

Alien species in Italian freshwater ecosystems: a macroecological assessment of invasion drivers

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Abstract

The relative role of propagule pressure, abiotic and biotic variables as determinants of alien species occurrence differs among studies. This limits the synthesis of emergent patterns in invasion ecology and generalisations for conservation actions. In order to produce a broad and general assessment of the invasion pattern in aquatic habitats we here propose a macroecological approach to assess the drivers of occurrence of alien species within the whole biota (microorganisms, plants and animals) across several natural freshwater ecosystems of Italy. We simultaneously tested three groups of variables (propagule pressure, abiotic and biotic characteristics), selected as putative predictors of invasibility of a site. Propagule pressure, expressed as proximity to larger inhabited areas, and differences in the native species richness of the receiving community, had a significant role in determining the number of alien species occurrences. Furthermore, body size influenced the occurrence and colonization processes of alien species. Finally, climatic characteristics were relevant in determining the chances that a site was invaded, confirming the role of these abiotic filters in the invasion process.

Key words: non-indigenous species, invasion ecology, propagule pressure, species richness, body size, climate influence

Introduction

Alien species are considered one of the major threats to biodiversity worldwide and their negative ecological and economic effects have been extensively documented (Strayer 2010; Simberloff 2011). Multiple factors can affect invasion success including: 1) introduction effort (i.e., propagule pressure), 2) the abiotic features of the colonised habitat (Catford et al. 2009; Keller et al. 2011a), and 3) the biotic features of the recipient communities. The last feature includes resistance to (Elton 1958) or facilitation of (Davies et al. 2005) alien species establishment; and introduced species traits, such as fecundity or tolerance to stressors (Kolar and Lodge 2001; Jeschke and Strayer 2006; Keller et al. 2011b). However, analyses of the mechanisms influencing the occurrence of alien species often have a limited taxonomic focus, and few studies have simultaneously investigated the combined effects of invader characteristics and those of the invaded ecosystems (Catford et al. 2011; Pyšek et al. 2010a).

Case studies on multiple alien species have disentangled the reasons why some species are more successful than others (e.g., Rejmanek and Richardson 1996; Hamilton et al. 2005; Van Kleunen et al. 2010; Thomaz et al. 2015), but the results of such studies tend to be context-dependent and their inference idiosyncratic. The relative importance of propagule pressure (i.e., the number of introduced individuals, seeds, eggs, etc.), and abiotic (i.e., climate) and biotic (i.e., the receiving community) variables, according to the Propagule, Abiotic, Biotic (PAB) framework (Catford et al. 2009) differs across case studies. This suggests that differences may be more important than similarities in invasion ecology (Catford et al. 2009), thereby hindering the synthesis of emergent patterns (McGeoch et al. 2010; Pyšek et al. 2010b). Undisputedly, humans always play a major role in the introduction of alien species, both directly by introducing species, and indirectly by altering habitats. Propagule pressure is a metric that considers both the number of introduction events and the number of introduced propagules (Lonsdale 1999; Lockwood et al. 2005; Simberloff 2011), often described as a major determinant of invasion success. The probability of an alien species successfully establishing in a site is proportional to the proximity of the potential source, which influences the number of propagules arriving in an area (MacIsaac et al. 2004; Muirhead and MacIsaac 2005). Unfortunately, accurate information on propagule pressure is scarce, and in most cases available only for deliberately introduced alien species (Ficetola et al. 2008), so that no general assessment has yet been performed.

In order to produce a broad and general picture of emerging patterns for alien species invasion, we propose a macroecological approach that simultaneously analyses occurrence patterns within several taxonomic groups (animals, plants, protists and prokaryotes) belonging to multiple freshwater ecosystems, taking advantage of the biodiversity dataset from Italian water bodies recently collated by the Lifewatch Italy infrastructure (Boggero et al. 2016). The Italian peninsula is a useful model for such a study, as it represents a limited, connected area, with high heterogeneity of habitats ranging from wet and cold alpine areas to dry and warm Mediterranean ones. Moreover, studies of alien species often focus on large, charismatic and/or pest species due to the difficulty in observing the occurrence of alien species in understudied taxa. Our study minimised this bias, because it's based on a dataset derived from broad-scale and long-term monitoring projects with highly detailed taxonomic resolution for several taxonomic groups usually neglected in studies on alien species, across orders of magnitude of body size.

