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Plant invasion risk inside and outside protected areas: Propagule pressure, abiotic and biotic factors definitively matter

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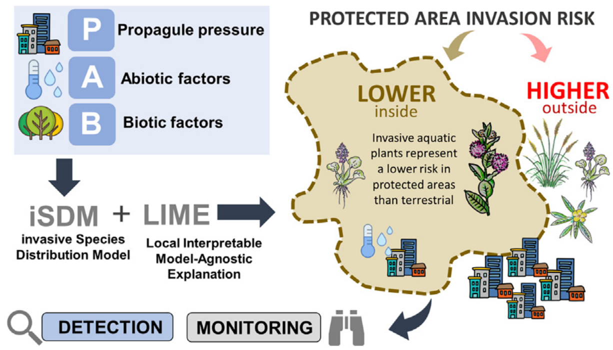
HIGHLIGHTS

- Plant invasions vary across realms, biogeographic regions and protection regimes.
- On a national scale invasion is promoted by abiotic factors and propagule pressure.
- On protected areas, low anthropic pressure and biotic filters, regulate invasions.
- Terrestrial plants represent a higher threat to protected areas than aquatic ones.
- Spatial modelling aid tailored management across spatial and administrative scales.

GRAPHICAL ABSTRACT



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ABSTRACT

Invasive alien species are among the main global drivers of biodiversity loss posing major challenges to nature conservation and to managers of protected areas.
The present study applied a methodological framework that combined invasive Species Distribution Models, based on propagule pressure, abiotic and biotic factors for 14 invasive alien plants of Union concern in Italy, with the local interpretable model-agnostic explanation analysis aiming to map, evaluate and analyse the risk of plant invasions across the country, inside and outside the network of protected areas.
Using a hierarchical invasive Species Distribution Model, we explored the combined effect of propagule pressure, abiotic and biotic factors on shaping invasive alien plant occurrence across three biogeographic regions (Alpine, Continental, and Mediterranean) and realms (terrestrial and aquatic) in Italy. We disentangled the role of propagule pressure, abiotic and biotic factors on invasive alien plant distribution and projected invasion risk maps. We compared the risk posed by invasive alien plants inside and outside protected areas.
Invasive alien plant distribution varied across biogeographic regions and realms and unevenly threatens protected areas. As an alien's occurrence and risk on a national scale are linked with abiotic factors followed by propagule pressure, their local distribution in protected areas is shaped by propagule pressure and biotic filters. The proposed modelling framework for the assessment of the risk posed by invasive alien plants across spatial scales and under different protection regimes represents an attempt to fill the gap between theory and practice in conservation planning helping to identify scale, site, and species-specific priorities of management, monitoring and control actions. Based on solid theory and on free geographic information, it has great potential for application to wider networks of protected areas in the world and to any invasive alien plant, aiding improved management strategies claimed by the environmental legislation and national and global strategies.

1. Introduction

Invasive alien species (IAS) are among the major drivers of global change and biodiversity loss, causing negative impacts on ecosystem services and functioning, impinging human health, and altering economic sustainability (IPBES, 2019; Stoett et al., 2019; Pyšek et al., 2020). Invasive species management is challenging (Early et al., 2016) and highly expensive, with costs that in some countries may reach hundreds of billions of euros per year (Pimentel et al., 2002; Diagne et al., 2021).

Biological invasions are globally addressed in a significant corpus of environmental legislation, national and global strategies (Meyerson et al., 2022) and technical documents or frameworks (e.g., United Nations Sustainable Development Goals, 2015; Global Biodiversity Framework CBD, 2021; EU's biodiversity strategy for 2030; Pergl et al., 2020; Wilson et al., 2020) and IAS management is a great challenge for managers of protected areas (Foxcroft et al., 2017). In the European Union a dedicated regulation "on the prevention and management of the introduction and spread of invasive alien species" (Regulation (EU) no. 1143/2014, hereafter, IAS Regulation) was adopted and came in force in 2015. The IAS Regulation identifies a list of invasive alien species of "Union concern" whose introduction or spread threaten or negatively impact biodiversity and ecosystem services and such adverse impacts require concerted actions at the European Union level (Regulation (EU) no. 1143/2014). The identification of invasive alien plants of Union concern follows a strict administrative and technical procedure that, besides documenting the species pressure on natural ecosystems, verifies their capability of establishing viable populations and spreading under current environmental conditions and in foreseeable climate change scenarios (Regulation (EU) no. 1143/2014).

Despite being regarded as primary assets for biodiversity conservation and as key barriers against the arrival, establishment, and spread of IAS (Gallardo et al., 2017), unfortunately, most protected areas worldwide are currently invaded by IAS, with negative impacts on natural habitats, ecosystem functions and biodiversity, and seriously threaten protected areas' core functions and roles (Foxcroft et al., 2017; Gallardo et al., 2017; Moodley et al., 2020). In the USA, for instance, alien plants affect eight million *ha* within national parks (Allen et al., 2009) and many park managers declared plant invasions as being of major concern (Moodley et al., 2020). In European protected areas, plant invasions are a worrying biodiversity threat (Genovesi and Monaco, 2014; Baquero et al., 2021; Moodley et al., 2022), second in importance after the fragmentation of habitats (Pyšek et al., 2013).

As generally agreed, one effective way for dealing with IAS is preventing their introduction and establishment and being prepared for early warning/early detection and rapid intervention (Leung et al., 2002; Holcombe et al., 2010; Srivastava et al., 2019; Pyšek et al., 2020). To effectively apply these proactive management techniques, invasive alien species distribution models (iSDMs) are among one of the available key tools (Srivastava et al., 2019; Reaser et al., 2020). Such models, depicting the statistical relationship between invasive species occurrence (e.g., presence/absence data) and the invaded range characteristics (environmental and other spatial variables), can be used to evaluate the risk of establishment and spread of alien species into non-native regions, offering, for example, sound bases for monitoring campaigns in areas susceptible to invasion under current environmental conditions and future global change scenarios (Thuiller et al., 2005, 2008; Bellard et al., 2018; Barral, 2019). Furthermore, iSDMs allow to identify areas where invasions may occur and the magnitude of spread (as a proxy of invasiveness; Elith and Leathwick, 2009), which in turn can support conservation decision-makers in defining several types of IAS management actions. To date, several studies have adopted model-based methodologies for dealing with invasive alien plants in the European Union protected areas (Dimitrakopoulos et al., 2017; Foxcroft et al., 2017; Moustakas et al., 2018; Moustakas and Katsanevakis, 2018). However, in Italy few of them have been deployed (e.g., Bazzichetto et al., 2018a, 2018b). As a consequence, further efforts aimed at bridging theory and practice in the application of iSDMs for conservation issues in the network of protected areas on a national scale in Italy are certainly needed.

In order to reduce such gaps of knowledge and tackle the lack in the availability of early warning tools required by the IAS Regulation, we created iSDMs for 14 invasive alien plants of Union concern occurring in Italy (hereafter invasive alien plants). Original occurrence data were collected during an intensive field work campaign by a national taskforce of botanists of the Italian Botanical Society. A set of variables (e.g., driving forces) referable to the PAB (propagule pressure, abiotic and biotic factors) invasion hypotheses (sensu Catford et al., 2009) were used to generate two classes of iSDMs, respectively for terrestrial and aquatic invasive alien plants (Yalcin and Leroux, 2017). We specifically explored the role of propagule pressure, abiotic and biotic factors on the occurrence of invasive alien plants in Italy, modelled their distribution, and evaluated in which way they threaten protected areas.

We assumed that the probability of invasion by alien plants is not homogeneous but varies across biogeographical regions and realms and that the protection regime does matter in shaping invasion risk. We hypothesized that propagule pressure, abiotic and biotic factors as well as protection regime play specific roles in facilitating or preventing plant invasions. By linking invasive alien plant occurrence probabilities with PAB drivers and by connecting invasion risk with the protection regime, we offer new scientific support for improving management policies and for tailoring monitoring and control actions across different spatial scales, management conditions and scenarios of global change.

