

Research Article**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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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 invasion 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 driest period of the year and low precipitation in the coldest period are the bioclimatic factors that most account for the potential distribution of the two species. The human footprint has a lower relative importance than bioclimatic variables. All Italian peninsula appears as a suitable bioclimatic environment for the invasion of the two *Ludwigia* species, with over 90% of areas with high suitability lying below 600 m altitude. Only mountain regions and the islands appear less suitable. The agricultural land at the foothill of the Apennine in the Mediterranean region 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.

Key words: invasion curves, freshwater ecosystems, aquatic plant species, herbarium records, GBIF, distribution models

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), besides being 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, characterized 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. 2023) 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 and Leathwick 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; Steen 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 *Ludwigia 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, sub *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, (including self-compatibility in short-styled morphotypes, cfr. Portillo Lemus et al. 2021) 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* subsp. *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 (Bolpagni and Piotti 2016; 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 thanks also to a strong allelopathic activity (Pelella et al. 2023). Both the European and the Italian legislation establish 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 predict with SDMs the climatic and human modified 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.

Materials and 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: www.itis.gov, <https://doi.org/10.5066/F7KH0KKBK>, <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 yielded 21 occurrence records and authors' unpublished records were 33, online databases yielded 30 records in Italy and 3 records were obtained from published data (Supplementary material File S1).

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* subsp. *montevidensis* and *L. hexapetala* occurrences in GBIF database (<https://www.gbif.org/>) at the global scale, including records in their native (Central and South America)

and invaded ranges (<https://doi.org/10.15468/dl.qyddsk>, <https://doi.org/10.15468/dl.9np9et>, <https://doi.org/10.15468/dl.24kbeu>). Again, the two species were searched under their current names and the above-mentioned synonyms. After removing duplicate records, we only considered records with coordinates uncertainty < 6000 m (average uncertainty of 806.31 m), and we limited the analysis to recent records (from 1970 onwards) to be consistent with the time period covered by the climatic observations. Overall, we included 3,705 of 9,940 records, including the Italian dataset (Supplementary material File 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, images and maps. We overlaid a 10×10 km grid to the presence points – the same grid applied to IUCN Red Lists Assessments (Murray 2017) – and retrieved one record for each grid cell, obtaining 1,422 final occurrence records (average uncertainty of 1,349 m) which were used to fit a first SDM (hereafter “Model 1”).

As predictors, we used bioclimatic variables from the WorldClim database (v. 2, Fick and Hijmans 2017, data relevant to the period 1970-2000) and the “human footprint index” layer (v. 2, indexing data of 2000; 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 (Thiébaud 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 (v. 2023.06.2+561) and Q-GIS were used to make the predictor layers available for downstream analysis.

The SDM was run with the sdm R package (v. 1.1.8; Naimi and Araújo 2016) in R Studio, with default settings, 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 background data (pseudo-absences), extracted from the geographical space where the studied species was not observed, thus reflecting information on species absence. These points were randomly chosen in a geographical space outside a 50 km radius buffer delimiting presence data. This approach, called the “buffer-out” approach, is commonly used to isolate potentially favourable areas around known presence points (Da Re et al. 2023). We

generated 1,422 background points (equal to the number of presence data – Iturbide et al. 2015) applying the same 10×10 km grid used for presence thinning. The mean of the four methods' 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. 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, we also applied a different modelling approach (hereafter “Model 2”). Model 2 was built using all 3,705 *Ludwigia* spp. records (Supplementary material File S2) and an equal number of background data, as in Model 1. Model 2 was fitted using the same four algorithms as Model 1 (MARS, SVM, BRT, RF) and the accuracy was assessed through the 5-fold cross-validation method. The predictive performance of Model 2 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, since a national map covering all waters bodies is not available at the national scale, for both models we analysed the areas with the highest probability of occurrence values (≥ 0.8) in terms of land cover and land use with Corine Land Cover (CLC) raster file (v. 2018_v20, © European Union, Copernicus Land Monitoring Service 2018, <https://land.copernicus.eu/pan-european/corine-land-cover>) using Q-GIS and GRASS-GIS (v. 7.8.7). We used the CLC raster file (including codes 411, 412, 421, 422, 423, 511, 512, 521, 522 and 523, i.e. wetlands and all aquatic habitats), 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) with QGIS.