We explored the drivers of alien species occurrence in freshwater ecosystems by assessing the relative contribution of the three main actors in the PAB framework. We explored explicit hypotheses for invasion success related to the effects of (i) propagule pressure, (ii) abiotic features of the receiving sites, and (iii) biotic features influencing the invading organisms.

As an indirect proxy for propagule pressure and human frequentation of a habitat, we used site accessibility (Nelson 2008; Uchida and Nelson 2010), defined as the travel time to a location of interest using land (road/off road) or water (navigable river, lake and ocean) based travel. Accessibility is evaluated using a cost-distance algorithm, which computes the "cost" of travelling between two locations on a regular raster grid. Generally, the cost is expressed in units of time. Previous studies have shown that site accessibility is positively correlated with the probability of introducing alien species in the wild (Strayer 2010; Weisz and Yan 2010). Thus, our hypothesis was that sites with higher human frequentation, closer to densely inhabited areas, would have a greater likelihood of alien species introduction than more remote and rarely visited sites.

For the effect of abiotic features, we evaluated the role of various metrics describing the nature of freshwater habitats using environmental descriptors (temperature and precipitation). Because of the peculiar shape of the Italian peninsula, we also included the geographical location of the sampled sites as a proxy for potentially unmeasured environmental latitudinal gradient (Mediterranean arid climate in the south vs continental climate in the north). Our hypothesis was

that specific environmental features would favour or hinder the occurrence of alien species.

For biotic features, we evaluated two distinct hypotheses, one regarding the effects of the recipient community, and one concerning the biological features of the invading organisms. For the effect of the recipient community, we explored whether alien species occurrence probability was correlated with the native species richness of the invaded community (Fridley et al. 2007). Earlier studies suggested that high native richness provides resistance against invasions (Elton 1958; Kennedy et al. 2002), although other works have suggested that the opposite pattern is also possible, with rich communities favouring invasion due to their high functional redundancy and potentially relaxed competition (Stohlgren et al. 1999; Davies et al. 2005; Poessel et al. 2013; Corriero et al. 2016). We thus did not have a specific prediction for this hypothesis, except that a general influence of the receiving community is expected. For the effect of the biological features of the invading organisms, we assessed the influence of body size. Body size is important in many ways in both macroecology and eco-evolutionary dynamics (Belgrano and Reiss 2011), and it may be a relevant trait in invasion biology (Amalfitano et al. 2015). Microscopic organisms are expected to have a much broader (possibly cosmopolitan) distribution than larger-bodied species; hence, a large proportion of the global species pool should be present locally (Fenchel and Finlay 2004; Fontaneto 2011). Small-bodied species may be less prone to invasion since very few species would be considered alien. Moreover, the taxonomy of small organisms raises many more problems than that of larger ones (Fontaneto 2011), and the occurrence of microscopic alien species may be underestimated due to taxonomic difficulties. Given that these two processes, wider distribution and troublesome taxonomy for smaller organisms, should act in the same direction, our expectation is that the number of effectively recognised alien species would be higher for larger species.

A previous study by Boggero et al. (2014) focused on the number and proportion of alien species in different freshwater habitats including two abiotic predictors (temperature and rainfall) and a biotic predictor (richness). Our study goes a step further, explicitly taking into account the effect of propagule pressure and including a better evaluation of the abiotic filtering effect. The current study, highlighting the relative contribution of different predictors of alien species occurrence probability at a site (site invasibility), can provide useful information for planning strategies to mitigate or prevent alien species invasions, identifying those areas that may potentially deserve more intensive monitoring efforts.

