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Disentangling the relative effects of environmental versus human factors on the abundance of native and alien plant species in Mediterranean sandy shores

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ABSTRACT

Aim Mediterranean coastal sand dunes are characterized by both very stressful environmental conditions and intense human pressure. This work aims to separate the relative contributions of environmental and human factors in determining the presence/abundance of native and alien plant species in such an extreme environment at a regional scale.

Location 250 km of the Italian Tyrrhenian coast (Region Lazio).

Methods We analysed alien and native plant richness and fitted generalized additive models in a multimodel-inference framework with comprehensive randomizations to evaluate the relative contribution of environmental and human correlates in explaining the observed patterns.

Results Native and alien richness are positively correlated, but different variables influence their spatial patterns. For natives, human population density is the most important factor and is negatively related to richness. Numbers of natives are unexpectedly lower in areas with a high proportion of natural land cover (probably attributable to local farming practices) and, to a lesser degree, affected by the movement of the coastline. On the other hand, alien species richness is strongly related to climatic factors, and more aliens are found in sectors with high rainfall. Secondarily, alien introductions appear to be related to recent urban sprawl and associated gardening.

Main conclusions Well-adapted native species in a fragile equilibrium with their natural environment are extremely sensitive to human-driven modifications. On the contrary, for more generalist alien species, the availability of limited resources plays a predominant role.

Keywords

Biological invasions, coastal dunes, diversity patterns, environmental and human determinants, exotic species, inference-based model.

INTRODUCTION

Many factors govern plant community assembly and invasibility (Richardson & Pyšek, 2006). Understanding which specific features affect native plant assemblages is ever more important in light of the increasing global loss of biodiversity. In general, environmental factors that have been found to influence patterns of species richness at a regional scale include climate, landscape heterogeneity, spatial patterns, geomorphologic processes and level of protection (van Rensburg *et al.*, 2002; Hawkins *et al.*, 2003; Davies *et al.*, 2005; Moser *et al.*, 2005; Thuiller *et al.*, 2006a). Moreover, human influence is nowadays one further important agent of change for species richness and diversity patterns (Maestre, 2004; Gaston, 2005). Human population density and proxies thereof have often been shown to correlate positively with species richness in response to similar factors, such as productivity (Balmford *et al.*, 2001; Araújo, 2003; Chown *et al.*, 2003), a congruence that suggests a marked conflict between conservation and development. However, depending on spatial scale and overall

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level of urbanization, intense human disturbance can finally lead to an inversion of this tendency with troubling effects on native biodiversity (e.g. Koh *et al.*, 2006).

At the same time, the abundance of alien species is also strongly affected by features of the recipient environment influencing community invasibility (Rejmánek *et al.*, 2005; Thuiller *et al.*, 2010). Pinpointing abiotic and socio-economic factors associated with greater abundances of neophytes and with higher levels of invasion can thus help elucidate the threat of biotic exchange (Dark, 2004; Richardson *et al.*, 2005). Human-related factors tend to be particularly important (O'Shea & Kirkpatrick, 2000; McKinney, 2002; Pyšek *et al.*, 2002; Liu *et al.*, 2005; Thuiller *et al.*, 2006b). This is consistent with theories that relate urbanization and other human activities to higher levels of propagule pressure (a measure of the number of individuals released into a region to which they are not native; Lockwood *et al.*, 2005; Wilson *et al.*, 2007; Britton-Simmons & Abbott, 2008) which increase chances of alien species establishment (Alston & Richardson, 2006). Studies considering both introduced and native species have also generally found a greater importance of factors associated with human disturbance for alien species (Deutschewitz *et al.*, 2003; Arévalo *et al.*, 2005).

Regional-scale observational studies consistently find a positive native–alien species richness correlation. Such emergent patterns have been partially explained in terms of ecological processes including species interactions and comparable responses to the same or covarying external factors (Stohlgren *et al.*, 1999, 2003; Sax, 2002; Fridley *et al.*, 2004; Davies *et al.*, 2005; Richardson *et al.*, 2005). However, how environmental and human determinants differentially influence alien species distribution patterns in contrast to native ones has not yet been convincingly clarified, particularly in very stressful ecosystems. Extrinsic factors that favour high numbers of native species may also directly increase niche opportunity for invaders or different specific determinants may facilitate the establishment of alien species (Davis *et al.*, 2000; Thuiller *et al.*, 2010).

We use Mediterranean coastal sand dunes as target ecosystems to tease apart environmental determinants from human-related parameters underlying patterns of richness for native and alien species. Sandy shores are a typical example of a severely constrained ecotone in which both kinds of determinants are particularly intense. Extreme physical stress and disturbance factors (e.g. sand burial, wind or salinity) act at very small spatial scales shaping community zonation along the dune profile in a gradient from pioneer communities on the beach to shrublands and macchias on fixed dunes (Wilson & Sykes, 1999; Acosta *et al.*, 2006, 2008). The total local species pool is moreover filtered by severe environmental conditions acting at the broad scale including summer droughts and coastline movements (Forey *et al.*, 2008). At the same time, human activities in littoral areas, including suburban development and touristic exploitation, have been historically widespread (Brown & McLachlan, 2002; Defeo *et al.*, 2009).

The aim of this work is therefore to explore how the interplay of environmental and human factors determines native–alien patterns of plant richness at a regional scale but focusing specifically on coastal dune habitats. Considering the level of transformation of Mediterranean coasts, we hypothesize a strong influence of human activity on both the native and alien flora. In particular, for alien species we may expect to find a strong role of human-mediated introduction and propagule pressure as the main drivers of invasions, whereas environmental factors, generally more important determinants of patterns of native species richness, should play a secondary role. To address this objective, we used an explicit treatment of multicolinearity together with a multimodal inference generalized additive framework accounting for spatial structures in the data. Randomization procedures were then used to estimate the absolute contribution of each selected variable to pattern of richness.

