Invasion trends of aquatic Ludwigia hexapetala and L. peploides subsp montevidensis (Onagraceae) in Italy based on herbarium records and global datasets

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Research Article

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Abstract

Identifying areas susceptible to invasion by an alien species is a strategy of prevention. We used national herbaria and global databases to assess the invasion trends of the two aquatic invasive species *Ludwigia hexapetala* and *Ludwigia peploides*subsp. *montevidensis* in Italy. We defined the invasion status with invasions curves and predicted potentially suitable areas with Species Distribution Models based on WorldClim variables and the human footprint index. Low seasonal variation in temperature and precipitation, temperature ≥ 20 °C in the warmest, driest and wettest periods of the year and precipitation in the coldest period are the bioclimatic factors that most account for the potential distribution of the two species. The human footprint has lower relative importance than bioclimatic variables. All Italian peninsula appears as a suitable bioclimatic environment for the invasion of the two *Ludwigia* species, except the Alps and the highest peaks in the Apennine. Based on the current distribution of the species in Italy and the mostly densely invaded areas globally, the agricultural land surrounding the current invaded areas and along the Italian coasts is the most vulnerable to the invasion. Considering the trend of the invasion curves, which have been sharply rising for the latest decades, there are reasons to expect that the alien *Ludwigia* species will continue their expansion, if no timely and effective actions are taken. Informative campaigns, accurate monitoring and prompt management are fundamental preventive tools in areas predicted as vulnerable to invasion by this study.

Introduction

Invasive alien species (hereafter IAS) are considered as one of the major threats to the conservation of biodiversity, natural and agricultural ecosystems and the related ecosystem services they offer (McNeely et al. 2001; Pyšek et al. 2020). The number of IAS is predicted to increase in every continent from 2005 to 2050 and, among taxa, the accumulation of introduced taxa is fastest for vascular plants, especially in North America and Europe (Seebens et al. 2021). The major drivers of IAS introduction are trade and transport, climate change, biodiversity loss, land-use change and human migrations and these factors are predicted to intensify in the future as well, increasing the invasion likelihood even further (Seebens et al. 2021). Aquatic habitats are the most vulnerable to invasions (Zedler and Kercher 2010; Brundu 2015) and the habitats that have been altered most by invasions (Bolpagni 2021). The «exocene» *sensu* Bolpagni (2021) is the dawn of a new epoch for freshwater ecosystems, characterised by the dominance of invasive plants, impaired ecosystem functioning and unknown evolution. In this scenario, prevention is the most effective and cost-efficient strategy for the conservative management and protection of ecosystems from invasions. Monitoring and early recording of IAS are the basis for prevention as well as for studying and learning from ongoing invasions. Records of alien plant species provided by herbaria and other global online databases (e.g. GBIF, iNaturalist) are extremely valuable to reconstruct biodiversity changes occurred in the past and the invasion history of IAS. For instance, invasion curves, i.e. the cumulative number of occurrence records of a species over time, can accurately give insight into temporal and spatial dynamics of specific IAS (Ceschin et al. 2018; Buldrini et al. 2022) or enlarged taxonomic groups (Seebens et al. 2021) and inform on the status of the invasion (i.e. whether the invasion is in an expansion or in a stable phase) and on invasiveness potential, deduced by the slope of the curve.

Invasion curves can be coupled with Species Distribution Models (hereafter SDMs), i.e. models that relate species distribution (obtained by occurrence records) with environmental factors at the sites of occurrence. SDMs can be used both to investigate the ecology of a species and to predict its distribution across an area (Elith et al. 2009), and were successfully employed to predict the potential distribution of several invasive aquatic species (Guo et al. 2013, 2018; Romero-Alvarez et al. 2017; Bart et al. 2019). Thus, SDMs can offer a powerful support to IAS management: when the model outputs are mapped to produce a species' potential distribution map, they may be used to identify areas where management efforts should be directed, in terms of early-warning actions, public awareness campaigns, early-detection and monitoring programs, risk of re-invasion after eradication or control efforts. These preventive measures are essential when working with neophytes with a particularly rapid and aggressive spreading.

Ludwigia peploides subsp. *montevidensis* (Spreng.) P.H. Raven and *L. hexapetala* (Hook. & Arn.) Zardini, H.Y. Gu & P.H. Raven are two invasive aquatic species that are currently spreading invasively in several European countries, including Italy (Dandelot et al., 2005; Bonali et al., 2006; Galasso et al., 2018). In Europe, the first introduction of *L. hexapetala* took place in France in 1823 and the first record of its populations growing wild is of 1830, still in France (Martins 1866 - with the previous name of *Jussiaea grandiflora* Mich. -; EPPO 2011; Thouvenot et al. 2013).

Both species belong to the Onagraceae family and are perennial hemicryptophytes native to Central and South America, in many countries of the temperate to intertropical regions (EPPO 2011). Both species live in stagnant to lentic freshwaters and were introduced to Italy as amenity species for aquatic gardens, producing many large yellow flowers (Banfi and Galasso 2010). They propagate mainly vegetatively, i.e. through stem fragment dispersal, but sexual reproduction is also possible (*L. peploides* subsp. *montevidensis* is even self-compatible) and can lead to the formation of large amounts of seeds, many of which are viable (Ruaux et al. 2009).

In Italy, *L. hexapetala* and *L. peploides* ssp. *montevidensis* are classified as «local invasive», as their presence is still restricted to a few sites, where, however, they cover large water surfaces and/or banks (Galasso et al. 2018). Nevertheless, biological invasions are dynamic processes and, considering the fast growth and the opportunistic traits of these two aquatic species, a further spread is very likely to occur within a short time. Several *Ludwigia* species are known to be potentially harmful, which is the reason why *L. grandiflora* (Michx.) Greuter & Burdet (of which *L. hexapetala* is often classified as a subspecies – *L. grandiflora* subsp. *hexapetala* (Hook. & Arn.) G.L. Nesom & Kartesz) and *L. peploides* were included in the List of IAS of (European) Union Concern (according to Regulation EU no. 1143/2014): they choke backwaters and inland freshwaters (even indirectly causing the onset of avian botulism infestations; see Lazzari 2019), intercept light penetration in water and alter ecological interactions. Both the European and the Italian legislation established restrictions on importing, selling, and growing alien *Ludwigia* species, and demand a national management plan to control the spreading of these IAS.

In the present study, we first define the current distribution and invasion curves of invasive *Ludwigia* species in Italy and the type of invaded habitats, based on occurrence records derived from herbaria and global databases. Then, we use the global distribution of the two species to elaborate SDMs and identify the country's areas that are most susceptible to invasion. With these models, we can provide local environmental agencies and managers with a prediction tool that can be used as an early-warning system to monitor and prevent further spreading of the two invasive species and the costly environmental and social impacts they may cause.