2. Material and methods

2.1. Study area and invasive alien plants of union concern

The study focused on 14 invasive alien plants of Union Concern currently established in Italy (302,068 km^2), and for which detailed information and occurrence records were available. These invasive alien plants are widely distributed in the country across its three biogeographical regions: Alpine, Continental, and Mediterranean (as defined by the map from the European Environment Agency, available at http://www.eea.europa.eu/). The Alpine region covers the Italian Alpine range and comparatively small areas in central Italy within the Apennines, for a total surface of approximately 52,000 km^2 (Bragazza, 2009), the Continental region covers around 88,000 km^2, and the Mediterranean one covers around 162,000 km^2, including the two largest Italian islands, i.e., Sicily (25,700 km^2) and Sardinia (24,100 km^2).

The 14 investigated invasive alien plants (scientific names are here reported exactly as in the Reg. no. 1143/2014) are 6 terrestrial species [*Asclepias syriaca* L.; *Baccharis halimifolia* L.; *Heracleum mantegazzianum* Sommier & Levier; *Impatiens glandulifera* Royle; *Pennisetum setaceum* (Forssk.) Chiov. − now accepted as *Cenchrus setaceus* (Forssk.) Morrone − and *Pueraria lobata* (Willd.) Ohwi], and 8 aquatic species [*Alternanthera philoxeroides* (Mart.) Griseb.; *Eichhornia crassipes* (Mart.) Solms − now accepted as *Pontederia crassipes* Mart.; *Elodea nuttallii* (Planch.) H.St.John); *Hydrocotyle ranunculoides* L.f.; *Lagarosiphon major* (Ridl.) Moss; *Ludwigia grandiflora* (Michx.) Greuter & Burdet − all records are currently referred to *L. grandiflora* subsp. *hexapetala* (Hook. & Arn.) G.L.Nesom & Kartesz, now considered as a distinct species, namely L. *hexapetala* (Hook. & Arn.) Zardini, H.Y.Gu & P.H.Raven; *Ludwigia peploides* (Kunth) P.H.Raven − in Italy, all records refer to *Ludwigia peploides* subsp. *montevidensis* (Spreng.) P.H.Raven − and *Myriophyllum aquaticum* (Vell.) Verdc.]. Each of these 14 invasive alien plants is established in at least one Italian administrative region (Galasso et al., 2018; Brundu et al., 2020).

2.2. Analytical framework

Since Italy includes just a portion of the global distribution ranges of the analyzed invasive alien plants, we structured iSDMs according to a hierarchical framework (Gallien et al., 2012), i.e., incorporating global predictions into regional scale models (Di Febbraro et al., 2018, 2019), as to avoid biased estimations of species niches (Raes, 2012). According to this framework, models were first calibrated on species occurrences at the global range scale and bioclimatic variables (i.e., global iSDMs). Then, we trained a second group of models at the Italian extent level (i.e., regional iSDMs), including predictions obtained from global iSDMs.

2.3. Data collection on invasive alien plants in Italy

Species occurrences for global iSDMs were retrieved from the Global Biodiversity Information Facility database (GBIF, available at: http://www.gbif.org, accessed in June 2021; the total number of geographic records used to create the models is reported in Table S1, in supplementary material). Records with insufficient spatial accuracy (≥ 5000 m radius), potential errors (duplicates of the same sample), and records that were outside of the coverage of the predictor layers (points occurring in the sea), were excluded, as well as records collected before 2000. As for regional iSDMs, detailed distribution data on the 14 selected invasive alien plants for Italy were collected by a dedicated taskforce of botanists within the Italian Botanical Society (Table S2). These experts collected distribution data using a standard template. All the records were carefully checked for accuracy before use. As a result, the number of georeferenced records available for this study was reduced to 25,860 for global iSDMs, with an average of 1989 records per species, and to 1081 for regional iSDMs, with an average of 77 records, of which: 576 in the Alpine region, 379 in the Continental and 126 in the Mediterranean.

2.4. Italian protected areas

The official list of protected areas in Italy includes 871 sites, of which >96 % are classified as terrestrial (Ministero dell'Ambiente e della Tutela del Territorio e del Mare, 2020). National protected areas cover a total surface of 64,100 km^2, which corresponds to 21 % of the Italian territory (D'Amen et al., 2011), and vary by their institution aims, reference regulation, and protection level. Moreover, 2314 Natura 2000 protected areas are recognised under the "Habitats" and "Birds" European Directives (Council Directive 92/43/EEC and Directive 2009/147/EC, respectively). The Natura 2000 protected area network in Italy covers about 58,200 km^2 (19 % of the Italian territory) and many of these sites are largely overlapping with other national protected areas (Sallustio et al., 2017). We searched the World Database on Protected Areas (https://www.protectedplanet.net, accessed in January 2021) to retrieve the GIS layers of the Italian protected areas belonging to IUCN categories I and II (i.e., nature reserves and national parks, respectively), and to Natura 2000 protected areas. In order to harmonise the spatial resolution of invasive alien plants occurrence and PAB predictors with the conservation network, we restricted the analysis to protected areas with an area > 1 km^2.

2.5. Global and regional environmental predictors for invasive terrestrial and aquatic plants

To calibrate global iSDMs, we relied on the 19 bioclimatic variables provided by the WorldClim database version 1.4 (https://www.worldclim.org;

Hijmans et al., 2005) and rasterised at a spatial resolution of ~10 km^2. This initial set was sub-selected by checking for multicollinearity, i.e., posing a variance inflation factor (VIF) < 5 (Zuur et al., 2010; usdm R package, Babak, 2017), retaining the following seven predictors: mean diurnal range (BIO2), temperature seasonality (BIO4), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO9), precipitation seasonality (BIO15), precipitation of warmest quarter (BIO18), precipitation of coldest quarter (BIO19).

For modelling terrestrial and aquatic invasive alien plants on a regional scale, we selected a set of predictors acting as proxy variables for propagule pressure, abiotic, and biotic factors (Table 1). The propagule pressure, i.e., the number of introduced propagules, is one of the most important factors explaining invasion success of a species (Lockwood et al., 2005; Malavasi et al., 2014; Bjarnason et al., 2017), while alien species establishment depends on the physical environment (abiotic; see e.g., Malavasi et al., 2018a, 2018b) and on the biological features of the recipient community (biotic; see e.g., Broennimann et al., 2012). As surrogates of propagule pressure, we adopted: a) the cover of artificial surfaces and urban areas (Carranza et al., 2010; Bazzichetto et al., 2018b; hereon urban built-up areas, from Tuanmu and Jetz, 2014 for terrestrial plant species and Domisch et al., 2015 for aquatic species); b) the distance from roads (Le Maitre, 2004; Drake et al., 2015; Bazzichetto et al., 2016; Bazzichetto et al., 2018a; Malavasi et al., 2018a, 2018b), and c) global urban and rural population count within the cells (McKinney, 2002; Gavier-Pizarro et al., 2010; Davis et al., 2016; Table 1). Urban built-up areas and urban/rural population present a dual role in providing new propagules from gardens and planting sites (e.g., Carranza et al., 2010; mostly invasive alien plants) and in creating disturbed and bare areas which are particularly prone to invasion (Bazzichetto et al., 2018b). Communication infrastructures are both important sources of propagules and can act as corridors favoring invasive alien plants dispersal (Le Maitre, 2004; Bjarnason et al., 2017).

As abiotic factors, we considered: a) slope; b) elevation; c) climatic variables; and d) the flow length (i.e., the sum of contributing grid cells for the entire sub-catchment; Table 1). Mean elevation was derived from the Shuttle Radar Topography Mission (SRTM) 90 m Digital Elevation Database (https://srtm.csi.cgiar.org/; Jarvis et al., 2008), and used to calculate also slope and flow length. Slope and elevation are good surrogates of water accumulation in the soil (MacMillan and Shary, 2009) affecting invasive alien plant settlement and growth as flow length summarizes water flow (i.e., hydrodynamic forces exerted on aquatic plants) (Bornette and Puijalon, 2011).

For modelling terrestrial and aquatic invasive alien plants on a regional scale climatic variables for terrestrial plants were retrieved from the WorldClim database (as for the global iSDMs), while for aquatic species, we collected freshwater-specific climate data from the Near-Global Environmental Information for Freshwater Ecosystems (Domisch et al., 2015). Domisch et al. (2015) for each grid cell along the hydrological network of

Table 1
Environmental predictors used in the iSDMs for the 14 invasive alien plants in Italy, as proxies of propagule pressure (P), abiotic (A), and biotic (B) factors (PAB framework), along with their detailed description and the data source. GLCC: a generalized land-cover class within nominal 1-km pixels based on the consensus land-cover dataset.

