

1 Research article

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3 **Modelling *Acacia saligna* invasion in a large Mediterranean island using PAB factors: a tool for**
4 **implementing the European legislation on invasive species**

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6 Vanessa Lozano^a, Flavio Marzialetti^{b*}, Maria Laura Carranza^b, Daniel Chapman^c, Etienne Branquart^d,
7 Klara Dološ^e, André Große-Stoltenberg^f, Michele Fiori^g, Paolo Capece^g, Giuseppe Brundu^a

8 ^a Department of Agriculture, University of Sassari, Via Italia 39, 07100, Sassari, Italy.

9 ^b EnviX-Lab, Dipartimento Di Bioscienze e Territorio, Università Degli Studi Del Molise, C. DaFonte
10 Lappone, 86090 Pesche, IS, Italy.

11 ^c Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK.

12 ^d Department of the Study of the Natural and Agricultural Environment, Public Service of Wallonia,
13 Belgium.

14 ^e Karlsruhe Institute of Technology, Institute of Geography and Geoecology, Karlsruhe, Germany.

15 ^f Division of Landscape Ecology and Landscape Planning, Institute of Landscape Ecology and Resources
16 Management, Justus-Liebig University Giessen, Germany.

17 ^g Regional Agency for the Environmental Protection of Sardinia, ARPAS, Sassari, Italy.

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19 *Corresponding author: Flavio Marzialetti: flavio.marzialetti@unimol.it; EnviX-Lab, Dipartimento Di
20 Bioscienze e Territorio, Università Degli Studi Del Molise, C. DaFonte Lappone, 86090 Pesche, IS, Italy.

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22 **Highlights**

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- 24 • SDM is an effective tool for predicting plant invasions
- 25 • An integrative PAB approach to explain *Acacia saligna* distribution in Sardinia
- 26 • Combined action of propagule pressure, abiotic, biotic factors promotes the invasion
- 27 • iSDM largely benefits from the use of high resolution and dedicated thematic layers
- 28 • iSDM is an effective tool for decision-making to prevent the invasion risk

29

30 **Abstract**

31 The present study aimed to investigate the role of propagule pressure (P), abiotic (A), and biotic (B) factors
32 (collectively indicated as PAB) on the suitability of the Mediterranean island of Sardinia (Italy) to be
33 invaded by the tree *Acacia saligna*, recently included in the list of invasive alien species of European Union
34 concern.

35 To this aim, a binomial Generalized Linear Model was applied for disentangling the relationship between
36 432 *A. saligna* occurrence records and 10 thematic layers, at high-resolution (10 x10 m), used as proxies
37 for the 3 categories of PAB variables. The 432 occurrence records of *A. saligna* were periodically monitored
38 (period 2000-2018) to check the persistence of the populations and their invasive status. The predictive
39 power of the model was evaluated by computing the mean of the AUC scores, through cross-fold validation.
40 The model adequately described how the PAB factors influence the presence of *A. saligna* which is mainly
41 shaped by abiotic factors such as topography, and biotic factors such as the presence of woody dune
42 vegetation, and to a lesser extent by other predictors. The projection of the model to the whole island clearly
43 shows that suitability varies at the landscape level due to the variation of the PAB across the territory. The
44 probability of *A. saligna* occurrence near the coast is higher in sand dunes. In the internal areas of the island
45 it occurs close to the roads and urban areas. This study and the tested methodology could represent a suitable
46 tool to prioritize areas for the monitoring of *A. saligna* to meet the requirements of the Regulation (EU) No.
47 1143/2014 on Invasive Alien Species (the IAS Regulation).

48

49 **Keywords** Conservation planning, Generalized Linear Model, Invasive Alien Species Regulation, invasive
50 Species Distribution Model, Sardinia.

51

52 **1. Introduction**

53 In 2002 the Conference of the Parties to the Convention on Biological Diversity (CBD) adopted the Guiding
54 Principles on Invasive Alien Species (IAS Decision VI/23) as a basic policy response. The first CBD
55 guiding principle states that prevention is generally far more cost-effective and environmentally desirable
56 than measures taken after IAS introductions. Therefore, the identification of the major pathways of
57 introduction and secondary spread, the areas and land uses more prone to invasion, and the implementation
58 of early warning-rapid interventions are all key actions to be included in a national strategy for preventing
59 IAS introduction, establishment and spread (Genovesi and Shine, 2004; Early et al., 2016). Predicting the
60 risk from IAS establishment and negative impacts is of great importance for policy makers, land managers
61 and other stakeholders, to delineate specific action plans and to choose or prioritize measures against IAS
62 (Venette, 2015; Bazzichetto et al., 2018a). Therefore, invasive alien species distribution models and habitat
63 suitability maps (iSDM) are a very useful tool producing reliable and repeatable information with which to
64 inform decisions (e.g., Guisan and Thuiller, 2005; Broennimann and Guisan, 2008; Jiménez-Valverde et
65 al., 2011; Petitpierre et al., 2012; Guisan et al., 2013). Nevertheless, application of iSDMs may have several
66 limitations as a result of the invasion process, e.g. violation of the equilibrium assumption and
67 underestimation the potential climatic niche of the species (e.g., Fournier et al., 2017; Barbet-Massin et al.,
68 2018; Chapman et al., 2019).

