RESEARCH ARTICLE



Modelling Acacia saligna invasion on the Adriatic coastal landscape: An integrative approach using LTER data

Flavio Marzialetti¹, Manuele Bazzichetto¹, Silvia Giulio², Alicia T.R. Acosta², Angela Stanisci¹, Marco Malavasi³, Maria Laura Carranza¹

I EnviX-Lab, Dipartimento Di Bioscienze e Territorio, Università Degli Studi Del Molise, C. DaFonte Lappone, 86090 Pesche, IS, Italy 2 Dipartimento di Scienze, Università Degli Studi di Roma Tre, V.le Marconi 446, 00146 Roma, Italy 3 Department of Applied Geoinformatics and Spatial Planning, Faculty of Environmental Sciences, Czech University of Life Sciences, Kamýcká 129, 165 21 Prague 6, Czech Republic

Corresponding author: Marco Malavasi (malavasi@fzp.czu.cz)

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Abstract

Invasive Alien Species (IAS) pose a major threat to biodiversity and ecosystem services worldwide. Even if preventing biological invasions should be the most cost-effective way to minimise the impact of IAS on biodiversity, new efforts are necessary to identify early signs of invasion and to assess invasion risk. In this context, the implementation of invasive Species Distribution Models (iSDMs) could represent a sound instrument that merits further research. *Acacia saligna* is an Australian vascular plant introduced into Europe during the last half century and is one of the most aggressive IAS in the Mediterranean basin.

In this work, we model the occurrence of *A. saligna* in the coastal landscapes of central Italy (Adriatic coast) while accounting for the simultaneous effect of multiple factors (propagule pressure, abiotic, biotic factors). The iSDM for *A. saligna* was implemented on a representative tract of the Adriatic coast in central Italy (Molise region), largely included in two Long-Term Ecological Research (LTER) sites which actively contribute to the description of the considered ecosystem status and possible future trends. By using a Generalised Linear Model (GLM) with a binomial distribution of errors based on field and cartographic geo-referenced data, we examined the statistical relationship between the occurrence of *A. saligna* and a comprehensive set of environmental factors. The iSDM effectively captured the role of the different vari-

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ables in determining the occurrence of *A. saligna* in the coastal dunes. Its occurrence is primarily related to Wooded dunes with *Pinus pinea* and/or *P. pinaster* (EU Habitat 2270) and distance from the sea and, to a lesser extent, with distance from roads and rivers. This research provides a first exploratory analysis of the environmental characteristics that promote the rapid growth and development of *A. saligna* in Italian dune ecosystems, identifying the habitats that are mainly affected by the invasive process in coastal areas and, by doing so, contributing to filling the gap between theory and practice in conservation decision-making. Finally, the LTER network benefitted from this research, confirming its relevance in providing useful information for modelling and monitoring invasion processes.

Keywords

Abiotic factors, Biotic factors, Invasive species distribution model, Propagule pressure, LTER

Introduction

Biological invasions are one of the major global drivers of biodiversity loss, often resulting in economic damage and public health care problems (Hulme et al. 2009, Simberloff et al. 2013).

The establishment, growth and expansion of invasive alien species depend on a combination of mechanisms related to both ecology of the species and the assembly of environmental factors (Lockwood et al. 2005, Richardson and Pyšek 2006, Malavasi et al. 2018). Indeed, biological invasions are promoted by a wide range of drivers that can be schematically grouped into three main components, the so called PAB factors: Propagule pressure (P), Abiotic characteristics of the invaded ecosystem (A) and Biotic interaction between invasive species and recipient community (B) (Catford et al. 2009). It is well known that invasions cannot occur without adequate propagule pressure (P), defined as the frequency of plant propagule introductions (Eppstein and Molofsky 2007). Although several authors agree that P represents the key driver in the invasion process (Lockwood et al. 2005, Colautti et al. 2006, Simberloff et al. 2013), abiotic drivers also play an essential role as the invasion will fail if the invading species cannot survive the environmental conditions of a site (Weiher and Keddy 1995, Gallien et al. 2014). Finally, an alien species entering into a new area can either gain or lose biotic interactions capable of facilitating or constraining the invasion (Mitchell et al. 2006).

In order to deal with biological invasions and for preventing their negative effects on ecosystem biodiversity and functioning (Hulme et al. 2009), the European Union adopted a new regulation (EU-No 1143/2014, hereinafter EU Alien regulation) which sets guidelines for the management of Invasive Alien Species (IAS). This regulation underlines the importance of invasion prevention, early warning and rapid response followed by eradication and control measures (Genovesi et al. 2015). As stated by the EU Alien regulation, preventing biological invasions should be the most cost-effective way to minimise the impact of IAS on biodiversity. Still, new methodologies aimed at identifying early signs of invasion are needed (Sitzia et al. 2016). In this context, the use of invasive Species Distribution Models (iSDMs), aimed at investigating the relationship between alien occurrence and PAB factors, should offer an effective tool to better understand biological invasions (Guisan and Thuiller 2005, Tulloch et al. 2016). Specifically, iSDMs analyse the statistical relationship between the presence of alien species (dependent variable) and environmental predictors (independent variables) (Elith and Leathwick 2009); they also allow both identification of the strength of the relationship between species presence and environmental variables and project the probability of occurrence of the species in wide areas in which the species is not present. Over the last twenty years, iSDMs have been widely implemented for conservation and management purposes (Elith and Leathwick 2009, Franklin 2010). Part of the research efforts has been devoted to unravelling the influence of different invasion drivers on the occurrence of some invasive species (Bazzichetto et al. 2018a, Bellard et al. 2016, Thuiller et al. 2005) and predicting the probability of invasion of one taxon (e.g. Gutierres et al. 2011) or a group of taxa (e.g. Malavasi et al. 2018).