Methods

Occurrence records

Ludwigia spp. occurrence records from Italy in the period 1850–2020 were obtained by screening and reviewing herbarium samples stored in 40 Italian herbaria (owned by universities, natural history museums, private citizens), published and unpublished (i.e. provided by the authors) records, and international online databases (GBIF, iNaturalist, Wikiplantbase#italia). The two species were searched under the currently used names and their synonyms (for *L. hexapetala*: *Jussiaea grandiflora* Ruiz & Pav. and *L. grandiflora* subsp. *hexapetala* (Hook. & Arn.) G.L. Nesom & Kartesz; for *L. peploides* subsp. *montevidensis*: *J. peploides* Kunth, *L. peploides* (Kunth) P.H. Raven). Since both species have high phenotypic plasticity in response to environmental variation (Dutartre et al. 2004; Muller 2004), the characters separating the two species are often blurred and, therefore, not always shared by the authors, causing taxonomic confusion (Azzella and Iberite 2010; Armitage et al. 2013; Buono et al. 2019). Some authors even proposed to treat the two species as subspecies of the same taxon (Nesom and Kartesz 2000). Herbarium data collections and species verification were therefore accurately done by the large team of Italian botanists authoring this article. For species names we followed the ITIS (Integrated Taxonomic Information System) (https://www.itis.gov/servlet/SingleRpt/SingleRpt). *Ludwigia hexapetala* plants are glabrous or sparsely hairy, with stems 20–200 cm long, partly erect and partly prostrate and floating, leaves narrowly elliptic to widely obovate, 1–11 cm long, sepals 11–19 mm long and petals 20–30 mm long, largely overlapping. *L. peploides* subsp. *montevidensis* plants are hairy, with stems 10–300 cm long, covering the soil or floating, leaves oblong to circular, less than 10 cm long, sepals 3–12 mm long, petals 7–24 mm long, not or scarcely overlapping (Banfi and Galasso 2010; Pignatti et al. 2017–2019). In Italy there is also a native species, *L. palustris* (L.) Elliott, which can easily be distinguished from the two introduced species by its much smaller dimensions (branches no more than 60 cm long) and solitary, small apetalous flowers (4 mm) with tiny green sepals (Pignatti et al. 2017–2019).

Herbaria and online databases yielded 50 and 30 occurrence records in Italy, respectively, including both species (SI1).

Records were classified according to the type of aquatic habitat (as indicated in the label of each herbarium specimen) in BOG = peatlands and bogs, CAN = canals, ditches, moats, LAK = natural lakes, PON = natural ponds, RIV = rivers, WET = wetlands and wet meadows, OTH = others (occasional and/or poorly described habitats), UD = undetermined. Whenever coordinates were not available, the localities were georeferenced on expert basis (e.g., locating the collection place on Google Earth imagery); the reference system used for all the analysis was WGS84. Records were then converted into a vector GIS format of points (shapefile) using the FLOSS software Q-GIS (v. 3.22.12) www.qgis.org).

Ludwigia *invasion curves*

The occurrence records for Italy were first used to elaborate invasion curves to highlight the spreading trends of each of the two *Ludwigia* species. We overlaid a 10×10 km grid (EEA 2013) to the record points and retrieved one occurrence record per grid cell per year to avoid redundancy, due to uneven sampling effort across the Italian territory (Antunes and Schamp 2017). Then, the sum of cells for each year where a species was present was plotted against the year of observation to obtain an invasion curve for each of the two species over time.

Species Distribution Models fitting and evaluation

We extended our data collection to all *L. peploides* ssp. *montevidensis* and *L. hexapetala* occurrences in GBIF database at the global scale, including records in their native (Central and South America) and invaded ranges. Again, the two species were searched under their current names and the above-mentioned synonyms. We only considered records with coordinates (average uncertainty of 2,826.25 m), which accounted for 9,940 records (links to the datasets: https://doi.org/10.15468/dl.qvddsk; https://doi.org/10.15468/dl.9np9et; https://doi.org/10.15468/dl.24kbeu – see GBIF 2022 – SI2). In the model building, the two species were pooled together because they could not be separated reliably, not only in the consulted bibliographic sources, but also in GBIF records and maps. After removing duplicate records, we overlaid a 10×10 km grid to the presence points and retrieved one record for each grid cell, obtaining 1,992 final occurrence records, which were used to fit a first SDM (hereafter «Model 1»).

As predictors, we used bioclimatic variables from the WorldClim database (vers. 2, Fick and Hijmans 2017) and the «human footprint index» layer (vers. 2; Wildlife Conservation Society et al. 2005). We initially considered 19 bioclimatic variables at 2.5 arc-min resolution, derived from monthly temperature and rainfall values. The human footprint index results from combining factors such as population density, land use and human infrastructures (Guo et al. 2013, 2018), and was added to the climatic layers because the presence of the two *Ludwigia* species is reported to be linked to high levels of habitat disturbance (Thiébaut and Dutartre 2009) and nutrient-enriched surface waters (Thouvenot et al. 2013). For all predictors, the Variance Inflation Factor (VIF) was calculated to detect multicollinearity and exclude statistically correlated variables (VIF threshold = 0.6; Elith and Franklin 2013). R Studio (vers. 1.2.5001) and Q-GIS were used to make the predictor layers available for downstream analysis.

The SDM was run with the *sdm* R package (vers. 1.1.8; Naimi and Araújo 2016) in R Studio, using four different commonly used methods: a regression-based algorithm (Multivariate Adaptive Regression Splines – MARS), and three machine-learning algorithms (Supported Vector Machine – SVM, Boosted Regression Trees – BRT, Random Forest – RF). All these modelling techniques require both occurrence presences and absences: as our occurrence data were presence-only, we generated pseudo-absences. These points were randomly chosen outside the favorable environment for *Ludwigia* spp. in terms of elevation, following the so-called «two-step pseudo-absences selection» method (Lobo and Tognelli 2011; Senay et al. 2013): this process reduces the bias associated with the use of pseudo-absences to build a SDM (Elith and Leathwick 2009; Lobo and Tognelli 2011). First, the elevation of *Ludwigia* spp. occurrence points was extrapolated from the European Environmental Agency's world digital elevation model (ETOPO5, European Environment Agency (EEA) 2022). Most of the records' elevation was around 100 m a.s.l. (115 ± 145 m). We thus randomly selected a number of pseudo-absences as equal as our species occurrences in areas of the world at higher altitude (800 m), where the two *Ludwigia* spp. are unlikely to be found according to GBIF database. The mean of the four models' predictions was calculated and the results projected on Italy. The final output was an occurrence probability map of the two invasive species in Italy. The probability of occurrence ranges from 0 to 1, where 0 means that none of the areas with those environmental conditions are expected to be suitable to the species, whereas 1 means that 100% of areas with those environmental conditions have the highest probability to host the species. In other terms, it represents a gradient of the most suitable areas to be colonised by one or the other *Ludwigia* species – and thus the most vulnerable to invasion. To assess the accuracy of the model we used the resampling method of 5-fold cross validation (Elith and Leathwick 2009) with 5 replications.