METHODS

Study area

The study was conducted along 250 km of the Italian Tyrrhenian coast within the limits of the region Lazio (42°23′ N, 11°39′ E to 41°11′ N, 13°20′ E). More than 90% of this coastline is composed of sandy beaches, although some rocky promontories and river outlets can be found. In this region, the coastal dune system has a relatively simple structure, consisting generally of embryo dunes followed by a main mobile dune ridge and a fixed dune ridge. This area is characterized by a Mediterranean climate, with high summer temperatures, dry summers and most of its annual rainfall distributed in autumn–winter (Carranza *et al.*, 2008).

Plant richness data

Plant richness data was obtained from a survey of the vascular flora of central Italian coastal dunes in 3′ by 5′ grid-cells (about 35 km^2) which followed the European Cartographic Project protocol (Ehrendorfer & Hamann, 1965; Acosta *et al.*, 2008). Since the focus was on coastal dune vegetation, sampling of the grid was limited to the geologic class of holocenic dunes, as outlined from a geologic map (Accordi & Carbone, 1988) and from orthophotographs. Fifty-six grid cells fall within the limits of the region Lazio; however 10 were removed because they either did not contain holocenic dunes or were too strongly urbanized. Within each grid cell, all vascular plant species (natives and aliens) were recorded wherever they occurred on recent dunes (Acosta *et al.*, 2008). Only neophytes (introduced after the 15th century) were classified as aliens in this study. Considering that the more non-native species are introduced in a region, the higher is the probability that some of them will establish and become invasive, patterns revealed by analysing the overall number of introduced species are relevant for gaining a broad-scale view of invasion success. In fact, several authors have explicitly relied on overall numbers of exotic species recorded in floras or in field sampling (irrespective of their estimated naturalization degree) as an indication of the threat of biological invasions (Pyšek *et al.*, 2002; Sobrino *et al.*, 2002; Deutschewitz *et al.*, 2003). We thus included in our classification of alien species both naturalized species (those with establishing, sustainable populations) and 'casuals' (those relying on repeated introduction by humans (Pyšek *et al.*, 2004) (see Table S1).

After verifying dependence on sampled holocenic dune area (A), we standardized richness (S) based on the logarithmic species–area relationship derived from the Arrhenius power function $S = cA^z$ (1921 – where *c* and *z* are constants varying among taxa and types of ecosystems), which best fitted our data (Lepš & Štursa, 1989; Lomolino, 2000). We therefore used residuals of LogS vs. LogA regressions for further analyses, since these represent variability unexplained by sampled dune surfaces.

External correlates

To analyse the main determinants of richness of both natives and neophytes in sandy shores, we calculated candidate variables within buffers of sampled areas. In a GIS environment, we created separately in each grid cell 1.5-km buffer areas surrounding sampled holocenic dunes, which were mapped along the coast as outlined previously. We chose 1.5-km buffers to consider only effects of local neighbouring factors.

Firstly, we classified the main possible factors in environmental/physical drivers (climate and coastline movements) and in human drivers (land cover, urbanization and tourism). For each driver, we selected a first set of variables of interest for a total of 25 predictors (see Table S2).

For climatic variables (average annual temperature, minimum January temperature, maximum July temperature and annual precipitation), we used mean climate grids derived from the statistical downscaling to 100-m resolution (as described in Zimmermann *et al.*, 2007) of 1-km Worldclim monthly maps (Hijmans *et al.*, 2005). The movement of the coastline between 1977 and 1998 (percentage eroding, stable or advancing) was estimated from recent updates of the atlas of Italian beaches (CNR, 1999; Aucelli *et al.*, 2006). Percentages of urban, agricultural and natural cover were calculated from the CORINE 2000 land cover map, which was obtained from the Italian Institute for Environmental Research and Protection (ISPRA – available at http://www.pcn.minambiente.it/) as was the percentage of protected areas. In addition, we considered several variables related both to propagule pressure for alien introduction and to disturbance for native species. Population density and a series of indicators of urban development (total density of buildings, density of buildings built before 1945 and density of buildings built after 1971; density of employees of construction activities) and of tourism pressure (density of employees of hotels, bars, restaurants, campsites, travel and tourism agencies and bathing establishments) were obtained from the 2001 census by the Italian Central Institute of Statistics (ISTAT – available at http://www.istat.it) at the level of census subunits, which represent the finest spatial resolution of Italian demographic surveys. Density of roads was calculated from a planar graph of the road network of the region.

To reduce colinearity, we only kept for model fitting the most meaningful and least interrelated variables identified by calculating a Pearson's correlation matrix. Variables related to population density and tourism pressure were strongly interrelated ($r > 0.5$) so we used only population density (per ha) as a proxy of overall level of human pressure and urban development as a whole. Only the density of buildings built after 1971 (per 10 m^2) indicating the degree of recent urban development was independent and was treated separately. This variable in the coastal context is a good proxy of coastal urban sprawl involving the proliferation of garden areas with many planted exotic species. Natural and agricultural land cover (%) were negatively correlated, so we only included natural cover ($r = -0.71$). Protected areas (%) were not correlated with natural areas. To represent the progress of the coastline, we included the percentage of advancing coast (%– inversely related to retreating coastline; $r = -0.4$). We included annual precipitation (mm – inversely related to minimum winter temperature; $r = -0.86$) to represent climatic influences. We thus used a total of six variables (population density, natural cover, protected areas, recent development, precipitation and advancing coast) for model fitting.

