largely European, due to preferential sampling (Chytrý,
403 2001).

404 *Ecological drivers of plant species richness*

405 GLMMs and variance partitioning revealed that environmental and anthropogenic factors (Fig. 4, 5)
406 acted differently on native and alien species. Climatic and ecological variables predict worldwide
407 patterns of native species richness. Usually, water-energy interactions exert strong effects on plant
408 species richness (Francis and Currie, 2003; Kreft and Jetz, 2007) and global diversity gradients in
409 general (Hawkins *et al.*, 2003). At a global scale, the distribution and the strong geographical
410 differentiation in the floristic composition of plant communities have been classically attributed to

411 climatic differences and regional-scale processes of speciation, extinction and dispersal (Ricklefs,
412 1987). Even though foredunes are deemed an azonal habitat, local climate seems to influence the
413 species present in the inner part of the beach (Mahdavi and Bergmeier, 2016; Del Vecchio *et al.*,
414 2018). The relationships between native species richness and anthropogenic factors such as
415 population density (proxy for urbanization) has been previously described in literature (Kühn *et al.*,
416 2004; Luck, 2007; Lucrezi *et al.*, 2014) suggesting a key role of nutrient enrichment and abundance
417 of resources. Regarding the year of sampling, a very weak positive relationship was observed
418 meaning that there was an increase of native species richness according to time of the survey.
419 However, due to the small value of the coefficient (< 0.001), this effect could be considered as
420 relatively weak.

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

433 It is generally accepted that islands are more invaded than mainland sites (Lonsdale, 1999; Pyšek
434 *et al.*, 2017; Moser *et al.*, 2018). In this study, we observed an opposite pattern with higher alien
435 species richness in coastal sand dunes in mainland areas than on islands (Fig. 4). This is consistent

436 with observations by Vilà *et al.* (2010), who compared Spanish coastal plant communities. The
437 smaller exotic species pool which is present on islands compared to mainland locations could result
438 from the lower human population density on islands compared to mainland in our dataset (average
439 density of 201.15 vs 515.52, respectively) which likely translates into lower propagule pressure.
440 Nonetheless, this pattern might just arise as a sampling effect due to the spatial distribution of our
441 data, being only few of our plots located on small islands, and even fewer on oceanic islands.

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

461 Chapman *et al.*, 2016; Bellard *et al.*, 2016) and intentionally (for instance by preventing sand drift or
462 by establishing ornamental plants). Thus, anthropogenic factors were primarily involved as drivers
463 of alien species richness patterns of coastal sand dune ecosystems worldwide.

464

465 **Conclusions**

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

480

481 **Acknowledgements**

482

483 We are grateful to Sam Provoost, Ana Vaz, Thomas Miller, and Augusto Giaretta for sharing their
484 data, thereby increasing the geographic coverage of this global dataset. HK acknowledges funding
485 from the German Research Foundation within the DynaCom project (DFG FOR 2716).

486

487 **Author contributions**

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

492

493 **Data availability statement**

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

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811 **Supporting Information**