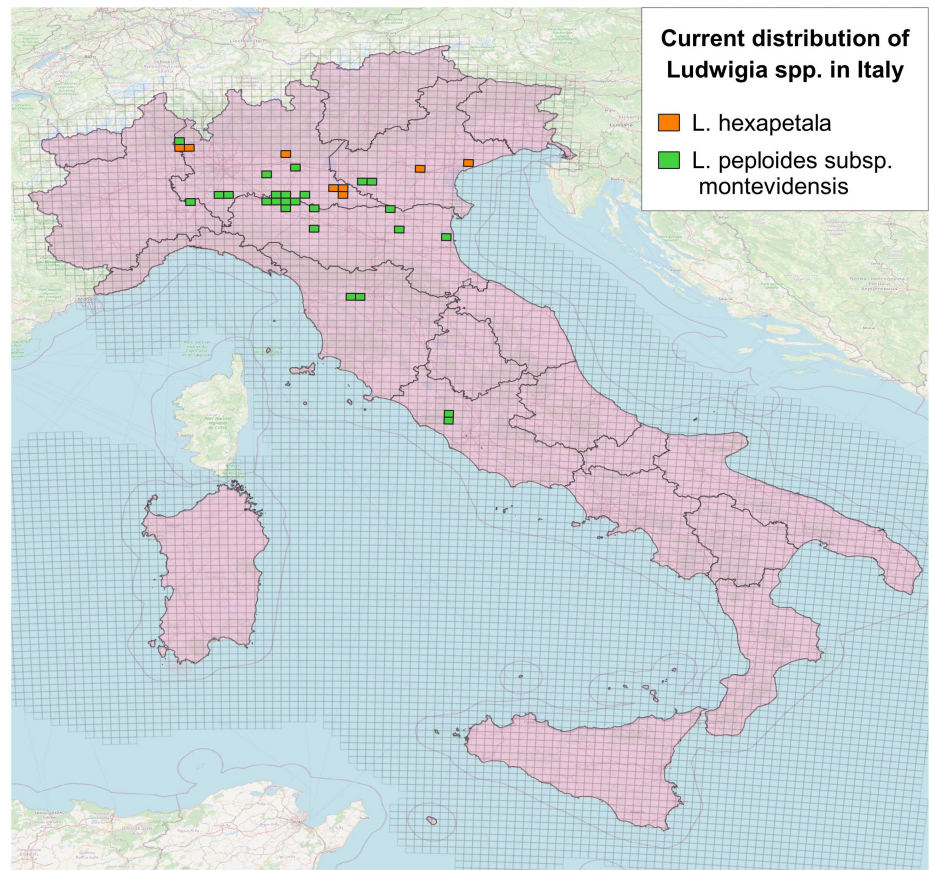


Figure 1. Current distribution of *Ludwigia* spp. in Italy. Green and orange 10×10 km squares contain one or more occurrence records.

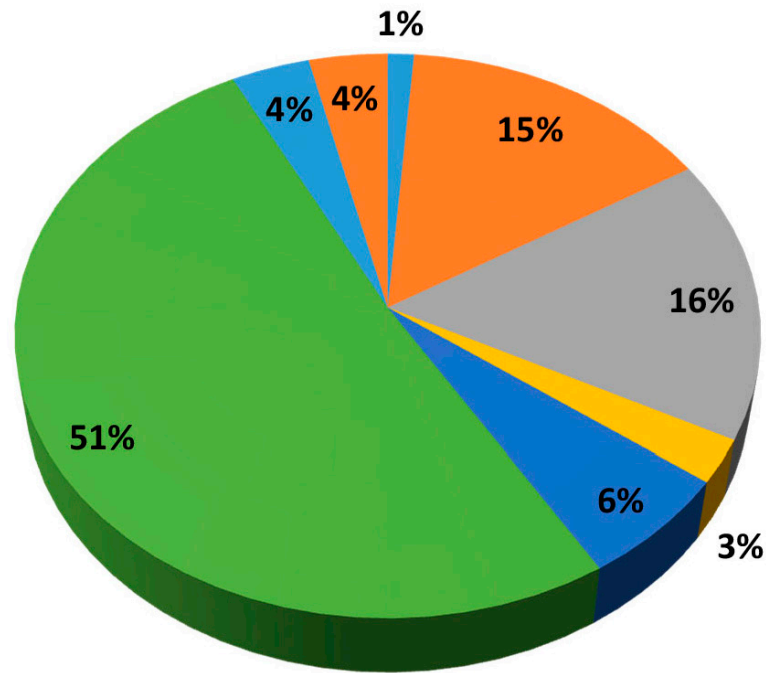
A spatial autocorrelation test (Moran's I test) was performed on the residuals for each model with `spdep` package in R (Bivand 2022). The autocorrelation was tested between geographic distances and the residuals of the two models, calculated as the difference between observed presence of the species and the mean predicted probability of occurrence (Gaspard et al. 2019) and statistical support was obtained with 1,000 permutations. Spatial autocorrelation in the models could be due to spatial dependency of the data, but also to co-varying key environmental variables that were not included in our dataset (Paradinas et al. 2023).

Results

Current distribution

The collection date of the 87 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 from the herbarium data, 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; Figure 1).