Model fitting

To explain the spatial pattern of native and alien richness as a function of environmental and human variables, we fitted generalized additive models (GAM) with two degrees of smoothing in a multimodal-inference framework, making inference from more than one single 'optimal' model (Link & Barker, 2006; Dormann *et al.*, 2008). Model weighting (w_i) was based on small-sample bias adjustment of Akaike Information Criteria (AICc). We estimated the weight of evidence with which each predictor explains the response variable (w_{pi}) as the sum of the AICs weights (w_i) over all models in which the selected predictor appeared. The predictor with the highest w_{pi} (the closest to 1) gets the highest weight of evidence to explain the response variable (the highest relative importance). Since spurious correlations between a predictor and a response variable may occur because of random or unexplained noises, a permutation procedure was then carried out to test the absolute weight of evidence of each presupposed important variable. The absolute weight of evidence in favour of a given variable was calculated by subtracting the median value of 1000 randomized w_{pi} from the original w_{pi}. Only determinants with positive values of absolute weights were considered important drivers (Thuiller *et al.*, 2007). We evaluated the overall explanatory power of our analysis by regressing observed richness values against fitted values and extracting the *R*-square of the relationship. To derive fitted values from our models, we averaged the predictions from each submodel weighted by the model w_i.

Spatial autocorrelation

Given our sampling design and the fact that invasions often start from few introduction sites, we tested for spatial autocorrelation (SA) using a Moran's *I* test (calculated in relation to the first nearest neighbour of each observation). In case of significant autocorrelation in the residuals of native and alien richness, we added to the model a spatial autocovariate term (SAC) which expresses the potential influence of the response variable at neighbouring sampling sites on local response values (Dormann *et al.*, 2007). This is a commonly used, relatively simple and straightforward method (Diniz-Filho *et al.*, 2008) that allowed us to correct for spatial autocorrelation within our multimodal-inference approach with comprehensive randomizations. We calculated the SAC term for each grid cell following Augustin *et al.* (1996), using 10 km as neighbourhood size and weighting by inverse distance among neighbouring observations.

Alien–Native relationship

We investigated the relationship between alien and native richness by testing the correlation among the two variables. Finally, to highlight processes that have a direct impact on alien patterns, not mediated by the influence that variables may have on natives, we fitted separate GAMs after controlling for native richness, i.e. using the residuals of simple linear regression of alien on native richness (not correlated with sampling area; $r = 0.035$, $P = 0.82$).

Spatial and statistical analyses were carried out with Arc Gis 9.2 (ESRI, 2006) and R 2.10.0 (R Development Core Team, 2008) respectively.

RESULTS

We found a total of 550 species on the entire Tyrrhenian coast. Alien species make up 8% of the total plant species richness in the study area (see Table S1). Moreover, alien and native richness are positively related ($r = 0.50$, $P < 0.001$; Fig. 1), but different external correlates determine their spatial pattern.

For natives, three variables had absolute weights greater than zero (Fig. 2a; Adj. R-square: 0.464, $P < 0.001$). Human population density (correlated with degree of urbanization) was the most important factor and was negatively related to richness (Fig. 3a). The negative effect of human impact on native species richness seems to level off at population densities greater than 40 residents per ha. Numbers of natives were also decreased by high proportions of natural land cover and, to a lesser degree, affected by the progress of the coastline (higher percentages of advancing coastline favour greater numbers of native dune species) (Fig. 3a; Fig. S1).

No spatial autocorrelation of native richness was detected by examining Moran Is (st. deviate = 0.937, P-value = 0.1744). However, we highlighted a certain degree of spatial clustering for alien richness (Moran I st. deviate = 1.608, P-value = 0.05), especially after controlling for native richness (Moran I st. deviate = 3.653, P-value < 0.001).

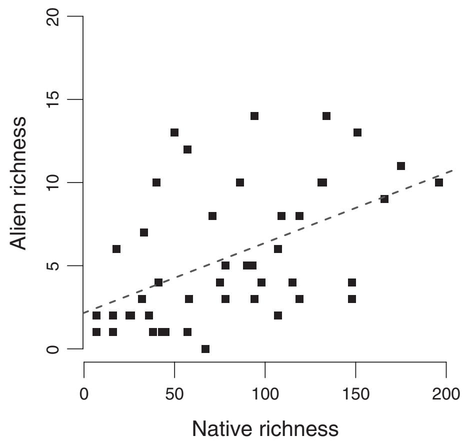

Figure 1 Positive relationship between alien and native species richness (Pearson correlation $r = 0.50$, $P < 0.001$).

The model for alien richness included five variables with positive absolute weights, with precipitation and natural surfaces as most important variables, followed by progress of the coastline, recent development and the spatial autocovariate (Fig. 2b; Adj. R-square = 0.373, $P < 0.001$). More aliens are found in sectors that receive greater precipitation and have lower winter temperatures (as they were negatively correlated) (Fig. 3b).

After controlling for natives, the SAC was the most important variable for alien patterns (Fig. 2c; Adj. R-square = 0.587, $P < 0.001$). As for the influence of human factors, alien introduction appears to be related not to overall degree of urbanization but only to recent urban development after the 70s (Fig. 2c). Alien richness tends to increase with density of recent buildings, but evens out at higher densities (Fig. 3c). Annual precipitation and advancing coast were again important variables for alien richness also after removing variability explained by native richness.

DISCUSSION

Tyrrhenian sandy shores sectors richer in native plant species harbour more introduced species as has been previously reported at comparable scales of analysis in other areas. Bruno *et al.* (2004) in particular observed this relationship even on coastal environments in North America. Several authors have observed that the same external factors were independently driving a similar response of both alien and indigenous species (Richardson *et al.*, 2005; Kumar *et al.*, 2006; Stohlgren *et al.*, 2006). In particular, Deutschewitz *et al.* (2003) found at a regional scale of analysis comparable to our study that similar factors were influencing both alien and native species, even if in different order of importance. The situation appears to be more complex in the coastal environment, where for a large part different and uncorrelated drivers regulate richness of native plants and abundance of alien species.