PAB factor	Predictor variable	Description of the predictor variable	Source of the predictor variable
Propagule pressure (P)	Road distance	Euclidean distance (m) from highways and primary roads	Italian National geodatabase (http://www.pcn.minambiente.it/mattm/servizi-di-scaricamento)
	Urban built-up areas	The extension (m) of artificial surfaces and associated areas (GLCC class 9)	Global 1-km Consensus Land Cover, originally at 30 arc-second resolution (~ 1 km2) Tuanmu and Jetz, 2014 (https://www.earthenv.org/landcover); Domisch et al., 2015 (http://www.earthenv.org/streams)
	Global urban population	Total urban population count per cell (N)	https://sedac.ciesin.columbia.edu/data/sets/browse?facets=data-type:raster&facets=theme:population
	Global rural population	Total rural population count per cell (N)	https://sedac.ciesin.columbia.edu/data/sets/browse?facets=data-type:raster&facets=theme:population
Abiotic (A)	Slope	Thematic layer (degrees) downloaded from SRTM 90 m DEM	Jarvis et al., 2008 (https://srtm.csi.cgiar.org/), Domisch et al., 2015 (http://www.earthenv.org/streams)
	Elevation	Thematic layer (m) downloaded from SRTM 90 m DEM	Jarvis et al., 2008 (https://srtm.csi.cgiar.org/), Domisch et al., 2015 (http://www.earthenv.org/streams)
	Flow length	Count of upstream stream grid cells	Domisch et al., 2015 (http://www.earthenv.org/streams)
	Temperature	For terrestrial plants: BIO3 (isothermality); BIO8 (mean temperature of wettest quarter); BIO9 (mean temperature of driest quarter). For aquatic plants: Hydro 2 (mean diurnal range); Hydro 4 (temperature seasonality); Hydro 8 (mean temperature of wettest quarter); Hydro 9 (mean temperature of driest quarter)	WorldClim version 1.4 climate data for 1970–2000 (https://www.worldclim.org; Hijmans et al., 2005), originally at 30 arc-second resolution (~ 1 km2). Domisch et al., 2015 (http://www.earthenv.org/streams)
	Precipitation	For terrestrial plants: BIO15 (precipitation seasonality); BIO18 (precipitation of warmest quarter); BIO19 (precipitation of coldest quarter). For aquatic plants: Hydro15 (precipitation seasonality); Hydro18 (precipitation of warmest quarter); Hydro19 (precipitation of coldest quarter)	WorldClim version 1.4 climate data for 1970–2000 (https://www.worldclim.org; Hijmans et al., 2005), originally at 30 arc-second resolution (~ 1 km2). Domisch et al., 2015 (http://www.earthenv.org/streams)
Biotic (B)	Evergreen broadleaf trees	Percentage of evergreen broadleaf trees (GLCC class 2)	Global 1-km Consensus Land Cover, originally at 30 arc-second resolution (~ 1 km2). Tuanmu and Jetz, 2014 (https://www.earthenv.org/landcover)
	Deciduous broadleaf trees	Percentage of deciduous broadleaf trees (GLCC class 3)	Global 1-km Consensus Land Cover, originally at 30 arc-second resolution (~ 1 km2). Tuanmu and Jetz, 2014 (https://www.earthenv.org/landcover)
	Mixed and other trees	Percentage of mixed and other trees (GLCC class 4)	Global 1-km Consensus Land Cover, originally at 30 arc-second resolution (~ 1 km2). Tuanmu and Jetz, 2014 (https://www.earthenv.org/landcover)
	Shrubs	Percentage of shrubs (GLCC class 5)	Global 1-km Consensus Land Cover, originally at 30 arc-second resolution (~ 1 km2). Tuanmu and Jetz, 2014 (https://www.earthenv.org/landcover)
	Herbaceous vegetation	Percentage of herbaceous vegetation (GLCC class 6)	Global 1-km Consensus Land Cover, originally at 30 arc-second resolution (~ 1 km2). Tuanmu and Jetz, 2014 (https://www.earthenv.org/landcover)
	Cultivated and managed vegetation	Percentage of cultivated and managed vegetation (GLCC class 7)	Global 1-km Consensus Land Cover, originally at 30 arc-second resolution (~ 1 km2). Tuanmu and Jetz, 2014 (https://www.earthenv.org/landcover)

the HydroSHEDS river layer (www.hydrosheds.org; Lehner and Grill, 2013; hereafter Hydro 1 to 19) report sub-catchment variables and summarise the upstream environment. For aquatic species, we also considered the flow length (derived from HydroSHEDS), a topography-based variable that is a good surrogate of the water movement (Bornette and Puijalon, 2011). To improve the information for aquatic ecosystems we collated to the above mentioned river network, the cells depicting lentic water bodies reported on the Global Lakes and Wetlands Cover database (Lehner and Döll, 2004). Climatic variables were considered as annual trends, seasonality and climatic stress which are key factors on regulating invasive alien plant distribution and their reproductive success (Pouteau et al., 2021).

Concerning the biotic factors for modelling terrestrial invasive alien plants, we used land–cover variables from the global dataset (Tuanmu and Jetz, 2014; hereon generalized land-cover classes GLCC), as a surrogate of species interactions (e.g., competition for light and water or facilitation synergies; Marzialetti et al., 2019; Lozano et al., 2020). For aquatic invasive alien plants, we extracted land cover data from a dedicated freshwater database (Domisch et al., 2015). For both terrestrial and aquatic land cover datasets, we gathered the percentage cover of the following six categories, which were used for all species: evergreen broadleaf trees, deciduous broadleaf trees, mixed/other trees, shrubs, herbaceous vegetation, and cultivated and managed vegetation.

All the PAB variables were reported at 1 × 1 km raster maps projected into WGS84 datum and the UTM 32 N projection system. In addition, as similarly done for global iSDMs, predictors were sub-selected according to collinearity (VIF < 5). After this check, we retained 19 variables for aquatic plants and 18 for terrestrial plants in the final regional models (Table 1).

2.6. Invasive alien species distribution models (iSDMs)

Both global and regional iSDMs were calibrated through an ensemble forecasting approach as developed in the R package "biomod2" (Thuiller et al., 2020). In both model sets, the following five algorithms were fitted: 1) Artificial Neural Networks (ANN); 2) Classification Tree Analysis (CTA); 3) Generalized Additive Models (GAM); 4) Generalized Linear Models (GLM); 5) Random Forest (RF). These algorithms have repeatedly been used in several studies on invasive alien species (see e.g., Daliakopoulos et al., 2017; De Castro et al., 2016). For each species and algorithm, model settings were optimally tuned as recommended in Breiner et al. (2018), selecting the best parameter configuration through 80–20 % bootstrap cross-validation scheme (see below; final settings for each species are reported in Table S3). For both global and regional iSDMs, a set of 10,000 background points was generated in an area encompassing all the Terrestrial Ecoregions of the World (Olson et al., 2001) where species records occurred (Barve et al., 2011). Since the occurrence records are often biased by oversampling in very intensively studied areas, we placed background points by mimicking the same spatial bias in occurrence data, i.e., according to the density of the occurrence data pooled among all the species (Chauvier et al., 2021), so that background points are more abundant where occurrence records are denser (Roy-Dufresne et al., 2019; Mondanaro et al., 2021).

As no independent data existed to evaluate the predictive performance of the models, each dataset was randomly split into 80 % for model training, and the remaining 20 % for model evaluation (Araújo and New, 2007). This split sampling was repeated ten times to account for the uncertainty associated with dataset partition (Thuiller et al., 2003). Model predictive performances were assessed by calculating the Area Under the Receiver-Operator Curve (AUC; Hanley and McNeil, 1982), the True Skill Statistic (TSS; Allouche et al., 2006), and the Continuous Boyce Index (CBI; Hirzel et al., 2006). Global iSDMs were averaged by calculating a committee averaging, which quantifies the percentage of agreement on the probability of species presence among various model projections (Thuiller et al., 2009). This outcome was then used to weight background points in regional iSDMs as described in Gallien et al. (2012). As for regional iSDMs, model averaging was performed by weighting the individual model projections by their AUC values and averaging the results (Marmion et al., 2009). The iSDMs for the 14 invasive alien plants were finally projected over Italian territory. In addition, we generated Multivariate Environmental Similarity Surfaces (MESS) for each species using the "dismo" R package (Hijmans et al., 2020), to identify areas where models extrapolated outside the environmental range of occurrence records (i.e., response variable estimation at unmeasured locations by extending a model to new places, see Elith et al., 2010).