69 The unified framework proposed by Blackburn et al. (2011) suggests that the invasion process can be
70 divided into a series of stages from introduction to successful establishment until invasion. Many studies
71 have addressed the interactions between alien species' invasive capacity and the susceptibility of habitats
72 or communities to invasion (e.g., Pyšek and Richardson, 2008; Mathakutha et al., 2019). In their review of
73 invasion ecology hypotheses, Catford et al. (2009) suggest considering each stage of invasion as a function
74 of propagule pressure (P), abiotic environment (A) and biotic relationships (B) (PAB hypothesis). The
75 propagule pressure, i.e. the number of introduced propagules, is a prerequisite for invasion (Colautti et al.,
76 2006; Malavasi et al., 2014), while alien species establishment depends on the physical environment
77 (abiotic filter; e.g., Malavasi et al., 2018) and on the biological features of the hosting community (biotic
78 filter; e.g., Broennimann et al., 2012).

79 We decided to apply the PAB hypothesis to the well-known globally invasive plant *Acacia saligna*, an
80 evergreen tree native to Western Australia (Maslin, 1974). It is a fast-growing tree that propagates both
81 vegetatively and sexually, is well adapted to semiarid landscapes and quite resilient to fire (George et al.,
82 2008). The current wide invasive range occupied by *A. saligna* is due to a combination of characteristics
83 such as the adaptability to different environmental conditions, the large seed production and easy
84 germination, the establishment of a rich seed-bank in the soil (Maslin and McDonald, 2004). *Acacia saligna*

85 is at the same time one of the most planted non-timber woody species used for soil protection, reforestation,
86 ornamental purposes, and for many other uses (Maslin and McDonald, 2004; Kull et al., 2011). In the
87 Mediterranean, many *Acacia* species were introduced and planted mainly for stabilizing sand dunes and for
88 preventing soil erosion (Del Vecchio et al., 2013). At present, *A. saligna* is widespread in Mediterranean
89 climates in its native range (Australia) and as an invasive non-native species (e.g., Algeria, Chile, Cyprus,
90 Israel, Italy, Morocco, Portugal, South Africa and Spain, Thompson et al., 2015) as well as in other areas
91 with seasonally dry conditions (e.g. Kenya) where it invades a great variety of habitat types (Le Maitre et
92 al., 2000; Lorenzo et al., 2010a b; Boudiaf et al., 2013; Hernández et al., 2014; Lazzaro et al., 2014; Celesti-
93 Grapow et al., 2016).

94 Invasion of *A. saligna* has detrimental effects on biodiversity and ecosystem functioning. *Acacia saligna*
95 invaded areas are characterized by dense thickets (Lehrer et al., 2013) in which natural biodiversity is
96 significantly modified (Del Vecchio et al., 2013). In addition to this, *A. saligna* invades several habitats of
97 conservation value (Stanisci et al., 2012) and protected areas (Pinna et al., 2015; Acunto et al., 2017).
98 Furthermore, it alters the runoff on slopes, modifies nutrient cycles and soil properties and decreases the
99 aesthetic and recreational value of invaded landscapes (Brundu et al., 2019). For these reasons, in the
100 European Union, *A. saligna* has been recently included in the list of invasive alien species of Union concern
101 (Regulation (EU) No. 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the
102 prevention and management of the introduction and spread of invasive alien species, hereafter, IAS
103 Regulation). In addition to a ban on trade, planting and use *A. saligna*, member states are committed to
104 surveillance to record occurrence in the environment and prevent its spread into or within the Union
105 (Beninde et al., 2015).

106 A few iSDM studies on *A. saligna* have been done for Europe (e.g., Gutierrez et al., 2011; Brundu et al.,
107 2019) and for the Italian mainland (Marzialetti et al., 2019). However, further modelling studies are
108 particularly urgent for the Mediterranean islands that are very well-known hotspots of biodiversity (Vilà et
109 al., 2006b; Fenu et al., 2015; Peruzzi et al., 2015) highly threatened by invasive alien species (Hulme, 2004;
110 Brundu, 2013; Malavasi et al., 2018). In addition, *A. saligna* is a neophyte in Sardinia (Galasso et al., 2018)
111 and has probably not yet invaded all potentially suitable areas. Thus, identifying the unoccupied areas at
112 risk of invasion provides crucial information for surveillance, management and prevention of impacts
113 across the entire island. Therefore, this study aims to disentangle the role of propagule pressure, abiotic and
114 biotic factors on the occurrence of *A. saligna* in the Mediterranean island of Sardinia. Our results provide
115 an approach for prioritization of prevention, monitoring and control efforts towards areas more susceptible
116 to be invaded, which would optimize the costs and time devoted to managing alien species.

117

118 **2. Materials and methods**

119 *2.1. Study area*

120 This study was conducted on Sardinia (Italy), the second largest island of the Mediterranean basin (24,100
121 km²) (Fig. 1). The elevation ranges from 0 to 1,834 m a.s.l. (Punta la Marmora, Gennargentu massif). The
122 climate is characterized by two main seasons, a hot-dry season and a cold-humid one. Annual mean
123 temperature ranges from 17-18 °C on the coast to 10-12 °C on the inland mountains (Arrigoni, 2006).
124 Annual precipitation varies greatly from the coast to the inland, from around 433 mm y⁻¹ in the southern
125 coast to 1,412 mm y⁻¹ in the North at 1000 m a.s.l. (Arrigoni, 2006). In addition, a summer period of aridity,
126 with low precipitation, marks the Sardinian climate typical Mediterranean *pluviseasonal-oceanic* (Rivas-
127 Martinez and Rivas-Saenz, 1996-2019).