POOR QUALITY FIG

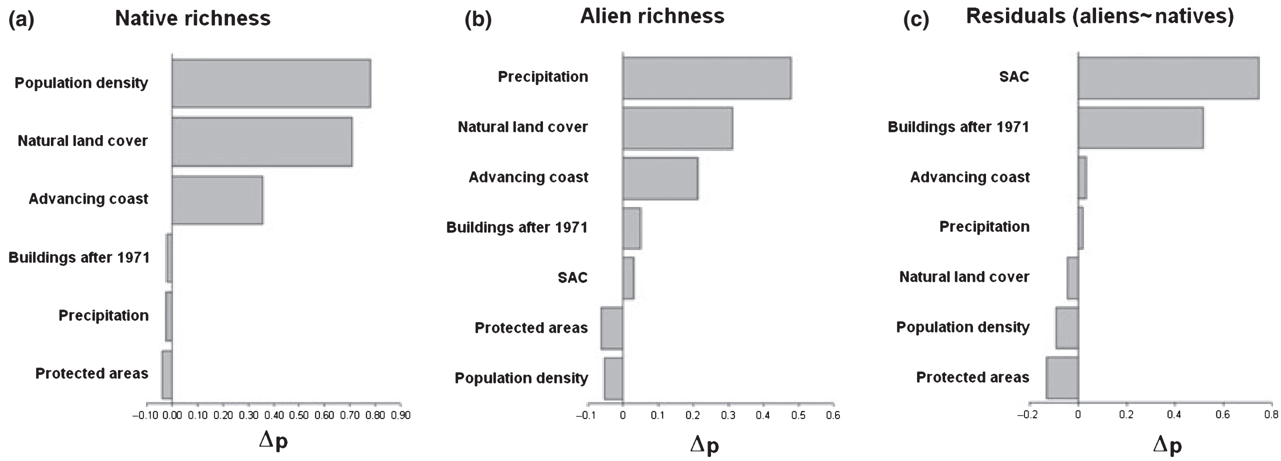

Figure 2 Absolute weights of evidence (Δ_p) of independent variables for explaining from left to right patterns of (a) native and (b) alien richness, and of (c) residuals of alien richness after simple linear regression on native richness.

While we assumed that physical environmental factors would be important determinants of the distribution of native plant species, we were only able to show a strong response to human pressure. Human population density (positively related to overall level of urbanization) negatively impacts native plant richness and is the predictor variable with the highest weight of evidence. This result is in contrast to the theory of coincidence of biodiversity with human population (Araújo, 2003). However, studies supporting this theory have generally been conducted at rather coarse scales, while it has been noted that at finer spatial resolutions, the relationship between species richness and human density may turn negative (Gaston, 2005; Pautasso, 2007). Nevertheless, Deutschewitz *et al.* (2003) still found a positive correlation with urbanization with the same grain used in our study. However, human pressure on Mediterranean shores is often quite extreme (Acosta *et al.*, 2006), and other authors have suggested that very intense human disturbance may also cause an inversion of the correlation with human population density (Koh *et al.*, 2006). Moreover, coastal environments are particularly sensitive to anthropogenic changes (Defeo *et al.*, 2009). In fact, there are a number of ways in which human disturbances can affect sandy shore habitats. A direct impact on the vegetation is related to exploitation for tourism (which in our study is correlated with population density; e.g. for bathing establishments $r > 0.5$), leading to trampling and destructive beach management practices. Intensive management typical of many touristic beaches of Lazio includes mechanical cleaning and dune flattening and affects primarily mature stands of the mobile dune but eventually also pioneer communities of the beach which is the most heavily exploited zone. Such a simplification of the community gradient in dunes inevitably leads to lower overall species richness at the grain examined in this study. Moreover, human disturbances can also have other more indirect effects (coastal erosion, infrastructural barriers landwards blocking the retreat of the vegetation, pollution) on diversity by altering the overall dynamic equilibrium of the coastal ecotone and the successional processes of the vegetation.

Richness of native plants was also inversely related to the percentage of natural land cover in the surrounding landscape, a fact which may appear somewhat surprising at first sight. However, natural cover is negatively correlated with agricultural land use, which may support the introduction of native weeds and ruderal species directly favoured by farming activities (Prach *et al.*, 2001). Moreover, private farmed lands represent quite effective barriers for touristic exploitation since they offer few public accesses to the beach. Conversely, Tyrrhenian natural areas are very fragmented and have often been inappropriately reforested (Bellarosa *et al.*, 1996) representing in this way rather an incentive for summer tourists, and consequently disturbance, with negative effects on native diversity.

Physical environmental factors appear to influence patterns of native species only moderately. In fact, only an effect of the movement of the coastline is supported by a small positive absolute weight of evidence. The advancing coastline, which is inversely related to coastal erosion, appears to favour native richness, probably by influencing the overall community zonation. The continuous deposition of sand is fundamental for the formation and conservation of a wide beach area, embryo dunes and mobile dunes (Packham & Willis, 1997). Several seaward plant communities (on the beach, embryo dunes and mobile dunes) are therefore more common on progressing coasts with more complex dune profiles leading to a more complete vegetation zonation and greater habitat heterogeneity. For example, progressing coastlines offer greater availability of beach habitat which is colonized by typical pioneer communities of specialized halophylous and psammophylous native species such as *Cakile maritima* and *Salsola kali* (e.g. Packham & Willis, 1997; Debez *et al.*, 2004). Moreover, many typical species of the mobile dune, *Ammophila arenaria* (L.) Link being the prime example, are very specialized and have particular adaptations for sand burial and accumulation (Maun, 1998) and are thus less frequent or declining in those coastal sectors where sand build up is not important.

