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**Plant invasions in Italy: An integrative approach using the European LifeWatch infrastructure database**

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1 **Plant invasions in Italy: an integrative approach using the European LifeWatch**  
2 **infrastructure database**

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38 **Abstract**

39 By using the LifeWatch database – a European e-science infrastructure on native and alien plant occurrence collected  
40 from a wide set of Italian terrestrial sites – we estimated the occurrence of alien species in a cross-habitat framework in  
41 relation to propagule pressure (P), abiotic (A) and biotic (B) conditions. The research represents an example of macro-  
42 ecological assessment of invasion risk at national scale claimed by the recent European regulation (EU 1143/2014) on  
43 invasive alien species. Based on a large vegetation dataset, we estimated alien and native species richness across a set of  
44 19 Italian terrestrial sites. By using a Generalized Linear Mixed Model, we investigated the relationship between the  
45 proportion of alien occurrence across sites and habitat types (EUNIS) at family level with PAB putative drivers derived  
46 from LifeWatch and other open access geographic databases. Our results support the full model as the best-fitting  
47 option, highlighting that plant invasion in the Italian terrestrial ecosystems is a function of the combination of PAB  
48 conditions. In the first step of the invasion process, the accessibility time from towns plays a major role. By contrast, the  
49 abiotic filter imposed by environmental condition (high temperatures and low precipitations) as well the competition  
50 with the native community (high species richness) may pose a limit to the settlement and spread of alien species.  
51 Because of the high availability of similar data on PAB conditions worldwide, this study represents an effective and  
52 easy tool to design appropriate biodiversity conservation policies focused on the prevention of alien spread.

53

54 **Keywords:** abiotic factors; biotic factors; climate; LifeWatch; LTER-Italy network; propagule pressure

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## 60 1. Introduction

61 Biological invasions have become a global issue constituting a major threat to biodiversity and requiring  
62 urgent solutions (Ehrenfeld, 2010; Early et al., 2016). Successful invasions are relatively rare (Williamson and Fitter,  
63 1996) and depend on the interaction of several drivers, but once the species is established in a new area, it is difficult to  
64 eradicate or control it effectively. The most valuable method to reduce its impact is to prevent establishment or spread  
65 in the first place (Duncan et al., 2003; Early et al., 2016). Determining what makes habitats vulnerable to biological  
66 invasion is therefore among the most important targets in ecology (Chytrý et al., 2008). However, in order to manage  
67 invasive species, an understanding of the mechanisms that contribute to the success of the invaders is required  
68 (Pauchard and Shea, 2006). Many hypotheses have been formulated to explain successful biological invasion, most of  
69 which attribute it to the interplay between invasiveness (i.e. the biologically-related property of species to become  
70 established, spread to or become abundant in new communities) and invasibility (i.e. the susceptibility of habitats to the  
71 establishment or proliferation of invaders) (Colautti et al., 2004). However, few studies have integrated these two  
72 aspects and most have instead generally focused on one single mechanism (Kueffer et al., 2013). Indeed, invasion  
73 success is due to a combination of factors and mechanisms, and it is likely to be context-dependent (Catford et al.,  
74 2009). There are high numbers of supported explanations for invasion success, but the main drivers thereof are usually  
75 tested in isolation (McGill et al., 2007), and consequently observations differ quite often among studies, sometimes  
76 showing opposite results (Lockwood et al., 2005). There is an increasing need for a synthetic approach in which as  
77 many drivers as possible are considered (Kueffer et al., 2013). Such an exhaustive approach has been proposed by  
78 Catford et al. (2009), in order to explain the invasion success of exotic species in a given site. The authors outline a  
79 wide range of non-exclusive drivers summarised into three major groups: propagule pressure, abiotic conditions of the  
80 invaded ecosystems and biotic characteristics (recipient community and invading species). They claim that the degree  
81 of invasion is driven by a combination of these three factors, even though their influence is unlikely to be equal and the  
82 incursion is usually interwoven with anthropogenically induced disturbances (Byers et al., 2002).

83 Propagule pressure is often the key driver of invasion and may reveal its idiosyncratic nature (Lockwood et al.,  
84 2005). Propagule pressure is defined as the number and frequency of propagules arriving at a site to which they are not  
85 native (Lonsdale, 1999), and is related with different factors, such as density of human population, numbers of visitors  
86 in nature reserves, proportion of urban or industrial land cover, land cover change, road density or the intensity of traffic  
87 and trade (Thuiller et al., 2005; Von der Lippe and Kowarik, 2007; Malavasi et al., 2014). Factors governing success  
88 also include an organism's ability to colonize and settle in specific abiotic conditions. An invasion will fail if the  
89 invading species cannot withstand the environmental filters and conditions of a site (Weiher and Keddy, 1995; Chytrý  
90 et al., 2008). Several hypotheses attribute invasion degree to environmental characteristics, together with a change in