The model's performance was evaluated in terms of predictive success (i.e. agreement between predictions and validation for each single algorithm) and consistency (i.e. agreement between predictions of the four algorithms). To assess the predictive performance of the models, the following statistics were calculated: sensitivity, specificity, True Skill Statistic, Area Under the (ROC) Curve (ROC = receiving operating characteristic) and correct classification rate (ccr). Consistency of the models was calculated using the argument «method = ensemble» of the *sdm* R function *ensemble*. Variable relative importance in determining the potential distribution was also calculated, as well as response curves to each unrelated variable.

As Model 1 predicted a high suitability for *Ludwigia* species in almost all the Italian peninsula, despite the large variation in climate along the altitudinal gradient of the Apennine chain and the very limited number of permanent water bodies in the predicted areas (that are mostly covered by dense forest along the whole peninsula), we applied also two different modelling approaches (hereafter «Model 2» and «Model 3»). Model 2 was built using all 9,940 *Ludwigia* spp. records and the same pseudo-absences as in Model 1. In this model, the bioclimatic and human footprint conditions in the areas most densely colonised by *Ludwigia* species have a higher predictive weight, and the most likely distribution is in areas that are most similar to those where *Ludwigia* occurrence records are most abundant. In Model 3 we focused on Italy only and defined a specific set of pseudoabsences selecting non-inhabited areas classified as «broad-leaved forests» and «coniferous forests» on the Corine Land Cover (CLC) raster file (v. 2018_v20, © European Union, Copernicus Land Monitoring Service 2018, – EEA). We used the 80 occurrence records found in the Italian territory as presence points and 80 pseudo-absence records as above defined for the SDM. Both Model 2 and Model 3 were fitted using the same four algorithms (MARS, SVM, BRT, RF) as Model 1 and their accuracy was assessed through the 5-fold cross-validation method. The predictive performance of the two models was again evaluated through the statistics of sensitivity, specificity, TSS, AUC and ccr, and the variable relative importance and response curves were calculated as well. In addition, for Model 2 and Model 3, using Q-GIS and GRASS-GIS (v. 7.8.7), we analysed the areas resulting to have the highest probability of occurrence values (≥ 0.8) in terms of land cover and land use with the CLC raster file, to understand in what types of landscape water habitats are more vulnerable to *Ludwigia* invasion. We also quantified the areas in each biogeographic region by overlaying potential distribution maps predicted with > 0.8 likelihood on the biogeographical regions' layer of the EEA (2016, (https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3) with QGIS.

Results

Current distribution

The collection date of the 80 Italian records of the invasive alien *Ludwigia* species (SI1) ranged between 1997 and 2020, except for one occurrence of *L. hexapetala* at Lake Iseo, dating back to 1939, that was planted in a peat bog for experiments of exotic species acclimatization (Arietti 1943; Banfi and Galasso 2010).

The two *Ludwigia* species investigated are mainly located in the north of Italy, along the River Po and smaller water bodies connected to it, and along the banks of some of the major Italian lakes (Lake Maggiore, Lake Iseo; Fig. 1). In central Italy, only two aquatic systems are currently invaded, corresponding to some sections of the River Arno and Lake Bracciano (the southernmost). As of yet, neither of the two alien *Ludwigia* species has been recorded in southern Italy and in the islands.

The most invaded aquatic habitats are lowland rivers (51% of occurrence records; Fig. 2). Almost 1/3 of occurrences were equally found in lakes and canals (including moats and ditches), and, according to land cover data, the occurrence records are located in landscapes dominated by urban or agricultural areas. The two invasion curves have different lag-phases length and steepness, but in both cases *Ludwigia* spp. populations have been constantly increasing in the past years (Fig. 3). *Ludwigia hexapetala* was introduced almost 50 years earlier than the other species, but its number of occurrence records has been overcome by the most recent *L. peploides* subsp. *montevidensis*. Since the early 2000s, the distribution of the latter has been constantly increasing, while *L. hexapetala* experienced a short lag phase between 2006 and 2016.

Predicted distribution

The Model 1 predicted most of the Italian peninsula and islands as a suitable environment for the establishment of *Ludwigia* species (Fig. 4A). Only the Alps and the highest peaks of the Apennines were predicted unsuitable for these species. The bioclimatic variables that are most important for this distribution are precipitation in the coldest quarter (bio19), and temperature (bio4) and precipitation (bio15) seasonality. For bio19 occurrence likelihood is highest with lowest precipitation, and for bio04 and bio15 for narrow temperature and precipitation variation ranges among seasons (Fig. 5A and 6A). The occurrence likelihood is highest for mean temperature in the driest (bio9; > 20°C) and wettest (bio8; around 20°C) quarters.

The outputs of Model 2 and Model 3 resembled each other to some extent and, in addition to highlighting a high suitability of those areas that are already invaded by *Ludwigia* species, they predicted other plain agricultural areas along the coasts of Italy and in the two major islands (Fig. 4B and 4C). Isothermality (bio3) is the most important predictor of Model 2 (Fig. 5B) and the probability of occurrence is highest with 50% isothermality, i.e. where the diurnal temperature range is half that of the annual temperature range (Fig. 6B). For Model 3, the mean temperature in the warmest quarter (bio10) is the most important predictor (Fig. 5C) and occurrence likelihood is highest for temperatures between 20 and 25°C (Fig. 6C). The human footprint had lower relative importance than bioclimatic variables in all models. Its contribution was highest in Model 2. The response to human pressure is a sigmoid curve, indicating a gradual increase in the probability of occurrence of *Ludwigia* species with human presence (Fig. 6A and 6B). All three models are acceptable, although accuracy decreases from Model 1 (from 0.895 TSS BRT to 0.990 AUC MARS) through Model 3 (from 0.823 TSS MARS to 0.984 sensitivity SVM; Table 1, SI3, SI4). Land use in the areas with invasion likelihood > 80% were non-irrigated arable land (about 4,600 km²), complex cultivation patterns (about 2,100 km²) and olive groves, accounting for 34, 16 and 11% of the total covered area, respectively, for Model 2, and non-irrigated arable land (about 11,000 km², 60%) for Model 3 (Table 2). The predicted area was larger in the Mediterranean than in the Continental biogeographic region for Model 2 (Fig. 7A, Fig. 8), whereas for Model 3 the predicted area was larger in the Continental biogeographic region (Fig. 7B, Fig. 8). All in all, Model 3 predicted a larger suitable area than Model 2 where the occurrence likelihood is higher than 0.8.