POOR QUALITY FIG

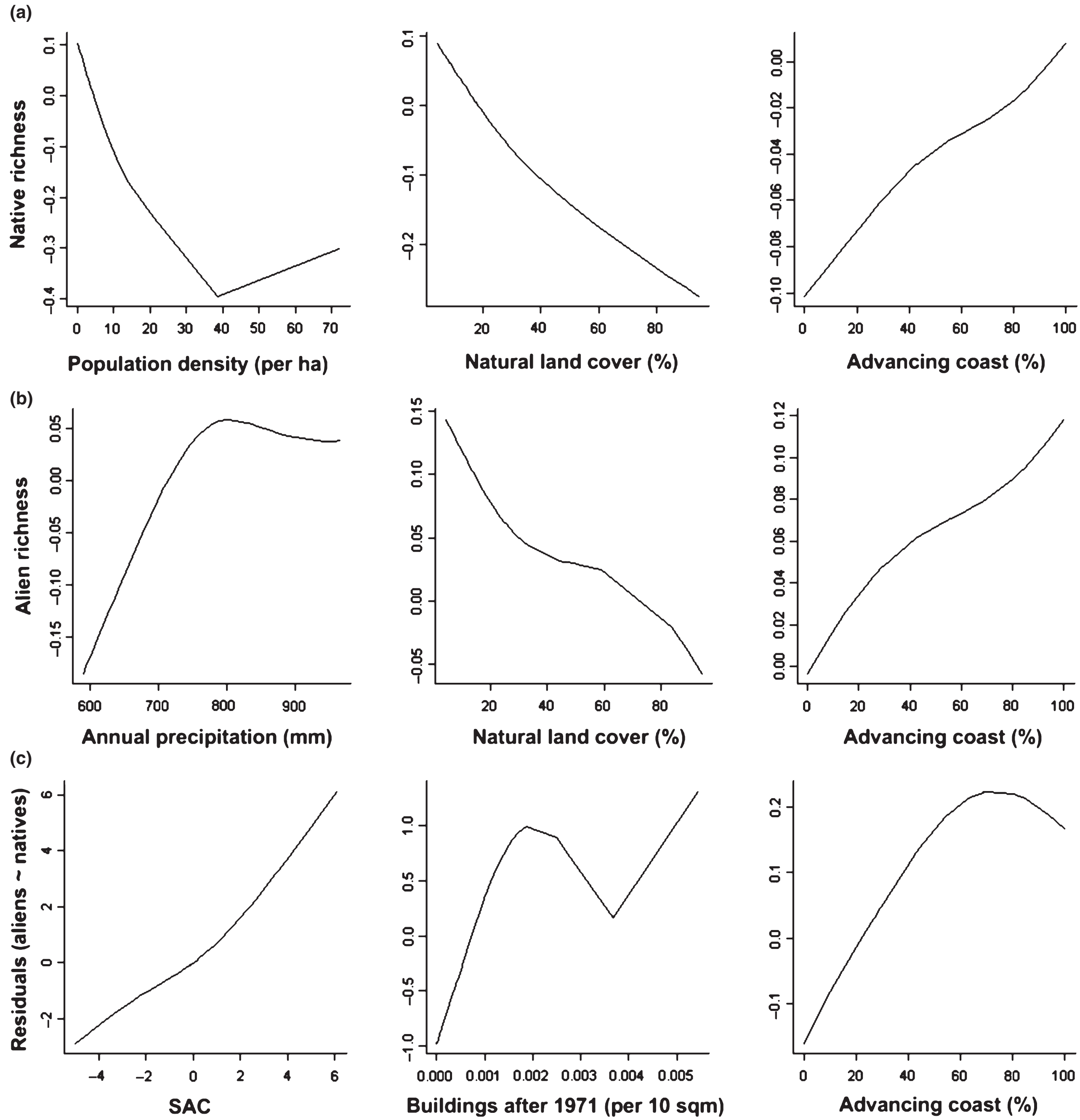

Figure 3 Response curves for the three most important independent variables of generalized additive models for native (a) and alien (b) richness, and for residuals of alien richness variability after simple linear regression on native richness (c). Additional response curves for the other independent variables in Supplementary material.

In contrast to patterns observed for native species, the key driver of alien plant richness was not anthropogenic but climatic. We found more introduced species in more mesic and cooler sectors of Tyrrhenian sandy shores. A strong positive effect of precipitation on the number of naturalized aliens has been reported even at the European level (Lambdon *et al.*, 2008). Even though the opposite trend has been reported as well, with more non-native species in warmer and drier sectors (Gasso *et al.*, 2009), it is a widely shared idea that alien species are more successful invaders where environmental conditions are not excessively harsh and resources are not limiting (e.g., light, nutrients and water). This is in relation to theories that suggest that competition intensity and thus biotic resistance are inversely correlated with the amount of resources available (Alpert *et al.*, 2000; Davis *et al.*, 2000; Richardson & Pyšek, 2006). From this point of view, in xeric environments such as coastal dune systems, the increase in water availability caused by higher precipitation may play an important role on alien plant abundance. Indeed, in other physically challenging semiarid environments, for example of North America, observational (Hobbs & Mooney, 1991; Hunter, 1991) as well as experimental (Milchunas & Lauenroth, 1995) studies have also found a positive influence of higher annual precipitation or water availability on invasion by aliens (Dukes & Mooney, 1999).

Two factors with influence on alien abundance (natural cover and advancing coastline) show similar relationships as with native species, a fact which may partially help explain the positive correlation among the two groups of species. Firstly, more neophytes are associated with fewer natural areas, probably again rather in relation to agricultural lands which may represent introduction sources for some species. However, other factors are also probably at play here, since farming does not seem to be a likely invasion pathway for many non-native species we recorded (Table S1). Secondly, progressing coastlines as highlighted for natives increase habitat heterogeneity and thus provide more opportunities for alien species as well as for natives (Deutschewitz *et al.*, 2003; Kumar *et al.*, 2006).