91 resource availability (Blumenthal, 2006); for example, when an increase in unused resources occurs, communities could  
92 be more susceptible to invasion (Melbourne et al., 2007). Generally, alien plants occurrence has a strong, significant  
93 relationship with water availability, and therefore climate, thereby increasing species richness when precipitation  
94 increases and the summer drought period becomes shorter (Martin-Fores et al., 2015). Moreover, an alien species  
95 entering a new area will gain or lose biotic interactions, which might promote or constrain invasion (Mitchell et al.,  
96 2006). Among these interactions, native richness is known to play a significant role in biotic resistance (Levine et al.,  
97 2004). Elton (1958) first forged the notion of biotic resistance to non-native invaders, defined as the degree of resistance  
98 offered by native communities, to explain the heavy invasion of species-poor systems such as island and  
99 anthropogenically disturbed areas. Higher native species richness is expected to reduce nutrient availability and  
100 intensify competition, predation, disease and parasites (Von Holle and Simberloff, 2005). In turn, these factors may  
101 reduce niche opportunities for invaders and play a role in biotic resistance (Shea and Chesson, 2002). However, the  
102 exact way in which native species richness influences alien invasion has not yet been clarified convincingly (Pauchard  
103 and Shea, 2006; Stohlgren et al., 2006; Carboni et al., 2013).

104 For many years, biological invasion studies were performed on single habitats or sites, or restricted to one or  
105 just a few species, and only with the recent compilations of large datasets of vegetation from all the major habitats of a  
106 country or large region, an increase in more extended studies has occurred (van Kleunen et al., 2015). Nonetheless,  
107 many of them are often confined to understanding different levels of invasion among habitats (Chytrý et al., 2009) by  
108 focusing on a single driver (Pyšek et al., 2010), species or taxonomical group (Feng et al., 2016; Taylor et al., 2016),  
109 while few have attempted to model invasion in a cross-habitat framework over a large set of taxonomic groups (Pyšek,  
110 and Chytrý, 2014; Bellard et al., 2016).

111 The impact of biological invasions has been a widespread problem in Europe, where it currently poses a major  
112 threat to both biodiversity conservation (DAISIE, 2009; EEC, 2014; Genovesi et al., 2015) and ecosystem functioning  
113 (Beninde et al., 2014), causing significant economic losses (Hulme et al., 2017). In response, the European commission  
114 proposed a strategy (EC, 2008) and a recent regulation on invasive alien species (EEC, 2014) that among others  
115 emphasizes prevention as one of the most cost-effective approaches. Still, the identification of different prevention  
116 actions depends on the national capacities to analyze and model species invasions and it should be favored by the  
117 existence of standardized open databases (DAISIE, 2009).

118 Based on this background, the challenge of this work is to apply an exhaustive synthetic approach whereby  
119 relative studies are placed within a robust, general theoretical framework proposed by Catford et al. (2009), in order to  
120 describe the context of plant invasion and to understand how the mechanisms relate to each other in such a macro-  
121 ecological environment. The here proposed analysis, developed using open data, sets a good example of macro-

122 ecological assessment of invasion risk at national scale which is claimed by the recent regulation (EU) No 1143/2014  
123 on invasive alien species (EEC, 2014; Genovesi et al., 2015; Beninde et al., 2015). In order to do this, we used the  
124 database assembled by LifeWatch, the e-Science and Technology European Infrastructure for Biodiversity and  
125 Ecosystem Research on native and alien plant occurrence (Basset and Los, 2012). LifeWatch aims to provide major  
126 contributions to addressing big environmental challenges by providing access through a pan-European distributed e-  
127 infrastructure to large sets of data, services and tools. The native and alien plant dataset is the result of systematically  
128 collating the species lists collected in a wide set of Italian terrestrial sites, including sites from the LTER-Italy network  
129 and the CONECOFOR ICP-Forest network. By using this dataset, we attempt to estimate the occurrence of plant alien  
130 species over a large set of taxonomic groups in a cross-habitat framework in relation to propagule pressure, abiotic and  
131 biotic conditions.

