

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

3
4

5 Malavasi Marco^{1*}, Acosta Alicia Teresa Rosario², Carranza Maria Laura³, Bartolozzi Luca^{4,15}, Basset Alberto^{5,15},
6 Bassignana Mauro⁶, Campanaro Alessandro⁷, Canullo Roberto⁸, Carruggio Francesca⁹, Cavallaro Viviana^{9,10},
7 Cianferoni Fabio^{4,15}, Cindolo Claudia¹¹, Cocciuffa Cristiana¹¹, Corriero Giuseppe^{10,15}, D'Amico Francesco Saverio^{9,10},
8 Forte Luigi^{9,10}, Freppaz Michele¹², Mantino Francesca⁹, Matteucci Giorgio^{13,15}, Pierri Cataldo^{10,15}, Stanisci Angela³,
9 Colangelo Paolo^{14,15}.

10

11 ¹ *Department of Applied Geoinformatics and Spatial Planning, Faculty of Environmental Sciences, Czech University of*
12 *Life Sciences, Kamycka 129,165 21 Prague 6, Czech Republic*

13 ² *Dipartimento di Scienze, Università degli Studi di Roma Tre, V.le Marconi 446, 00146 Roma , Italy*

14 ³ *Dipartimento di Bioscienze e Territorio, Università del Molise, V. Duca degli Abruzzi, 86039 Termoli (CB), Italy*

15 ⁴ *Natural History Museum of the University of Florence, Zoological Section "La Specola", via Romana 17, 50125*
16 *Florence, Italy*

17 ⁵ *Department of Science and Biological and Environmental Technology, University of Salento, Piazza Tancredi 7,*
18 *73100 Lecce, Italy*

19 ⁶ *Institut Agricole Régional, Rég. La Rochère, 1/A, 11100 Aosta, Italy*

20 ⁷ *National Centre for the Study and Conservation of Forest Biodiversity "Bosco della Fontana", National Forest*
21 *Service, Marmirolo, Mantova, Italy*

22 ⁸ *School of Biosciences and Veterinary Medicine - Plant Diversity and Ecosystems Management unit University of*
23 *Camerino - V. Pontoni, 5 - 62032 Camerino (Italy)*

24 ⁹ *Botanic Garden and Museum of the University of Bari, Via Orabona 4, 70125 Bari*

25 ¹⁰ *Department of Biology, University of Bari "Aldo Moro", Via Orabona 4, 70115 Bari, Italy*

26 ¹¹ *Corpo Forestale dello Stato - CONECOFOR*

27 ¹² *Università degli Studi di Torino, DISAFA-NatRisk, Largo Braccini 2, 10095 Grugliasco (To), Italy*

28 ¹³ *Consiglio Nazionale delle Ricerche, Istituto di Biologia Agroambientale e Forestale, Monterotondo Scalo, RM, Italy*

29 ¹⁴ *CNR, Institute of Agro-environmental and Forest Biology, Via Salaria km 29.300, 00015 Monterotondo (Rome, Italy)*

30 ¹⁵ *LifeWatch-Italy*

31

32 *Corresponding author:

33 Marco Malavasi

34 Department of Applied Geoinformatics and Spatial Planning, Faculty of Environmental Sciences, Czech University of
35 Life Sciences, Kamycka 129,165 21 Prague 6, Czech Republic

36 malavasi@fzp.czu.cz

37 telephone: [+420735193473](tel:+420735193473)

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

55

56

57

58

59

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.