128 The coastal dunes of Sardinia harbor many ecosystems of priority conservation concern in Europe, listed
129 by the “Habitats” Directive 92/43/EEC (e.g., HD 2250* - Coastal dunes with *Juniperus* spp., HD 2130* -
130 Grey dunes, HD 2270*- Wooded dunes with *Pinus pinea* and/or *P. pinaster*). Importantly, the wooded
131 dunes with *P. pinea* and/or *P. pinaster* in Italy and Sardinia are planted forests established for land
132 reclamation and to protect agricultural areas and roads from sand (Falcucci et al., 2007; Malavasi et al.,
133 2013). Besides invasive alien species, Sardinian and Mediterranean coastal ecosystems are jeopardized by
134 a number of anthropogenic pressures (Falcucci et al., 2007; Malavasi et al., 2013) and widespread erosion
135 (Drius et al., 2013; Camarda et al., 2015; Acosta et al., 2007; Malavasi et al., 2018).

136

137 *2.2. Study species*

138 *Acacia saligna* (Labill.) H.L.Wendl (Fabaceae) is an alien species that invades a large number of natural
139 ecosystems in Sardinia and in the Mediterranean such as sand dune vegetation (e.g., Arrigoni, 2010;
140 Gutierrez et al., 2011; Meloni et al., 2013), and riparian plant communities (Lorenzo et al., 2010a; Del V
141 ecchio et al., 2013; Lazzaro et al., 2014; Celesti-Grapow et al., 2016).

142 In Sardinia and in other regions in Italy, *A. saligna* was massively planted in the 1950’s (Pavari and de
143 Philippis, 1941; Del Vecchio et al., 2013) to stabilise sand dunes and protect *Pinus* spp. plantations from
144 wind and sea spray (Maniero, 2000; Celesti-Grapow et al., 2009; Del Vecchio et al., 2013) and as an
145 ornamental plant. In the invaded areas *A. saligna* forms dense thickets, including within wooded pine dunes
146 (HD 2270*) and Mediterranean scrublands (HD 2260; Del Vecchio et al., 2013; Marzialetti et al., 2019).
147 In addition, *A. saligna* outcompetes many Sardinian endemic species, in particular *Anchusa crispa* Viv.
148 subsp. *maritima* (Vals.) Selvi & Bigazzi (Farris et al., 2013) typical of fixed coastal dunes with herbaceous
149 vegetation (grey dunes - HD 2130*) and invades coastal dunes with *Juniperus* spp (HD 2250*) (Pinna et

150 al., 2015; Acunto et al., 2017). Through nitrogen-fixation, *A. saligna* thickets promote the establishment of
151 ruderal and nitrophilous species, simplifying and homogenising native plant communities (Caruso, 2012;
152 Calabrese et al., 2017).

153 Under a Mediterranean climate, *A. saligna* can grow with mean annual temperature ranging from 11 to 23
154 °C and with annual precipitations from 240 to 1160 mm (Maslin and McDonald, 2004). Its persistence in
155 the invaded sites is promoted by vegetative propagation (suckering) and by the establishment of a large
156 persistent seed bank characterized by physical dormant seeds (Mehta, 2000; Strydom et al., 2012; Abd El-
157 Gawad and El-Amier, 2015, Cohen et al., 2018).

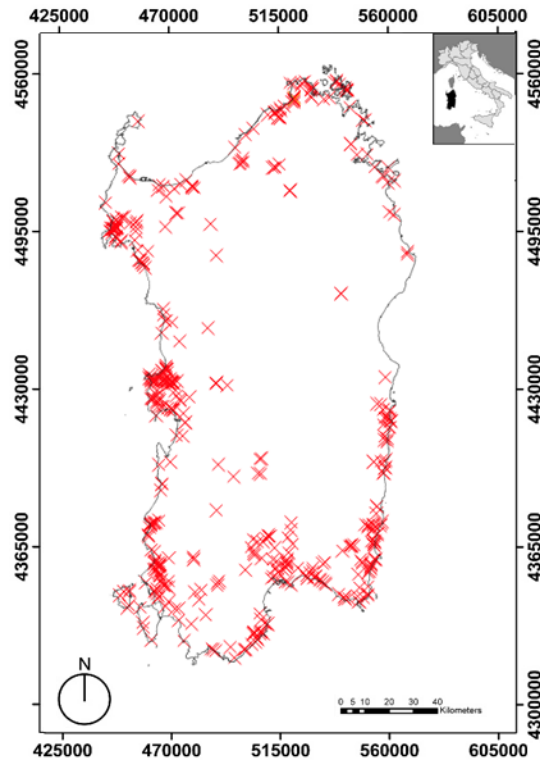
158

159 *2.3. Acacia saligna occurrence data*

160 We used 432 georeferenced presence records of *A. saligna* collected around the invaded areas in Sardinia,
161 and all these sites were periodically monitored (period 2000-2018), every two years, to check the
162 persistence of the populations and their invasive status, i.e. whether only planted, casual or naturalised
163 (Brundu et al., 2003; Camarda et al., 2016; Galasso et al., 2018). Field observations were georeferenced by
164 means of a portable GPS (Garmin GPS 12 channels) and crosschecked on Google Earth imagery. For
165 modelling these presences, 1000 pseudo-absence records were randomly generated across the entire study
166 area excluding the areas occupied by the patches of *A. saligna*. Pseudo-absences were located at least 100
167 m apart from each other and the presence records were masked using a buffer with a radius of 150 m. The
168 procedure was implemented in QGIS environment (3.2. “Bonn” version 2018).