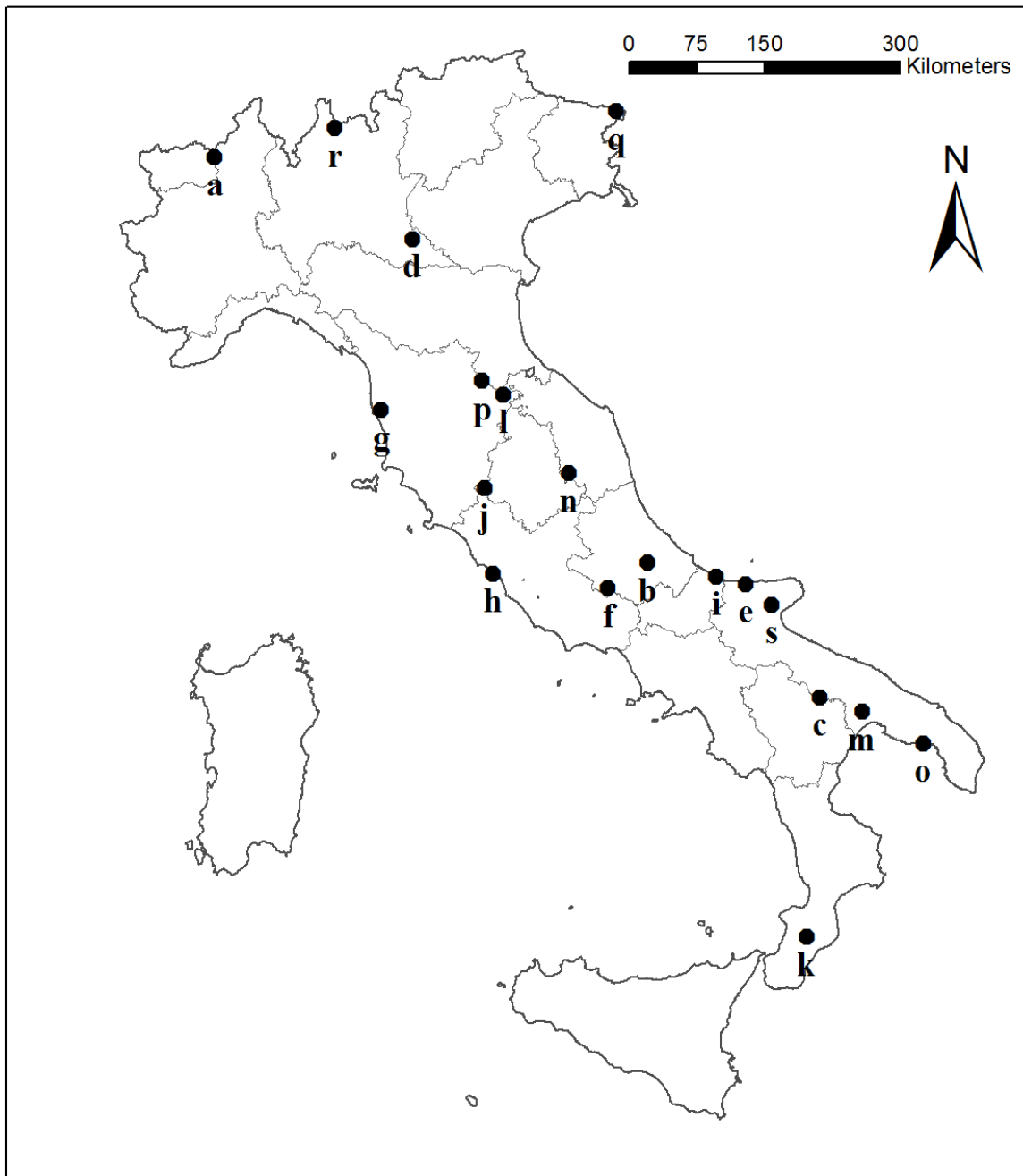
132

## 133 **2. Materials and Methods**

### 134 *2.1. Study area*

135 In Italy, 13.4% of the national vascular flora is represented by non-native taxa (Celesti-Gradow et al., 2009).  
136 Their introduction and establishment may date back thousands of years, because of Italy's historical position at the  
137 centre of the main trade routes and a long history of human activity (Celesti-Gradow et al., 2009). Moreover, offering a  
138 wide range of environmental contexts, Italy represents a worthwhile model for study. To our knowledge, at the Italian  
139 national level, only Celesti-Gradow et al. (2009) have attempted to identify the main large-scale drivers of alien species  
140 invasion, albeit only accounting for differences in the numbers of alien species between administrative regions, and  
141 excluding the biotic factor.

142 The study was conducted in terrestrial sites of the LifeWatch network in Italy (Fig 1). LifeWatch  
143 (<http://www.lifewatch.eu>) is a European e-science infrastructure offering ecological informatics services and tools to  
144 scientists and other public and private institutions involved in biodiversity and ecosystem research (Basset and Los,  
145 2012). The analysed area includes 19 sites distributed across the Italian peninsula. It includes a wide variety of  
146 ecosystems, which ranges from coasts to high mountains, from temperate to Mediterranean areas, from scarcely  
147 vegetated formations to closed forests and encompasses different levels of disturbance and anthropic pressure thus  
148 representing an interesting training ground for implementing a macro-ecological modelling approach on plant invasions.