2.7. Factors influencing invasive alien plants suitability inside and outside Italian protected areas

To assess if the current spatial configuration of the two main types of protected areas considered in the present study (i.e., national protected areas in the narrow sense, i.e., distinct from Natura 2000 protected area network) plays a role in shaping invasive alien plants habitat suitability in Italy, we set a randomization experiment similar to the one developed by Gallardo et al. (2017). For each invasive alien plant, we first calculated the difference between the mean values of habitat suitability inside and outside Italian protected areas, i.e., the observed values. Then, we assessed the statistical significance of these observed differences by randomly generating 999 alternative configurations of the same number of original protected areas (national protected areas and Natura 2000 protected areas), changing their geographic position but not their area. For each of these randomly generated configurations, we calculated the difference between the mean values of habitat suitability inside and outside of simulated protected areas, thus obtaining a random distribution of differences. If, for a given species, the observed difference fell above/below the density of 95 % of the simulated values, we then considered that difference as being lower/higher than expected by chance.

We further refined the outcome of the randomization experiment by inspecting which were the most influential, local factors that made protected areas significantly less suitable than the remaining landscape portions. For this purpose, we deployed the so-called "LIME" framework (Local Interpretable Model-agnostic Explanations; Ryo et al., 2021), specifically focusing on those species that exhibited a significantly lower suitability inside than outside the Italian protected areas. This post-hoc interpretation approach attempts to explain how a complex model (iSDMs, in our case) provides a certain prediction for a given area by fitting a simpler, "surrogate" model calibrated only in the local area of interest. Once the algorithm identifies the best surrogate model by assessing how good it mimics the more complex one, the most important predictors emerging in the simple model represent those that influence most of the predictions in the local area of interest (for further details, see Ryo et al., 2021). We applied this framework dividing the protected areas in three groups, according to their location in one of the three biogeographical regions of Italy (Alpine, Continental, and Mediterranean).

3. Results

3.1. Invasive alien species occurrence and distribution models (iSDMs)

According to our data collection, *Impatiens glandulifera* scored the highest number of occurrences (514) in Italy, followed by *Elodea nuttallii* (125). *Impatiens glandulifera* was the most widely spread invasive alien plant in the Alpine biogeographic region (432 records), *E. nuttallii* in the Continental region (103), and *Cenchrus setaceus* in the Mediterranean region (53) (Table S2).

Of the 1081 invasive alien plant records, 173 were inside protected areas. The number of occurrences was higher inside the Natura 2000 protected area network than inside the national protected areas. Some species such as *Impatiens glandulifera*, *Lagarosiphon major*, and *Ludwigia peploides* subsp. *montevidensis* had higher occurrences inside the protected areas (Table S4).

The regional iSDMs of the 14 invasive alien plants achieved good to excellent predictive performances sensu Swets (1988) and Landis and Koch (1977), with AUC > 0.8 (mean AUC = 0.93; SD = 0.03), TSS > 0.5 (mean TSS = 0.78; SD = 0.07), and CBI > 0.7 (mean CBI = 0.84; SD = 0.09; Table S5).

Impatiens glandulifera showed the highest suitability in the Alpine biogeographical region, followed by *Heracleum mantegazzianum* in the same bioregion, and by *Pontederia crassipes* in the Mediterranean (Table S6). We found that the Continental biogeographical region was particularly affected by *Asclepias syriaca* and *Elodea nuttallii*, and that was likely suitable for the establishment of both terrestrial and aquatic invasive alien plants (Table S6, Figs. S1 and S2). However, the overall potential distribution of the aquatic invasive alien plants (Figs. S2) mainly insists in the Mediterranean biogeographical region.

Among the most important predictors determining a high probability of invasion in Italy for aquatic and terrestrial invasive alien plants, we found the mean temperature of driest and wettest quarter, precipitation of warmest quarter, precipitation seasonality, elevation, and slope (Figs. S3 and S4).

According to the MESS index, there was evidence of some "novel" (i.e., non-analogue) environments occupied in Italy. For example, the environmental spaces occupied by *Alternanthera philloxeroides*, *Baccharis halimifolia, Cenchrus setaceus*, *Hydrocotyle ranunculoides,* and *Ludwigia hexapetala* include climatic conditions not available in their native range (non-analogue), evidencing that these species had colonised novel environmental conditions. Similar shifts were detected for *Elodea nuttallii*, *Lagarosiphon major*, *Myriophyllum aquaticum*, and *Pontederia crassipes,* though to a lesser extent. Furthermore, the MESS revealed the occurrence of extrapolation in most of the projection modelling area for *A. philoxeroides*, *B. halimifolia*, *H. ranunculoides*, and L. *peploides* subsp. *montevidensis*. Weakly negative MESS values occurred for most of the invasive alien plants (Figs. S5 and S6).

3.2. Invasion risk and PAB predictors in the Italian protected areas

The analysis of predicted invasive alien plants distribution (i.e., suitability) and, in particular, the density curves (Fig. 1) showed that six of the eight aquatic plants (*A. philoxeroides*, *E. nuttallii*, *L. major*, *L. peploides*, *M. aquaticum*, and *P. crassipes*) had significantly lower suitability values inside the national protected areas and, other than that, *A. philoxeroides* was the only one who had significantly lower suitability values also inside Natura 2000 protected areas.

Two of the six terrestrial plants (*A. syriaca*, and *C. setaceus*) had significantly lower suitability in both national and Natura 2000 protected areas, while *Pueraria lobata* showed significantly lower suitability in Natura 2000 sites. Only for *Heracleum mantegazzianum* significantly higher suitability values inside national protected areas were observed.

No significant differences inside and outside protected areas for the other four species (i.e., two aquatic and two terrestrial) were found (see Fig. 1).

Importantly, *I. glandulifera* did not show significant values, as the difference between inside and outside protected areas is almost equal to zero, which means that the probability of finding this alien species inside or outside protected areas is almost the same.

The overall cumulative suitability (i.e., predicted distribution) for the 14 selected invasive alien plants within the national protected areas and the Natura 2000 protected areas network is shown in Fig. 2. In national protected areas, high risk of invasion is mainly predicted on coastal landscape and sites with low elevation and close to urban settlements (e.g., in the UNESCO MAB Biosphere Reserve Cilento and Val de Diano, a 395 km^2 area in south-central Italy Tyrrhenian coast). Also, invasion risk inside protected areas is lower with respect to non-protected areas in relation with higher altitudes and distances from urban centers and roads (e.g., Gran Paradiso National Park, 703 km^2 are on western Alps ranging from 800 to 4061 m a.s.l; Filippa et al., 2022) underlying the differentiated incidence of propagule pressure and abiotic factors acting on areas with different protection regimes. The Natura 2000 network, conformed by numerous small widespread sites often close to urban centers or embedded on artificial contexts (e.g., Sughereta del Sasso at Rome, Mediterranean region), presented higher invasion risk than the national parks on both terrestrial and aquatic realms (e.g., Boschi del Ticino, Continental region).

Overall, a lower probability of occurrence of invasive alien plants was found inside protected areas compared to outside. Therefore, the LIME framework (Local Interpretable Model-agnostic Explanations) was performed for the invasive alien plants inside national protected areas (see Figs. 3 and 4) and inside Natura 2000 protected area network (see Figs. S7 and S8) with a significant difference in suitability ($p < 0.05$, see Fig. 1) between inside-outside protected areas in Italy.

LIME analysis clustered propagule pressure, abiotic and biotic factors into groups and explained invasive alien plants presence and suitability within the protected areas. However, the results did not show consistent differences between the three Italian biogeographical regions. The variables that most influenced the presence of terrestrial invasive alien plants within protected areas were the mean temperature of driest quarter, the slope, urban built-up, urban population, and rainfall seasonality (Fig. 3), whilst for the aquatic invasive alien plants we found a high influence of the elevation, but exclusively in the Alpine and Continental biogeographical regions. However, the other predictors showed a similar trend in the three biogeographical regions without major differences (Fig. 4).