Material and methods

Dataset preparation

In this study we used the occurrence data collected in Boggero et al. (2016), which extended the dataset of a previous macroecological analysis on the same geographical area (4300 occurrence data points – Boggero et al. 2014). The dataset spans approximately 50 years of monitoring programs on different taxonomic groups from a wide variety of permanent freshwater habitats (including springs, streams, lakes, fountains designated through the EUNIS classification system) covering almost all taxa, from prokaryotes to fish and macrophytes. For this reason, the dataset is particularly well suited for a study exploring invasion biology through a macroecological approach. The information on species presence at each site comes from published papers, including reports from universities and research institutions, as well as notes in technical reports from local authorities. Unfortunately, the dataset does not report the exact dates of species findings in a site so we cannot analyse invasions as a dynamic process through time. We considered the dataset (covering a 50 year period) as representative of recent invasion processes and we are confident that this approximation does not affect our results. For more detailed information about the dataset, the sites and their typology classification, the geographic coverage and the LifeWatch Italy network organisation see Boggero et al. (2016).

Previous studies focused on the fact that man-made aquatic environments or reservoirs could be more prone to alien invasions (Havel et al. 2015) or could disproportionately contribute to the secondary spread of invasive species (Hulme 2006) by functioning as invasion hubs for freshwater invaders (Muirhead and MacIsaac 2005). Therefore, in this study we explicitly chose to focus on natural and semi-natural environments only, excluding man-made sites (EUNIS code J5: [highly artificial man-made waters and associated structures](#)). We also excluded macrophytes because of the difficulties in obtaining a reliable estimate of their size. Furthermore, because of the macroecological focus of this work we included only those sites where at least two different phyla were sampled. The original dataset from Boggero et al. (2016) was thus pruned by removing macrophytes and non-natural sites. The final dataset included 5299 occurrence data from 139 sites (85 lentic and 54 lotic) distributed across the Italian peninsula (see Appendix 1 and Figure 1). Of the 1630 species (22 phyla, 244 families) included, 51 are alien species, representing ~ 3% of the total species diversity. The frequency of alien species presence in our database is consistent with percentages previously reported for Italian freshwaters

(Gherardi et al. 2008; Boggero et al. 2014), suggesting that our data were not biased towards a misleadingly larger representation of native versus alien species.

The dataset was aggregated at the family level to provide comparable levels of diversity for the statistical analyses to be applied. We are aware that species within a family may differ in autoecological requirements. However, we analysed very different families so that intra-family diversities are almost negligible with respect to inter-family differences. Thus, aggregating species at the family level allowed us to group species with homogeneous ecological features and body size. Native species richness and alien species richness were calculated for each family in each water body. The family-level and site-level aggregated dataset, together with the associated covariates, is available in Appendix 2.

Estimates of body size for each species (maximum length in mm) were obtained from literature; we mostly used monographs on Italian species (e.g., Ruffo 1977–1985). When data were not available in monographs, we searched for additional literature at the European scale (e.g., John et al. 2002; Wiederholm 1983). Given the wide range in body size, from cyanobacteria (0.001 mm) to fish (> 1 m), we assumed that small differences in body size between populations of the same species would not affect our inferences. The body sizes of species were averaged per family and subsequently log-transformed.

In this work, we focus on the available data for Italian freshwater systems and we used the lentic/lotic dichotomy only as random effect in the models below. The varied geographic coordinates for lakes (north) vs rivers (central, south) (see Figure 1) supports our choice to exclude man-made systems, which usually occur in central-southern Italy to provide drinking water in areas more likely subject to prolonged drought. Unfortunately, there are insufficient data available to analyse in detail the different probabilities of alien species occurrence in northern and southern Italy. This is due to national monitoring programs based on a family/genus level approach undermining the results that could be achieved through a species level approach.

Site climatic variables were obtained from the Worldclim database (Hijmans et al. 2005). Values for five bioclimatic variables, namely annual mean temperature, temperature mean diurnal range, temperature seasonality, annual precipitation, and precipitation seasonality, were extracted from 2.5 arc-minute resolution (approximately 5 km) raster layers. The combination of these five variables provides a good picture of Italian climatic conditions at the scale of our investigation. Next, to avoid problems