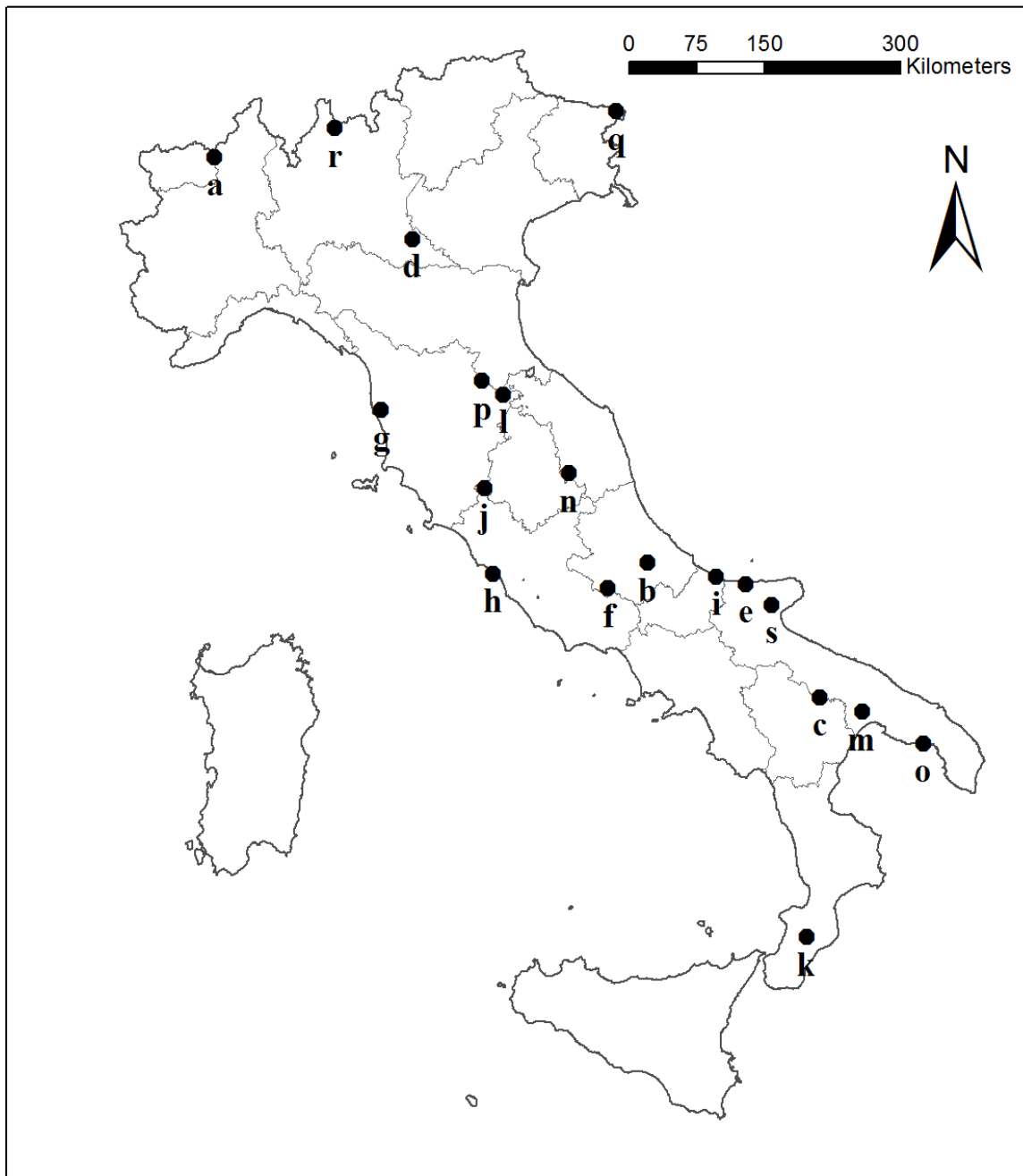
132

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-Grapow 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-Grapow 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-Grapow 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 km² (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 km² 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	P	http://forobs.jrc.ec.europa.eu/products/gam/
AMT (°C)	Annual Mean temperatures		http://worldclim.org/version2
MT-Coldest (°C)	Mean temperature of the coldest quarter		http://worldclim.org/version2
MT-Warmest (°C)	Mean temperature of the warmest quarter	A*	http://worldclim.org/version2
Pp-Wettest (mm)	Precipitations of the wettest quarter		http://worldclim.org/version2
Pp-Driest (mm)	Precipitations of the driest quarter		http://worldclim.org/version2
Native richness	Number of native species	B	LTER and CONECOFOR database (http://www.lteritalia.it/ ; http://icp-forests.net/)