The framework results showed that *C. setaceus,* in the Mediterranean region, is highly influenced by coverage of mixed trees but is not affected by mean temperature of driest quarter as in the Alpine and Continental regions. These results also evidenced a preference of *A. syriaca* for urbanized areas, close to roads, with low to medium slopes and low moisture accumulation (Fig. 3). Another finding was the general relation among the proximity to road networks and urbanized areas and invasive alien plants distribution inside the protected areas (Figs. 3 and 4).

The framework analysis applied to the aquatic invasive alien plants (Fig. 4) showed a preference for altitudes of ca. 300 m a.s.l. in the case of *A. philoxeroides* and of ca. 800 m a.s.l. for *E. nuttallii*, and L. *major* on both Alpine and Continental regions. On the other hand, in the Mediterranean biogeographic region of Italy, *P. crassipes,* a very well-known global invasive and widespread species, is positively affected by the surrounding urban population.

4. Discussion

Overall, the methodology applied in the present study - integrating propagule pressure, abiotic and biotic factors into iSDMs - delivered invasion risk models for 14 terrestrial and aquatic invasive alien plants (of Union concern) in Italy, across three biogeographical regions, and their suitability inside and outside protected areas, increasing our knowledge on both the distribution of invasive alien plants in the entire country and on the factors promoting or limiting plant invasions inside and outside protected areas. National risk models can inform managers of protected areas and help them to identify effective management measures and to support surveillance and monitoring strategies at different geographic scales and administrative levels.

As documented by previous studies on a global scale (e.g., Gallardo et al., 2015; Foxcroft et al., 2017), also regionally, in Italy, the occurrence of invasive alien plant species in protected areas can be explained by propagule pressure, abiotic and biotic (PAB) factors (e.g., human population density, climatic conditions, land degradation/naturalness) and protection regime (see also Genovesi and Monaco (2013) and Moustakas et al. (2018)).

4.1. Invasion risk in the three biogeographical regions of Italy

The invasion risk of the 14 invasive alien plants varied across realms (e.g., terrestrial and aquatic) and biogeographical regions. Aquatic ecosystems presented a higher invasion risk in Continental and Mediterranean bioregions while terrestrial ones resulted highly susceptible to invasions across all biogeographical regions.

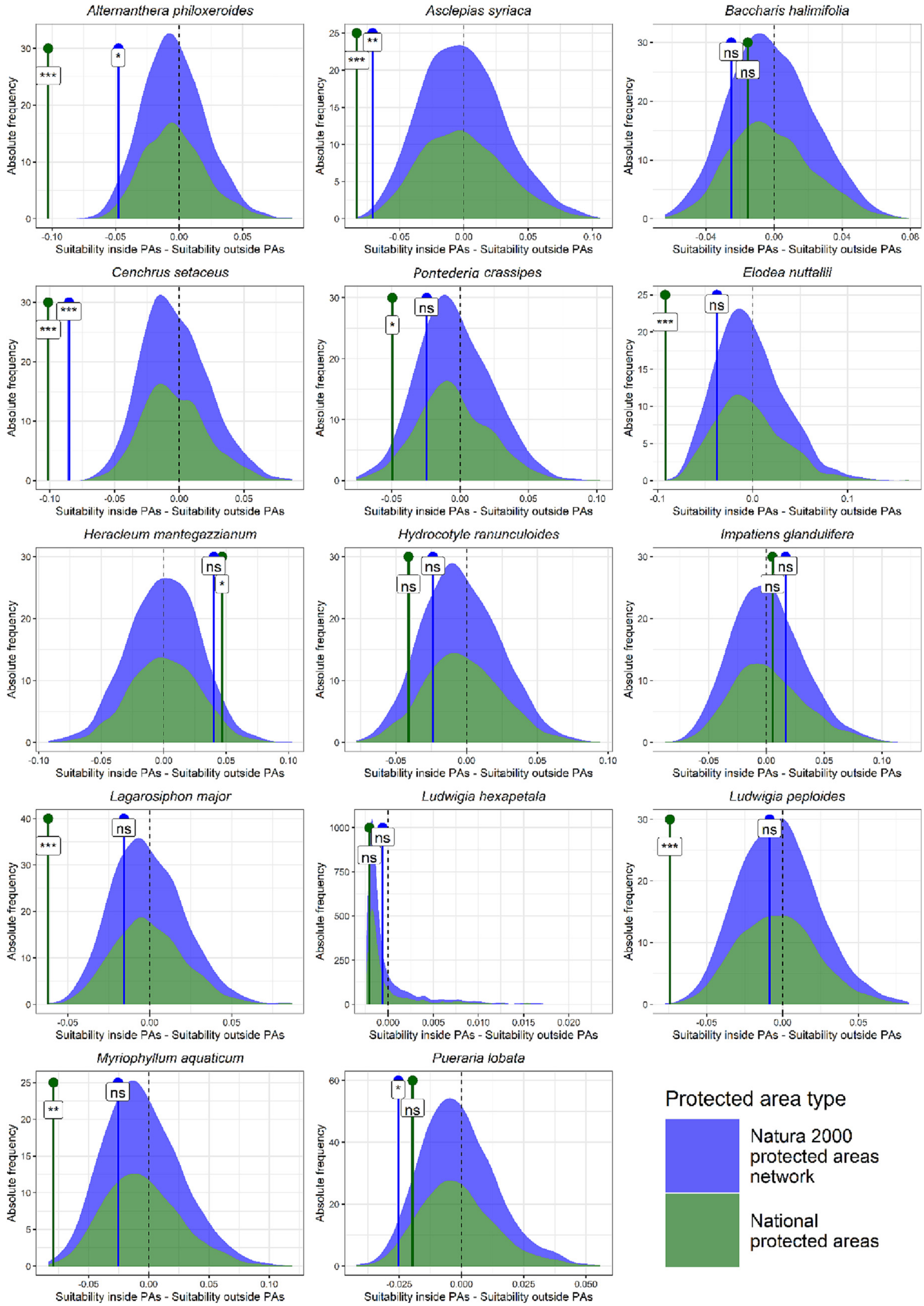

Fig. 1. Density curves of predicted invasive alien plant distributions inside and outside the two main types of protected areas (Natura 2000 protected area network, blue; national protected areas, green), along with the 95 % confidence intervals (CI, shaded areas).