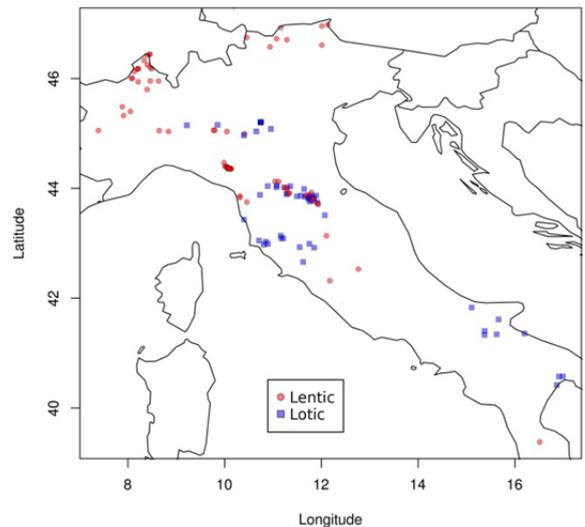


Figure 1. Geographic locations of sampled freshwater systems (for details see Appendix 2).

of autocorrelation and to reduce the number of variables included in the statistical models, a principal component analysis (PCA) was performed using the five bioclimatic variables. The scores of the first and the second components of the bioclimatic PCA, accounting for 85% of the total variance (Appendix 3), formed the abiotic predictors of site invasibility used in the statistical analyses. The first principal component from the environmental variables PCA (PC1env) was positively correlated with average annual precipitation, and negatively correlated with the other bioclimatic variables (see Appendix 3). The positive values of PC1env thus represent sites with high average annual precipitation, low mean annual temperature and low seasonality of rainfall and temperature (i.e., mountain sites in the Alps and in the Apennines). On the contrary, the second principal component, PC2env was positively correlated with rainfall seasonality and negatively correlated with average annual precipitation (bio12), temperature diurnal range (bio2) and seasonality (bio4). Therefore, sites with positive values are those with low rainfall predominantly in one season, and found mainly in the southern and western coastal area of Italy.

A second PCA was performed using the geographical coordinates (latitude and longitude) of each site. The score of the first component (PC1geo), accounting for 91% of the total variance (Appendix 3), identifies an axis from south-eastern (negative values) to north-western Italy (positive values). The

score was included in the subsequent model to test for a potential geographical trend in invasion probability along the Italian peninsula and to control for spatial autocorrelation among sample sites.

Site accessibility, expressed as the fastest travel time in minutes (either by car, bike, boat, or on foot) from the nearest city with more than 50,000 inhabitants to the centroid coordinates of a site, was derived from spatial maps provided by Nelson (2008). Larger values for accessibility indicate sites requiring longer travel time (i.e. remote sites or those with restricted access). Previous studies have demonstrated that this measure, even if apparently very coarse, provides a good representation of site accessibility for humans, and that this variable can be successfully integrated into ecological models (Ficetola et al. 2013).

Statistical analyses

We investigated the effect and the importance of the set of biological and environmental variables previously described as predictors of the probability of occurrence of alien species.

We used generalized linear mixed models (GLMM) to determine which variables best predicted alien species occurrence. GLMMs have the flexibility of generalized linear models in handling non-normal data distribution (Crawley 2013), and the advantage of accounting for potential violations of the assumption of independence of observations (Bunnfeld and Phillimore 2011; Beckerman 2014).

GLMMs were performed using the package *lme4* 1.1-7 (Bates et al. 2014) in R 3.1.1 (R Development Core Team 2014). We evaluated the invasibility (i.e., the probability of occurrence of an alien species) as the proportion of alien species observed in each site by taxonomic group. The proportion of alien species, weighed by sample size (total number of species observed), was then used as a response variable in a GLMM with a binomial distribution. As explanatory variables, we considered the three groups of variables within the PAB framework as candidate explanatory variables: (1) site accessibility as a proxy for propagule pressure; (2) the first and the second PC score axes from the environmental PCA (PC1env and PC2env) and the first PC score axis from the geographic PCA (PC1geo) as descriptors for abiotic features; (3) species richness and body size as proxies for biotic features.