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

813 **Appendix S1.** Model specifications

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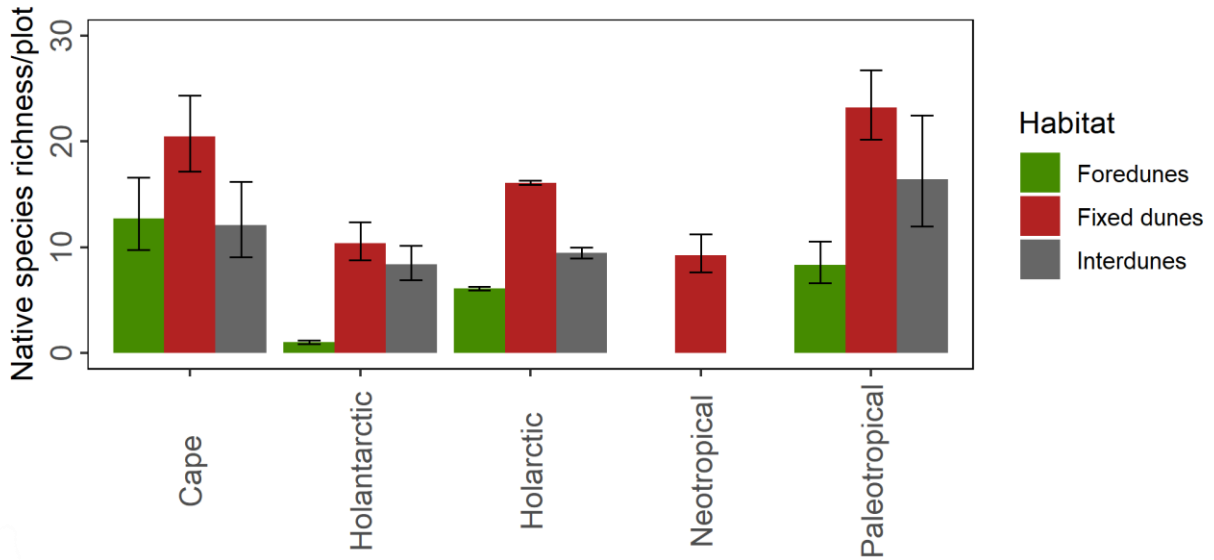
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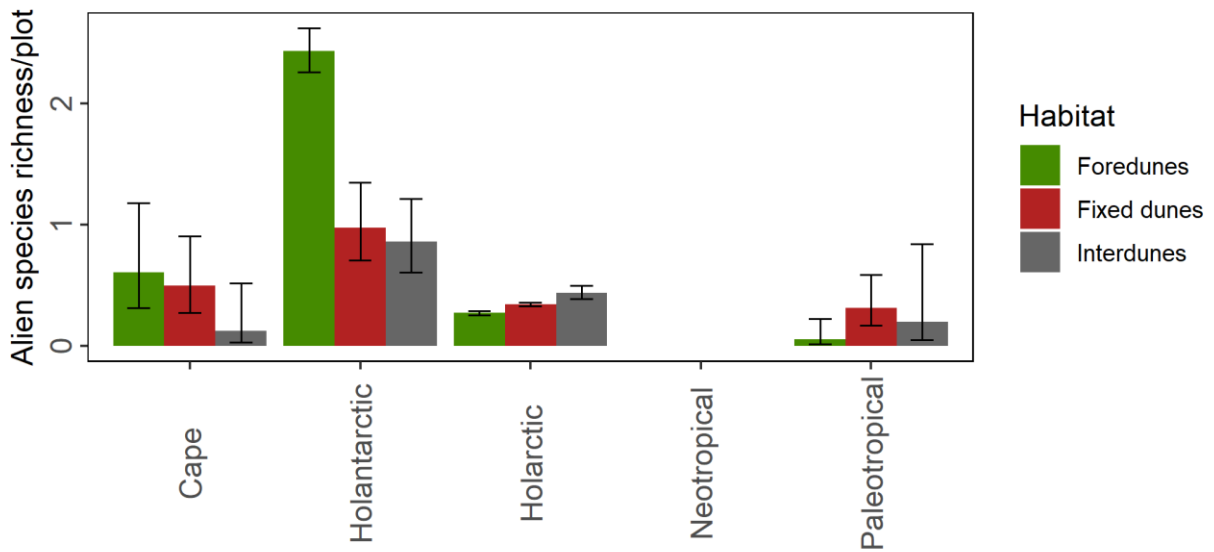
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823 **Figures**

(a)



(b)



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825 **Figure 1.** Bar charts displaying the effect of habitat across floristic kingdoms on a) Native species,

826 b) Alien species. Values reported are estimated species richness per plot \pm 95% confidence intervals

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833 **Figure 2.** Global map showing the distribution of the vegetation plots according to Takhtajan floristic
834 kingdoms (Takhtajan, 1986). Please note that the size of the symbol is proportional to the absolute
835 number of alien species; lower inset represents a detail of Cape and Paleotropical kingdoms