169

170



171

172 **Figure 1.** The study area and the distribution of the 432 *Acacia saligna* records (red crosses). The coordinate
 173 reference system is UTM (WGS84) zone 32 N.

174

175 2.4. Predictor variables

176 We selected a set of predictors for the presence of *A. saligna* acting as proxy variables for propagule
 177 pressure (P), abiotic (A) and biotic factors (B) (see Table 1 for detailed description).

178 The following variables have been used as measures of propagule pressure: (i) the locations in which *A.*
 179 *saligna* was planted for afforestation purposes in the past; (ii) the distance from roads (Le Maitre, 2004;
 180 Drake et al., 2015; Bazzichetto et al., 2016; Bazzichetto et al., 2018; Malavasi et al., 2018); and (iii) the
 181 extension of artificial surfaces (from CORINE land cover, CLC 2012). It is widely agreed that one of the
 182 main sources of propagule pressure for forest trees are tree nurseries and plantations (Malavasi et al., 2014),
 183 therefore, we classified the presence and pseudo-absence records as being inside or outside plantations of
 184 *A. saligna*. The locations of *A. saligna* afforestation were achieved from the published official maps of the
 185 Sardinian forest services (EFS, 2013), which at the moment are updated until 2013. We calculated the
 186 Euclidean distance of *A. saligna* wild populations from highways and primary roads due to the role of
 187 communication infrastructures in favoring alien species dispersal and the presence of planted individuals
 188 along the roads. Finally, in order to account for the dual role of urbanisations in providing new propagules

189 from gardens, in which *A. saligna* is frequently planted (Carranza et al., 2010) and creating disturbed and
190 bare areas more prone to invasion (Bazzichetto et al., 2018b) we considered the percentage of artificial
191 surfaces (hereon ART; including urban fabrics; industrial and commercial units; mine, dump and
192 construction sites, as defined in the Corine Land Cover CLC 2012 map for Italy) converted into a raster
193 layer by a moving window of 11 x 11 pixels (see Marzialetti et al., 2019).

194 The following abiotic factors (A) were considered: (i) slope; (ii) average temperature; (iii) the distance from
195 coastline, and (iv) frequency of wild fires. We included in the model a slope map in degrees extracted from
196 a 10 x 10 m digital elevation model (resampled from 1 x 1 m Lidar data) because it is generally considered
197 a good surrogate of water accumulation in the soil (MacMilland and Shary, 2009) affecting the suitability
198 for *A. saligna* (Le Maitre, 2004; Gutierrez et al., 2011). The thematic layer on the mean annual temperature
199 for Sardinia for the period 1971-2000 was provided by the *Agenzia Regionale per la Protezione*
200 *dell'Ambiente della Sardegna* (ARPAS - <http://www.sardegnaambiente.it/arpas/>). The sea-inland stress
201 gradient that drives invasion on coastal areas (Carranza et al., 2011; Bazzichetto et al., 2016, 2018) was
202 measured as the Euclidean distance to the nearest seashore. Then, as *A. saligna* successfully colonizes
203 burned areas in the Mediterranean region (Bell et al., 1993) we included in the analysis a raster layer with
204 the total number of wild fire events from 2005-2016.

205 Concerning biotic factors (B) facilitating or avoiding *A. saligna* invasion (Marzialetti et al., 2019) we
206 considered the abundance of different natural and seminatural vegetation types. We calculated the
207 percentage of cover of the following categories: coastal dunes with *Pinus* spp. plantations (AFF); dunes
208 with woody vegetation, and degradation stages (WDH) and dune vegetation (DUN) using a moving window
209 of 11 x 11 pixels (supplementary Table 1).

210 For all 18 variables, raster grid maps for the whole island of Sardinia were produced at 10 x 10 m resolution
211 using the WGS84 datum and UTM 32N projection system (EPSG code: 32632) (supplementary Table 2) .
212 However, to minimize collinearity only 10 were used in the final model (Table 1) selected according to
213 Variance Inflation Factor (VIF).

214

215 **Table 1.** Predictor variables selected for building the iSDM, serving as proxies of propagule pressure (P),
216 abiotic (A) and biotic (B) factors, along with their detailed description, the data source and the original
217 scale. For a detailed explanation of the land cover types see supplementary materials, Table 2.