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

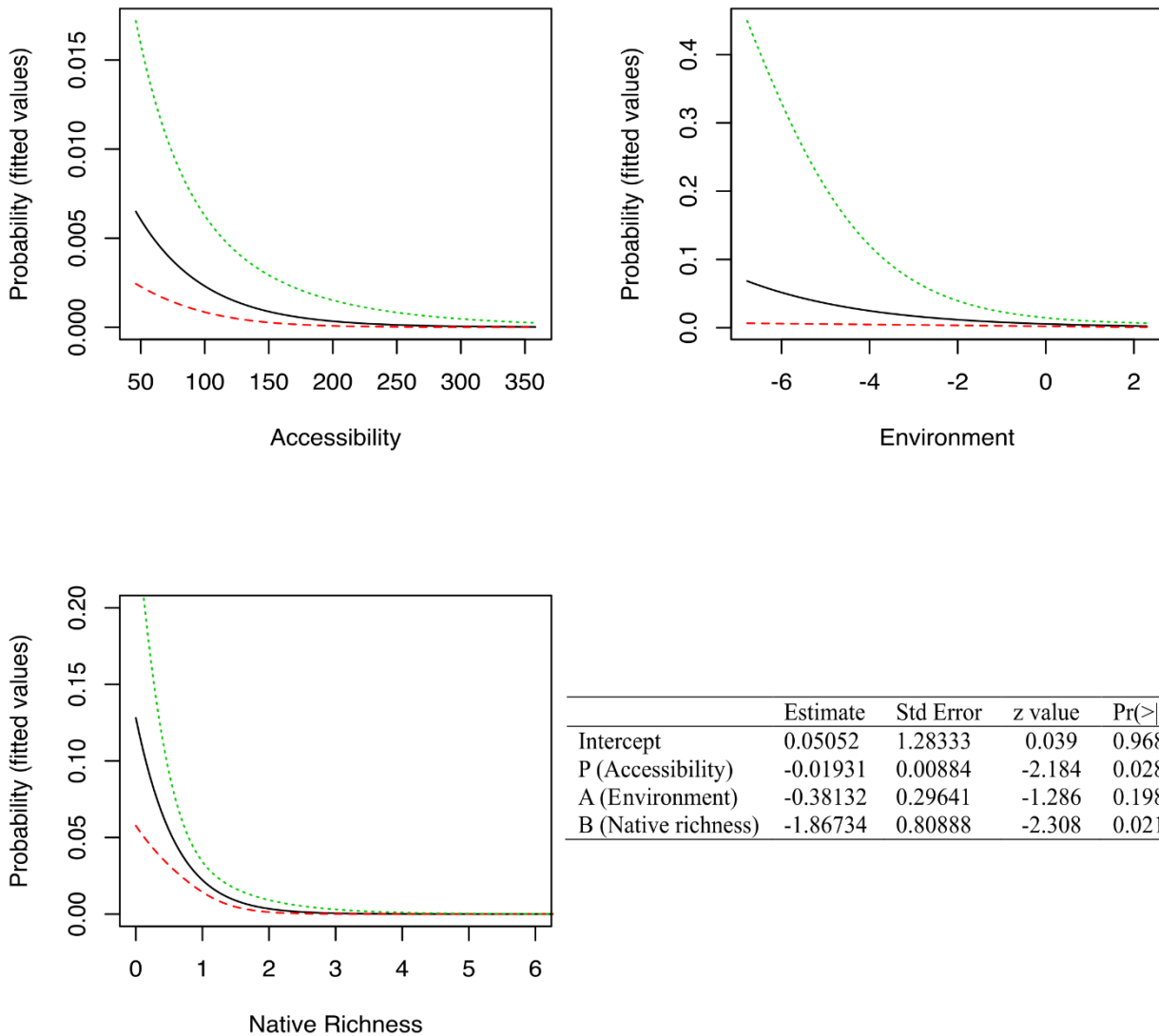
239 **3. Results**

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 Δ_{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	Δ_{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