Despite all these efforts, further research is still necessary, orientated towards implementing invasive species distribution models for supporting IAS management. A taxon for which important research efforts have been undertaken, but still requiring multivariate analysis of the different invasion drivers, is the Australian genus *Acacia*. *Acacia* sp. is a highly aggressive genus and one of the major invaders in the world (Castro-Díez et al. 2011, Richardson et al. 2011, Richardson and Rejmánek 2011). Amongst them, *A. saligna* (Labill.) H. L. Wendl. is one of the most invasive taxa of the genus (Richardson and Rejmánek 2011) and its spread is particularly worrisome in Italy and the rest of Europe (Wilson et al. 2011). Although the high potential of invasion of *A. saligna* is acknowledged and the role of several environmental factors in driving its invasion has been separately investigated (Hadjikyriakou and Hadjisterkotis 2002, Nsikani et al. 2017, Yelenik et al. 2004), studies exploring the simultaneous influence of these factors are needed.

In light of this, the present study sets out to model the occurrence of *A. saligna* in coastal landscapes of central Italy (Adriatic coast) while accounting for the simultaneous effect of propagule pressure, abiotic and biotic factors. By implementing an iSDM, based on field and cartographic geo-referenced data, we explored the relationship between the presence of *A. saligna* and PAB factors. We assumed that the invasion by *A. saligna* across the dune mosaic is not homogeneous, but varies through space, according to the distribution of the main PAB factors.

By identifying the factors related to higher occurrence values of the alien taxa and by mapping the areas with different probabilities of occurrence, we can identify new tools able to contribute to the prioritisation of conservation actions in coastal ecosystems, as required by the EU Alien regulation.

It is also worth mentioning that such iSDM implementation benefitted from the presence within the study area of two Long-Term Ecological Research sites (LTER) (http://www.lter-europe.net/), which actively contributed to the description of the considered ecosystem status and its possible future trends. Indeed, the LTER network in which ecosystem experts monitor a wide range of environmental variables may offer a rich overview of alien species distribution and invasion drivers across different ecosystems and geographical areas.

Materials and methods

Target species

A. saligna is one of the most invasive taxa of the genus *Acacia* (Richardson and Rejmánek 2011). The species was introduced into the coastal areas of South Africa and of the Mediterranean basin for reforestation, dune stabilisation and ornamental purposes (Bar Kutiel et al. 2004, Gutierres et al. 2011,Wilson et al. 2011). It expanded in an uncontrolled manner in coastal areas of Algeria, Cyprus, Israel, Italy, Kenya, Morocco, Portugal, South Africa and Spain (Wilson et al. 2011, Yelenik et al. 2004). It successfully colonised arid environments of the Mediterranean region with poor and periodically burnt soils (Bell et al. 1993). In Italy, *A. saligna* was introduced in the 1950s for the stabilisation of inner dunes (Izzi et al. 2007; Tulloch et al. 2016). Nowadays, the species is present in many coastal areas of Italy (Celesti-Grapow et al. 2010; Del Vecchio et al. 2013) and it tends to colonise a narrow coastal strip between the Mediterranean scrubs and the *Pinus* sp. woodlands of the fixed dunes (Del Vecchio et al. 2013).

A. saligna has several ecological features that favour its expansion in non-native environments. The clonal and sexual reproduction, high rate of growth, short juvenile period and high tolerance to environmental stress (Del Vecchio et al. 2013, Milton and Hall 1981, Witkowski 1994) are all traits that allow its expansion in a wide variety of ecosystems. Furthermore, the production of a huge number of long-lived seeds and the secretion of allelopathic substances ensure the persistence of the species in the soil seed bank and its chance to sprout over long periods (Mehta 2000, Abd El-Gawad and El-Amier, 2015, Strydom et al. 2012). *A. saligna* forms dense monospecific stands in which several native species are excluded (Yelenik et al. 2004), leading to a simplification of the structure and diversity of native plant communities (Calabrese et al. 2017, Cohen and Bar Kutiel 2017, Del Vecchio et al. 2013, Hadjikyriakou and Hadjisterkotis 2002). It also alters the soil properties as its invasion promotes changes in microclimatic conditions (Mehta 2000, Richardson et al. 2011, Calabrese et al. 2017) and to hydrological and nutrient cycles (Witkowski 1991, Yelenik et al. 2004), in particular the N-cycle (Yelenik et al. 2004; Le Maitre et al. 2011)

Study area

The study was carried out on a representative tract of the Adriatic coast of central Italy (Molise region). The coast is mainly composed of recent sandy dunes (Holocene), which occupy a narrow strip along the seashore. The dune system has a simple structure, being usually characterised by a single dune ridge with low elevation (less than 10 metres) (Acosta et al. 2009, Carranza et al. 2008). Here, the psammophilous vegetation distributes following a well-defined coastal zonation due to the presence of a sea-inland environmental gradient (Acosta et al. 2003, Prisco et al. 2012).

The intense and rapid land use change (Malavasi et al. 2013, 2016) and the introduction of exotic species are amongst the main threats affecting native communities of Adriatic coastal ecosystems (Romano and Zullo 2014, Calabrese et al. 2017, Malavasi et al. 2018). Nonetheless, the coastal dunes of Molise still host many ecosystems of conservation concern in Europe (the so-called EU habitat types according to the European Directive 92/43/EEC; Stanisci et al. 2014). Most of the analysed coastal sectors are included in Sites of European Conservation Concern (Foce Trigno – Marina di Petacciato: IT7228221; Foce Biferno -Litorale di Campomarino: IT7222216; Foce Saccione-Bonifica Ramitelli: IT7222217) and belong to the European LTER network (Bertoni 2012, Drius et al. 2013) (Fig. 1).

Acacia saligna occurrence records

To implement the analysis, we used presence data of *A. saligna* mostly collected inside LTER sites during the years 2013-15 (Calabrese et al. 2017, Del Vecchio et al. 2013). We used 30 presence points and 95 random-absences collected at a minimum distance of 100 m between each other and distributed along the whole coastal dunes in the area (Hijmans 2012). The number of absences was chosen in order to guarantee model adequacy and provide an accurate prediction (Franklin 2010).