Table 1

Performance of the three models evaluated by AUC (Area Under the (ROC) Curve), Sensitivity, Specificity, TSS (True Skill Statistics) and ccr (Correct Classification Rate) for each modelling algorithm: SVM (Supported Vector Machine), RF (Random Forest), BRT (Boosted Regression Trees) and MARS (Multivariate Adaptive Regression Splines). Mean values and s.d. (standard deviation for 5 replications of 5-fold cross-validation runs).

Model	Algorithm	AUC	s.d.	sensitivity	s.d.	specificity	s.d	TSS	s.d	ccr	s.d
MODEL 1	SVM	0.993	0.003	0.979	0.008	0.978	0.009	0.957	0.011	0.979	0.006
	RF	0.996	0.002	0.980	0.011	0.987	0.008	0.967	0.009	0.983	0.005
	BRT	0.985	0.005	0.957	0.016	0.937	0.018	0.895	0.022	0.947	0.011
	MARS	0.990	0.004	0.965	0.012	0.965	0.012	0.930	0.012	0.965	0.006
MODEL 2	SVM	0.992	0.001	0.973	0.007	0.952	0.008	0.924	0.007	0.959	0.004
	RF	0.999	0.001	0.988	0.004	0.990	0.004	0.977	0.004	0.989	0.002
	BRT	0.976	0.003	0.929	0.010	0.922	0.009	0.851	0.013	0.924	0.013
	MARS	0.981	0.003	0.933	0.013	0.936	0.010	0.869	0.010	0.935	0.005
MODEL 3	SVM	0.980	0.021	0.984	0.028	0.925	0.072	0.910	0.074	0.954	0.038
	RF	0.975	0.023	0.959	0.055	0.948	0.050	0.910	0.064	0.953	0.032
	BRT	0.965	0.029	0.969	0.046	0.905	0.081	0.873	0.079	0.936	0.040
	MARS	0.912	0.065	0.953	0.059	0.870	0.099	0.823	0.124	0.910	0.062

Table 2

Land use in areas predicted by Model 2 and Model 3 with likelihood > 0.8. Corine Land Cover code (CLC code), area (% and Km2) occurring within each land use type.

CLC code	Description	Model 2		Model 3	
		%	km^2	%	km^2
111	Continuous urban fabric	2.04	282	0.47	94
112	Discontinuous urban fabric	7.82	1057	8.25	1604
121	Industrial or commercial units	3.17	430	2.73	532
122	Road and rail networks and associated land	0.27	36	0.18	36
123	Port areas	0.10	14	0.00	0
124	Airports	0.15	21	0.20	39
131	Mineral extraction sites	0.30	42	0.24	47
132	Dump sites	0.05	6	0.02	5
133	Construction sites	0.05	6	0.09	17
141	Green urban areas	0.20	27	0.10	19
142	Sport and leisure facilities	0.27	36	0.17	35
211	Non-irrigated arable land	**34.32**	**4665**	**60.07**	**11667**
212	Permanently irrigated land	0.06	8	0.03	6
213	Rice fields	0.16	21	3.01	579
221	Vineyards	5.62	780	1.80	353
222	Fruit trees and berry plantations	1.62	225	1.68	352
223	Olive groves	**11.38**	**1571**	1.38	276
231	Pastures	0.54	73	0.77	149
241	Annual crops associated with permanent crops	0.65	91	0.12	35
242	Complex cultivation patterns	**15.91**	**2177**	7.85	1545
243	Land principally occupied by agriculture with significant areas of natural vegetation	4.26	583	3.27	654
244	Agro-forestry areas	0.00	0	0.00	0
311	Broad-leaved forest	4.95	676	3.43	680
312	Coniferous forest	0.73	100	0.17	35
313	Mixed forest	1.46	196	0.48	94
321	Natural grasslands	0.41	57	0.10	22
322	Moors and heathland	0.00	0	0.00	0
323	Sclerophyllous vegetation	0.98	134	0.12	25
324	Transitional woodland-shrub	0.84	114	0.99	191

CLC code	Description	Model 2		Model 3	
331	Beaches dunes sands	0.06	8	0.22	43
332	Bare rocks	0.00	31	0.00	0
333	Sparsely vegetated areas	0.22	2	0.20	42
334	Burnt areas	0.01	2	0.01	2
335	Glaciers and perpetual snow	0.00	0	0.00	0
411	Inland marshes	0.28	38	0.20	39
412	Peat bogs	0.00	0	0.02	3
421	Salt marshes	0.13	17	0.00	0
422	Salines	0.00	0	0.00	0
423	Intertidal flats	0.00	0	0.00	0
511	Water courses	0.41	55	0.62	121
512	Water bodies	0.31	43	1.01	196
521	Coastal lagoons	0.27	35	0.00	0
522	Estuaries	0.00	0	0.00	0
523	Sea and ocean	0.00	0	0.00	0
TOTAL		100.00	13,659	100.00	19,537

Discussion

The long history of introduction and management of *L. hexapetala* and *L. peploides* subsp. *montevidensis* in France – where these species are shortlisted among the most invasive species – provides lessons and clear examples of what the situation could be in Italy (both ecologically and economically) if no timely measures were adopted (Dandelot et al. 2005; Dutartre et al. 2007; Thiébaut and Dutartre 2009). Once established and widespread, *Ludwigia* spp. populations are difficult to control, impossible to eradicate, and extremely expensive to manage: over 1 billion €/year was estimated in France between 2009 and 2013 (Wittmann and Flores-Ferrer 2015). Since the presence of *Ludwigia* spp. in Italy is still restricted to some areas, there is still the possibility to develop and adopt successful strategies to control the existing populations and prevent their spread to new areas. According to the invasion curves, the populations occurring in Italy are currently expanding. The number of occurrences of the two *Ludwigia* species has been steeply increasing in recent decades. This trend is affected also by improved data availability, thanks to open and shared global species databases, and likely also by a deeper awareness of the problems caused by invasive alien species, with special concern to those that are included in the Union list. The slower expansion of *L. hexapetala* that followed its introduction might be due to unconcern for this invasive species in the past, and thus an underestimation of its abundance and distribution (Dutartre et al. 2007). *Ludwigia peploides* subsp. *montevidensis* has apparently overcome *L. hexapetala* in number of occurrence records and might be more fit than the latter in expanding its range and in resilience in Italy. This fitness can be associated with the generally more temperate climate in the native range (temperate vs. subtropical in *L. hexapetala* – POWO 2022). In any case caution is needed in interpreting this phenomenon, given the ecological plasticity of both species (EPPO 2011; Genitoni et al. 2020) and of other species within this genus (Khalifa et al. 2017). An alternative or additional explanation may be provided by the breeding system of *L. peploides* subsp. *montevidensis*, which is a self-compatible species. Self-compatibility could, in fact, provide advantages both for dispersal (seeds in addition to clonal propagules) and for evolving adaptability (Dandelot et al. 2005).