149

150 **Fig 1:** Study area (Italy). Letters indicate the analyzed terrestrial sites of the LifeWatch network. (a) Alpi nord  
 151 occidentali; (b) Appennino centro meridionale; (c) Bosco Difesa Grande; (d) Bosco Fontana; (e) Bosco Isola di Lesina;  
 152 (f) Collelongo-Selva Piana; (g) Colognole - broadleaved woodland; (h) Dune costiere del Lazio; (i) Dune costiere del  
 153 Molise; (j) Monte Rufeno; (k) Piano Limina; (l) PNFC – Camaldoli – mixed woodland; (m) PNR Terra delle Gravine –  
 154 Comune di Palagianello; (n) Riserva Naturale Montagna di Torricchio; (o) Salina Vecchia Torre di Colimenna; (p)  
 155 Sasso Fratino – mixed woodland; (q) Tarvisio; (r) Val Masino; (s) Versante meridionale Gargano. For further  
 156 information about each site see Supplementary Material, Table A.1.

157

158 2.2. Floristic Data

159 For what concerns the data on flora, the LifeWatch database collates the georeferenced occurrence data  
160 systematically collected in the long-term ecological research network sites (LTER-Italy; <http://www.lteritalia.it/>) and  
161 the Italian CONECOFOR ICP-Forest network (<http://icp-forests.net/>). The sites are described according to the European  
162 Nature Information System (EUNIS) classification of habitats (Davies et al., 2004). Here, we considered four level-1  
163 EUNIS habitats: coastal habitats (B), grasslands and lands dominated by forbs, mosses or lichens (E), heathland, scrub  
164 and tundra (F), woodland, forest and other wooded land (G). We excluded from the analyses highly anthropic sites and  
165 non-terrestrial plants. The floristic database, describing species occurrence across 19 different sites, consists of 4878  
166 occurrences. Out the observed taxa, 2152 are native, while 138 are considered as alien species. The correct  
167 identification of the alien status was checked using the list reported for Italy by Celesti-Grapow et al. (2009). In order to  
168 produce a reliable analysis in a macro-ecological framework, the obtained set of data was aggregated by site, EUNIS  
169 habitat and taxonomical group (family level; see Supplementary Material, Table A.1), and native and alien richness  
170 were calculated. The floristic dataset, including a subset of the total non-native Italian flora distributed along a limited  
171 number of terrestrial sites is a subset of the total non-native Italian flora, so partially representative of the Italian  
172 peninsula. Still, it allows exploring the relationship between the observed occurrences of alien species and a set of  
173 potential drivers. Before calculating native and alien taxonomic richness per site, abiotic and propagule pressure  
174 variables were also determined (Tab. 1).

175

### 176 *2.3. Propagule pressure and abiotic variables*

177 In a GIS environment (ArcGis 10.3, ESRI, Redlands, CA, USA), two sets of variables were extracted:  
178 propagule pressure and abiotic variables (Table 1). The sites included in the LifeWatch database cover large areas of  
179 different extent and the only comparable and available georeferenced information between all the sites is the centroid of  
180 the sampled area, therefore, these variables were calculated as the mean value in a wide buffer area around the centroid.  
181 Considering the lack of a detailed geographic information, the utilization of a standard 30 km in radius buffer around  
182 the centroid coordinates represents a reasonable and effective way to describe the general climatic and accessibility  
183 conditions at national scale and across different sites. Still, due to the large geographical extent of the investigated area,  
184 we assumed that the potential bias introduced by averaging parameters in a buffer of 30 km would be negligible at this  
185 scale.

186 Whereas the accessibility constitutes a primary driver in promoting invasive plant introductions (von der Lippe  
187 and Kowarik, 2007), we used as propagule pressure proxy, a site accessibility parameter (Vicente et al., 2010) extracted  
188 from the Global Map of Accessibility, with a spatial resolution of 1 km<sup>2</sup> (Nelson, 2008). Accessibility is defined herein  
189 as the travel time in minutes to a location of interest, using land- (road/off road) or water- (navigable river, lake and



190 ocean) based travel from the nearest major city (cities of 50,000 or more people in year 2000).

191 Climate has a major role in shaping alien species occurrence at wide scales (Thuiller et al., 2005) so as abiotic  
192 factor we considered a set of climatic variables calculated for each site. Both, temperature (Godoy et al., 2011) and  
193 water regime (Bradley et al., 2010) are crucial in determining the distribution of aliens so we accounted of: Annual  
194 Mean Temperature, Mean Temperature of the Warmest Quarter, Mean Temperature of the Coldest Quarter and  
195 Precipitation of the Wettest Quarter and Precipitation of the Driest Quarter. A quarter is defined as a period of three  
196 months (1/4 of the year). Climate data were derived from the WorldClim, an accurate and free climate database for  
197 ecological modeling and GIS (Hijmans et al., 2005), which is a set of global climate layers with several spatial  
198 resolutions. For our analysis ~1 km<sup>2</sup> spatial resolution was used. WorldClim has several advantages if compared to other  
199 global climatic databases, as the high spatial resolution, the high density of weather station records, the improved  
200 elevation data and detailed information about spatial patterns of uncertainty (see Hijmans et al., 2005 for details).

