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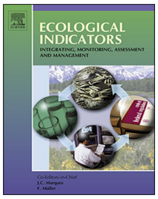

Original Articles

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

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ABSTRACT

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

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1. Introduction

Biological invasions have become a global issue constituting a major threat to biodiversity and requiring urgent solutions (Ehrenfeld, 2010; Early et al., 2016). Successful invasions are relatively rare (Williamson and Fitter, 1996) and depend on the interaction of several drivers, but once the species is established in a new area, it is difficult to eradicate or control it effectively. The most valuable method to reduce its impact is to prevent establishment or spread in the first place (Duncan et al., 2003; Early et al., 2016). Determining what makes habitats vulnerable to biological invasion is therefore among the most important targets in ecology (Chytrý et al., 2008). However, in order to manage invasive species, an understanding of the mechanisms that contribute to the success of the invaders is required (Pauchard and Shea, 2006). Many hypotheses have been formulated to explain successful biological invasion, most of which attribute it to the interplay between invasiveness (i.e. the biologically-related property of species to become established, spread to or become abundant in new communities) and invasibility (i.e. the susceptibility of habitats to the establishment or proliferation of invaders) (Colautti and MacIsaac, 2004). However, few studies have integrated these two aspects and most have instead generally focused on one single mechanism (Kueffer et al., 2013). Indeed, invasion success is due to a combination of factors and mechanisms, and it is likely to be context-dependent (Catford et al., 2009). There are high numbers of supported explanations for invasion success, but the main drivers thereof are usually tested in isolation (McGill et al., 2007), and consequently observations differ quite often among studies, sometimes showing opposite results (Lockwood et al., 2005). There is an increasing need for a synthetic approach in which as many drivers as possible are considered (Kueffer et al., 2013; Bazzichetto et al., 2018). Such an exhaustive approach has been proposed by Catford et al. (2009), in order to explain the invasion success of exotic species in a given site. The authors outline a wide range of non-exclusive drivers summarised into three major groups: propagule pressure, abiotic conditions of the invaded ecosystems and biotic characteristics (recipient community and invading species). They claim that the degree of invasion is driven by a combination of these three factors, even though their influence is unlikely to be equal and the incursion is usually interwoven with anthropogenically induced disturbances (Byers, 2002).

Propagule pressure is often the key driver of invasion and may reveal its idiosyncratic nature (Lockwood et al., 2005). Propagule pressure is defined as the number and frequency of propagules arriving at a site to which they are not native (Lonsdale, 1999), and is related with different factors, such as density of human population, numbers of visitors in nature reserves, proportion of urban or industrial land cover, land cover change, road density or the intensity of traffic and trade (Thuiller et al., 2005; Von der Lippe and Kowarik, 2007; Malavasi et al., 2014). Factors governing success also include an organism's ability to colonize and settle in specific abiotic conditions. An invasion will fail if the invading species cannot withstand the environmental filters and conditions of a site (Weiher and Keddy, 1995; Chytrý et al., 2008). Several hypotheses attribute invasion degree to environmental characteristics, together with a change in resource availability (Blumenthal, 2006); for example, when an increase in unused resources occurs, communities could be more susceptible to invasion (Melbourne et al., 2007). Generally, alien plants occurrence has a strong, significant relationship with water availability, and therefore climate, thereby increasing species richness when precipitation increases and the summer drought period becomes shorter (Martin-Fores et al., 2015). Moreover, an alien species entering a new area will gain or lose biotic interactions, which might promote or constrain invasion (Mitchell et al., 2006). Among these interactions, native richness is known to play a significant role in biotic resistance (Levine et al., 2004). Elton (1958) first forged the notion of biotic resistance to non-native invaders, defined as the degree of resistance offered by native communities, to explain the heavy invasion of species-poor systems such as island and anthropogenically disturbed areas. Higher native species richness is expected to reduce nutrient availability and intensify competition, predation, disease and parasites (Von Holle and Simberloff, 2005). In turn, these factors may reduce niche opportunities for invaders and play a role in biotic resistance (Shea and Chesson, 2002). However, the exact way in which native species richness influences alien invasion has not yet been clarified convincingly (Pauchard and Shea, 2006; Stohlgren et al., 2006; Carboni et al., 2013).