348 **6. References**

- 349 Alpert, P., 2006. The advantages and disadvantages of being introduced. *Biol. Invasions* 8, 1523-1534
- 350 Basset, A., Los, W., 2012. Biodiversity e-Science: LifeWatch, the European infrastructure on biodiversity and
351 ecosystem research. *Plant Biosyst.* 146, 780–782.
- 352 Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.*
353 67, 1-48.
- 354 Bellard, C., Leroy, B., Thuiller, W., Rysman, J.F., Courchamp, F., 2016. Major drivers of invasion risks throughout the
355 world. *Ecosphere* 7:e01241. doi: 10.1002/ecs2.1241.
- 356 Beninde, J., Fischer, M.L., Hochkirch, A., Zink, A., 2015. Ambitious advances of the European Union in the legislation
357 of invasive alien species. *Conserv. Lett.* 8, 199-205.
- 358 Bradley, B.A., Wilcove, D.S., Oppenheimer, M., 2010. Climate change increases risk of plant invasion in the Eastern
359 United States. *Biol. Invasions* 12, 1855-1872.
- 360 Blumenthal, D.M., 2006. Interactions between resource availability and enemy release in plant invasion. *Ecol. Lett.* 9,
361 887–895.
- 362 Byers, J.E., 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection
363 regimes. *Oikos* 97, 449-458.
- 364 Carboni, M., Münkemüller, T., Gallien, L., Lavergne, S., Acosta, A., Thuiller, W., 2013. Darwin's naturalization
365 hypothesis: scale matters in coastal plant communities. *Ecography* 36, 560-568.
- 366 Catford, J.A., Jansson, R., Nilsson, C., 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a

367 single theoretical framework. *Divers. Distrib.* 15, 22–40.

368 Celesti-Grapow, L., Alessandrini, A., Arrigoni, P.V., Banfi, E., Bernardo, L., Bovio, M., Brundu, G., Cagiotti, M.R., et
369 al., 2009. Inventory of the non-native flora of Italy. *Plant Biosyst.* 143, 386-430.

370 Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L., & Danihelka, J., 2008. Separating habitat
371 invasibility by alien plants from the actual level of invasion. *Ecology* 89, 1541-1553. doi:10.1890/07-0682.1.

372 Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L.C., Vilà, M., 2009. European map of alien plant invasions based on
373 the quantitative assessment across habitats. *Divers. Distrib.* 15, 98-107.

374 Colangelo, P., Fontaneto, D., Marchetto, A., Ludovisi, A., Basset, A., Bartolozzi, L., Bertani, I., Campanaro, A., et al.,
375 2017. Alien species in Italian freshwater ecosystems: a macroecological assessment of invasion drivers. *Aquat.*
376 *Invasion* 3, 299-309.

377 Colautti, R.I. and MacIsaac, H.J., 2004. A neutral terminology to define ‘invasive’ species. *Divers. Distrib.* 10, 134-
378 141.

379 Colautti, R.I., Grigorovich, I., MacIsaac, H., 2006. Propagule pressure: a null model for biological invasions. *Biol.*
380 *Invasions* 8, 1023-1037.

381 Corriero, G., Pierri, C., Accoroni, S., Alabiso, G., Bavestrello, G., Barbone, E., Bastianini, M., Bazzoni, A.M., et al.,
382 2015. Ecosystem vulnerability to alien and invasive species: a case study on marine habitats along the Italian coast.
383 *Aquat. Conserv.* 26, 392-409. doi:10.1002/aqc.2550.