218

PAB factors	Predictor variables	Detailed description of the predictor variables	Source of the predictor variables
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Propagule pressure (P)	Artificial areas (ART)	Percentage of artificial areas (CLC 2012 class 1) within a 100 m radius circular buffer	Corine Land Cover (CLC) 2012 vector map (scale 1:100000) (https://land.copernicus.eu/pan-european/corine-land-cover)
	<i>A. saligna</i> afforestation	Euclidean distance (m) from <i>Acacia</i> plantations	EFS (Ente Foreste della Sardegna 2013) (10 m spatial resolution)
	Road distance	Euclidean distance (m) from highways and primary roads	Regional geodatabase (scale 1:25000) (http://dati.regione.sardegna.it)
Abiotic (A)	Coastline distance	Euclidean distance (m) from the coastline	Regional geodatabase (scale 1:2000) (http://dati.regione.sardegna.it)
	Slope	Degrees, thematic layer produced by GIS analysis from a DEM with 10 x 10 m geometric resolution	Regional topography geodatabase (http://www.sardegnaeoportale.it)
	Temperature	Annual mean temperature (°C)	Original raster layer produced by <i>Agenzia Regionale per la Protezione dell'Ambiente della Sardegna</i> - ARPAS (250 m spatial resolution)
	Fire frequency	Number of wildfire events in the period 2005-2016	Regional wildfire geodatabase (vector format) (scale 1:25000) (http://www.sardegnaeoportale.it)
Biotic (B)	Afforestation(AFF)	Percentage of <i>Pinus</i> plantations (CLC 2012 class 3.12) within a 100 m radius circular buffer	Corine Land Cover (CLC) 2012 vector map (scale 1:100000) (https://land.copernicus.eu/pan-european/corine-land-cover)
	Dune vegetation (DUN)	Percentage of dune vegetation (CLC 2012 class 3.31) within a 100 m radius circular buffer	Corine Land Cover (CLC) 2012 vector map (scale 1:100000) (https://land.copernicus.eu/pan-european/corine-land-cover)
	Woody dune habitat (WDH)	Percentage of dunes with woody vegetation, and degradation stages (CLC 2012 class 3.2) within a 100 m radius circular buffer	Corine Land Cover (CLC) 2012 vector map (scale 1:100000) (https://land.copernicus.eu/pan-european/corine-land-cover)

219

220 2.5. Invasive alien species distribution model iSDM

221 We modeled the relationship between *A. saligna* occurrence and the PAB predictor variables (Table 1)
 222 using a Generalized Linear Model (GLM, *dismo* R package 1.1-4, Hijmans et al., 2017). We first extracted
 223 the PAB values at the presences and pseudo-absence records. We set the presence/pseudo-absence of the
 224 invasive alien plant as response variable and PAB predictors as covariates. Then we computed the Variance
 225 Inflation Factor (VIF, *usdm* R package, Babak, 2017) in order to exclude multi-collinearity between PAB

226 proxy variables (Guisan and Thuiller, 2005). A predictor was excluded for VIF values higher than 3 (see
227 supplementary Table 3 for collinearity analysis and variables selection). We fitted the GLM implementing
228 when necessary polynomial transformations for non-linear responses (Venables and Ripley, 1994).

229

230 2.5.1. Model evaluation and predictions

231 We evaluated the performance of the model by the area under the receiver operator curve (AUC) (Pearce
232 and Ferrier, 2000). AUC represents the probability that a randomly selected presence has a higher model-
233 predicted suitability than a randomly selected background location (Manel et al., 2001). Specifically, for
234 cross-validating the model we randomly partitioned the data and fitted the GLM 100 times, each time
235 selecting 75% of points for model training and the remaining 25% for testing prediction accuracy. The
236 iSDM predictive performance was summarized by averaging the cross-validated AUC values (LeDell et
237 al., 2015). In addition, we obtained the goodness-of-fit of the model using the Nagelkerke R^2
238 (Nagelkerke, 1991), which estimates the proportion of variance explained by the iSDM.

239 Finally, in order to schematically summarize the main trends and areas of invasibility in the island of
240 Sardinia we projected the probabilities of invasion in the study area, and we classified them into five classes
241 ranging from very low to very high (very low = suitability < 0.1 , low = suitability ≥ 0.1 and < 0.3 ,
242 intermediate = suitability ≥ 0.3 and < 0.5 , high = suitability ≥ 0.5 and < 0.7 , very high = suitability ≥ 0.7).
243 Then for each *A. saligna* suitability class we calculated the respective percentage relative to the island
244 extent.

245

246 3. Results

247 *PAB predictors and Acacia saligna occurrence*

248 The fitted GLM explained 75% of the variation in occurrence (Nagelkerke $R^2 = 0.75$) and had excellent
249 predictive power (cross-validated mean AUC = 0.94 ± 0.007 sd). The model underlined the specific role of
250 propagule pressure, abiotic and biotic factors in determining *A. saligna* occurrence across the island of
251 Sardinia (Fig 2; Tab. 2).