On the other hand, population density, although strongly correlated with several urbanization, tourism and beach exploitation indicators (all sources of propagule pressure in coastal environments), does not have a positive effect on numbers of aliens. Chytrý *et al.* (2008) focusing on many different habitats and multispecies assemblages also found that the effect of propagule pressure (human-related proxy variables) on the abundance of alien species was very small relative to the effect of local habitat properties. Indeed, the relative contribution of propagule pressure to abundances of alien species may vary widely depending on the habitat examined. Under the extreme conditions typical of coastal habitats, propagule pressure appears to play a less important role for the abundance of non-native species, in contrast to trends observed in other environments for several alien species (Rouget & Richardson, 2003; Lockwood *et al.*, 2005). In our study, the only strong exception is recent coastal suburbanization after controlling for native richness, which appears to be the most effective source of propagules for aliens in the study area (besides perhaps a minor role of farming). Garden areas associated with urban sprawl and with summer structures built after the 70s, often without clear urban plans and with gardens directly facing the beach, support the continuous introduction of alien plants on the neighbouring sand dune system. In fact, for a noticeable proportion of the alien flora found on natural dunes, including the invasives *Carpobrotus acinaciformis* and *Agave americana*, gardening is the most likely invasion pathway. Alien richness thus increases with coastal urban sprawl up to a certain point, levelling off only when extreme suburbanization removes out a number of propagule sources for alien species, like gardens and intensive crops, leading to a decrease of the exotic flora.

While no spatial autocorrelation could be detected for native richness, we highlighted the spatial clustering of alien richness, in particular after removing variability explained by natives (in which case spatial patterning was the most important explanatory variable). Autocorrelation is especially interesting in the case of alien plants because it suggests a spreading trend related to one or few specific source sites that account for the majority of introductions (Pino *et al.*, 2005). For instance, hotspots of alien richness may be related to larger urban nuclei in the inland (e.g. Rome; Fig. 4).

Conclusions

On Tyrrhenian Italian sandy coasts, while native and alien richness are positively correlated, by and large different variables influence their spatial patterns. Contrary to what we might have expected, native plants are more affected by human factors than alien species, which at this resolution are strongly influenced by environmental conditions. The physical harshness of the coastal environment may play an important role in explaining this apparent paradox on multiple grounds. Specialized and well-adapted native species in a fragile equilibrium with their natural environment are extremely sensitive to environmental modifications brought about by humans. On the other hand, for more generalist alien species known to naturalize across a wide range of niches in Mediterranean systems, the availability of the limited resources plays a predominant role. In this context, quite surprisingly, overall human development appears to be less important for the abundance of introduced species than may have been anticipated.

From a conservation perspective, these findings can offer important guidance for regional-level managers of coastal sandy systems in the Mediterranean. First of all, there appears to be a strong conflict between human activities close to the coastal landscape (residential and related to tourism, which is highly important for the local economy of many Mediterra-

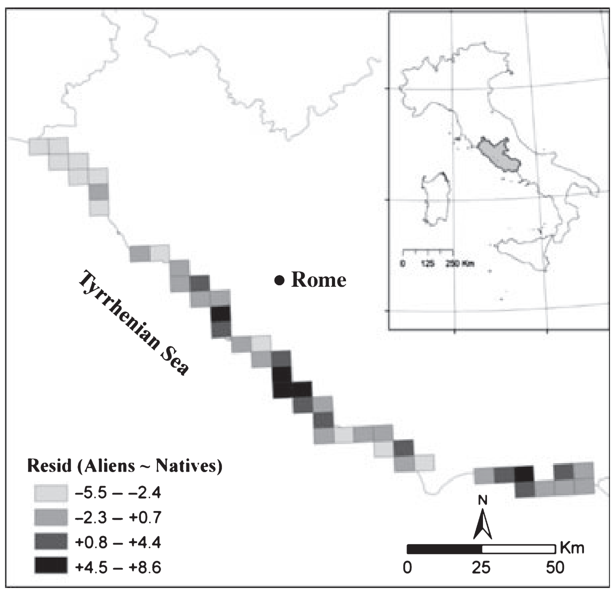

Figure 4 Map of residuals of alien richness after simple linear regression on native richness along the coast of the Region Lazio (42°23′ N, 11°39′ E to 41°11′ N, 13°20′ E).

nean areas) and the preservation of native plant biodiversity on dunes. The importance of more sustainable beach management practices on Mediterranean coastal dunes cannot be overemphasized. On the other hand, exotic species control measures in these physically challenging semiarid environments need to be carried out keeping in mind that sectors with greater availability of limiting resources (e.g. water) may be more exposed to alien species establishment. On the introduction front, urban sprawl and garden areas should be closely monitored, as they appear to be the key sources of propagules in these environments.

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REFERENCES

Accordi, G. & Carbone, F. (1988) Carta delle litofacies del Lazio-Abruzzo ed aree limitrofe. *Quaderni della Ricerca Scientifica*, **114**(5), CNR.

Acosta, A., Ercole, S., Stanisci, A. & Blasi, C. (2006) Sandy coastal ecosystems and effects of disturbance in central Italy. *Journal of Coastal Research*, **2**, 985–989.

Acosta, A., Carranza, M.L., Di Martino, L., Frattaroli, A., Izzi, C.F. & Stanisci, A. (2008) Patterns of native and alien plant species occurrence on coastal dunes in Central Italy. *Plant invasions: human perception, ecological impacts and management* (ed. by B. Tokarska-Guzik, J.H. Brock, G. Brundu, L. Child, C.C. Daehler and P. Pyšek), pp. 235–248, Backhuys Publishers, Leiden.

Alpert, P., Bone, E. & Holzapfel, C. (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 52–66.

Alston, K.P. & Richardson, D.M. (2006) The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. *Biological Conservation*, **132**, 183–198.