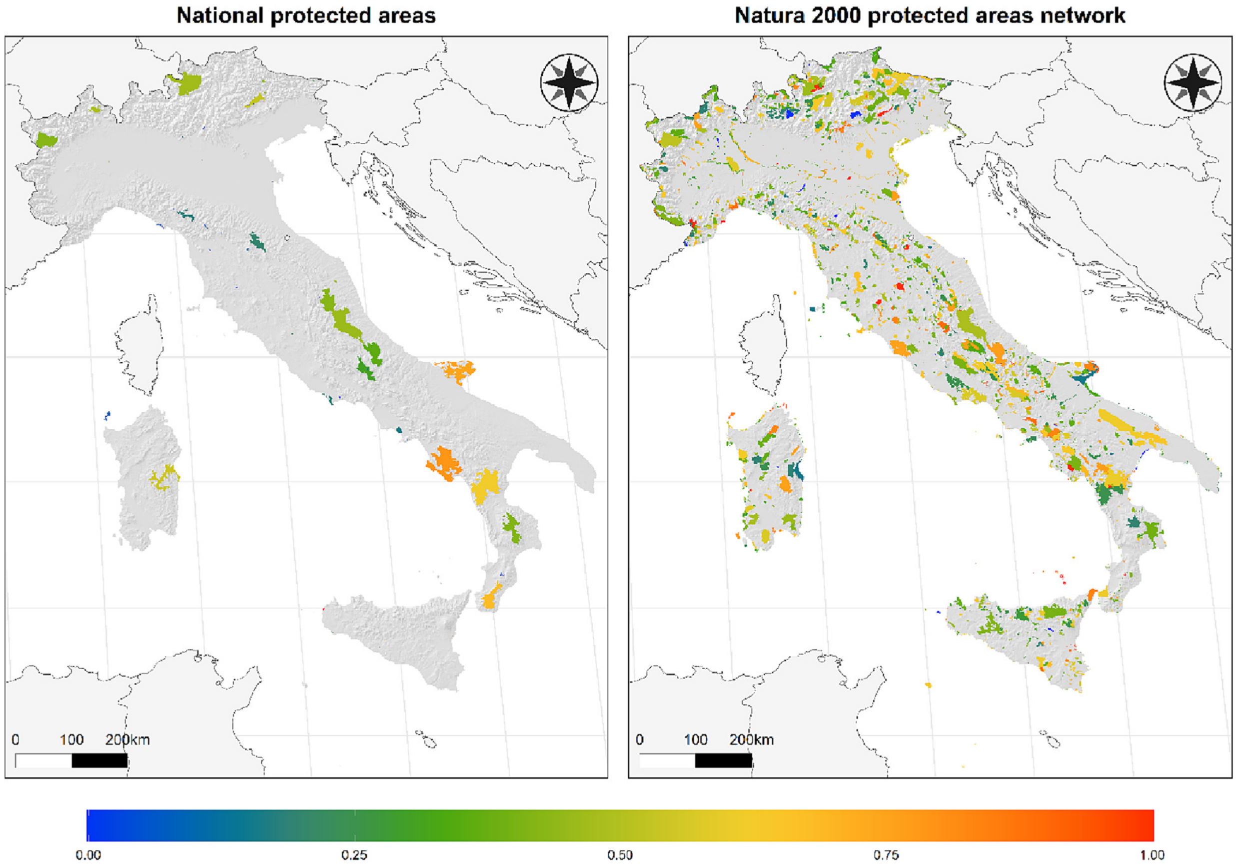

Fig. 2. Invasion risk map across the national protected areas (left) and the Natura 2000 protected areas network (right) in Italy, based on the ensemble modelling for the selected 14 invasive alien plants of Union concern. Colors ranging from red (high invasion risk) to dark blue (low invasion risk) represent the cumulative probability of occurrence for all species.

The high invasion risk on terrestrial ecosystems of the Continental and Mediterranean biogeographical regions for most of the analyzed species may be fueled by intense human pressure (e.g., tourism settlements in coastal areas, agriculture in lowland and close to riparian habitats; Hulme et al., 2008; Bjarnason et al., 2017; Di Gristina et al., 2021; Spampinato et al., 2022), natural disturbances such as wildfires (Stinca and Motti, 2017) and in some cases by the occurrence of unsaturated communities with weakly competitive native species (Hulme, 2004). Furthermore, the subtropical regions of the world provided the Mediterranean region with several invasive species (e.g., *Baccharis halimifolia, Cenchrus setaceus*) and some of them became very widespread in Italy, probably because they are well adapted to regional environmental conditions, or tolerate well summer droughts and fires as in the specific case of *Cenchrus setaceus* (Adkins et al., 2011; Esler et al., 2018).

The presence with low invasion risk of common terrestrial invasive alien plants (e.g., *A. syriaca* and *P. lobata*) in the Italian Alpine biogeographical region might suggest that mountains are threatened by invasive species already present on lower altitudes (e.g., Schmeller et al., 2022 and articles cited therein) which gradually colonize and adapt to alpine environmental conditions (e.g., by phenotypic plasticity or genotypic differentiation) more than by the arrival of pre-adapted species (see also Alexander et al., 2011). Importantly, *Pueraria lobata* (kudzu-vine), could further expand its distribution in Italy following climates resembling its native range (Asia-Pacific) as in the case of Alpine valleys at the border with Switzerland and Northwestern Alps (see Montagnani et al., 2022) and could also expand, as already occurred in North America, into climatically novel areas (Callen and Miller, 2015).

The eight studied aquatic invasive alien plants mainly persist on the Continental and Mediterranean biogeographic regions, and this may be partially due to the presence of highly populated areas affecting the major river basins, to the topography, and to mild environmental conditions. In fact, despite the efforts made in the last century to counteract the nutrient enrichment from diffuse and point-sources, the excess of nitrogen and phosphorous is among the main causes of degradation of European rivers, including in Italy (Erba et al., 2022). For instance, the high risk in the Po River and its catchment may be related to intense anthropogenic activities in the agricultural sector and inland urban centers (Buldrini et al., 2022). Furthermore, *Myriophyllum aquaticum* and *Ludwigia* sp. pl. are expected to expand their invasive range in Europe in response to climate change, as showed by Gillard et al. (2017), and this expansion may be expected in Italy as well.

4.2. PAB framework and invasion risk in Italy

By coupling propagule pressure, abiotic, and biotic factors and alien species occurrence within iSDMs we successfully identified the role of environmental and anthropic factors in determining invasive alien plant invasion risk. In fact, abiotic factors, in particular climatic, such as mean temperature of driest and wettest quarter, precipitation of warmest quarter, precipitation seasonality, and geomorphological ones (e.g., elevation, and slope) resulted in being the most important drivers for invasion risk in Italy. For instance, *C. setaceus* and *B. halimifolia* resulted more common and abundant in the Mediterranean region which is characterized by summer drought that facilitates the establishment of species tolerant to aridity stress (similar results were showed also by Albuquerque et al., 2020 for *C. setaceus*). On the other hand, there is evidence that global warming may favour the shift towards higher altitudes of invasive alien species (e.g., Tasser et al., 2017) as in the case of *H. mantegazzianum* in the Italian Alpine region. At the same time, cold stress which is an important factor shaping invasive alien species distribution (Lozano, 2021; Pouteau