Figure. I Study area. Sites of European Conservation concern and LTER sites are shown in black. Coordinates are given in Datum: WGS 84.

Environmental data

In an ArcGIS environment (ArcGIS 10.2.2), a set of environmental variables was computed related to propagule pressure (P), abiotic (A) and biotic factors (B) and which were expected to influence the expansion of A. saligna. We selected road distance as a proxy of propagule pressure (Malavasi et al. 2014, Bazzichetto et al. 2018a), while sea distance and river distance were used as surrogates of abiotic conditions (Gutierres et al. 2011, Bazzichetto et al. 2018a). Finally, Pinus sp. wooded dune land cover and herbaceous dune vegetation land cover were used as a proxy of biotic conditions (Del Vecchio et al. 2013) (Table 1). Concerning propagule pressure, the distance from roads was considered because of its acknowledged role in favouring alien species dispersal (Le Maitre et al. 2004, Jørgensen and Kollmann 2009). Road distance was computed as the Euclidean distance between each point of occurrence of the invasive species and the closest road, including paved roads and secondary pathways (road data retrieved from https://planet.openstreetmap.org/; OpenStreetMap contributors 2017) that cross the dune systems. For abiotic factors, sea distance was considered because, in coastal dunes, it properly depicts the ecological conditions along the sea-inland stress gradient (Acosta et al. 2003, Drius et al. 2013, Bazzichetto et al. 2016). This sea distance was measured as the Euclidean distance of each point of occurrence from the shore line (obtained through photo-interpretation by Malavasi et al. 2013). Considering that A. saligna tends to prefer mesic conditions on arid landscapes, we used river/stream distance as a proxy of water supply (Le Maitre 2004, Gutierres et al. 2011). The distance from rivers was derived using the hydrography map and measured as the Euclidean distance of each point from principal rivers and streams of the Molise region (river data retrieved from https://planet.openstreetmap.org/; OpenStreetMap contributors 2017). Finally, as biotic factors, we considered the relationship between A. saligna occurrence with two natural dune vegetation types widely spread along the coast and characterised by different spatial structures and plant strategies: closed formations of Pinus woods and the herbaceous dune vegetation growing on fore dunes. We derived the percentage (%) of Pinus sp. woodlands and of herbaceous dune vegetation by ap-

Factor	Proxy variables (predictors)	Description		
Р	Road distance (m)	Euclidean nearest distance (m) from paved roads and secondary pathways		
A	Sea distance (m)	Euclidean distance (m) from shoreline		
	River distance (m)	Euclidean distance (m) from nearest river (main streams, river courses)		
В	% Pinus sp. wooded dunes Percentage of Pinus sp. wooded dunes within a 30 m radius			
		Includes EU Habitat: 2270 – Wooded dunes with Pinus pinea and/or Pinus		
		pinaster		
	% Herbaceous dune	Percentage of herbaceous vegetation within a 30 m radius window. Includes		
	vegetation	embryonic shifting dunes (EC-2110), shifting dunes along the shoreline		
		with Ammophila arenaria (EC – 2120) and Malcolmietalia dune grasslands		
		(EC –2230).		

Table 1. Predictors analysed. Propagule pressure (**P**), abiotic (**A**) and biotic (**B**) factors along with the corresponding proxy variables (predictors) used for implementing the iSDM.

plying a moving window procedure (buffer 30 m radius) FRAGSTATS; (McGarigal et al. 2012) across a fine scale (1:5000) land-cover map (Malavasi et al. 2013). The land-cover map conforms to the CORINE land-cover mapping procedure extended to a fourth level of detail for the forested and semi-natural categories (see Acosta et al. 2005 for details). The considered cover categories in the study area are linked with habitats of European conservation concern: wooded dunes with *Pinus pinea* and/or *Pinus pinaster* (EC-2270) and herbaceous dune vegetation, that includes the embryonic shifting dunes (EC-2110), shifting dunes along the shoreline with *Ammophila arenaria* (EC – 2120) and *Malcolmietalia* dune grasslands (EC – 2230). All the variables were reported into raster layers with 5 m resolution, which is an adequate spatial resolution for analysing the coastal dune environments in the Mediterranean basin (Bazzichetto et al. 2018a, Malavasi et al. 2018).

Species distribution models

The iSDM was based on a binomial Generalised Linear Model (GLM) aimed at analysing the relationship between the occurrence of *A. saligna* and the PAB variables (Hosmer and Lemeshow 2000). First, we performed collinearity analysis between these variables (see Appendix 1 for details) in order to exclude multi-collinearity (Brauner and Shacham 1998). Collinearity was assessed by means of Spearman's rank correlation (Ps) and by computing the Variance Inflation factor (VIF) (Brauner and Shacham 1998, Guisan and Thuiller 2005). A predictor was excluded by the model in case of high correlation, i.e. whenever the Spearman's correlation coefficient (Ps) was higher than 0.7 or lower than -0.7 and when VIF was higher than 3 (see Appendix 1 for collinearity analysis and variables selection).

Model performance was evaluated using two measures: the McFadden's R squared (McFadden 1973) and the area under the receiver operator curve (AUC) (Pearce and Ferrier 2000). The McFadden's R squared index, as the classical R squared, can assume continuous values from 0 to 1, with 0 indicating minimum and 1 maximum variability "explained" by the model (McFadden 1973). AUC has been widely used as a standard measure for assessing the predictive accuracy of SDMs (Lobo et al. 2008, Pearce and Ferrier 2000). In particular, the AUC was used to estimate the capacity of the model in predicting the presence of the species in location where the species was actually present and its absence where it was not recorded. AUC values between 0.5 and 0.7 indicate a poor discrimination capacity of the model, values between 0.7 and 0.9 represent a reasonable discrimination and an AUC greater than 0.9 indicates a very good discrimination capacity of the model (Pearce and Ferrier 2000). A robust estimation of the AUC can be gathered by cross-validating the model and averaging the single AUC values obtained from each cross-validation run. With this aim, the dataset was randomly partitioned into five subsets, using a 75% for model training and the remaining 25% to test prediction accuracy. Then, a final AUC value was computed by averaging between a single AUC obtained in each cross-validation run (Le Dell et al. 2015, Millar et al. 2011).