201 All abiotic variables were summarised into a single predictor for modelling and subsequently describing alien  
202 species patterns. To synthesize the abiotic variables, principal component analysis (PCA) was performed on a matrix  
203 composed of climatic variables, in order to extract PC axes that would provide a synthetic but reliable picture of  
204 environmental variation across different regions of the Italian peninsula. The first Principal Components (PC1)  
205 accounting for more than 80% of the total variability was then used in the model (See Supplementary Material, Table  
206 B.1) as an “Environment” predictor. This approach has the advantage of reducing considerably the number of variables  
207 in the model and solving the problem of autocorrelation often observed in climatic variables.

208

Predictors	Description	Factors	Source
Accessibility (minutes)	Travel time to a location from the nearest major cities	<b>P</b>	<a href="http://forobs.jrc.ec.europa.eu/products/gam/">http://forobs.jrc.ec.europa.eu/products/gam/</a>
AMT (°C)	Annual Mean temperatures		<a href="http://worldclim.org/version2">http://worldclim.org/version2</a>
MT-Coldest (°C)	Mean temperature of the coldest quarter		<a href="http://worldclim.org/version2">http://worldclim.org/version2</a>
MT-Warmest (°C)	Mean temperature of the warmest quarter	<b>A*</b>	<a href="http://worldclim.org/version2">http://worldclim.org/version2</a>
Pp-Wettest (mm)	Precipitations of the wettest quarter		<a href="http://worldclim.org/version2">http://worldclim.org/version2</a>
Pp-Driest (mm)	Precipitations of the driest quarter		<a href="http://worldclim.org/version2">http://worldclim.org/version2</a>
Native richness	Number of native species	<b>B</b>	LTER and CONECOFOR database ( <a href="http://www.lteritalia.it/">http://www.lteritalia.it/</a> ; <a href="http://icp-forests.net/">http://icp-forests.net/</a> )

209 **Table 1** GIS-derived predictors for propagule pressure (P), abiotic (A) and biotic (B) factors calculated for a buffer area  
210 of 30 km radius around each plot. A brief description and the sources used to derive them and the unit of measure (in  
211 brackets) are also reported. \* abiotic variables were summarized into a single “Environment” predictor (First Principal  
212 Components – PC1, Table B.1)

213

214

## 215 2.4. *Statistical analyses*

216 The proportion of alien species occurring at each site was estimated using a generalised linear mixed model  
217 (GLMM). For statistical analyses, the dataset was aggregated at the family level, to provide comparable units of  
218 diversity for the analyses.

219 Similarly, to the statistical workflow proposed by Corriero et al. (2016) and Colangelo et al. (2017) for  
220 freshwater and marine ecosystems, the observed proportion of alien species at the family level within the sampled sites  
221 was included as a dependent variable in the model, assuming a binomial distribution of the error. Given that site  
222 invasion success depends on multiple factors, namely biotic, abiotic and propagule pressure variables, we  
223 simultaneously tested them as predictors (i.e. fixed effect) of alien species occurrence. Besides, the first PC axis scores  
224 from the PCA, based on climatic and geographic variables, were used as descriptors of abiotic conditions at each site  
225 (Table B.1). Finally, as a measure of the biotic complexity of the receiving community, we used the native richness  
226 calculated at each site for each family (Table 1).

227 In order to control for potential bias due to a different sampling effort across taxonomic group and habitat, and  
228 uneven sampling across different habitats at the same site, we included the family of the taxa and EUNIS habitat type  
229 nested in the site name as a random intercept. Furthermore, because the numbers of observed native species may vary  
230 across different families, we included native richness as a random slope.

231 Seven different models, plus a null model, were compared using the Akaike information criterion correction  
232 for finite sample sizes (AICc), in order to identify the best-fitting model.

233 To estimate the explained variance of the best model, we calculated both conditional and marginal  $R^2$  values  
234 (R package MuMIn, Barton, 2013). Conditional  $R^2$  accounts for the explanatory power of both fixed and random  
235 effects, whereas marginal  $R^2$  only accounts for fixed effects (Nakagawa & Schielzeth, 2013).

236 Statistical analyses were performed in R 3.1.1 (R Development Core Team 2014), using the package *lme4* 1.1-  
237 7 (Bates et al. 2015) for GLMMs.