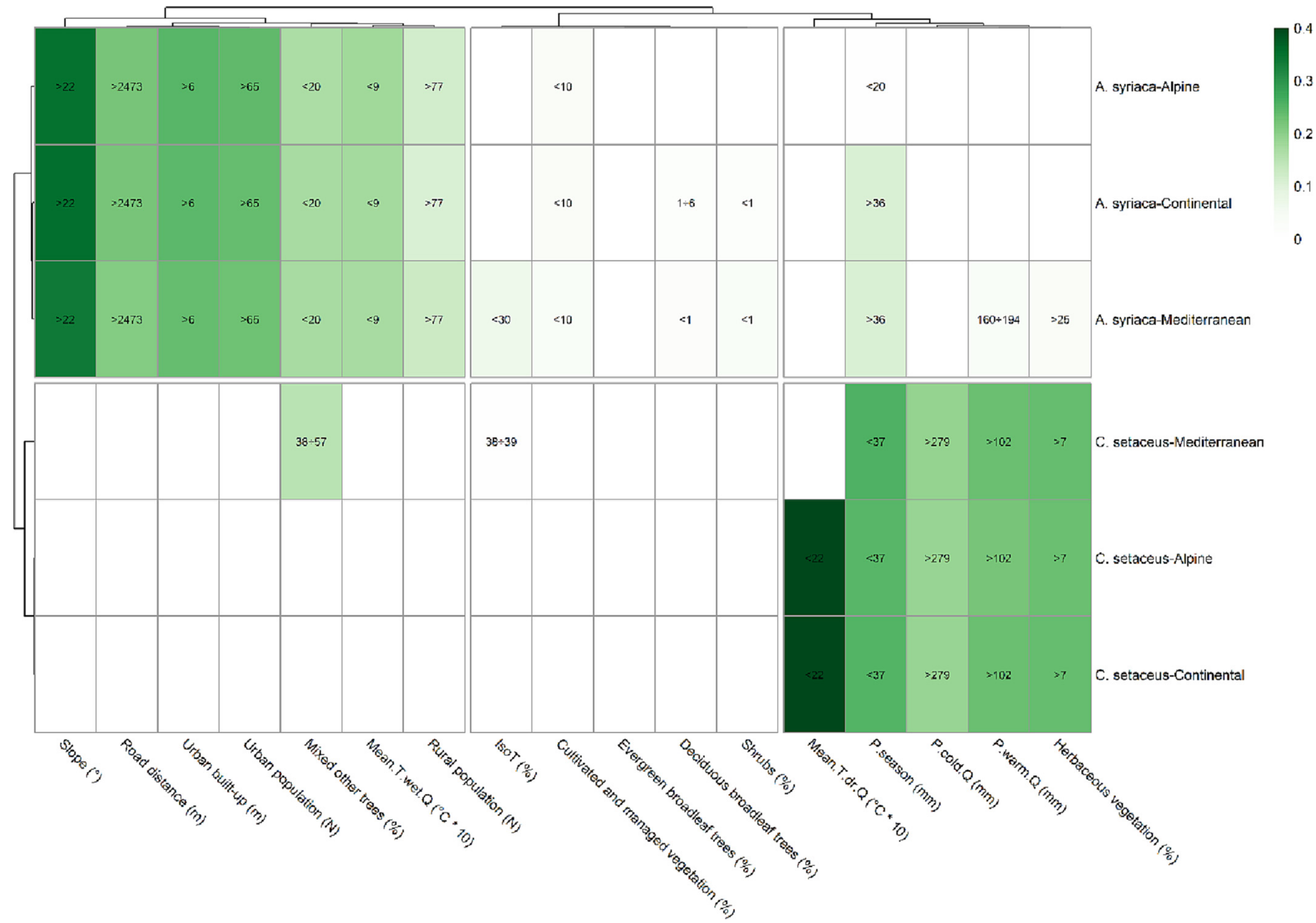

Fig. 3. Local Interpretable Model-Agnostic Explanation (LIME) analysis, showing the propagule pressure, abiotic and biotic predictors related to terrestrial invasive alien plants occurrence inside national protected areas across the different biogeographic regions (Mediterranean, Alpine, Continental). The analysis was performed only for terrestrial invasive alien plants with significant differences in suitability values between inside and outside national protected areas ($p < 0.05$, see Fig. 1). Colour intensity indicates variable importance from light green (0: low) to dark green (0.4: high). Absolute variable values are reported inside each cell. For description of variables see Table 1.

et al., 2021) partially explains why alpine landscapes in Italy hosted fewer invasive alien plants in comparison to Mediterranean and Continental regions.

In the Italian water ecosystems, as previously observed throughout the world (Gallardo et al., 2015; Bellard et al., 2016), climatic seasonality as well as mean annual values of temperature or precipitation resulted as good predictors of the distributions of invasive alien plants. For instance, Mediterranean temporary ponds and small streams potentially provide suitable habitat for invasive species such as *P. crassipes* (Brundu, 2013). In these habitats, the rapid expansion of alien macrophytes is generally related to the low or absent competition with native aquatic plant species and the water quality which is altered by human activities (Brundu et al., 2012).

In the Mediterranean region, the predicted drier and warmer conditions (Lionello et al., 2014) may have different effects on invasive alien plants, reducing for instance the invasion risk of aquatic species on lakes and ponds and increasing it on irrigation channels and other human infrastructures for storing and transporting water, constructed for keeping agricultural lands productive (e.g., Fraga et al., 2020). Furthermore, the invasion risk of several invasive alien plants, weakly adapted to cold stress (e.g., coming from tropical/sub-tropical areas; Alexander et al., 2016), will be reshaped in the forecasted scenarios with harsher climatic conditions (e.g., as *M. aquaticum*; Gillard et al., 2017; Lozano, 2021).

However, MESS analysis revealed that the extrapolation, due to the combination of propagule pressure, abiotic and biotic factors, may be affected by slight overestimation. Our research identified wide vacant areas in Italy susceptible to be invaded where invasion has not already taken place, probably due to stochastic factors, the date of introduction of the invasive alien species (Gillard et al., 2017), and the presence of dispersal barriers. Our results suggested that several invasive alien plants are still spreading (Alexander and Edwards, 2010), calling for monitoring campaigns in uninvaded areas and for preventing their spread and establishment in new areas.

4.3. Invasion risk in the Italian protected areas

The main driver of invasive alien plant distribution, in both national protected areas and Natura 2000 protected areas, was propagule pressure (e.g., urban built-up) followed by abiotic factors (e.g., slope, and temperature) and such influence varied across the different biogeographical regions and realms (as in Wan et al., 2021). Propagule pressure has already been described in literature as an important local driver of alien species invasions in protected areas (e.g., Meyerson and Pyšek, 2013; Pyšek et al., 2013; Ribeiro et al., 2019). Terrestrial invasive alien plants distribution is also influenced by climatic seasonality (e.g., the mean temperature of driest quarter). In this context climate change would promote an expansion of invasive alien plants in most protected areas (Wan et al., 2021). On the other hand, the distribution of aquatic invasive alien plants in the national protected areas is mainly influenced by elevation that, related to microclimatic variability, may restrict invasive alien plant occurrence (see Pauchard and Alaback, 2004).

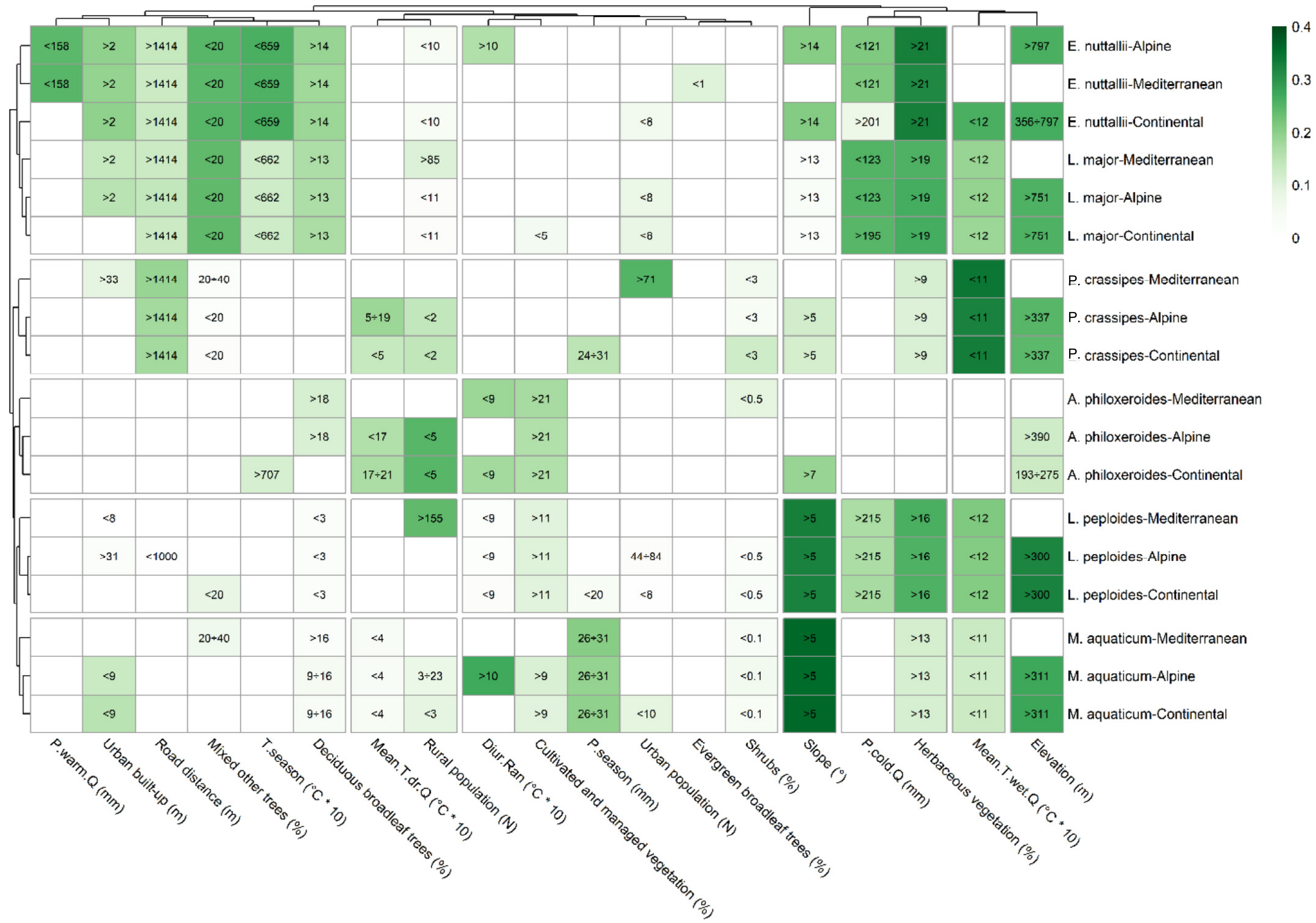

Fig. 4. Local Interpretable Model-Agnostic Explanation (LIME) analysis, showing the propagule pressure, abiotic and biotic predictors related to aquatic invasive alien plants occurrence inside national protected areas across the different biogeographic regions (Mediterranean, Alpine, and Continental). The analysis was performed only for aquatic invasive alien plants presenting significant difference in suitability values between inside and outside national protected areas (p value <0.05, see Fig. 1). Colour intensity indicates variable importance from light green (0: low) to dark green (0.4: high). Absolute variable values are reported inside each cell. For description of variables see Table 1.