The current distribution of the two species is almost completely confined to northern Italy, apart from few spots in the central parts of the peninsula. Based on the data collected from herbarium accessions, the species were most often found in rivers (Fig. 2), despite our recent field observations would suggest that they occur more frequently in stagnant waters. In rivers, the habitats that we observed being colonized by *Ludwigia* spp. are in the riparian belts or in places with lentic water.

According to the SDMs, all Italian peninsula has suitable bioclimatic conditions for the establishment of *Ludwigia* spp. Only the Alps and the highest mountains in the Apennines have a low probability of being colonised according to Model 1. The invasion risk of *Ludwigia* species appears therefore very high all over the peninsula. Model 2 and Model 3 can be interpreted as the most vulnerable areas where the bioclimatic conditions are most similar to those where the species are most abundant globally (Model 2) and already occurring in Italy (Model 3). In these areas, the two species would be likely able to immediately establish and spread, if introduced. Water bodies in agricultural landscapes have the highest likelihood of being invaded according to both Model 2 and Model 3.

All models are consistent concerning the bioclimatic conditions that can predict the distribution of the two species: low seasonal variation in temperature and precipitation and high isothermality, as well as high temperature in the warmest, driest and wettest periods of the year (average ≥ 20°C). It is known, in fact, that the temperature *optimum* for the development of these species ranges from 20 to 30°C (Ruaux 2008) and at 40°C the growth rate is still very notable, although no flowers are produced (Yen and Myerscough 1989): in other words, they would be favored by a climate similar to that of the subtropical and intertropical regions they come from. Precipitation in the coldest period (Model 1) seems to have a negative effect on the occurrence of the two species. In the aquatic environment this bioclimatic condition causes high and cold water, suggesting that high cold water can be a limiting factor. The coldest period corresponds to the winter months (November-February) in Italy and in the temperate regions of the Northern Hemisphere, during which the two species are dormant. These bioclimatic requirements can be expected for tropical and subtropical species and indicate low evolutionary divergence of invasive from native populations in climatic adaptation. Range expansion is therefore most likely driven by climate change, rather than by adaptive evolution occurred in the introduced range. The Mediterranean bioclimatic region, characterized by warm, dry summers and mild and moderately wet winters, and where seasonality is lower than in the Continental region, appears extremely vulnerable to the invasion of *Ludwigia* species, especially along the coasts where the climate is not mitigated by the altitude of the Apennine chain (Model 2). The unchanged climatic pre-adaptation of these species, however, suggests that the Mediterranean climate has already been shifting into the Continental region, where the species already occurs and can potentially expand further finding suitable conditions (Model 3) in this transition zone (Vennetier 2007; Hernandez et al. 2017).

Low tolerance to precipitation in the coldest period has important implications for management. Wherever water level can be regulated, maintenance of a high water level during winter could prove to be an effective method to control the spreading of these species and/or could prolong the positive effects of the mechanical control (Legrand 2002; Meisler 2009; Thiébaut and Dutartre 2009; Hussner et al. 2016 etc.). Being both the inclusion of *Ludwigia* species in the Union list and the invasion process in Italy quite recent events, the national action plan is under preparation, and practical control experiences are lacking with a few exceptions (Montagnani et al. 2018; Life TIB project 2011–2015). Therefore much still remains to be understood and experimented to manage – and, whenever still possible, locally eradicate – the populations of *Ludwigia hexapetala* and *L. peploides* subsp. *montevidensis* in Italy.

Conclusions

Overall, this study aimed at investigating the current distribution of the local invasive *Ludwigia* spp. and predicting their potential suitability and spread over the Italian country. The habitat-based approach used, combined with SDMs, proved to be a suitable procedure to assess the invasion potential of *Ludwigia* spp. in different types of aquatic habitats in Italy. Indeed, risk analysis, monitoring and management of alien plants can greatly benefit from detailed information on the identity of receptor habitats (Guarino et al. 2021) and areas most vulnerable to invasion.

In all sites where *Ludwigia* spp. occur, a deeper understanding of local relationships among hydrology, climate and water management, as well as resource availability and biotic interactions are critical to plan successful strategies for the control and containment of these IAS. In the meantime, a meticulous monitoring of water systems, especially of those where occurrence likelihood is highest, is probably the best recommended preventive action to undertake. We believe the harmful consequences that *Ludwigia* spp. can cause are still unknown to many stakeholders involved in environmental and landscape management: informative campaigns and meetings can surely bring positive outcomes, as people's knowledge and awareness are powerful tools for detecting major threats to ecosystem conservation, such as the arrival and the invasion of new alien species (McNeely et al. 2001).

Declarations

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Competing interests

Authors declare they have no financial interests.

Author contributions

BG analysed the data and drafted the manuscript. FB coordinated the herbarium collections. CL, FB and GP designed the study. FB and CL coordinated the contributions of the authors and all phases of the work. All authors searched and provided data, read, commented and approved the manuscript.