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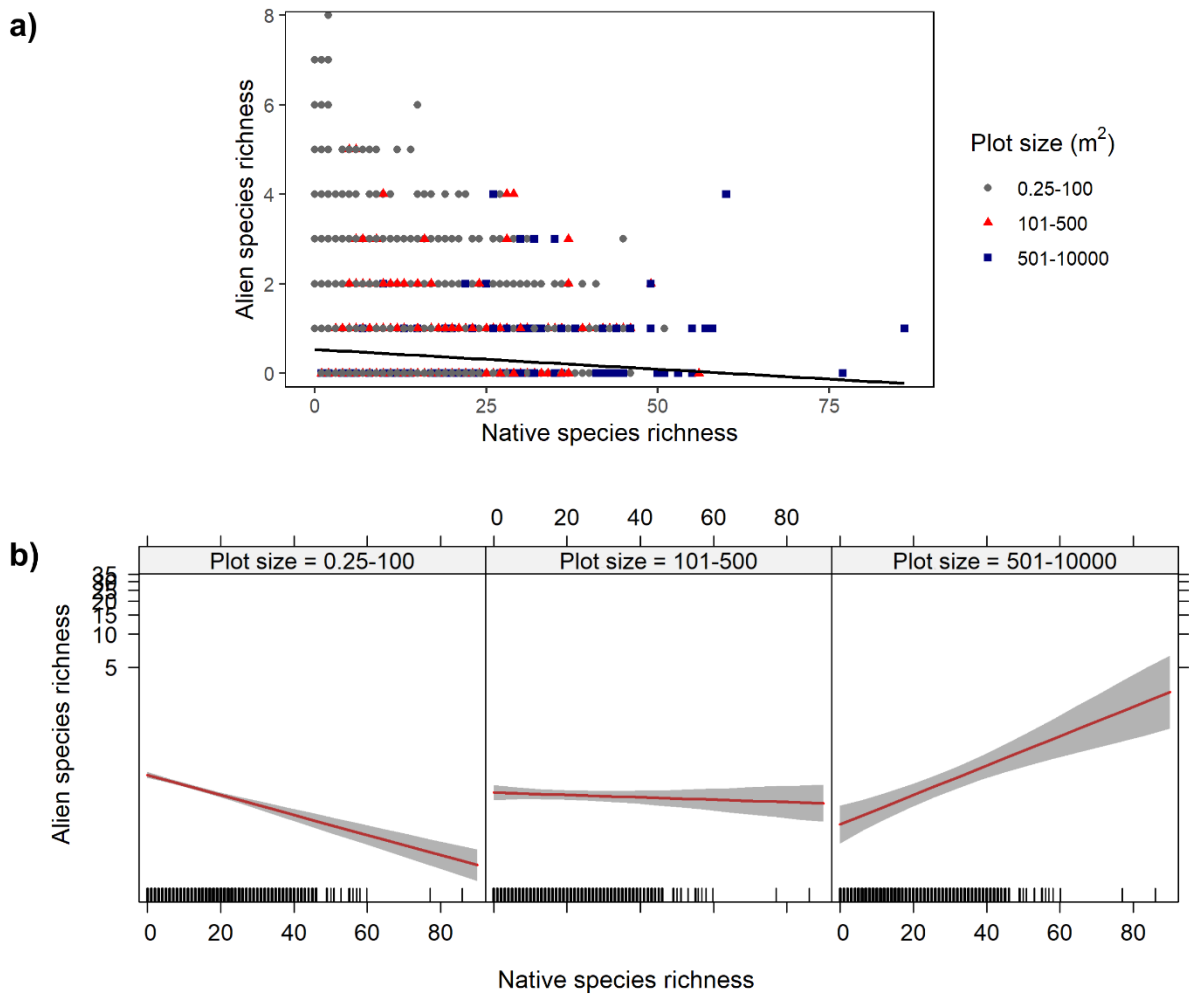
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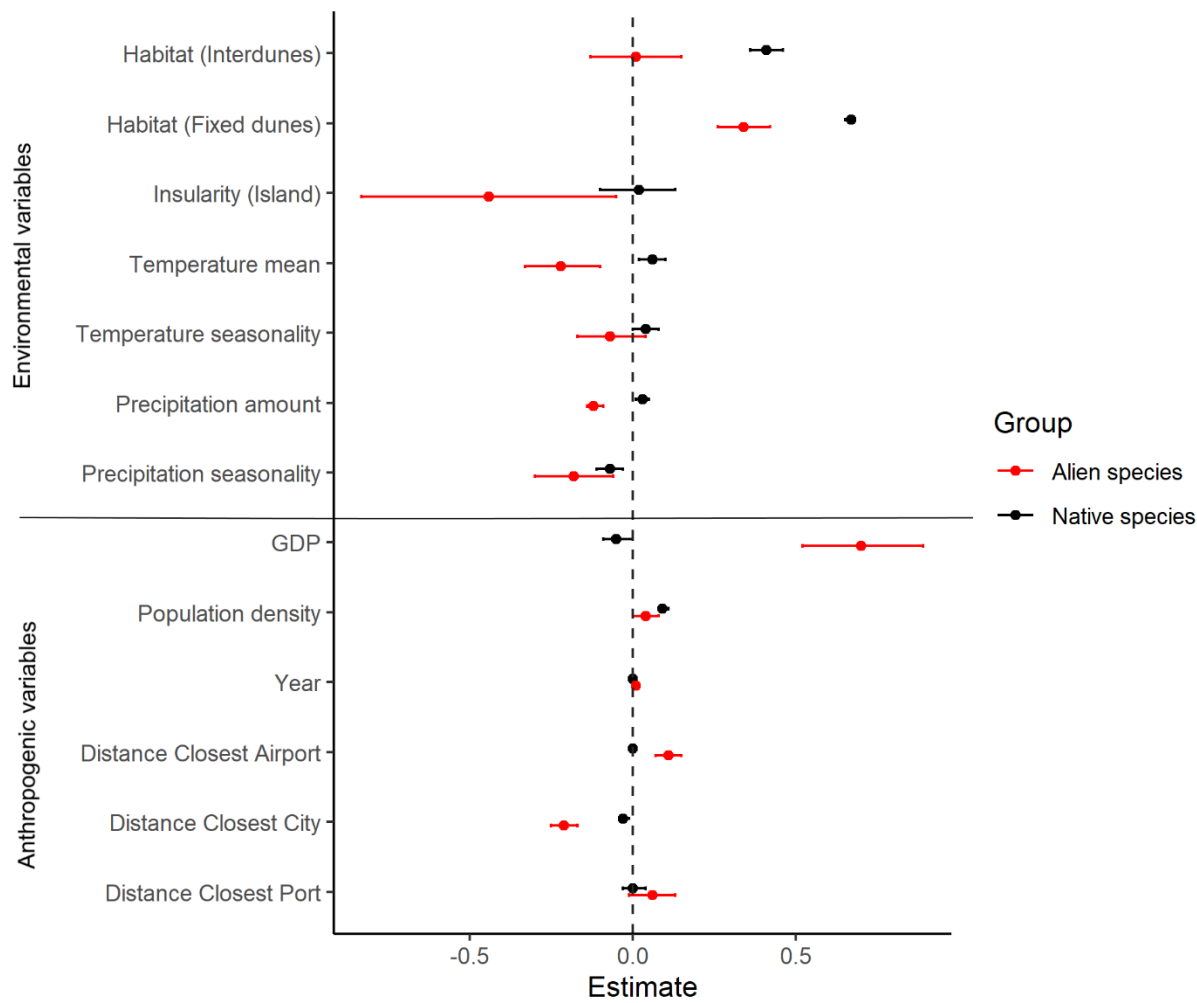
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843 **Figure 3.** a) Scatterplot illustrating the relationship between alien and native species richness. Solid
 844 line represents the overall regression trend. b) Effect plot displaying the dynamic pattern between
 845 alien species richness and native species richness according to plot size. Shaded areas represent 95%
 846 confidence intervals. Plots were grouped in three classes according to their size (0.25-100,101-500,
 847 501-10000 m²) for ease of interpretation.