384 DAISIE, 2009. Handbook of alien species in Europe, ed. Springer, Berlin.

385 Davies, C.E., Moss, D., Hill, M.O., 2004. EUNIS habitat classification revised 2004. European Environment Agency,
386 Copenhagen and European Topic Centre on Nature Protection and Biodiversity, Paris.

387 Davis, M.A., 2003. Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience* 53,
388 481–489.

389 Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of
390 invasibility. *J.Ecol.* 88, 528–534.

391 Duncan, R.P., Blackburn, T.M., Sol, D., 2003. The ecology of bird introductions. *Annu. Rev. Ecol. Evol. Syst.* 34, 71–
392 98.

393 Early, R., Bradley, B.A., Dukes, J.S., Lawler, J.J., Olden, J.D., Blumenthal, D.M., Gonzalez, P., Grosholz, E.D., et al.,
394 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat.*
395 *Commun.* 7, 12485. doi.org/10.1038/ncomms12485.

396 EEC, 2014. Council Directive 1143/2014/EC of 22 october 2014 on the prevention and management of the
397 introduction and spread of invasive alien species. *Off. J. L.* 317/35, 4/11/2014.

- 398 Ehrenfeld, J.G., 2010. Ecosystem consequences of biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 41, 59-80.
- 399 Elton, C.S., 1958. *The ecology of invasions by animals and plants*, ed. Methuen, London.
- 400 EC, 2008. *Towards an EU Strategy on Invasive Species [COM(2008) 789, EC, Brussels 2008]*.
- 401 Feng, Y., Maurel, N., Wang, Z., Ning, L., Yuand, F.H., van Kleunen, M., 2016. Introduction history, climatic
402 suitability, native range size, species traits and their interactions explain establishment of Chinese woody species in
403 Europe. *Glob. Ecol. Biogeogr.* 25: 1356-1366. doi:10.1111/geb.12497.
- 404 Genovesi, P., Carboneras, C., Vilà, M., Walton, P., 2015. EU adopts innovative legislation on invasive species: a step
405 towards a global response to biological invasions? *Biol. Invasions* 17, 1307-1311.
- 406 Godoy, O., Pires de Lemos-Filho, J., Valladares, F., 2011. Invasive species can handle higher leaf temperature under
407 water stress than Mediterranean natives. *Environ. Exp. Bot.* 71, 207-214.
- 408 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate
409 surfaces for global land areas. *Int. J. Climatol.* 25, 1965-1978.
- 410 Hulme, P.E., Pyšek, P., Nentwig, W., Vilà, M., 2009. Will threat of biological invasions unite the European Union?
411 *Science* 324, 40–41.
- 412 Kueffer, C., Pyšek, P., Richardson, D.M., 2013. Integrative invasion science: model systems, multi-site studies, focused
413 meta-analysis and invasion syndromes. *New Phytol.* 200, 615-633.
- 414 Levine, J.M., Adler, P.B., Yelenik, S.G. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.*
415 7, 975–989.
- 416 Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. *Trends*
417 *Ecol. Evol.* 20, 223–228.
- 418 Lonsdale, W.M., 1999. Global patterns of invasions and the concept of invasibility. *Ecology* 80, 1522-1536.
- 419 Malavasi, M., Carboni, M., Cutini, M., Carranza, M.L., Acosta, A.T.R., 2014. Landscape fragmentation, land-use
420 legacy and propagule pressure promote plant invasion on coastal dunes: a patch-based approach. *Landscape Ecol.*
421 29, 1541-50.
- 422 Martin-Fores, I., Sanchez-Jardon, L., Acosta-Gallo, B., del Pozo, A., Castro, I., de Miguel, J.M., Ovalle, C., Casado,
423 M., 2015. From Spain to Chile: environmental filters and success of herbaceous species in Mediterranean-climate
424 region. *Biol. Invasion* 17, 1425-1438.
- 425 McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., et al.,
426 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological
427 framework. *Ecol. Lett.* 10, 995–1015.
- 428 Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., et

429 al., 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol. Lett.* 10, 77–94.