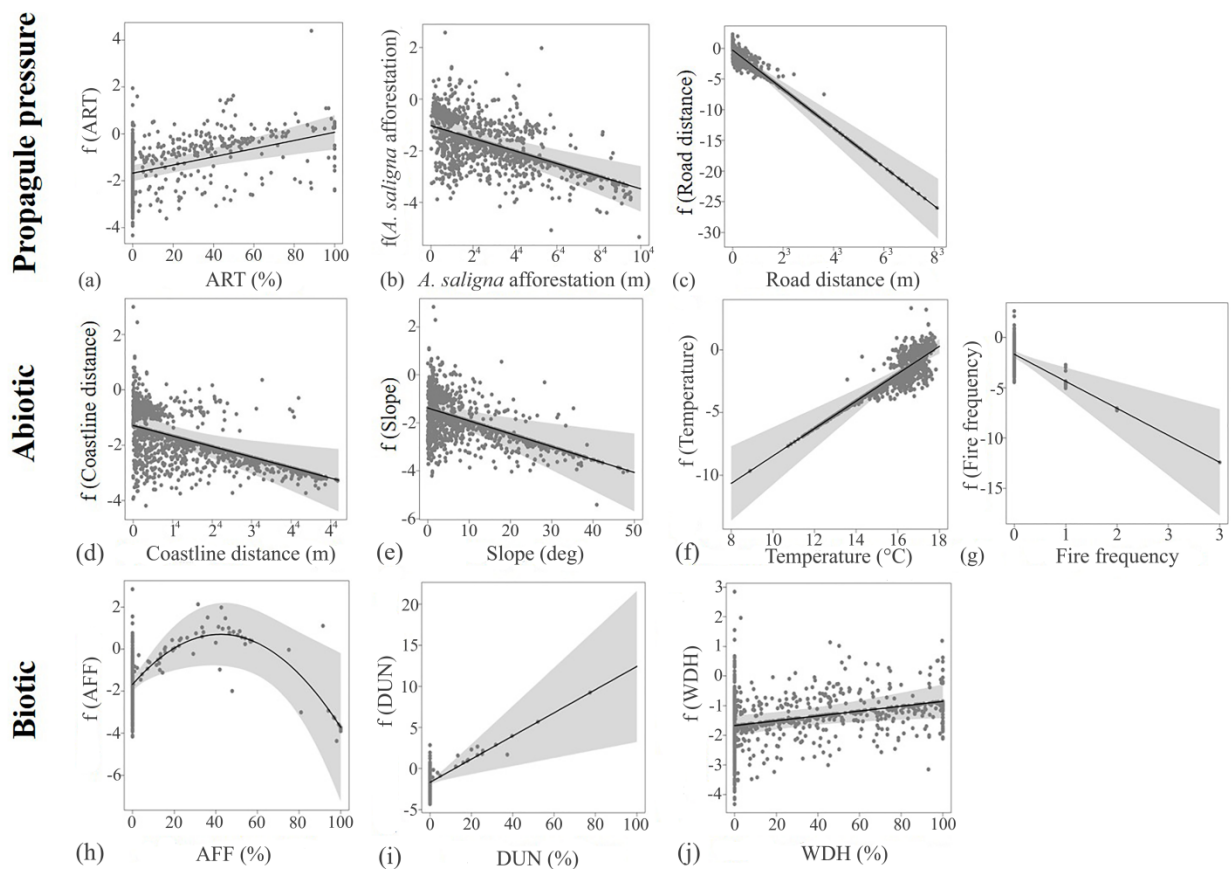
252 Among propagule pressure (P) proxy variables, *A. saligna* tends to preferentially occur in areas with higher
253 levels of urbanisation, close to roads and close to areas in which it has been planted (Fig. 2, Table 2). Among
254 abiotic factors (A), *A. saligna* has a significant relationship with coastline distance and slope, indicating its
255 preference for coastal and flat areas with moisture accumulation. *A. saligna* also preferred areas with low
256 fire frequency and warmer conditions (Fig. 2, Table 2). All the biotic factors (B) showed a significant

257 relationship with *A. saligna* occurrence. In relation to *Pinus* spp. plantation cover (AFF), *A. saligna*
 258 exhibited a parabolic trend with maximum suitability at around 40% AFF cover. *A. saligna* also prefers
 259 areas with woody vegetation (WDH) and semi-natural dune vegetation (DUN) (Fig. 2, Table 2).

260 The suitability map for Sardinia produced from the model (Fig. 3) yielded suitability classes for the whole
 261 island in the following proportions: 4.8 % very high, 4.7 % high, 5.8 % intermediate, 10.4 % low, and 74.3
 262 % very low. Higher probabilities of *A. saligna* occurrence are located close to urban areas and roads, in
 263 coastal areas and on flat slopes (Fig. 3).

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266

267 **Figure 2.** Regression plots along with confidence intervals (CI, grey shadowed area) showing the
 268 relationship between *Acacia saligna* occurrence (grey dots) and the PAB predictor variables: a) percentage
 269 of artificial areas, b) *A. saligna* afforestation distance, c) road distance, d) coastline distance, e) slope, f)
 270 annual mean temperature, g) fire frequency, h) percentage of *Pinus* sp. afforestation, i) percentage of
 271 herbaceous dune natural vegetation and j) percentage of dunes with woody vegetation, and degradation

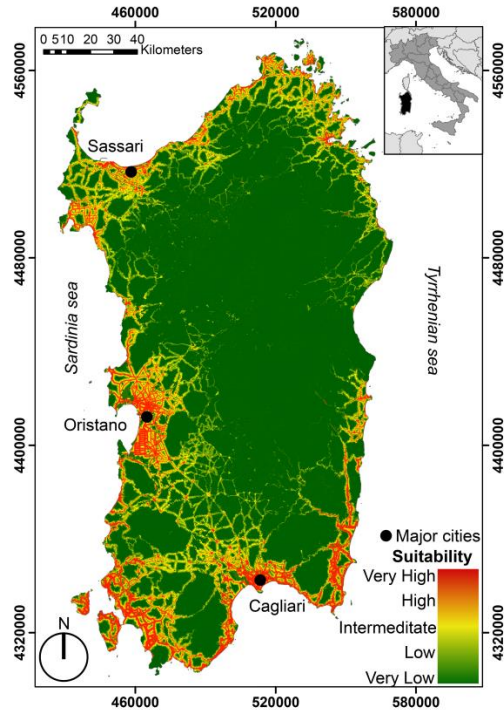
272 stages (see Table 1). Predictor values are shown on the x-axes while partial suitability values are plotted on
 273 the y-axis (fitted value (f) of predictor variables).