Araújo, M.B. (2003) The coincidence of people and biodiversity in Europe. *Global Ecology and Biogeography*, **12**, 5–12.

Arévalo, J.R., Delgado, J.D., Otto, R., Naranjo, A., Salas, M. & Fernández-Palacios, J.M. (2005) Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspectives in Plant Ecology Evolution and Systematics*, **7**, 185–202.

Aucelli, P.P.C., Aminti, P.L., Amore, C., Artom, C., Bellotti, P., Bozzano, A., Caputo, C., Castellini, G., Cipriani, L.E. & Cocco, E. (2006) Le spiagge del Lazio. *Studi Costieri*, **10**, 21–26.

Augustin, N.H., Mugglestone, M.A. & Buckland, S.T. (1996) An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology*, **33**, 339–347.

Balmford, A., Moore, J.L., Brooks, T., Burgess, N., Hansen, L.A., Williams, P. & Rahbek, C. (2001) Conservation conflicts across Africa. *Science*, **291**, 2616–2619.

Bellarosa, R., Codipietro, P., Piovesan, G. & Schirone, B. (1996) Degradation, rehabilitation and sustainable management of a dunal ecosystem in central Italy. *Land Degradation & Development*, **7**, 297–311.

Britton-Simmons, K.H. & Abbott, K.C. (2008) Short- and long-term effects of disturbance and propagule pressure on a biological invasion. *Journal of Ecology*, **96**, 68–77.

Brown, A.C. & McLachlan, A. (2002) Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. *Environmental Conservation*, **29**, 62–77.

Bruno, J.F., Kennedy, C.W., Rand, T.A. & Grant, M.B. (2004) Landscape-scale patterns of biological invasions in shoreline plant communities. *Oikos*, **107**, 531–540.

Carranza, M.L., Acosta, A., Stanisci, A., Pirone, G. & Ciaschetti, G. (2008) Ecosystem classification and EU habitat distribution assessment in sandy coastal environments. *Environmental Monitoring and Assessment*, **140**, 99–107.

Chown, S.L., van Rensburg, B.J., Gaston, K.J., Rodrigues, A.S.L. & van Jaarsveld, A.S. (2003) Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications*, **13**, 1233–1241.

Chytrý, M., Jarošik, V., Pyšek, P., Hajek, O., Knollova, I., Tichy, L. & Danihelka, J. (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, **89**, 1541–1553.

CNR (1999). *Atlante delle Spiagge Italiane* (ed. by G. Fierro). SELCA, Firenze.

Dark, S.J. (2004) The biogeography of invasive alien plants in California: an application of GIS and spatial regression analysis. *Diversity and Distributions*, **10**, 1–9.

Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A. & Rice, K.J. (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology*, **86**, 1602–1610.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.

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

Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M. & Scapini, F. (2009) Threats to sandy beach ecosystems: a review. *Estuarine Coastal and Shelf Science*, **81**, 1–12.

Deutschewitz, K., Lausch, A., Kühn, I. & Klotz, S. (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, **12**, 299–311.

Diniz-Filho, J.A.F., Rangel, T. & Bini, L.M. (2008) Model selection and information theory in geographical ecology. *Global Ecology and Biogeography*, **17**, 479–488.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemuller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.

Dormann, C.F., Schweiger, O., Arens, P. *et al.* (2008) Prediction uncertainty of environmental change effects on temperate European biodiversity. *Ecology Letters*, **11**, 235–244.

Dukes, J.S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology and Evolution*, **14**, 135–139.

Ehrendorfer, F. & Hamann, U. (1965) Vorschlaege zu einer floristichen Kartierung von Mitteleuropa. *Berichte der Deutschen Botanischen Gesellschaft*, **78**, 35–50.

ESRI (2006). *ArcGIS 9.2*, Environmental Systems Research Institute, Inc. (ESRI), Redlands, CA.

Forey, E., Chapelet, B., Vitasse, Y., Tilquin, M., Touzard, B. & Michalet, R. (2008) The relative importance of disturbance and environmental stress at local and regional scales in French coastal sand dunes. *Journal of Vegetation Science*, **19**, 493- U10.

Fridley, J.D., Brown, R.L. & Bruno, J.E. (2004) Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology*, **85**, 3215–3222.

Gasso, N., Sol, D., Pino, J., Dana, E.D., Lloret, F., Sanz-Elorza, M., Sobrino, E. & Vilà, M. (2009) Exploring species attributes and site characteristics to assess plant invasions in Spain. *Diversity and Distributions*, **15**, 50–58.

Gaston, K.J. (2005) Biodiversity and extinction: species and people. *Progress in Physical Geography*, **29**, 239–247.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hobbs, R.J. & Mooney, H.A. (1991) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology*, **72**, 59–68.

Hunter, R. (1991) Bromus invasions on the Nevada test site – present status of *B. rubens* and *B. tectorum* with notes on their relationship to disturbance and altitude. *Great Basin Naturalist*, **51**, 176–182.

Koh, C.N., Lee, P.F. & Lin, R.S. (2006) Bird species richness patterns of northern Taiwan: primary productivity, human population density, and habitat heterogeneity. *Diversity and Distributions*, **12**, 546–554.

Kumar, S., Stohlgren, T.J. & Chong, G.W. (2006) Spatial heterogeneity influences native and nonnative plant species richness. *Ecology*, **87**, 3186–3199.

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

Lepš, J. & Štursa, J. (1989) Species-area curve, life-history strategies, and succession – a field-test of relationships. *Vegetatio*, **83**, 249–257.

Link, W.A. & Barker, R.J. (2006) Model weights and the foundations of multimodel inference. *Ecology*, **87**, 2626–2635.

Liu, J., Liang, S.C., Liu, F.H., Wang, R.Q. & Dong, M. (2005) Invasive alien plant species in China: regional distribution patterns. *Diversity and Distributions*, **11**, 341–347.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.