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

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

Based on this background, the challenge of this work is to apply an exhaustive synthetic approach whereby relative studies are placed within a robust, general theoretical framework proposed by Catford et al. (2009), in order to describe the context of plant invasion and to understand how the mechanisms relate to each other in such a macroecological environment. The here proposed analysis, developed using open data, sets a good example of macro-ecological assessment of invasion risk at national scale which is claimed by the recent regulation (EU) No 1143/2014 on invasive alien species (EEC, 2014; Genovesi et al., 2015; Beninde et al., 2015). In order to do this, we used the database assembled by LifeWatch, the e-Science and Technology European Infrastructure for Biodiversity and Ecosystem Research on native and alien plant occurrence (Basset and Los, 2012). LifeWatch aims to provide major contributions to addressing big environmental challenges by providing access through a pan-European distributed e-infrastructure to large sets of data, services and tools. The native and alien plant dataset is the result of systematically collating the species lists collected in a wide set of Italian terrestrial sites, including sites from the LTER-Italy network and the CONECOFOR ICP-Forest network. By using this dataset, we attempt to estimate the occurrence of plant alien species over a large set of taxonomic groups in a cross-habitat framework in relation to propagule pressure, abiotic and biotic conditions.

2. Materials and methods

2.1. Study area

In Italy, 13.4% of the national vascular flora is represented by nonnative taxa (Celesti-Grapow et al., 2009). Their introduction and establishment may date back thousands of years, because of Italy's historical position at the centre of the main trade routes and a long history of human activity (Celesti-Grapow et al., 2009). Moreover, offering a wide range of environmental contexts, Italy represents a worthwhile model for study. To our knowledge, at the Italian national level, only Celesti-Grapow et al. (2009) have attempted to identify the main large-scale drivers of alien species invasion, albeit only accounting for

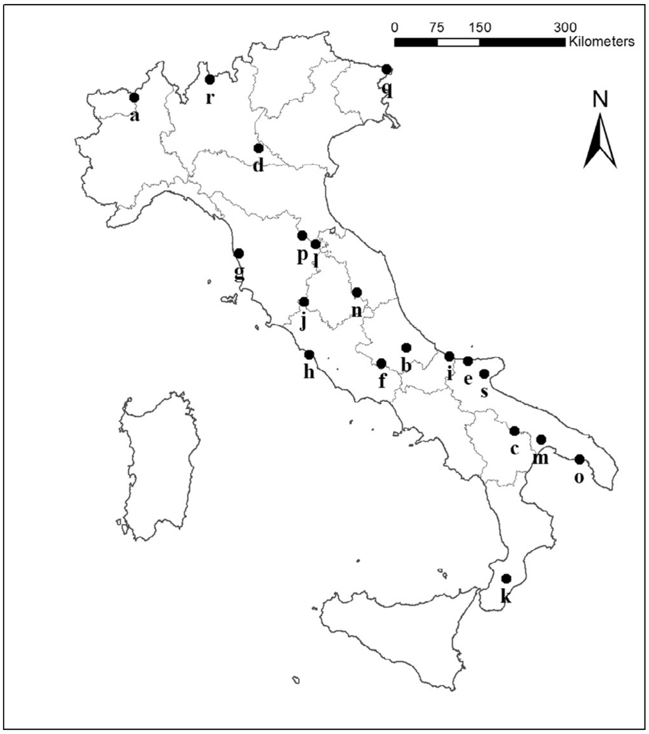


Fig. 1. Study area (Italy). Letters indicate the analyzed terrestrial sites of the LifeWatch network. (a) Alpi nord occidentali; (b) Appennino centro meridionale; (c) Bosco Difesa Grande; (d) Bosco Fontana; (e) Bosco Isola di Lesina; (f) Collelongo-Selva Piana; (g) Colognole – broadlived woodland; (h)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

differences in the numbers of alien species between administrative regions, and excluding the biotic factor.

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

2.2. Floristic data

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

2.3. Propagule pressure and abiotic variables

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

Whereas the accessibility constitutes a primary driver in promoting invasive plant introductions (von der Lippe and Kowarik, 2007), we used as propagule pressure proxy, a site accessibility parameter (Vicente et al., 2010) extracted from the Global Map of Accessibility, with a spatial resolution of 1 km^2 (Nelson, 2008). Accessibility is defined herein as the travel time in minutes to a location of interest, using

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

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	**A***	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		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/)

Table 2

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

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

land- (road/off road) or water- (navigable river, lake and ocean) based travel from the nearest major city (cities of 50,000 or more people in year 2000).