Results

According to the GLM model, the different PAB factors showed specific and significant relationships with the occurrence of *A. saligna*. (Table 2).

The variables, considered for modelling species occurrence, were independent with no significant Spearman's rank correlation coefficient and VIF values (see Appendix 1 for details).

The occurrences of *A. saligna* were associated with propagule pressure (P) (Table 2), with higher probabilities of finding the species in proximity to roads (Fig. 2). Concerning the abiotic variables (A), sea distance showed a significant and negative relationship with the presence of *A. saligna*, indicating that the species occurred in a specific sector of the dune system (50 – 100 metres to sea) (Table 2, Fig. 2). Similarly, *A. saligna* showed a significant negative relationship with river distance, indicating a link to humid conditions (Table 2, Fig. 2). Amongst the biotic factors (B), *A. saligna* was significantly associated with *Pinus* sp. dune woods. In particular, the probability of occurrence of *A. saligna* increased with higher percentages of *Pinus* dune woods (Fig. 2).

The fitted GLM explained 0.70 of the variability (McFadden's R squared= 0.70) and good predictive power (AUC mean = 0.96).

Discussion

In this study, we modelled the occurrence of *A. saligna* along the Adriatic coast in central Italy and identified the specific role of propagule pressure, abiotic and biotic factors in determining the presence of the species. The model showed a good power of prediction, as highlighted by the explained variability of the McFadden's R squared and predictive accuracy of the mean AUC, obtained through cross-validation.

Table 2. GLM model outcome. Response variable: *Acacia saligna* presence/absence; predictors: Propagule pressure, abiotic and biotic factors. For a detailed description of the predictors and the land cover types see Table 1.

Predictors	Estimate	Std. Error	Z value	p-value			
Intercept	2.08	1.24	1.68	p>0.05			
P (Propagule pressure)							
Road distance	-0.004	0.002	-2.059	*			
A (Abiotic)							
Sea distance	-0.025	0.010	-2.639	**			
River distance	-0.001	0.000	-2.289	*			
B (Biotic)							
Pinus sp. dune wood	0.073	0.019	3.884	***			
Herbaceous dune vegetation	0.003	0.016	0.202	p>0.05			

*** p< 0.001;

** p < 0.01;

* p<0.05)



Figure 2. Regression curves. Relationship between *A. saligna* occurrence and the PAB predictors **a** Road distance **b** Sea distance **c** River distance **d** % of *Pinus* sp. dune wood). On the x-axis: predictors with the corresponding unit of measurement. On the y-axis: the residual values for each predictor.

Our results highlighted that the invasion by *A. saligna* was not spatially homogeneous, but varied across the coastal landscape, following the spatial distribution of the different PAB factors. *A. saligna* preferentially occurred close to the coastal pine forest, at an intermediate distance from the coastline, preferably 50-100 metres from sea and its presence was also related to distance from roads and rivers. Specifically, *A. saligna* occurrence is promoted by propagule pressure, which along the Mediterranean coasts can be related to distance from roads (Arévalo et al. 2005, Malavasi et al. 2014, Bazzichetto et al. 2018b). In addition to the acknowledged role of roads in supporting alien species dispersal (Jørgensen and Kollmann 2009, Le Maitre et al. 2004), roads can also fragment forested areas, thus altering the undergrowth light conditions (Gutierres et al. 2011) and creating gaps of favourable habitat for *A. saligna* (Flory and Clay 2006, Gutierres et al. 2011, Parendes and Jones 2000). Indeed, forest edges are characterised by microclimatic conditions of temperature and soil moisture (Brothers and Spingarn 1992, Gehlhausen et al. 2000) that promote the growth of edge species (Carranza et al. 2012), most of them being weeds and aliens (Spellerberg 1998).

Moreover, the model also highlighted that abiotic factors regulated *A. saligna* invasion. Coastal dune ecosystems are characterised by a mosaic of habitats in which the gradual change in abiotic conditions shapes the growth of the species, thus determining the typical sea-inland ecological gradient (Acosta et al. 2003, Drius et al. 2013). Sea distance is a good proxy of such gradient (Bazzichetto et al. 2016) and the observed correlation of *A. saligna* occurrence with sea distance underlined the influence of this complex environmental gradient on the invasion process. Indeed, *A. saligna* tends to invade specific sectors of the dune system (Cohen et al. 2008, Midgley and Turnbull 2003) and, according to our results, this species preferentially occurred on sparsely vegetated fixed dunes. Probably this trend is also related with soil characteristics that, in the inner dune sectors, are more compact and with lower salt concentration (Santoro et al. 2011).

Similar behaviour was observed in other ecosystems characterised by dry sandy soils, (e.g. South-African fynbos, coastal sand dunes of Israel) in which *A. saligna* invades areas with open or patchy vegetation (Mehta 2000, Bar Kutiel et al. 2004) and it was attributed to its good competitive strategy for using water resources (Witkowski 1991, Yelenik et al. 2004).

In confirmation of this, river distance (a proxy of soil moisture) seems to favour *A. saligna* growth in this Adriatic sector. The observed correlation highlighted the tendency of the species to grow and develop in the most humid areas of arid coasts of the Mediterranean climatic region (Bar Kutiel et al. 2004; Gutierres et al. 2011). Due to its preference for mesic conditions on arid landscapes, *A. saligna* is commonly associated with areas close to the river courses on both inland sectors and dunes (Gutierres et al. 2011). Furthermore, the proximity of rivers, besides indicating the availability of moisture, should imply the presence of disturbance that removes competing plants, making such landscapes particularly sensitive to invasion (Mehta 2000, Gutierres et al. 2011).