Because our data came from sites distributed across different freshwater (lotic and lentic) systems, and richness at the site level might be influenced by habitat specific characteristics and by an uneven sampling effort within each habitat, the classification

of a site as lotic or lentic was included as a random intercept in the model. Furthermore, to account for taxonomic bias, family was also included as a random intercept allowing richness to vary across families (random slope). The impact of the introduction of the random effects was evaluated by running four full models varying the structure of random effect terms (i.e., removing each of the random effects in turn). The models were compared using Akaike's Information Criterion, and the preliminary results suggested that the inclusion of all three terms significantly improved the model fit (Appendix 4).

Our final full model included six predictors (no interactions between variables were considered in the model). Because a number of well-supported models for each response variable (or a combination of these) are possible, GLMM parameter estimates were obtained by model averaging considering all models within a 95% AICc confidence interval. This method has numerous advantages over traditional approaches, where support of the best model is estimated by an arbitrary threshold, and provides a measure of the importance of explanatory variables (Burnham and Anderson 2002). The relative importance (RI) of variables is calculated as the sum of their Akaike weights in the models in which the variable appears; so that a variable that contributes more to model fit will have a higher RI value. The R package MuMin 1.10.5 (Barton 2014) was used for model comparison and to compute the average model estimates.

Results

According to the AICc, the best fitting model included all the predictors with the only exception being the second environmental PC axis (PC2env), whereas the full model was the second best fitting model (Table 1). When considering the 95% delta AICc interval, five different models can be retained to estimate model parameters (Table 1).

Regarding the importance of the variables in the model-averaging estimates, accessibility, body size and native species richness had the highest relative importance (Table 2). Among the environmental variables, the first PC axis (PC1env) had higher relative importance than the second PC axis (PC2env), whereas the effect of geography (PC1geo) had the lowest relative importance.

According to these estimates, the probability of occurrence of alien species decreased very rapidly with the increase in native richness and the increase in the time necessary to reach a site (Figure 2). On the contrary, larger body size was associated with a higher probability of occurrence of alien species in a site (Figure 2).

Table 1. Factors related to the proportion of alien species in freshwater systems: 95% AICc best fitting models. Models are sorted according to the best AICc score. Predictors included in the models are denoted by an X. The retained models are based on 4 to 6 predictors: accessibility, native richness, body size, score on the first and second axis of the environmental PCA (PC1env and PC2env, respectively) and score on the first axis of the geographic PCA (PC1geo).

Model number	Accessibility	Native richness	Body size	PC1env	PC2env	PC1geo	df	logLik	AICc	Δ_{AICc}	AICc weight
1	X	X	X	X		X	10	-180.54	381.19	0.00	0.57
2	X	X	X	X	X	X	11	-180.54	383.19	2.00	0.21
3	X	X	X	X			9	-183.26	384.61	3.42	0.10
4	X	X	X	X	X		10	-182.67	385.43	4.24	0.07
5	X	X	X			X	9	-183.92	385.91	4.73	0.05

Table 2. Factors related to the proportion of alien species in freshwater systems: averaged coefficients of the Binomial GLMM. For each predictor, full-averaged coefficients, standard (std.) errors, significance (p), and variables relative importance (RI) are reported. For abbreviation of predictors see Table 1 legend.

Predictors	Estimate	Std. error	Adjusted SE	z value	p	RI
(Intercept)	6.791172	2.602285	2.603624	2.608	0.009097	
Log Accessibility	-0.679659	0.258201	0.258323	2.631	0.008511	1
Log Size	0.610709	0.175495	0.175589	3.478	0.000505	1
Native richness	-14.172474	2.904901	2.906462	4.876	1.10E-06	1
PC1env	-0.509716	0.250974	0.251077	2.03	0.042344	0.95
PC2env	-0.314222	0.213014	0.213077	1.475	0.140297	0.83
PC1geo	0.005871	0.092418	0.092458	0.063	0.949369	0.28

For the abiotic predictors, the first environmental PC (PC1env) was negatively correlated with the probability of occurrence of alien species, suggesting a decreased likelihood of finding them at high elevations (Figure 2). The same occurred with the second environmental PC (PC2env) suggesting a decreased likelihood of finding alien species with high rainfall seasonality and low average annual rainfall (Figure 2; see Appendix 1 for correlations between environmental variables and PC axes).

Finally, geographical location seems to play a very marginal role, although a slight increase in alien species presence can occur at higher latitudes (Table 2).