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Figures

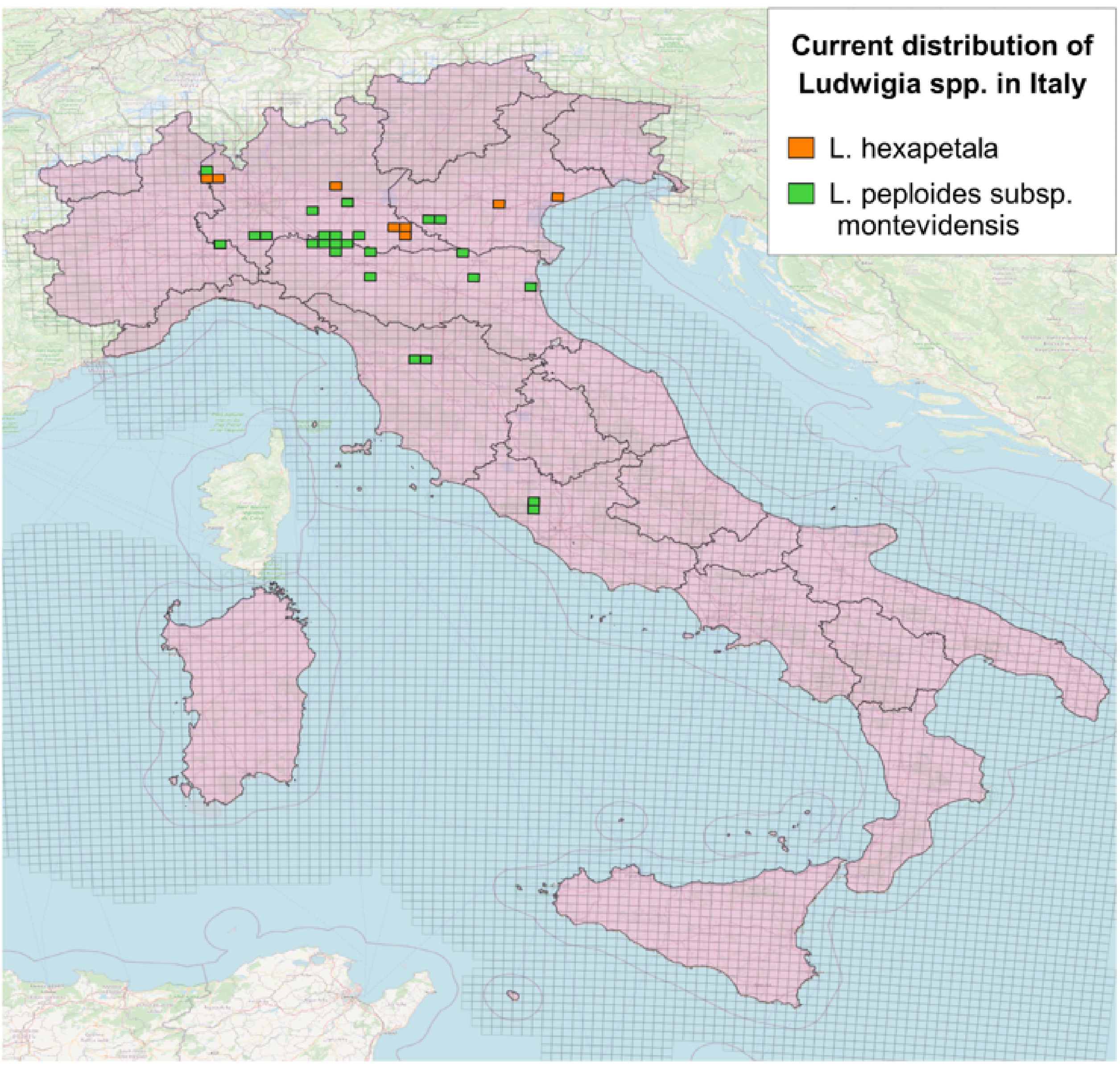

Figure 1

Current distribution of *Ludwigia*spp. in Italy. Green and orange 10×10 km squares contain one or more occurrence records.

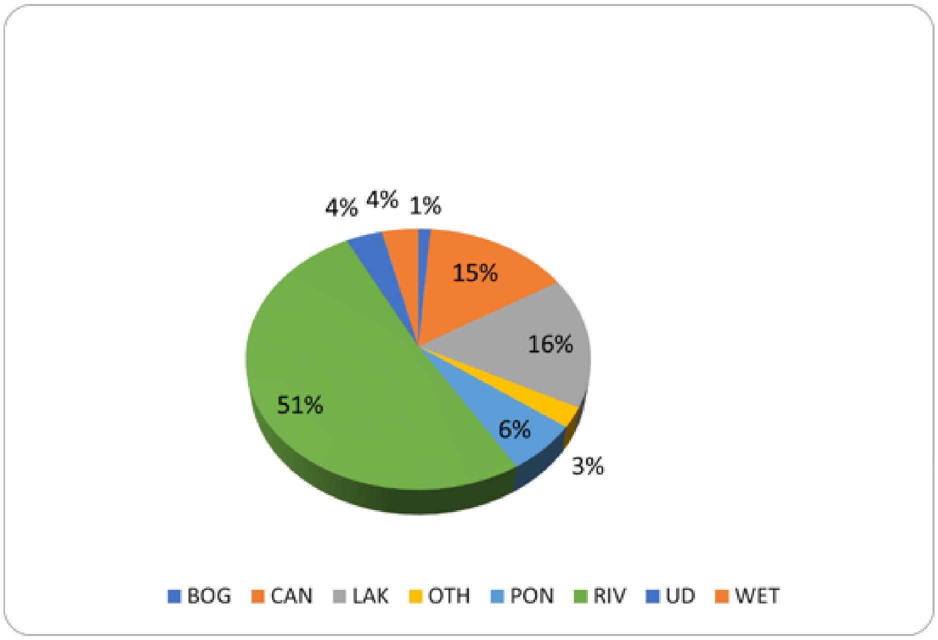

Figure 2

Types of habitats invaded by *Ludwigia*spp. in Italy. BOG = peat bogs; CAN = canals, ditches, moats; LAK = natural lakes; PON = natural ponds; RIV = natural rivers; WET = wetlands and wet meadows; OTH = others (occasional and poorly described habitats); UD = undetermined.

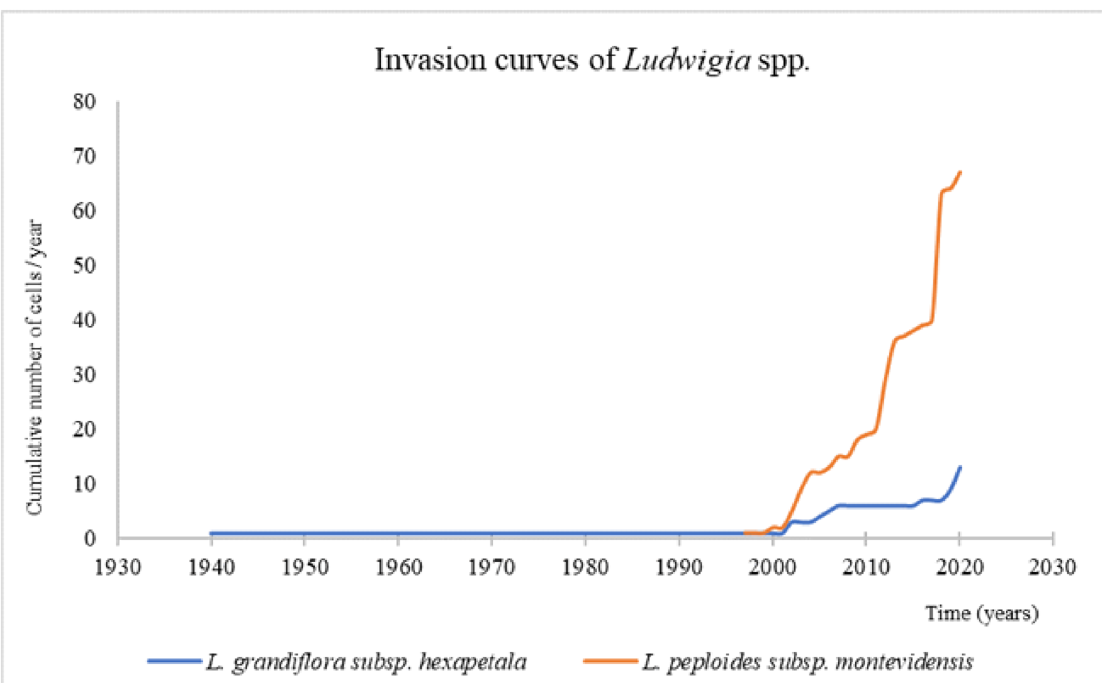

Figure 3

Invasion curve of *Ludwigia hexapetala* and *L. peploides* subsp. *montevidensis* in Italy.