Biotic conditions also affected the distribution of *A. saligna*, which preferentially invaded areas close to pine forests. The preference of the invader for pine forests on Mediterranean coasts is particularly worrisome because this formation, with high historical and social value for the territory (Del Vecchio et al. 2013), is a priority habitat of European conservation concern (Habitat 2270* Wooded dunes with *Pinus pinea* and/or *P. pinaster*) (Bonari et al. 2017, 2018). Thus, our results pinpointed the need for defining adequate management actions to counteract the invasion risk. Most of the areas covered by Wooded dunes with *Pinus pinea* and/or *P. pinaster* in the Italian peninsula derive from old afforestations (Falcucci et al. 2007) carried out to protect the inner coastal plains and for land reclamation purposes (Malavasi et al. 2013). The structure and floristic composition of these old pine formations has evolved over time and now is characterised by the presence of a good cohort of Mediterranean scrub species that forms the understorey corresponding to canopy gaps. The presence of canopy gaps that

allow the settlement of fast-growing and light-demanding species would make old pine forests particularly vulnerable to alien invasions (Burnham and Lee 2010, Del Vecchio et al. 2013, Gray 2005, Selmants and Knight 2003) and be threatened specifically by *A. saligna*. The results obtained using LTER data, should offer the basis for prioritising monitoring efforts on areas more susceptible to invasion, thus optimising the resources and time devoted to managing alien species expansion.

Similarly to that observed by Malavasi et al. (2018) using the LifeWatch biological database, the utilisation of the LTER network constitutes a sound tool for modelling biological invasions, promoting the sharing of unprecedented amounts of data amongst ecologists. Furthermore, the multi-temporal nature of LTER data offers a unique opportunity to monitor variations and environmental conditions over time and also to identify, through multi-temporal iSDMs (e.g. Carone et al. 2014), the factors and phenomena that underlie the changes occurring in invasive alien species distribution over time.

Conclusion

This integrative analysis of the occurrence of the non-native species *A. saligna* in coastal landscapes, including a single model using the simultaneous effect of propagule pressure, abiotic and biotic factors, allowed us to effectively depict those critical drivers for determining the presence of this highly invasive plant in the Mediterranean dunes and to define areas with different probabilities of invasion. Invasion by *A. saligna* was not homogeneous but varied across the coastal landscape, following the spatial distribution of different factors. Indeed, invasion preferentially occurred on coastal fixed dunes close to pine forests. The implemented iSDM provided valuable insights into the invasion process and it supplied an efficient prediction of the invasion processes in this stretch of the Adriatic coast, providing the necessary instruments for the assessment of invasion risks claimed by the EU Alien regulation (EEC 2014).

Finally, as the presence of a valuable amount of data collected across a network of LTER sites supported the implementation of a more effective iSDM, it is also true that the LTER network benefitted from such research, confirming its relevance in providing useful information for modelling and monitoring invasion processes. Furthermore, by monitoring variations in environmental conditions, it is possible to identify, through multi-temporal iSDMs, the factors and phenomena that allow alien species expansion over time. With this in mind, we hope that other LTER network-based case studies could be further carried out to provide integrated information across a wide range of monitored ecosystems and for increasingly larger areas.

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References

- Abd El-Gawad AM, El-Amier YA (2015) Allelopathy and potential impact of invasive *Acacia saligna* (Labill.) wendl. on plant diversity in the Nile delta coast of Egypt. International Journal of Environmental of Research 9: 923–932.
- Acosta A, Blasi C, Carranza ML, Ricotta C, Stanisci A (2003) Quantifying ecological mosaic connectivity and hemeroby with a new topoecological index. Phytocoenologia 33(4): 623–631. https://doi.org/10.1127/0340-269X/2003/0033-0623
- Acosta A, Carranza ML, Izzi F (2005) Combining Land cover mapping of coastal dunes with vegetation analyses. Applied Vegetation Science 8(2): 133–138. https://doi.org/10.1111/ j.1654-109X.2005.tb00638.x
- Acosta A, Carranza ML, Izzi CF (2009) Are there habitats that contribute best to plant species diversity in coastal dunes? Biodiversity and Conservation 18(4): 1087–1098. https://doi.org/10.1007/s10531-008-9454-9
- Arévalo JR, Delgado JD, Otto R, Naranjo A, Salas M, Fernández-Palacios 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(3): 185–202. https://doi.org/10.1016/j.ppees.2005.09.003
- Bar Kutiel P, Cohen O, Shoshany M (2004) Invasion rate of the alien species Acacia saligna within coastal sand dune habitats in Israel. Israel Journal of Plant Sciences 52: 115–124. https://doi.org/10.1560/8BK5-GFVT-NQ9J-TLN8
- Bazzichetto M, Malavasi M, Acosta ATR, Carranza ML (2016) How does dune morphology shape coastal dune EC-habitat distribution? A remote sensing approach using Airborne LiDAR in the Mediterranean coast. Ecological Indicators 71: 618–626. https://doi. org/10.1016/j.ecolind.2016.07.044
- Bazzichetto M, Malavasi M, Barták V, Acosta ATR, Moudrý V, Carranza ML (2018a) Modeling plant invasion on Mediterranean coastal landscapes: An integrative approach using remotely sensed data. Landscape and Urban Planning 171:98–106. https://doi.org10.1016/j.landurbplan.2017.11.006
- Bazzichetto M, Malavasi M, Bartak V, Acosta ATR, Rocchini D, Carranza ML (2018b) Plant invasion risk: A quest for invasive species distribution modeling in managing Natura 2000 sites. Ecological Indicators 95: 311–319. https://doi.org/10.1016/j.ecolind.2018.07.046
- Bell DT, Plummer JA, Taylor SK (1993) Seed germination ecology in southwestern Western Australia. Botanical Review 59(1): 24–73. https://doi.org/10.1007/BF02856612
- Bellard C, Leroy B, Thuiller W, Rysman JF, Courchamp F (2016) Major drivers of invasion risks throughout the world. Ecosphere 7(3): 1–14. https://doi.org/10.1002/ecs2.1241
- Bertoni R (2012) La Rete Italiana per la ricerca ecologica a lungo termine (LTER-Italia). Aracne Editrice (Roma) 2012: 99–107.
- Bonari G, Acosta ATR, Angiolini C (2017) Mediterranean coastal pine forest stands: Understorey distinctiveness or not? Forest Ecology and Management 391: 19–28. https://doi. org/10.1016/j.foreco.2017.02.002
- Bonari G, Acosta ATR, Angiolini C (2018) EU priority habitats: Rethinking Mediterranean coastal pine forests. Rendiconti Lincei. Scienze Fisiche e Naturali 29(2): 295–307. https:// doi.org/10.1007/s12210-018-0684-9