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

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

2.4. Statistical analyses

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

Similarly, to the statistical workflow proposed by Corriero et al. (2015) and Colangelo et al. (2017) for freshwater and marine ecosystems, the observed proportion of alien species at the family level within the sampled sites was included as a dependent variable in the model, assuming a binomial distribution of the error. Given that site invasion success depends on multiple factors, namely biotic, abiotic and propagule pressure variables, we simultaneously tested them as predictors (i.e. fixed effect) of alien species occurrence. Besides, the first PC axis scores from the PCA, based on climatic and geographic variables, were used as descriptors of abiotic conditions at each site (Table B.1). Finally, as a measure of the biotic complexity of the receiving community, we used the native richness calculated at each site for each family (Table 1).

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

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

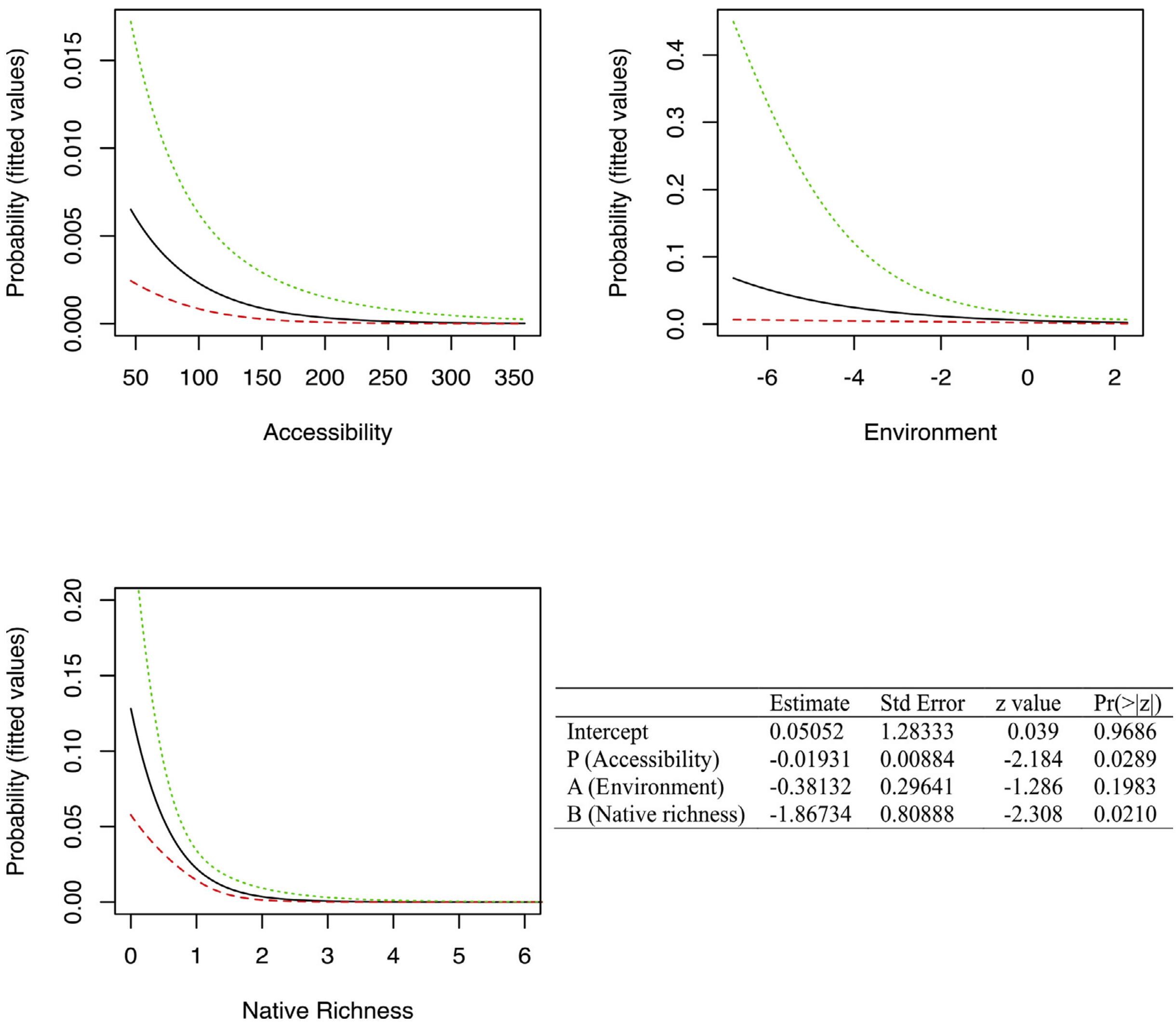
To estimate the explained variance of the best model, we calculated both conditional and marginal R^2 values (R package MuMln, Barton, 2013). Conditional R^2 accounts for the explanatory power of both fixed and random effects, whereas marginal R^2 only accounts for fixed effects (Nakagawa & Schielzeth, 2010).