Discussion

Since the discovery of the New World, many species have been moved through deliberate introductions, aquaculture, ballast water transport, fish for restocking, movements of boats, and aquarium cleaning (Nunes et al. 2014). In Italy, notwithstanding the presence of the Alps acting as a physical barrier and its poor connection with the Danube river basin, species invasion into lake and river watersheds does not represent a remote case (Gherardi et al. 2008). Major vectors of introduction in Italian freshwaters are stock enhancement and culture causing the actual presence of around 40 alien species representing

about 3% of the total freshwater richness analysed (Boggero et al. 2014). Vulnerability of freshwater systems is thus less related to the geographic isolation of the Italian peninsula and more a product of the intensive use of freshwaters by humans, and the dispersal capability of aquatic organisms (Beisel 2001; Ricciardi 2001). Therefore, understanding the drivers of biological invasions is crucial for the conservation and proper management of freshwater ecosystems and their biodiversity.

In line with the above considerations, we proposed a comprehensive analysis of invasibility in Italian freshwater sites across a broad range of taxa. This study represents a further development of previous analyses (Boggero et al. 2014), and includes a larger dataset and a more formal theoretical approach within the PAB framework (Catford et al. 2009). We included a large set of variables but we are aware that underlying co-varying factors that were not measured may exist. For instance, in this paper, we do not consider lake/river morphometry as while it is easy to relate the biodiversity of small rivers/lakes to their surface area, this relationship fails when considering large rivers/lakes where only two or three stretches along their perimeters/major axis are considered during monitoring. In particular, in the case of rivers, biodiversity significantly changes from sources to river mouths, so that it will confound