- Brauner N, Shacham M (1998) Role of range and precision of the independent variable in regression of data. American Institute of Chemical Engineers 44(3): 603–611. https://doi. org/10.1002/aic.690440311
- Brothers TS, Spingarn A (1992) Forest fragmentation and alien plant invasion of central Indiana old- growth forests. Conservation Biology 6(1): 91–100. https://doi.org/10.1046/ j.1523-1739.1992.610091.x
- Burnham KM, Lee TD (2010) Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest. Biological Invasions 12: 1509–1520. https://doi.org/10.1007/s10530-009-9563-8
- Calabrese V, Frate L, Iannotta F, Prisco I, Stanisci A (2017) *Acacia saligna*: an invasive species on the coast of Molise (southern Italy). Foresta – Journal of Silviculture and Forest Ecology 14: 28–33. https://doi.org/10.3832/efor2211-013
- Carone MT, Guisan A, Cianfrani C, Simoniello T, Loy A, Carranza ML (2014) A multi-temporal approach to model endangered species distribution in Europe: The case of the Eurasian otter in Italy. Ecological Modelling 274: 21–28. https://doi.org/10.1016/j.ecolmodel.2013.11.027
- Carranza ML, Acosta ATR, Stanisci A, Pirone G, Ciaschetti G (2008) Ecosystem classification for EU habitat distribution assessment in sandy coastal environments: An application in central Italy. Environmental Monitoring and Assessment 140(1-3): 99–107. https://doi. org/10.1007/s10661-007-9851-7
- Carranza ML, Frate L, Paura B (2012) Structure, ecology and plant richness patterns in fragmented beech forests. Plant Ecology & Diversity 5(4): 541–551. https://doi.org/10.1080 /17550874.2012.740509
- Castro-Díez P, Godoy O, Saldaña A, Richardson DM (2011) Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use. Diversity & Distributions 17(5): 934–945. https://doi.org/10.1111/j.1472-4642.2011.00778.x
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity & Distributions 15(1): 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x
- Celesti-Grapow L, Pretto F, Carli E, Blasi C (2010) Flora vascolare alloctona e invasive delle regioni d'Italia. Casa Editrice Università La Sapienza (Roma) 2010: 1–208.
- Cohen O, Bar Kutiel P (2017) The impact of *Acacia saligna* invasion on the indigenous vegetation in various coastal habitats in Israel and its implication for nature conservation. Israel Journal of Plant Sciences 64(1–2): 1–11.
- Cohen O, Riov J, Katan J, Gamliel A, Bar Kutiel P (2008) Reducing persistent seed banks of invasive plants by soil solarization – The case of *Acacia saligna*. Weed Science 56: 860–865. https://doi.org/10.1614/WS-08-073.1
- Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: A null model for biological invasions. Biological Invasions 8(5): 1023–1037. https://doi.org/10.1007/s10530-005-3735-y
- Del Vecchio S, Acosta A, Stanisci A (2013) The impact of *Acacia saligna* invasion on Italian coastal dune EC habitats. Comptes Rendus Biologies 336(7): 364–369. https://doi. org/10.1016/j.crvi.2013.06.004
- Drius M, Malavasi M, Acosta ATR, Ricotta C, Carranza ML (2013) Boundary-based analysis for the assessment of coastal dune landscape integrity over time. Applied Geography (Sevenoaks, England) 45: 41–48. https://doi.org/10.1016/j.apgeog.2013.08.003

- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology Evolution and Systematics 40(1): 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159
- Eppstein MJ, Molofsky J (2007) Invasiveness in plant communities with feedbacks. Ecology Letters 10(4): 253–263. https://doi.org/10.1111/j.1461-0248.2007.01017.x
- Falcucci A, Maiorano L, Boitani L (2007) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. Landscape Ecology 22(4): 617–631. https://doi.org/10.1007/s10980-006-9056-4
- Flory SL, Clay K (2006) Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. Plant Ecology 184(1): 131–141. https://doi. org/10.1007/s11258-005-9057-4
- Franklin J (2010) Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, New York, 320 pp.
- Gallien L, Carboni M, Münkemüller T (2014) Identifying the signal of environmental filtering and competition in invasion patterns a contest of approaches from community ecology. Methods in Ecology and Evolution 5(10): 1002–1011. https://doi.org/10.1111/2041-210X.12257
- Gehlhausen SM, Schwartz MW, Augspurger CK (2000) Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology 147(1): 21–35. https://doi.org/10.1023/A:1009846507652
- Genovesi P, Carboneras C, Vilà M, Walton P (2015) EU adopts innovative legislation on invasive species: A step towards a global response to biological invasions? Biological Invasions 17(5): 1307–1311. https://doi.org/10.1007/s10530-014-0817-8
- Gray AN (2005) Eight nonnative plants in western Oregon forests: Associations with environment and management. Environmental Monitoring and Assessment 100(1–3): 109–127. https://doi.org/10.1007/s10661-005-7060-9
- Guisan A, Thuiller W (2005) Predicting species distribution: Offering more than simple habitat models. Ecology Letters 8(9):993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x
- Gutierres F, Gil A, Reis E, Lobo A, Neto C, Calado H, Costa JC (2011) *Acacia saligna* (Labill.)
 H. Wendl in the Sesimbra County: Invaded habitats and potential distribution modeling. Journal of Coastal Research 64: 403–407.
- Hadjikyriakou G, Hadjisterkotis E (2002) The adventive plants of Cyprus with new records of invasive species. Zeitschrift fur Jagdwissenschaft 48: 59–71. https://doi.org/10.1007/ BF02192393
- Hijmans RJ (2012) Cross-validation of species distribution models: Removing spatial sorting bias and calibration with a null model. Ecology 93(3): 679–688. https://doi. org/10.1890/11-0826.1
- Hosmer DW, Lemeshow S (2000) Interpretation of the fitted logistic regression model. In: Hosmer DW, Lemeshow S (Eds) Applied Logistic Regression. John Wiley & Sons, New York, 47–90.
- Hulme PE, Pyšek P, Nentwig W, Vilà M (2009) Will threat of biological invasions unite the European Union? Science 324(5923): 40–41. https://doi.org/10.1126/science.1171111
- Izzi CF, Acosta A, Carranza ML, Ciaschetti G, Conti F, Di Martino L, D'Orazio, Frattaroli A, Pirone G, Stanisci A (2007) Sampling the vascular flora in coastal dune ecosystems of Central Italy. Fitosociologia 44(1): 129–137.