274
 275 **Table 2.** Results of the GLM analysis of *Acacia saligna* presence/pseudo-absence, modelled using
 276 predictors relating to propagule pressure (P), abiotic (A) and biotic (B) factors. Significance codes: 0 ‘***’
 277 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’.

278

Predictors	Estimate	Std. Error	Z value	p-value
Intercept	-1.63E+01	2.95E+00	-5.519	3.41 10 ⁻⁸ ***
Propagule pressure (P)				
ART	1.74E+00	4.07E-01	4.288	1.80 10 ⁻⁵ ***
<i>A. saligna</i> afforestation	-3.07E-05	5.36E-06	-5.728	1.02 10 ⁻⁸ ***
Road distance	-3.29E-03	3.23E-04	-10.172	< 2 10 ⁻¹⁶ ***
Abiotic (A)				
Coastline distance	-3.77E-05	1.35E-05	-2.797	0.00515**
Slope	-8.67E-02	1.66E-02	-5.21	1.89 10 ⁻⁷ ***
Temperature	1.09E+00	1.76E-01	6.228	4.73 10 ⁻¹⁰ ***
Fire	-2.74E+00	6.83E-01	-4.014	5.96 10 ⁻⁵ ***
Biotic (B)				
AFF	-1.53E+01	5.36E+00	-2.858	0.00426**
DUN	1.41E+01	4.72E+00	2.99	0.00279**
WDH	8.21E-01	3.48E-01	2.359	0.0183*

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280

281 **Figure 3.** Suitability map for *Acacia saligna* in Sardinia based on the regional-scale invasive species
 282 distribution model (iSDM). Shading shows model predicted relative probabilities of occurrence. The
 283 coordinate reference system is UTM (WGS84) zone 32 N.

284

285 4. Discussion

286 This iSDM-based study explored whether 10 independent predictor variables explained the distribution of
 287 the invasive populations of *A. saligna* in the Mediterranean island of Sardinia and provided a high-
 288 resolution suitability map as a tool for managing this highly invasive species. Strong modelled responses
 289 to the predictor variables demonstrated the importance of propagule pressure (P), abiotic (A) and biotic (B)
 290 factors in determining suitability for *A. saligna* invasion. The predictive performance of the model,
 291 according to the cross-validated AUC, was very high (mean AUC = 0.94), allowing us to produce a highly
 292 informative high-resolution suitability map from the model.

293 Predictors relating to propagule pressure gave the strongest explanation of the occurrence of *A. saligna* in
 294 Sardinia. Specifically, our results show that proximity to *A. saligna* plantations, road networks and artificial
 295 or urbanised areas are important drivers of invasion. Indeed, we observed a higher chance of invasion close
 296 to past *A. saligna* plantations or roads and with medium coverage of built areas. The occurrence of *A.*
 297 *saligna* records close to the plantations established in the 1950s for stabilizing sand dunes and for other
 298 purposes (Pavari and De Philippis, 1941; Celesti-Grappo et al., 2009; Del Vecchio et al., 2013) suggests

299 the species has spread from those plantations and confirms the importance of enforcing the ban on *A. saligna*
300 introduction and further plantation enshrined in the IAS Regulation. The preference we found for road
301 infrastructure and urbanised areas also suggests these locations increase the chance of propagule dispersal
302 and subsequent establishment of *A. saligna*, similarly to patterns reported for many other IAS (e.g., Alpert,
303 2006; Hobbs et al., 2009, Wilson et al., 2011) including other *Acacia* spp. invasions in Europe (Gutierrez
304 et al., 2011; Marziales et al., 2019). Indeed, our results are consistent with previous results showing that
305 invasive success of Australian acacias in general is correlated with propagule pressure and the extent of its
306 use and dissemination within new regions (i.e. “human usage factors”) (Castro-Díez et al. 2011).

307 Abiotic conditions were also very useful to explain the occurrence of *A. saligna* in Sardinia. The model
308 shows that the invader thrives in warmer conditions with greater moisture accumulation and that are less
309 fire prone (over the time period investigated). The model also found the species to be more common near
310 to the coast. Overall, this is consistent with broader scale analysis showing that *A. saligna* has great potential
311 to invade the Mediterranean area (Castro-Díez et al., 2011). However, previous findings showed that *A.*
312 *saligna* avoids the highly stressful saline conditions found in immediate proximity to the seashore
313 (Bazzichetto et al., 2016; Marziales et al., 2019) due to suppression of seed germination and seedling
314 survival (Meloni et al., 2013). Concerning fire frequency during the investigated decade (2005-2016), we
315 observed a higher suitability on non-burnt or burned only-once locations. Such apparent inconsistency with
316 previous research that suggested an important role fires in explaining *A. saligna* distribution in the
317 Mediterranean biome (Bell et al., 1993; Wilson et al., 2011) is probably related to the limited time interval
318 for which mapped fires are available. The time series of fire occurrence might be not long enough to
319 adequately describe the current invasion. Considering the observed preponderant role of propagule pressure
320 and, that *Acacia saligna* afforestation dates back to the fifties, it is highly probable that also in Sardinia the
321 fire have promoted invasions and favored germination from the seed bank (Richardson and Kluge, 2008)
322 but in locations that have burnt before the analyzed decade (2005-2016). Our results suggest that, besides
323 the utilization of high-resolution spatial data, the integration of temporal series data and landscape legacy
324 could greatly help to further improve our knowledge on species invasions (Malavasi et al., 2014).