Lomolino, M.V. (2000) Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography*, **27**, 17–26.

Maestre, F.T. (2004) On the importance of patch attributes, environmental factors and past human impacts as determinants of perennial plant species richness and diversity in Mediterranean semiarid steppes. *Diversity and Distributions*, **10**, 21–29.

Maun, M.A. (1998) Adaptations of plants to burial in coastal sand dunes. *Canadian Journal of Botany-Revue Canadienne de Botanique*, **76**, 713–738.

McKinney, M.L. (2002) Do human activities raise species richness? Contrasting patterns in United States plants and fishes. *Global Ecology and Biogeography*, **11**, 343–348.

Milchunas, D.G. & Lauenroth, W.K. (1995) Inertia in plant community structure – state changes after cessation of nutrient-enrichment stress. *Ecological Applications*, **5**, 452–458.

Moser, D., Dullinger, S., Englisch, T., Niklfeld, H., Plutzar, C., Sauberer, N., Zechmeister, H.G. & Grabherr, G. (2005) Environmental determinants of vascular plant species richness in the Austrian Alps. *Journal of Biogeography*, **32**, 1117–1127.

O'Shea, E.M. & Kirkpatrick, J.B. (2000) The impact of suburbanization on remnant coastal vegetation in Hobart, Tasmania. *Applied Vegetation Science*, **3**, 243–252.

Packham, J.R. & Willis, A.J. (1997) *Ecology of dunes, salt marsh and shingle*, Chapman & Hall, Cambridge.

Pautasso, M. (2007) Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecology Letters*, **10**, 16–24.

Pino, J., Font, X., Carbó, J., Jové, M. & Pallarès, L. (2005) Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). *Biological Conservation*, **122**, 339–350.

Prach, K., Pyšek, P. & Bastl, M. (2001) Spontaneous vegetation succession in human-disturbed habitats: a pattern across seres. *Applied Vegetation Science*, **4**, 83–88.

Pyšek, P., Jarošik, V. & Kučera, T. (2002) Patterns of invasion in temperate nature reserves. *Biological Conservation*, **104**, 13–24.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M. & Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131–143.

R Development Core Team (ed.) (2008). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available online at http://www.R-project.org.

Rejmánek, M., Richardson, D.M. & Pyšek, P. (2005) Plant invasions and invasibility of plant communities. *Vegetation ecology* (ed. by E. van der Maarel), pp. 332–355, Blackwell Science, Oxford, UK.

van Rensburg, B.J., Chown, S.L. & Gaston, K.J. (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *The American Naturalist*, **159**, 566–577.

Richardson, D.M. & Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409–431.

Richardson, D.M., Rouget, M., Ralston, S.J., Cowling, R.M., Van Rensburg, B.J. & Thuiller, W. (2005) Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *Ecoscience*, **12**, 391–402.

Rouget, M. & Richardson, D.M. (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *The American Naturalist*, **162**, 713–724.

Sax, D.F. (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions*, **8**, 193–210.

Sobrino, E., Sanz-Elorza, M., Dana, E.D. & Gonzalez-Moreno, A. (2002) Invasibility of a coastal strip in NE Spain by alien plants. *Journal of Vegetation Science*, **13**, 585–594.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.

Stohlgren, T.J., Barnett, D.T. & Kartesz, J. (2003) The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment*, **1**, 11–14.

Stohlgren, T.J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J. & Master, L.L. (2006) Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasions*, **8**, 427–447.

Thuiller, W., Midgley, G., Rouget, M. & Cowling, R. (2006a) Predicting patterns of plant species richness in megadiverse South Africa. *Ecography*, **29**, 733–744.

Thuiller, W., Richardson, D.M., Rouget, M., Proches, S. & Wilson, J.R.U. (2006b) Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology*, **87**, 1755–1769.

Thuiller, W., Slingsby, J.A., Privett, S.D.J. & Cowling, R.M. (2007) Stochastic species turnover and stable coexistence in a species-rich, fire-prone plant community. *PLoS ONE*, **2**, e938.

Thuiller, W., Gallien, L., Boulangeat, I., de Bello, F., Münkemüller, T., Roquet-Ruiz, C. & Lavergne, S. (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions*, **16**, 461–475.

Wilson, J.B. & Sykes, M.T. (1999) Is zonation on coastal sand dunes determined primarily by sand burial or by salt spray? A test in New Zealand dunes *Ecology Letters*, **2**, 233–236.

Wilson, J.R.U., Richardson, D.M., Rouget, M., Proches, S., Amis, M.A., Henderson, L. & Thuiller, W. (2007) Residence time and potential range: crucial considerations in modelling plant invasions. *Diversity and Distributions*, **13**, 11–22.

Zimmermann, N. E., Edwards, T. C., Moisen, G. G., Frescino, T. S. & Blackard, J. A. (2007) Remote sensing-based predictors improve distribution models of rare, early successional and broadleaf tree species in Utah. *Journal of Applied Ecology*, **44**, 1057–1067.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article: 4

Figure S1 Response curves of GAMs for native species richness.

Figure S2 Response curves of GAMs for alien species richness.

Figure S3 Response curves of GAMs for residuals (aliens~natives).

Table S1 List of alien species recorded.

Table S2 Table of all 25 predictors analysed.

BIOSKETCH

This work was part of **Marta Carboni's** PhD thesis under the supervision of **Alicia Acosta,** in collaboration with **Wilfried Thuiller**. For her PhD M. Carboni is studying the mechanisms and patterns underlying the distribution of alien plant species in Central Italian coastal dune ecosystems at multiple spatial scales.

Author contributions: A.A. conceived the ideas; F.I. and M.C. collected the data; W.T. and M.C. analysed the data; All authors contributed to the writing of the manuscript, which was led by M.C.

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