- Jiménez-Valverde A (2012) Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. Global Ecology and Biogeography 21: 498–507. https://doi.org/10.1111/j.1466-8238.2011.00683.x
- Jørgensen RH, Kollmann J (2009) Invasion of coastal dunes by the alien shrub Rosa rugosa is associated with roads, tracks and houses. Flora Morphology Distribution Functional Ecology of Plants 204(4): 289–297. https://doi.org/10.1016/j.flora.2008.03.002
- Le Dell E, Petersen M, van der Laan M (2015) Computationally efficient confidence intervals for cross- validated area under the ROC curve estimates. Electronic Journal of Statistics 9(1): 1173–1178. https://doi.org/10.1126/science.1249098.Sleep
- Le Maitre DC (2004) Predicting invasive species impacts on hydrological processes: The consequences of plant physiology for landscape processes. Weed Technology 18(sp1): 1408– 1410. https://doi.org/10.1614/0890-037X(2004)018[1408:PISIOH]2.0.CO;2
- Le Maitre DC, van Wilgen BW, Chapman RA (2004) Alien plant invasions in South Africa: Driving forces and the human dimension. South African Journal of Science 100: 103–112.
- Le Maitre DC, Gaertner M, Marchante E, Ens EJ, Holmes PM, Pauchard A, O'Farrell PJ, Rogers AM, Blanchard R, Blignaut J, Richardson DM (2011) Impacts of invasive Australian acacias: Implications for management and restoration. Diversity & Distributions 17(5): 1015–1029. https://doi.org/10.1111/j.1472-4642.2011.00816.x
- Lobo JM, Jiménez-valverde A, Real R (2008) AUC: A misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17(2): 145–151. htt-ps://doi.org/10.1111/j.1466-8238.2007.00358.x
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20(5): 223–228. https://doi.org/10.1016/j. tree.2005.02.004
- Malavasi M, Santoro R, Cutini M, Acosta ATR, Carranza ML (2013) What has happened to coastal dunes in the last half century? A multitemporal coastal landscape analysis in Central Italy. Landscape and Urban Planning 119: 54–63. https://doi.org/10.1016/j.landurbplan.2013.06.012
- Malavasi M, Carboni M, Cutini M, Carranza ML, Acosta ATR (2014) Land use legacy, landscape fragmentation and propagule pressure promote plant invasion on coastal dunes. A patch based approach. Landscape Ecology 29(9): 1541-1550, https://doi.org/10.1007/ s10980-014-0074-3
- Malavasi M, Santoro R, Cutini M, Acosta ATR, Carrana ML (2016) The impact of human pressure on landscape patterns and plant species richness in Mediterranean coastal dunes. Plant Biosystems 150: 73–82. https://doi.org/10.1080/11263504.2014.913730
- Malavasi M, Acosta ATR, Carranza ML, Bartolozzi L, Basset A, Bassignana M, Campanaro A, Canullo R, Caruggio F, Cavallaro V, Cianferoni F, Cindolo C, Cocciuffa C, Corriero G, D'Amico FS, Forte L, Freppaz M, Mantino F, Matteucci G, Pierri C, Stanisci A, Colangelo P (2018) Plant invasions in Italy: An integrative approach using the European LifeWatch infrastructure database. Ecological Indicators 91: 182–188. https://doi.org/10.1016/j.ecolind.2018.03.038
- McFadden D (1973) Conditional logit analysis of qualitative choice behavior. In: Zarembka P (Ed.) Frontiers in Econometrics. Wiley, New York, 105–142.

- McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. http://www.umass.edu/landeco/research/fragstats/ fragstats.html
- Mehta S (2000) The invasion of South African fynbos by an Australian immigrant: The story of *Acacia saligna*. Restoration and Reclamation Review 6(5): 1–10.
- Midgley SJ, Turnbull JW (2003) Domestication and use of Australian acacias: Case studies of five important species. Australian Systematic Botany 16(1): 89–102. https://doi. org/10.1071/SB01038
- Millar MA, Byrne M, O'Sullivan W (2011) Defining entities in the Acacia saligna (Fabaceae) species complex using a population genetics approach. Australian Journal of Botany 59(2): 137–148. https://doi.org/10.1071/BT10327
- Milton SJ, Hall AV (1981) Reproductive biology of Australian acacias in the south-western cape province, South Africa. Transactions of the Royal Society of South Africa 44(3): 465– 487. https://doi.org/10.1080/00359198109520589
- Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vázquez DP (2006) Biotic interactions and plant invasions. Ecology Letters 9(6): 726–740. https://doi.org/10.1111/ j.1461-0248.2006.00908.x
- Nsikani MM, Novoa A, van Wilgen BW, Keet JH, Gaertner M (2017) Acacia saligna's soil legacy effects persist up to 10 years after clearing: Implications for ecological restoration. Austral Ecology 42(8): 880–889. https://doi.org/10.1111/aec.12515
- Parendes L, Jones J (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J.Andrews experimental forest, Oregon. Conservation Biology 14(1): 64–75. https://doi.org/10.1046/j.1523-1739.2000.99089.x
- Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133(3): 225–245. https://doi.org/10.1016/ S0304-3800(00)00322-7
- Prisco I, Acosta ATR, Ercole S (2012) An overview of the Italian coastal dune EU habitats. Annali di Botanica 2: 39–48. https://doi.org/10.4462/annbotrm-9340
- Richardson DM, Pyšek P (2006) Plant invasions: Merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30(3): 409–431. https://doi. org/10.1191/0309133306pp490pr
- Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species a global review. Diversity & Distributions 17(5): 788–809. https://doi.org/10.1111/j.1472-4642.2011.00782.x
- Richardson DM, Carruthers J, Hui C, Impson FA, Miller JT, Robertson MP, Rouget M, Le Roux JJ, Wilson JRU (2011) Human-mediated introductions of Australian acacias – a global experiment in biogeography. Diversity & Distributions 17(5): 771–787. https:// doi.org/10.1111/j.1472-4642.2011.00824.x
- Romano B, Zullo F (2014) The urban transformation of Italy's Adriatic coastal strip: Fifty years of unsustainability. Land Use Policy 38: 26–36. https://doi.org/10.1016/j.landusepol.2013.10.001
- Santoro R, Jucker T, Carranza ML, Acosta ATR (2011) Assessing the effects of *Carpobrotus* invasion on coastal dune soils. Does the nature of the invaded habitat matter? Community Ecology 12(2): 234–240. https://doi.org/10.1556/ComEc.12.2011.2.12

- Selmants PC, Knight DH (2003) Understory plant species composition 30–50 years after clearcutting in southeastern Wyoming coniferous forests. Forest Ecology and Management 185(3): 275–289. https://doi.org/10.1016/S0378-1127(03)00224-X
- Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courcham F, Galil B (2013) Impacts of biological invasions: What's what and the way forward. Trends in Ecology & Evolution 28(1): 58–66. https://doi.org/10.1016/j.tree.2012.07.013
- Sitzia T, Campagnaro T, Kowarik I, Trentanovi G (2016) Using forest management to control invasive alien species: Helping implement the new European regulation on invasive alien species. Biological Invasions 18(1): 1–7. https://doi.org/10.1007/s10530-015-0999-8
- Spellerberg I (1998) Ecological effects of roads and traffic: A literature review. Global Ecology and Biogeography Letters 7(5): 317–333. https://doi.org/10.2307/2997681
- Stanisci A, Acosta ATR, Carranza ML, de Chiro M, Del Vecchio S, Di Martino L, Frattaroli AR, Fusco S, Izzi CF, Pirone G, Prisco I (2014) EU habitats monitoring along the coastal dunes of the LTER sites of Abruzzo and Molise (Italy). Plant Sociology 51: 51–56. https:// doi.org/10.7338/pls2014512S1/07
- Strydom M, Esler KJ, Wood AR (2012) Acacia saligna seed banks: Sampling methods and dynamics, Western Cape, South Africa. South African Journal of Botany 79: 140–147. https://doi.org/10.1016/j.sajb.2011.10.007
- Thuiller W, Richardson DM, Pyšek P, Midgley GF, Hughes GO, Rouget M (2005) Nichebased modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11(12): 2234–2250. https://doi.org/10.1111/j.1365-2486.2005.001018.x
- Tulloch AIT, Sutcliffe P, Naujokaitis-Lewis I, Tingley R, Brotons L, Ferraz KM, Possingham H, Guisan A, Rhodes JR (2016) Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes. Biological Conservation 199: 157–171. https://doi.org/10.1016/j.biocon.2016.04.023
- Weiher E, Keddy PA (1995) Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns. Oikos 74(1): 159–164. https://doi.org/10.2307/3545686
- Wilson JRU, Gairifo C, Gibson MR, Arianoutsou M, Bakar BB, Baret S, Celesti-Grapow L, DiTomaso JM, Dufour-Dror JM, Kueffer C, Kull CA, Hoffman JH, Impson FAC, Loope LL, Marchante E, Marchante H, Moore JL, Murphy DJ, Tassin J, Witt A, Zenni RD, Richardson DM (2011) Risk assessment, eradication, and biological control: Global efforts to limit Australian acacia invasions. Diversity & Distributions 17(5): 1030–1046. https:// doi.org/10.1111/j.1472-4642.2011.00815.x
- Witkowski ETF (1991) Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. Journal of Applied Ecology 28(1): 1–15. https://doi. org/10.2307/2404109
- Witkowski ETF (1994) Growth of seedlings of the invasives, Acacia saligna and Acacia cyclops, in relation to soil phosphorus. Australian Journal of Ecology 19(3): 290–296. https://doi. org/10.1111/j.1442-9993.1994.tb00492.x
- Yelenik SG, Stock WD, Richardson DM (2004) Ecosystem level impacts of invasive Acacia saligna in the South African fynbos. Restoration Ecology 12: 44–51. https://doiorg/10.1111/j.1061–2971.2004.00289.x

Appendix I

The variables considered for modelling species occurrence are lower than the threshold values of both Spearman's rank correlation coefficient and VIF values (Table A1). Sea distance and herbaceous dune vegetation are the variables with greater correlation score (-0.6); instead the lowest correlation was found between herbaceous dune vegetation and road distance (0.00). Pinus dune wood in the multi-collinearity test has the higher VIF (2.56), while road distance has the lowest (1.12).

Table A1. Correlation analysis. Spearman's rank correlation coefficient and Variance Inflation factor(VIF) for all predictors.

Predictors	Spearman's rank correlation					VIF
-	Pinus sp.	Road	Herbaceous	Sea distance	River	
	dune wood	distance	dune		distance	
			vegetation			
Pinus dune wood						2.56
Road distance	0.15					1.12
Herbaceous dune	0.01	0.00				1.22
vegetation						
Sea distance	-0.35	-0.05	-0.60			1.43
River distance	-0.07	0.17	-0.04	0.06		1.19