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

3. Results

According to the AICc, the model No. 4 including accessibility and native richness as predictors of alien invasion was the best-fitting GLMM (Table 2). However, the full model including all the three potential predictors (PAB factors) shows a Δ_{AICc} far less than 2; such threshold is usually considered the minimum in order to reject a model 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 the full model in order to give a broader picture of invasion drivers.

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



	Estimate	Std Error	z value	Pr(>|z|)
Intercept	0.05052	1.28333	0.039	0.9686
P (Accessibility)	-0.01931	0.00884	-2.184	0.0289
A (Environment)	-0.38132	0.29641	-1.286	0.1983
B (Native richness)	-1.86734	0.80888	-2.308	0.0210

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

4. Discussion

This paper represents a pioneering attempt to implement a synthetic macro-ecological approach for investigating drivers of alien plant species invasion over a large set of taxonomic groups in an Italian cross-habitat framework. This attempt, supported by a free database describing alien distribution and geographic and environmental variables in Italy, offers an effective and feasible support for identifying the national strategy of prevention claimed the European regulation on invasive alien species (EEC, 2014). Specifically, we found support for the full model as the best-fitting option, confirming that plant invasion in Italy is a function of the combination of propagule pressure, abiotic and biotic conditions of the invaded ecosystem. All three drivers are supposed to contribute to an increase in alien species proportion, with the following trend combination: high accessibility by humans, favourable abiotic conditions, such as water availability, and sites with low or lower native richness.

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

As regards abiotic variables, our results show that by moving towards areas with higher precipitation and lower mean temperature, we have a higher proportion of alien species. This notion supports the increased resource availability hypothesis (Davis et al., 2000, Chytrý et al., 2008), namely colonisation promoted by an enrichment in the main limiting resources. We propose that water availability is one of the main limiting factor, and this is particularly true for the Mediterranean climate, where wetter areas are more susceptible to non-native species establishment (Martin-Fores et al., 2015). The resource availability hypothesis suggests that colonisation is promoted by higher resource availability, due to either higher resource supply or lower resource uptake by competing species (Davis et al., 2000). Either way, the resource availability hypothesis alone is not exhaustive in explaining invasion success; for instance, it is not clear why high resource levels would facilitate exotic species in particular rather than native ones (Davis et al., 2000). Blumenthal (2006) proposes that this can be explained in combination with the enemy release hypothesis (ERH) (Elton, 1958). Once a high resource-demanding species goes in an exotic range, natural enemies are absent and they have a competitive advantage over native species, benefiting from both high resource availability and enemy release (Blumenthal, 2006), with abiotic and biotic factors being clearly interrelated.

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

5. Conclusion

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

This study represents an important step in evaluating and possibly managing and preventing alien spread at the national level which is claimed by the EU regulation on invasive alien species (EU 1143/2014) and that needs of further efforts in Italy as in other countries. Once the main causal factor for successful invasion is determined, the mechanism associated with the factor can be effectively explored in detail. For instance, if propagule pressure is found to drive invasions, the relative importance of abiotic and biotic factors can be assessed afterwards through a top-down approach, starting with the major driver and increasing in complexity as propagule pressure, abiotic and biotic factors are independently investigated. In particular, our findings could provide useful insights for conservation-oriented measures such as promoting recovering processes or developing alien control measures.

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

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2018.03.038.

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