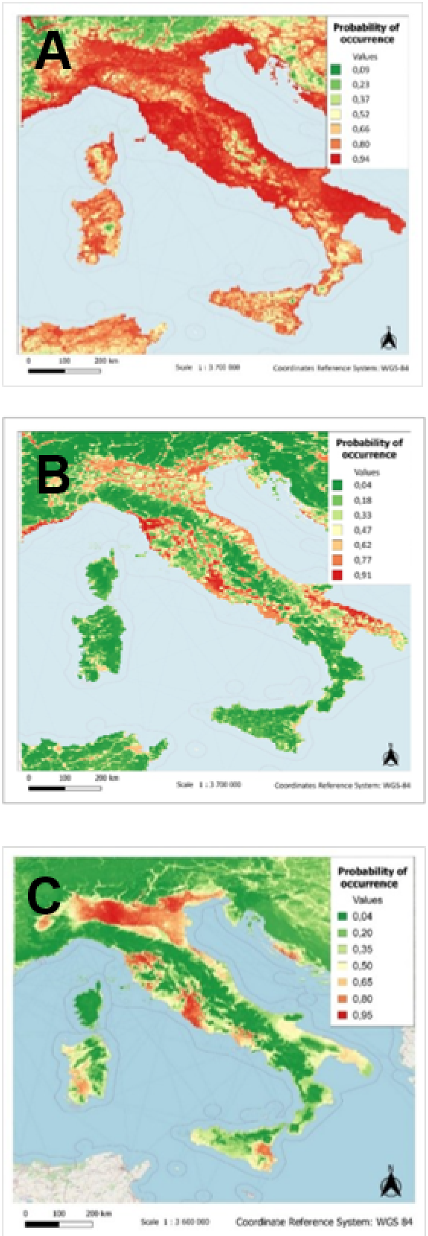

Figure 4

Predicted distribution of *Ludwigia* spp. in Italy. A) Model 1, B) Model 2, C) Model 3. Occurrence likelihood is indicated by different colours.

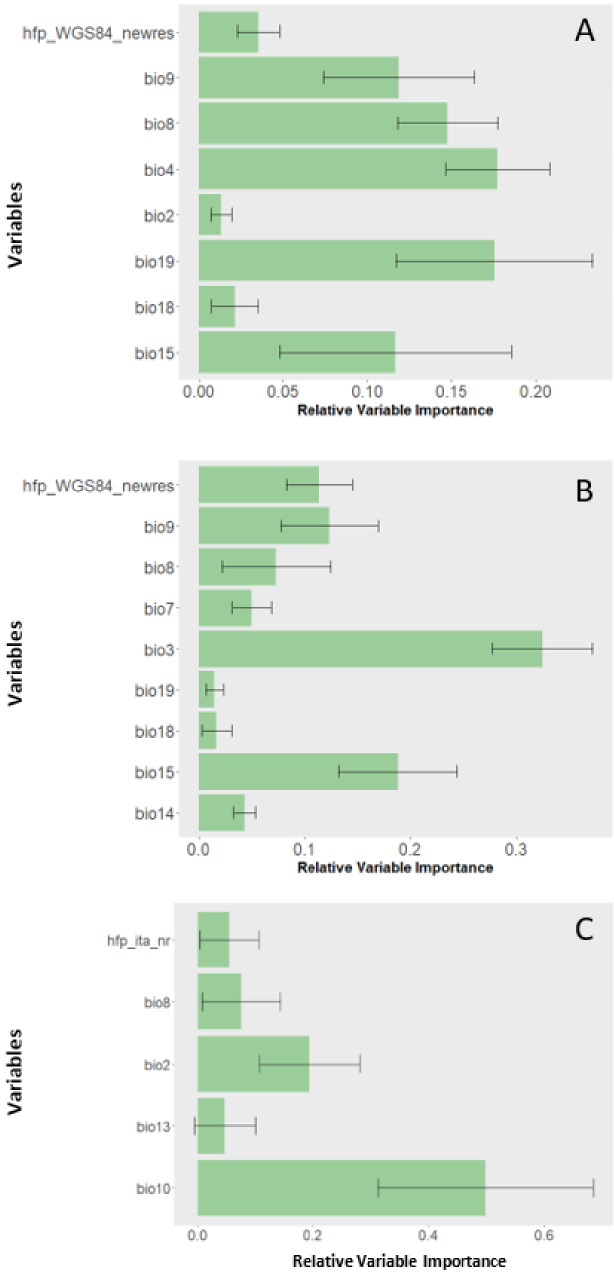

Figure 5

Relative variable importance of predictors in Model 1 (A), Model 2 (B) and Model 3 (C). hfp_WGS84_newres (human footprint layer), bio2 (mean diurnal range), bio3 (isothermality), bio4 (temperature seasonality), bio7 (temperature annual range), bio8 (mean temperature of wettest quarter), bio9 (mean temperature of driest quarter), bio10 (mean temperature of warmest quarter), bio13 (precipitation of wettest month), bio14 (precipitation of driest month), bio15 (precipitation seasonality), bio18 (precipitation of warmest quarter, bio19 (precipitation of coldest quarter).