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849 **Figure 4.** Summary of GLMMs. x-axis reports the estimate \pm 95% Wald confidence interval, y-axis
 850 the model's predictors.

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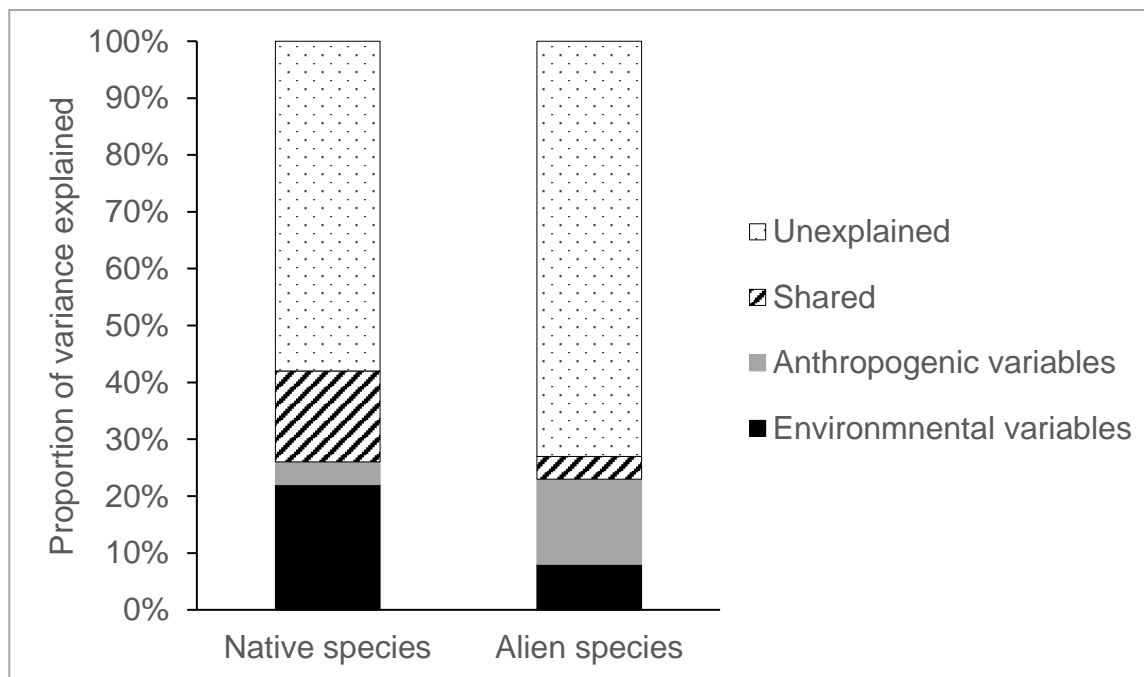
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859 **Figure 5.** Variation partitioning reporting the proportion of variance explained expressed as
860 percentage by environmental variables and anthropogenic variables for native and alien species
861 richness

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