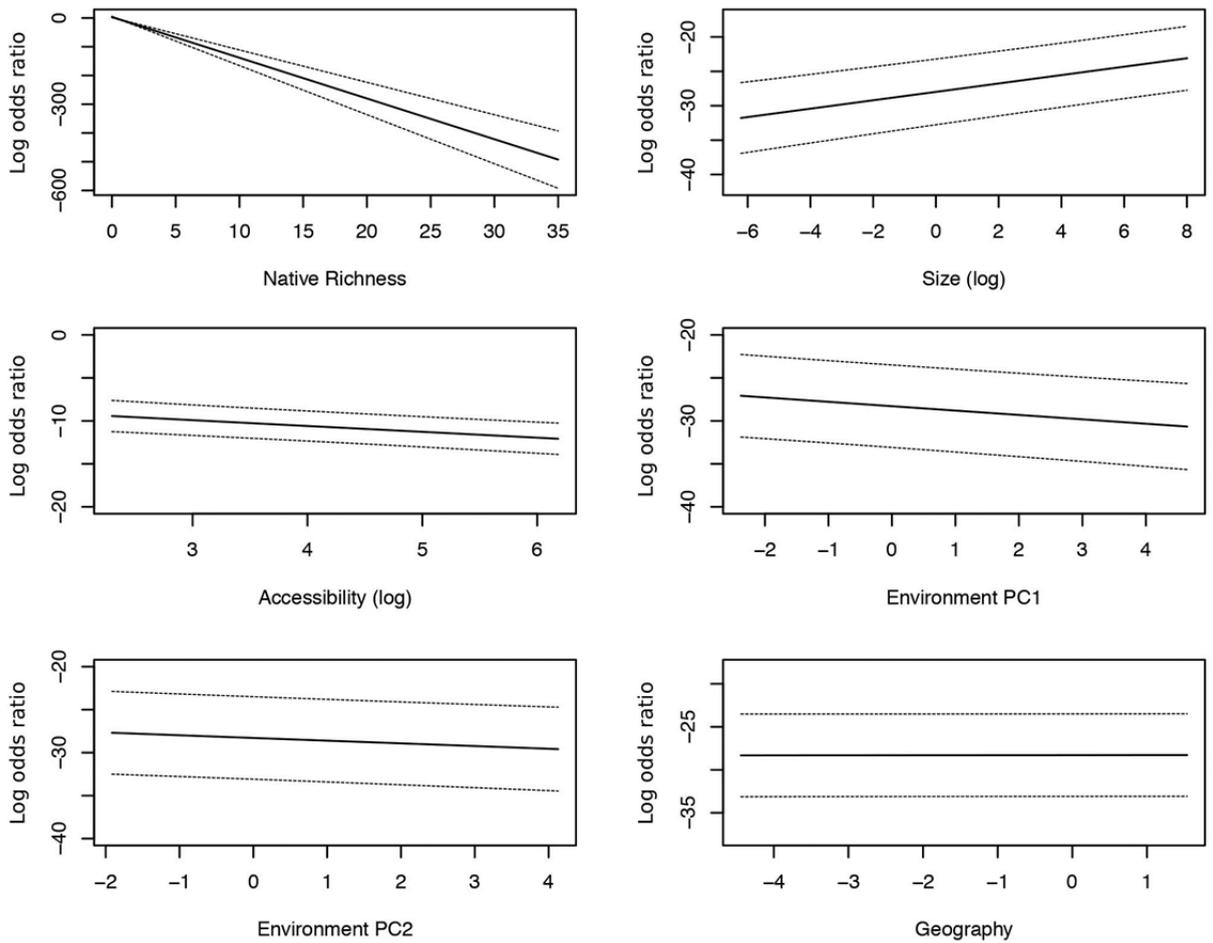


Figure 2. Full-averaged model estimates: predicting capabilities of each of the independent variables included in the GLMM. Estimated probability (solid line) and standard error (dashed lines) of alien species occurrence are reported as the log-odds ratio on the Y axis.

any type of hypothesis. We chose to focus only on variables that can be measured for all the systems considered and we are confident that the selected set of variables can make an important contribution to the understanding of biological invasions in Italian freshwater systems. The simultaneous evaluation of multiple predictors for several different taxa allowed us to test the relative contribution of anthropogenic, biotic and abiotic variables to the establishment of alien species in natural freshwater systems. Our findings suggested that most of the investigated variables were important in explaining the pattern of alien species occurrence. This provided us with a more comprehensive picture of site invasibility in a PAB framework.

Site accessibility, a proxy for propagule pressure driven by anthropic activity (transport, tourism, etc.), was of primary importance in explaining the occurrence of alien species.

Undoubtedly, alien species cannot colonize new areas if propagules do not arrive at the sites. Thus, the proximity of a site to human agglomerates and roads becomes a relevant variable in explaining the probability of their occurrence. This finding is in general agreement with other studies that have assessed the role of introduction effort (e.g., Von Holle and Simberloff 2005; Colautti et al. 2006; Ricciardi et al. 2011), although this is the first time that the effect of propagule pressure is demonstrated over a broad taxonomic range spanning several groups of prokaryotes and eukaryotes. The role of human activities is important in biological invasions (Pyšek et al. 2010a), and may help explain the inconsistent and idiosyncratic results obtained by species-specific and context-dependent studies, that do not explicitly consider the effect of propagule pressure (Lonsdale 1999; Lockwood et al. 2005;

Catford et al. 2009). Our results confirm that propagule pressure should certainly be taken into account in any analysis of site invasibility (Colautti et al. 2006; Simberloff 2009). Although our proxy for propagule pressure is a rather coarse approximation, it still provides useful insights into the processes driving alien species colonisation of new environments over broad spatial scales.

The biotic variables (native richness and body size) included in the model had a significant effect on site invasibility. However, it is important to stress the meaning of the two biotic predictors tested: species richness is a measure of community complexity, while body size is a proxy for the phenotype of single taxonomic groups. Our results suggest that both community structure and biotic features of taxa can be relevant in determining the probability of occurrence of alien species. Species richness identifies the capacity of the native community to reduce establishment probability; body size stresses the importance of a phenotypic character in determining the invasiveness of a specific taxon. Particularly relevant is the drastic decrease in alien species occurrence probability with increasing native species richness. This negative relationship supports the hypothesis that species richness of the receiving community negatively influences invasion patterns in aquatic habitats and may act as a buffer against invasibility (Elton 1958; Kennedy et al. 2002; Eisenhauer et al. 2013). We must note that in Boggero et al. (2014), native richness was positively correlated to alien species occurrence. This incongruence is possibly due to the difference in datasets between the two studies. We used a much larger dataset and aggregated the data at family level, while Boggero et al. (2014) used different taxonomic levels. We also explored the potential influence of random effects by excluding native species richness as random slope. The obtained pattern is congruent with the results we presented. Moreover, the inclusion of native richness as random slope in our model accounted for the very large variance (Appendix 3) in this parameter across different families, thus producing a significant increase in model fit.