238

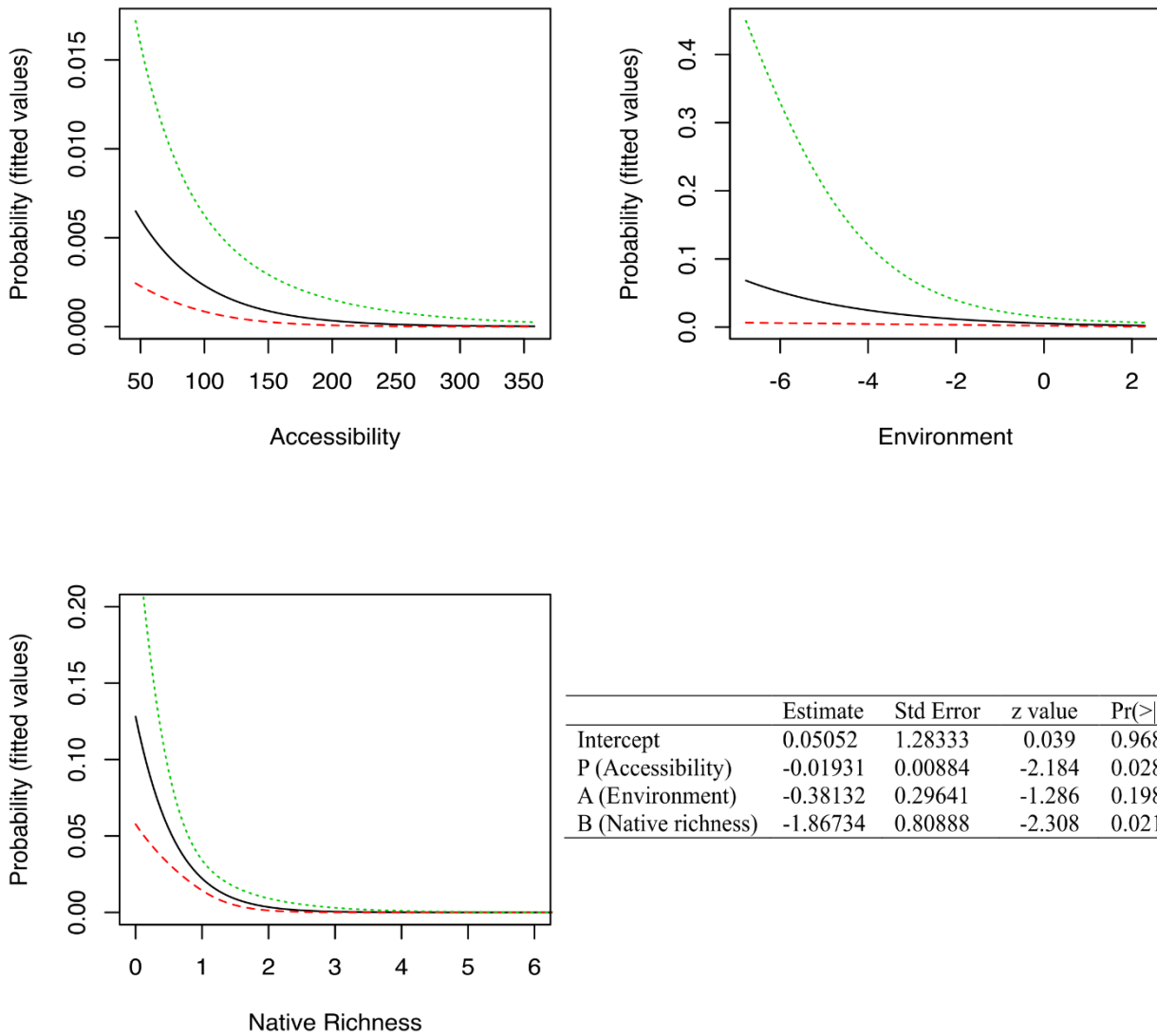
## 239 **3. Results**

240 According to the AICc, the model No. 4 including accessibility and native richness as predictors of alien  
241 invasion was the best-fitting GLMM (Table 2). However, the full model including all the three potential predictors  
242 (PAB factors) shows a  $\Delta_{AICc}$  far less than 2; such threshold is usually considered the minimum in order to reject a model  
243 in favor of another. Thus, it is possible to consider the full model valid as well as the model n° 4. Here we will report  
244 the full model in order to give a broader picture of invasion drivers.