Concerning the function of biotic factors on shaping terrestrial alien species distribution in protected areas, our results confirmed the role of semi-natural land cover classes on curtailing plant invasions (Bazzichetto et al., 2018a, 2018b; Carranza et al., 2010). Furthermore, as suggested by other researches, the most important biotic factors locally regulating alien plants occurrence and abundance are the coverage of natural vegetation and the level of habitat fragmentation (Malavasi et al., 2014; Malavasi et al., 2018b).

The lower probability of occurrence of invasive alien plants inside the Italian protected areas may be partially related to the low accessibility of a number of national parks, often placed on remote locations, far from densely populated urban centers and above 600 m a.s.l. (Romano et al., 2021, e.g., in the case of the Gran Paradiso National Park, in the western Italian Alps). However, such a general trend varies between National protected areas, mainly restricted to remote mountain regions and Natura 2000 sites which are widespread in lowlands, coastal landscape with intensive agricultural areas (Romano et al., 2021) and close to large urban settlements (Concepción, 2021). Our results also highlighted a particularly low risk of aquatic plants invasion in protected areas, coupled with modest propagule pressure, geomorphological factors impeding alien spread and moderate-low anthropic pressure (see also Moustakas et al., 2018).

The LIME analysis on terrestrial invasive alien plants, with significant differences in suitability values between inside and outside protected areas, gives evidence that the occurrence of several terrestrial invasive alien species, such as *C. setaceus*, is influenced by the combination of abiotic (e.g., temperature of driest quarter and seasonal precipitation) and biotic filters (e.g., low coverage of mixed trees). *Cenchrus setaceus* is native to North Africa and the Middle East and grows primarily in the seasonally dry tropical biome. According to our results, also in the invaded range, *C. setaceus* thrives in warm and arid climatic conditions. On the other hand, *A. syriaca* occurrence is related to propagule pressure (e.g., urbanized areas) and as in the case of several aliens, it is facilitated by the proximity to roads (Malavasi et al., 2018a, 2018b; Follak et al., 2018; Lozano et al., 2020).

Concerning aquatic species, the analysis evidenced a relationship between invasive alien plants and the protected area's altitude. For instance, the presence of stable populations of *M. aquaticum* above 300 m a.s.l. may be related to its native range on South American mountain areas (Hussner et al., 2009). In accordance with previous research, *P. crassipes* preferentially grows on protected areas with wetter conditions, (Cordeiro et al., 2020) avoiding the low temperatures (e.g., related with high altitudes). *Pontederia crassipes* is one of the most widespread and invasive alien species worldwide and its occurrence is known to be highly aided by propagule pressure (e.g., Cordeiro et al., 2020). As a result, several sites of conservation concern and designated within the intergovernmental Ramsar Convention on Wetlands (e.g., in Tuscany, Italy) are at high invasion risk due to their proximity to urban areas and human infrastructures, and our results confirmed the role of cities in intensifying propagule pressure and indirectly affecting water bodies. Results obtained by other authors (e.g., Gallardo et al., 2015) are in accordance with our findings, indicating that some proxies of propagule pressure (e.g., population density, road proximity and urbanization) amplify the potential for invasion.

4.4. Prioritization and management of invasive alien plants

Our results highlighted a clear relationship among propagule pressure, abiotic and biotic factors and invasion risk inside Italian protected areas. In addition, they showed the importance of accounting for the biogeographic region (i.e., Alpine, Continental, and Mediterranean), the realm (aquatic and terrestrial) and the protection regime, i.e., the difference in invasion risk inside and outside protected areas (see also Foxcroft et al., 2017; Ziller et al., 2020).

The 14 investigated invasive alien plants are already established in Italy and some of them are quite widespread, requiring long-term persistent controls (Brundu et al., 2020). However, our results can support priority-setting, suggesting that the always limited available resource for IAS management should be preferentially addressed to tackle invasive alien plants in the Mediterranean and Continental bioregions. Furthermore, considering that climate change scenarios predict an increment of two factors that at present limit invasive alien plants altitudinal spread (e.g., temperatures and precipitations, e.g., Pérez et al., 2022), an expansion in Alpine region could be also expected and should be prevented.

The most important factors shaping invasive alien plants occurrence inside Italian protected areas are propagule pressure and abiotic filters, and such information is crucial to define adequate strategies for prevention and monitoring of uninvaded areas.

As demonstrated by previous studies (e.g., Colautti et al., 2006; Carranza et al., 2010), invasive alien plant occurrence inside Italian protected areas is fueled by urban areas providing propagules (e.g. gardens and urban green areas) and by infrastructures (see also Malavasi et al., 2018a, 2018b) assuring dispersal corridors for alien species that move from disturbed landscapes to natural ones included in protected areas.

The managers of protected areas should pay particular attention to the presence of communication infrastructures as well as to the local landscape which may have crucial roles in promoting or preventing plant invasions. The staff of protected areas should conduct periodical field surveys in particular on areas with high/medium invasion risk to record the presence of alien species and their invasion stage. Furthermore, protected area managers, by integrating invasion risk maps with the distribution of threatened or endemic species, should better identify conservation priorities (e.g., Ziller et al., 2020; El-Barougy et al., 2021).

5. Conclusions

The adopted modelling framework, based on the statistical relation among alien plant occurrence and environmental characteristics, effectively modelled invasion risk in Italy for terrestrial and aquatic alien plants, across biogeographical regions and protection regimes and it is important in several ways.

The improved understanding of invasion processes and their interplay with environmental drivers at different scales may help to define priorities of intervention tailored for each site (e.g., biogeographical region or protected areas), accounting of distinct invasion drivers (PAB factors) and species features (e.g., which invasive alien plants should be tackled first). For instance, in Italy, invasion risk inside protected areas is lower than outside and such a trend is particularly evident on national parks often placed on remote mountain areas far from populated urban centers. On the other hand, protected areas placed on lowlands and coastal zones embedded in agricultural lands and urbanized areas (e.g., several Natura 2000 sites) resulted threatened by alien plants, the most important local factors aiding invasion processes being propagule pressure and abiotic features. Knowing which ecosystems and protected areas are at high invasion risk help decision makers to prioritize cost effective surveillance and early detection strategies as well as to plan dedicated monitoring activities.

The adopted national scale of analysis, allowed to build a sound information frame useful to support specific management strategies and tailored conservation actions at different levels ranging from the single protected area to a group of areas or the entire network of Parks and Natura 2000 sites. National risk models and the comprehensive view of invasion processes in the entire network of protected areas and on its surrounding landscape can inform and help managers to identify effective conservation measures aimed at contrasting the negative impacts of alien plants on natural habitats, ecosystem functions and biodiversity.

The proposed approach is based on free geographic information, so similar procedures can be extended to wider networks of protected areas in the world and to any invasive alien plant (not included in the Reg. no. 1143/2104 Union list), aiding improved management strategies and action plans. This is particularly important because a conservation strategy across countries and regions claimed by international regulations requires a common approach in which the ecological theory and the alien species management practice converge towards shared goals.

CRediT authorship contribution statement

VL, MF, MLC, GBr: conceptualization, methodology, data processing, writing – original draft, writing – review and editing; MLC, GBr: supervision; VL, MF: formal analysis; AA, NMGA, EB, GBed, LCG, KC, AC, GD, SF, GF, BF, MI, LLas, LLaz, AM, FM, CH, CMM, SO, SP, LPe, LPo, CP, FP, AR, LR, ASan, ASel, GS, ASti, GV, MV, CS: data curation, writing – review and editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162993.

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