Body size is important in many ways in both macroecology and eco-evolutionary dynamics, and may be a relevant trait in invasion biology (Kolar and Lodge 2001; Amalfitano et al. 2015). In our study, alien species were found across the whole range of body size values, from the smallest (i.e., Cyanobacteria and Rotifera) to the largest (i.e., fish) organisms. Body size emerged as an important variable in the models: the likelihood of finding an alien species increased if the invading species belonged to a taxonomic group with larger body size

(Figure 2). Within our dataset, most of the alien species were fish and other relatively large bodied taxa, whereas taxa with a smaller body size were less represented. Large taxa species are more likely to have been transported intentionally by humans because of their commercial value. Indeed, large taxa such as fish are heavily introduced for angling, and they are among the taxonomic groups showing the highest invasion rates at a global scale (Copp et al. 2005). Moreover, larger taxa are likely to occupy higher trophic levels (this could be particularly relevant for fish at the community level, see Persaud et al. 2011) and, in turn, this could favour alien species establishment because they may be less subject to predation by, and competition with, the native community. However, the effect of body size could also be at least partly explained by the difficulty in observing alien species in taxonomic groups with smaller size and high taxonomic uncertainties, and by the larger biogeographical ranges of very small species (Fontaneto 2011). The effect of alien species in the microbial world is not clearly understood and ecological facilitation could be more common than ecological damage in microbial communities (Horňák and Corno 2011; Mächler and Altermatt 2011; Amalfitano et al. 2015). Regardless of which processes are responsible for the effect of body size on invasiveness, the pattern is present and clear, with alien species occurrence positively correlated with body size.

We also show that the suitability of the abiotic features of a site is an important prerequisite for the successful establishment of alien species, although it has less importance than the previously described variables. Indeed, our models highlighted the potential filtering effect of abiotic constraints, regardless of the distance from a propagule source. In particular, the relationship between alien species occurrence and environmental variables suggested a lower invasibility for high elevation sites, distributed along the Apennines and the Alps, and for sites with low average annual rainfall concentrated in one season, typical of southern Italy. This could easily be explained by the fact that the low temperatures in mountain sites and the shortage of rainfall in southern Italy can act as limiting factors in the establishment of alien species poorly adapted to these harsh climates. In this context, climatic variables likely reflect that both alien and native species are constrained by environmental conditions and that certain conditions (e.g., low temperatures, arid climates) function as environmental filters that pose major physiological constraints that hamper the introduction and establishment of alien species without specific adaptations.

Conclusions

An important feature of our models was to simultaneously consider different taxa, multiple habitats and multiple putative drivers of alien species occurrence, providing a holistic picture of invasibility of freshwater habitats. We identified site-related features, showing that specific climatic conditions coupled with high site accessibility produced a relatively higher risk of invasibility. Moreover, the biological features of both the receiving community and the invading taxa act in synergy with abiotic drivers and propagule pressure. Our results also highlighted that strategies and priorities aiming to prevent alien species introduction and establishment need to consider all taxonomic groups, and not only the charismatic ones.

From the perspective of conservation and management of freshwater ecosystems, our analysis focusing on the probability of invasion provides a measure of the invasibility risk of a site. Through a more holistic view of the ecological complexity of sites and of their biodiversity, we provide evidence of areas potentially at risk of invasion along the Italian peninsula. This could be of help to managers in making decisions about where and on which systems to focus their attention to prevent alien species arrival.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Used dataset pruned from Boggero et al. (2016).

Appendix 2. Aggregated dataset used to build GLMMs.

Appendix 3. Description of the procedure for the preparation of the environmental and geographical variables.

Appendix 4. Test for the random effect term used in the GLMM.