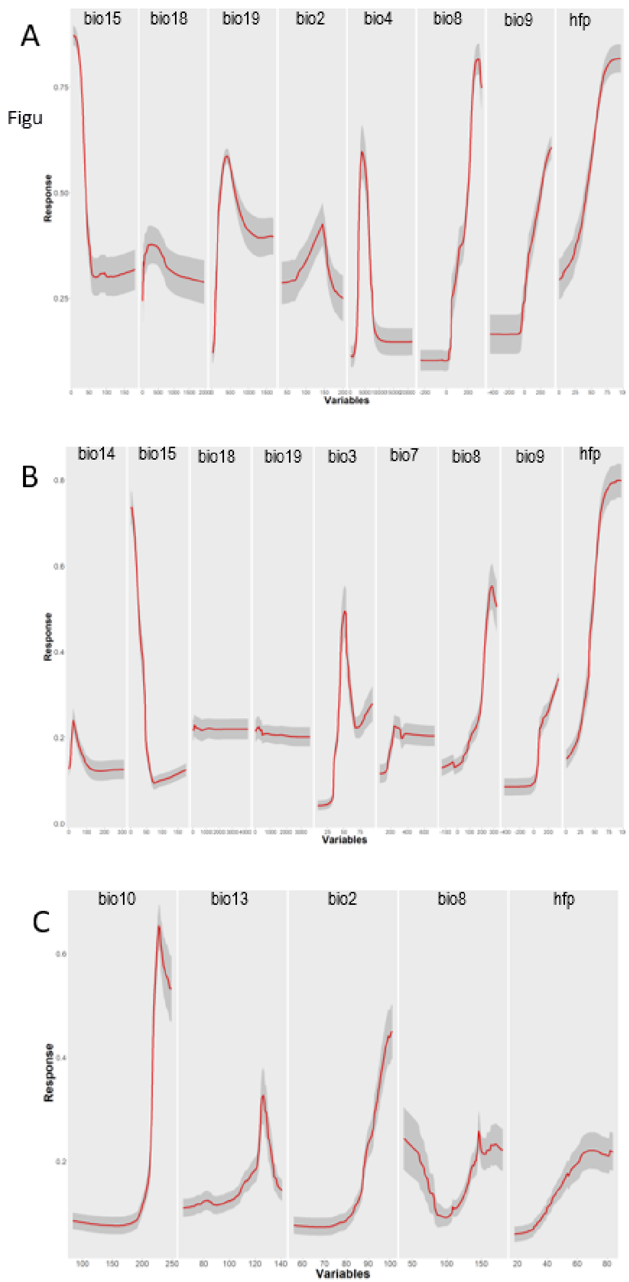

Figure 6

Response curve of the probability of *Ludwigia* spp. occurrence to the variables used as predictors for Model 1 (A), Model 2 (B) and Model 3 (C). hfp (human footprint layer), bio2 (mean diurnal range_°C), bio3 (isothermality_%), bio4 (temperature seasonality_°C), bio7 (temperature annual range_°C), bio8 (mean temperature of wettest quarter_°C), bio9 (mean temperature of driest quarter_°C), bio10 (mean temperature of warmest quarter_°C), bio13 (precipitation of wettest month_mm), bio14 (precipitation of driest month_mm), bio15 (precipitation seasonality_%), bio18 (precipitation of warmest quarter_mm), bio19 (precipitation of coldest quarter_mm). Temperatures are 10x.

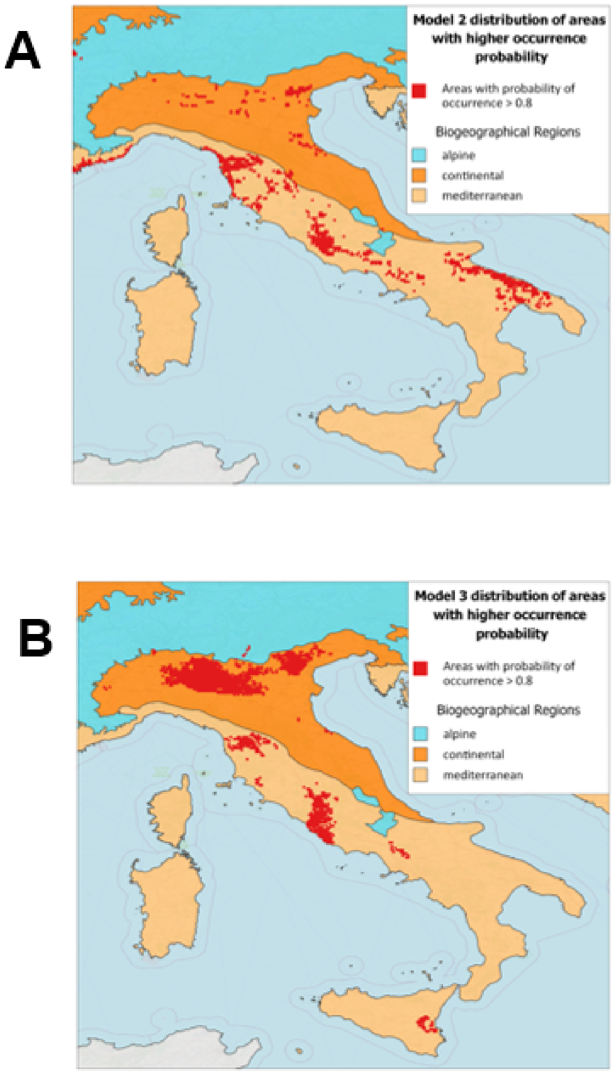

Figure 7

Predicted distribution of Model 2 and Model 3 (likelihood >0.8) in each biogeographic region in Italy.

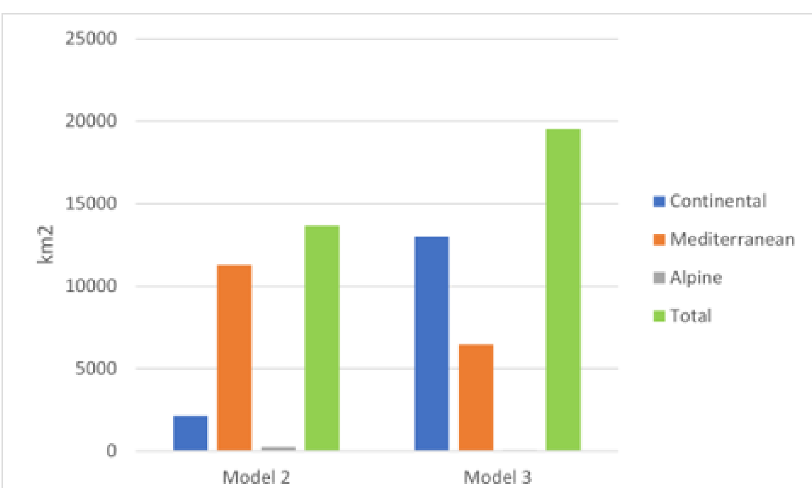

Figure 8

Predicted distribution area (km^2) of Model 2 and Model 3 (likelihood >0.8) in each biogeographic region in Italy.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SI1.OccurrencerecordsIT.xlsx
- SI2.GBIF.xlsx
- SI3.Probabilitydistributionmaps.pdf
- SI4.Modelperformacestatistics.xlsx