325 For Sardinia, biotic predictors also helped to explain the distribution of *A. saligna*, demonstrating
326 preferences for sand dunes with open vegetation (DUN), sand dunes with woody vegetation (WDH) and
327 plantations with intermediate cover of *Pinus* spp. (AFF). In these habitats *A. saligna* is competitive and has
328 very clear negative impacts. As a result, management activities are in progress in these priority habitats,
329 aiming for local eradication or population control, as defined by the European Directive 92/43/EEC, and
330 for protection of critically endangered endemic species (IUCN 2001, 2003, 2006; Domina and Mazzola,
331 2008; Caruso, 2012; Del Vecchio et al., 2013; Brundu, 2013). Similar incidence of *A. saligna* on bare lands,

332 and sparsely scattered vegetation has been described for arid ecosystems with sandy substrate in other
333 regions (e.g., South-African fynbos, coastal sand dunes of Israel; Mehta, 2000; Bar Kutiel et al., 2004), and
334 it could be explained by low competition with native species and efficient water uptake by *A. saligna*
335 (Witkowski, 1991; Yelenik et al., 2004).

336 As well as providing understanding of the factors limiting *A. saligna* invasion, the model also allowed us
337 to produce a high-resolution risk map for the whole island of Sardinia. The projected suitability map
338 suggests a high risk of invasion in proximity to sand dunes, in the coastal plains and close to roads and
339 other areas with strong human influence (see Angiolini et al., 2013). These results could help to optimize
340 monitoring and prevention efforts, and to improve the existing management practice aimed at containing
341 the invasion. For instance, we suggest directing early-warning monitoring campaigns along roads and
342 railways as well cleaning and maintaining transportation infrastructure borders in order to reduce the
343 presence of open disturbed areas in which seedlings can establish and spread. Wild fires or prescribed
344 burning should also be limited as much as possible in any habitat where *A. saligna* is already established as
345 occasional fires might strongly enhance seed germination from the soil seed-bank. In addition, we
346 recommend the gradual removal of *A. saligna* from private and public gardens, botanic gardens or arboreta
347 and other plantations from which they may escape and spread towards and establish within uninvaded
348 habitats (Brundu et al., 2019).

349 The high and unrealized invasion risk also supports the recent inclusion of *A. saligna* in the list of invasive
350 alien species of European Union concern, banning its intentional introduction in the European Union under
351 article 7.1 of the IAS Regulation. However, the expected efficiency of these prevention measures may be
352 of moderate effectiveness as *A. saligna* is already present in most of the EU Member States (Brundu et al.,
353 2019). In fact, *A. saligna* could be declared a *widespread* species in several Member States (e.g., Cyprus,
354 Croatia, France, Greece, Italy, Malta, Portugal and Spain). Under article 3 (point 16) of the IAS Regulation,
355 a widespread species is an “*invasive alien species whose population has gone beyond the naturalization*
356 *stage, in which a population is self-sustaining, and has spread to colonize a large part of the potential*
357 *range where it can survive and reproduce*”. For such widespread species it is very likely too late to apply
358 eradication, except in restricted and priority areas. The majority of Member States shall have to put in place
359 effective management (art. 19 of the IAS Regulation), so that their impact on biodiversity, the related
360 ecosystem services, and, where applicable, on human health or the economy are minimized. Nevertheless,
361 prohibition measures should limit further entry and introduction of new genotypes or provenances, and
362 limit spread and re-invasion in sites where removal or control intervention are taking place. Finally, these
363 prevention measures should be accompanied as much as possible by informative campaigns aiming to

364 inform citizens, to increase public awareness, as unaware citizens frequently contribute to spread the
365 invasive species (Brundu et al., 2019).

366 **5. Conclusion**

367 The iSDM developed based on high resolution thematic layers representing a range of PAB predictors
368 explained the current distribution of *A. saligna* in Sardinia to a high degree of predictive accuracy. The
369 model identified the important roles of propagule pressure, abiotic conditions and biotic factors in
370 determining invasion risk and allowed the production of a suitability map for the Sardinian territory
371 identifying locations at risk of further invasion. Such methodology could be further used for regional-scale
372 modelling of other invasive species, including those listed in the IAS Regulation. We are convinced that
373 our results and the chosen methodology match the demand of the Regulation for new early warning tools
374 i.e. for predicting the location of new outbreaks, for establishing priorities for monitoring and control of
375 widespread invasive species, and confirm the usefulness of predictive models for IAS management.

376

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382

383 **ORCID**

384 Vanessa Lozano <https://orcid.org/0000-0001-5910-0995>

385 Flavio Marzialetti <https://orcid.org/0000-0001-5661-4683>

386 Maria Laura Carranza <http://orcid.org/0000-0001-5753-890X>

387 Daniel Chapman <https://orcid.org/0000-0003-1836-4112>

388 André Große-Stoltenberg <http://orcid.org/0000-0001-6075-5497>

389 Giuseppe Brundu <https://orcid.org/0000-0003-3076-4098>

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