245 Overall,  $R^2$  values highlighted a relatively high explanatory power of the full model, where 50% of the  
 246 variance is explained by the predictors (conditional  $R^2 = 0.97$ , marginal  $R^2 = 0.5$ ). Estimated coefficients for the full  
 247 model (Fig. 2) and regression plots suggest that the higher the accessibility of the site, with less than one hour's travel  
 248 from the nearest major cities, the higher the proportion of an alien species occurring (Fig. 2). On the other hand, the  
 249 proportion of aliens drastically decreases in sites with intermediate levels of accessibility reaching very low asymptotic  
 250 values on sites distant more than three hours from major cities. Abiotic variables were also highly correlated with the  
 251 proportion of alien species (Fig. 2). Given that the first PC score is positively correlated with temperatures and  
 252 negatively correlated with precipitation and latitude (Table B.1), the result obtained in the investigated habitat should be  
 253 considered as an indication of a decrease in the chances of finding an alien species in sites characterised by high  
 254 temperature and low precipitation, such as in southern Italy. On the contrary, sites characterised by higher precipitation  
 255 and less extreme temperatures (i.e. in central Italy) are more susceptible to alien species invasion. Finally, lower is the  
 256 native species richness, lower the proportion of alien species occurrence and increasing values of native richness  
 257 determines a steep reduction in the probability of finding an alien species in a site.  
 258

Model n°	P (Accessibility)	A (Environment)	B (Native richness)	df	logLik	AICc	$\Delta_{AICc}$
4	X		X	8	-328.605	673.3	0.00
8	X	X	X	9	-327.734	673.6	0.29
7		X	X	8	-329.851	675.8	2.49
3			X	7	-330.894	675.9	2.55
2	X			7	-340.298	694.7	21.36
6	X	X		8	-339.532	695.2	21.85
5		X		7	-341.492	697.1	23.75
1				6	-342.503	697.1	23.75

259 **Table 2** Selection table comparing seven different models explaining the proportion of alien species at each site  
 260 resulting from the GLMM, using the Akaike information criterion correction for finite sample sizes (AICc). P:  
 261 Propagule Pressure; B: Biotic Factors; A: Abiotic Factors.



262

263 **Fig. 2** Regression plot along with standard deviations based on the full model. The proportion of alien species against  
 264 Propagule pressure (accessibility), expressed in minutes away from the nearest town with >50,000 inhabitants (see  
 265 materials and methods), Abiotic (Environment) expressed as the first principal component from the PCA, based on  
 266 climatic and geographic variables, and Biotic (Native Species Richness) factors. The table with the estimated  
 267 coefficients for the full model is also reported.

268

#### 269 4. Discussion

270 This paper represents a pioneering attempt to implement a synthetic macro-ecological approach for  
 271 investigating drivers of alien plant species invasion over a large set of taxonomic groups in an Italian cross-habitat  
 272 framework. This attempt, supported by a free database describing alien distribution and geographic and environmental  
 273 variables in Italy, offers an effective and feasible support for identifying the national strategy of prevention claimed the

274 European regulation on invasive alien species (EC, 2014). Specifically, we found support for the full model as the best-  
275 fitting option, confirming that plant invasion in Italy is a function of the combination of propagule pressure, abiotic and  
276 biotic conditions of the invaded ecosystem. All three drivers are supposed to contribute to an increase in alien species  
277 proportion, with the following trend combination: high accessibility by humans, favourable abiotic conditions, such as  
278 water availability, and sites with low or lower native richness.

279         Accessibility, accounting for propagule pressure, is correlated positively with an increase in the proportion of  
280 alien species. Relying on our results, we can claim that accessibility by humans is a successful driver of invasion: those  
281 sites for which less than one hour's travel is needed from the nearest major cities, are those with a higher chance of  
282 invasion. The extent and rate of species transfer around the globe has increased due the intensification of national and  
283 international travel, trade and transport where, a higher number of human visitors to a site may lead to an increase in the  
284 number of exotic species (Alpert, 2006). This accessibility reveals the presence and intensity of intercontinental  
285 commerce and travel (e.g. ballast, seed, contaminants, horticultural trade) and local transport networks (e.g. roadsides,  
286 canals and railways), both known to promote the spread of non-native species (Pyšek and Hulme, 2005). Besides, such  
287 local networks may constitute remarkable opportunities for the secondary dispersal of invasive species in different  
288 biogeographic regions as the Mediterranean (Celesti-Grapow et al., 2009) and the temperate one (Chytrý et al., 2009).  
289 Indeed, the understanding that successful invasion requires adequate propagule pressure is now common to all theories  
290 of invasion ecology (Simberloff, 2009) as dominant pathways for species invasions are similar across different regions  
291 (Turbelin et al., 2017). Colautti et al. (2006) proposed that propagule pressure should form the basis of a null model for  
292 invasion studies, because invasion cannot occur without propagules and because, if excluded, it has the potential to  
293 mislead the interpretation of invasion patterns. Therefore, accessibility measures, as well as being a proxy of human  
294 disturbances, seem to be a suitable tool for accounting for such dispersal processes. However, the strong relationship  
295 between propagule pressure and establishment success do not exclude the role both of the abiotic and the recipient  
296 community. The interaction of these factors with propagule pressure might turn out to be the more informative step,  
297 able to further our understanding of invasion processes (Lockwood et al., 2005).