430 Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N., Maron J.L., Morris, W.F.,
431 et al., 2006. Biotic interactions and plant invasion. *Ecol. Lett.* 9, 726–740.

432 Nakagawa, S. & Schielzeth, H., 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for
433 biologists. *Biol. Rev. Camb. Philos. Soc.* 85, 935–956.

434 Nelson, A., 2008. Travel time to major cities: A global map of Accessibility. Global Environment Monitoring Unit -
435 Joint Research Centre of the European Commission, Ispra. <http://forobs.jrc.ec.europa.eu/products/gam/> (accessed 26
436 June 2016).

437 Pauchard, A., Shea, K., 2006. Integrating the study of non-native plant invasions across spatial scales. *Biol. Invasions* 8,
438 399–413.

439 Pyšek, P., Chytrý, M., 2014. Habitat invasion research: where vegetation science and invasion ecology meet. *J. Veg.*
440 *Sci.* 25, 1181–1187. doi:10.1111/jvs.12146.

441 Pyšek, P., Hulme, P.E., 2005. Spatio-temporal dynamics of plant invasions: linking pattern to process. *Ecoscience* 12,
442 302–315.

443 Pyšek, P., Jarošík, V., Hulme, P.E., Kühn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., et al., 2010.
444 Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proc. Natl.*
445 *Acad. Sci. U.S.A.* 107, 12157–12162.

446 Rejmánek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? *Ecology* 77, 1655-
447 1661.

448 Rose, K.C., Graves, R.A., Hansen, W.D., Harvey, B.J., Qiu, J., Wood, S.A., Ziter, C., Turner, M.G., 2016. Historical
449 foundations and future directions in macrosystems ecology. *Ecol. Lett.* 20, 147-157. doi:10.1111/ele.12717.

450 Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*
451 17, 170-176.

452 Simberloff, D., 2009. The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 40, 81–102.

453 Stohlgren, T., Jarnevich, C., Chong, G.W., Evangelista, P.H., 2006. Scale and plant invasions: a theory of biotic
454 acceptance. *Preslia* 78, 405–426.

455 Taylor, K.T., Maxwell, B.D., Pauchard, A., Nuñez, M.A., Peltzer, D.A., Terwei, A., Rew, L.J., 2016. Drivers of plant
456 invasion vary globally: evidence from pine invasions within six ecoregions. *Glob. Ecol. Biogeogr.* 25, 96-106.

457 Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O., Rouget, M., 2005. Niche-based modelling as a
458 tool for predicting the risk of alien plant invasions at a global scale. *Glob. Ecol. Biogeogr.* 11, 2234-2250.

459 Turbelin, A. J., Malamud, B. D. and Francis, R. A., 2017. Mapping the global state of invasive alien species: patterns of

460 invasion and policy responses. *Glob. Ecol. Biogeogr.* 26, 78–92.

461 Van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., et al., 2015. Global
462 exchange and accumulation of non-native plants. *Nature* 525, 100-103. doi:10.1038/nature14910.

463 Vicente, J., Alves, P., Randin, C., Guisan, A., & Honrado, J., 2010. What drives invasibility? A multi-model inference
464 test and spatial modelling of alien plant species richness patterns in northern Portugal. *Ecography* 33, 1081-1092.

465 Von der Lippe, M., & Kowarik, I., 2007. Long-Distance Dispersal of Plants by Vehicles as a Driver of Plant
466 Invasions. *Conserv. Biol.* 21, 986-996.

467 Von Holle, B., Simberloff, D., 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure.
468 *Ecology* 86, 3212-3218.

469 Weiher, E., Keddy, P.A., 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns.
470 *Oikos* 74,159-164.

471 Williamson, M., Fitter, A., 1996. The varying success of invaders. *Ecology* 77, 1661-1666.

472