298         As regards abiotic variables, our results show that by moving towards areas with higher precipitation and lower  
299 mean temperature, we have a higher proportion of alien species. This notion supports the increased resource availability  
300 hypothesis (Davis et al., 2000, Chytrý et al., 2008), namely colonisation promoted by an enrichment in the main  
301 limiting resources. We propose that water availability is one of the main limiting factor, and this is particularly true for  
302 the Mediterranean climate, where wetter areas are more susceptible to non-native species establishment (Martin-Fores  
303 et al., 2015). The resource availability hypothesis suggests that colonisation is promoted by higher resource availability,  
304 due to either higher resource supply or lower resource uptake by competing species (Davis et al., 2000). Either way, the

305 resource availability hypothesis alone is not exhaustive in explaining invasion success; for instance, it is not clear why  
306 high resource levels would facilitate exotic species in particular rather than native ones (Davis et al., 2000). Blumenthal  
307 (2006) proposes that this can be explained in combination with the enemy release hypothesis (ERH) (Elton, 1958).  
308 Once a high resource-demanding species goes in an exotic range, natural enemies are absent and they have a  
309 competitive advantage over native species, benefiting from both high resource availability and enemy release  
310 (Blumenthal, 2006), with abiotic and biotic factors being clearly interrelated.

311 Here comes into play native richness, which is negatively correlated with an increase in the proportion of alien  
312 species. Many authors have observed the existence of this negative correlation, explaining this phenomenon through  
313 species competition (Martin-Fores et al., 2015). Communities with higher species richness are more “stable” and less  
314 susceptible to invaders, as more niches are used and fewer remain available to be occupied (Pauchard and Shea, 2006).  
315 However, some authors have proven that the naturalisation of exotic species decreases native biodiversity (Davis,  
316 2003), and consequently, it is difficult to establish whether the invasion success originated from low native richness or  
317 if the invasion caused a decrease in native richness. Overall, there is little evidence to support the hypothesis that native  
318 species richness is directly responsible for greater resistance to invasion (Rejmánek, 1996; Stohlgren et al., 2006),  
319 thereby suggesting that other biotic factors (e.g. native parasites, predators, grazers) may be more responsible for the  
320 unsuccessful naturalisation of alien species may be due to (Levine et al., 2004). Biotic resistance constrains the  
321 abundance of invasive species once they have successfully established, rather than preventing their occurrence within  
322 communities, thus suggesting a more important role for abiotic factors in regulating invasions (Levine et al., 2004,  
323 Chytrý et al., 2008).

324

## 325 **5. Conclusion**

326 This work confirms the simultaneous contribution of the three factors for invasion success at a macro-  
327 ecological scale. First of all, it is appropriate to consider propagule pressure, because invasion cannot occur without it:  
328 high accessibility to a site seems to trigger the presence of non-native species. Human travel, trade and transport are  
329 proxy of propagule pressure, and, given that they do not show signs of reduction, accessibility needs to be considered in  
330 future studies about invasion spread and monitoring. Resource availability detected by climate variables turned out to be  
331 a suitable predictor, whereas native richness showed a negative correlation with alien occurrence, even though we  
332 cannot infer direct causalities.

333 This study represents an important step in evaluating and possibly managing and preventing alien spread at the  
334 national level which is claimed by the EU regulation on invasive alien species (EU 1143/2014) and that needs of further  
335 efforts in Italy as in other countries. Once the main causal factor for successful invasion is determined, the mechanism

336 associated with the factor can be effectively explored in detail. For instance, if propagule pressure is found to drive  
337 invasions, the relative importance of abiotic and biotic factors can be assessed afterwards through a top-down approach,  
338 starting with the major driver and increasing in complexity as propagule pressure, abiotic and biotic factors are  
339 independently investigated. In particular, our findings could provide useful insights for conservation-oriented measures  
340 such as promoting recovering processes or developing alien control measures.

341 Finally, because of the high availability of such propagule pressure, abiotic and biotic data worldwide, we  
342 claim the reproducibility of such a macro-ecological approach in modelling and monitoring biological invasions. In this  
343 context, the use of the LifeWatch dataset successfully allowed to test such an approach, thereby highlighting and  
344 promoting the sharing of the unprecedented amounts of data that ecology is facing. Still, the proposed macro-ecological  
345 approach could be extended across a large set of scales and landscapes thus providing further indications on invasion  
346 risk in different countries and biogeographical regions.

347

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