■ BOG ■ CAN ■ LAK ■ OTH ■ PON ■ RIV ■ UD ■ WET
Figure 2. Habitat types 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 (based on herbarium record labels)

In central Italy, only two aquatic systems are currently invaded, corresponding to some sections of the River Arno and Lake Bracciano (the southernmost). So far, neither of the two species has been recorded in southern Italy nor in the islands.

Based on the information obtained from the herbarium labels, the most invaded aquatic habitats are lowland rivers (51% of occurrence records; Figure 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 urban or agricultural areas. The two invasion curves have different lag phase length and steepness, but in both cases *Ludwigia* spp. populations have been constantly increasing in the past years (Figure 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

Model 1 predicted most of the Italian peninsula as a suitable environment for the establishment of *Ludwigia* species (Figure 4A). The Alps and the highest peaks of the Appennine were predicted unsuitable for these species, as well as

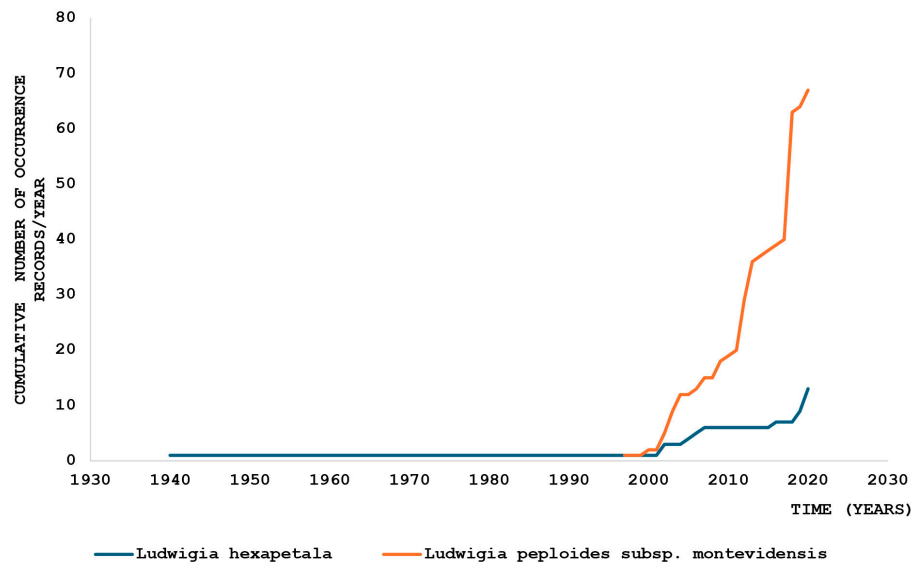


Figure 3. Invasion curve of *Ludwigia hexapetala* and *L. peploides* subsp. *montevidensis* in Italy.

the mountainous parts of Calabria at the southern tip of the Italian peninsula and the islands. Of the land cover with occurrence probability >0.8 , 93.8% was predicted between 0 and 600 m a.s.l., and 99.2% was predicted below 1000 m a.s.l. The maximum altitude predicted by Model 1 is between 2600–2800 m (for an area of 0.7 km²). The bioclimatic variables that are most important for this distribution are temperature seasonality (bio4), precipitation in the coldest quarter (bio19), mean temperature in the warmest quarter (bio9) and precipitation seasonality (bio15). Occurrence likelihood is highest for narrow temperature (bio4) and precipitation (bio15) seasonality, mean temperature $\geq 20^{\circ}\text{C}$ in the driest quarter (bio9) and low precipitation (around 50 mm) in the coldest quarter (bio19) (Figures 5 and 6).

The output of Model 2 resembled that of Model 1 although it predicted lower likelihood along the Appennine chain and in the Po plain (Figure 4B). Indeed, here the maximum altitude predicted was 2200 m a.s.l., for an area of only 0.02 km². The most important variables for Model 2 were the same as for Model 1, with similar patterns. Differently from Model 1, precipitation in the warmest quarter (bio18), that was important for Model 1, although with a small weight, was not relevant for Model 2. The human footprint had lower relative importance than bioclimatic variables in both models. The response to human pressure resembles a sigmoid curve, indicating a gradual increase in the probability of occurrence of *Ludwigia* species with human presence (Figure 6). Both models are acceptable, although accuracy is slightly higher for Model 2 (from 0.891 TSS BRT and MARS to 0.996 AUC RF) than for Model 1 (from 0.858 TSS BRT to 0.990 AUC RF; Table 1, Supplementary material Files S4 and S5). Although the autocorrelation was significant for both models (Moran I = 0.52 and 0.60 for Model 1 and Model 2, respectively, p-values < 0.0001), the correlation curves were not those expected for autocorrelation (correlation of residuals vs. geographical distance),

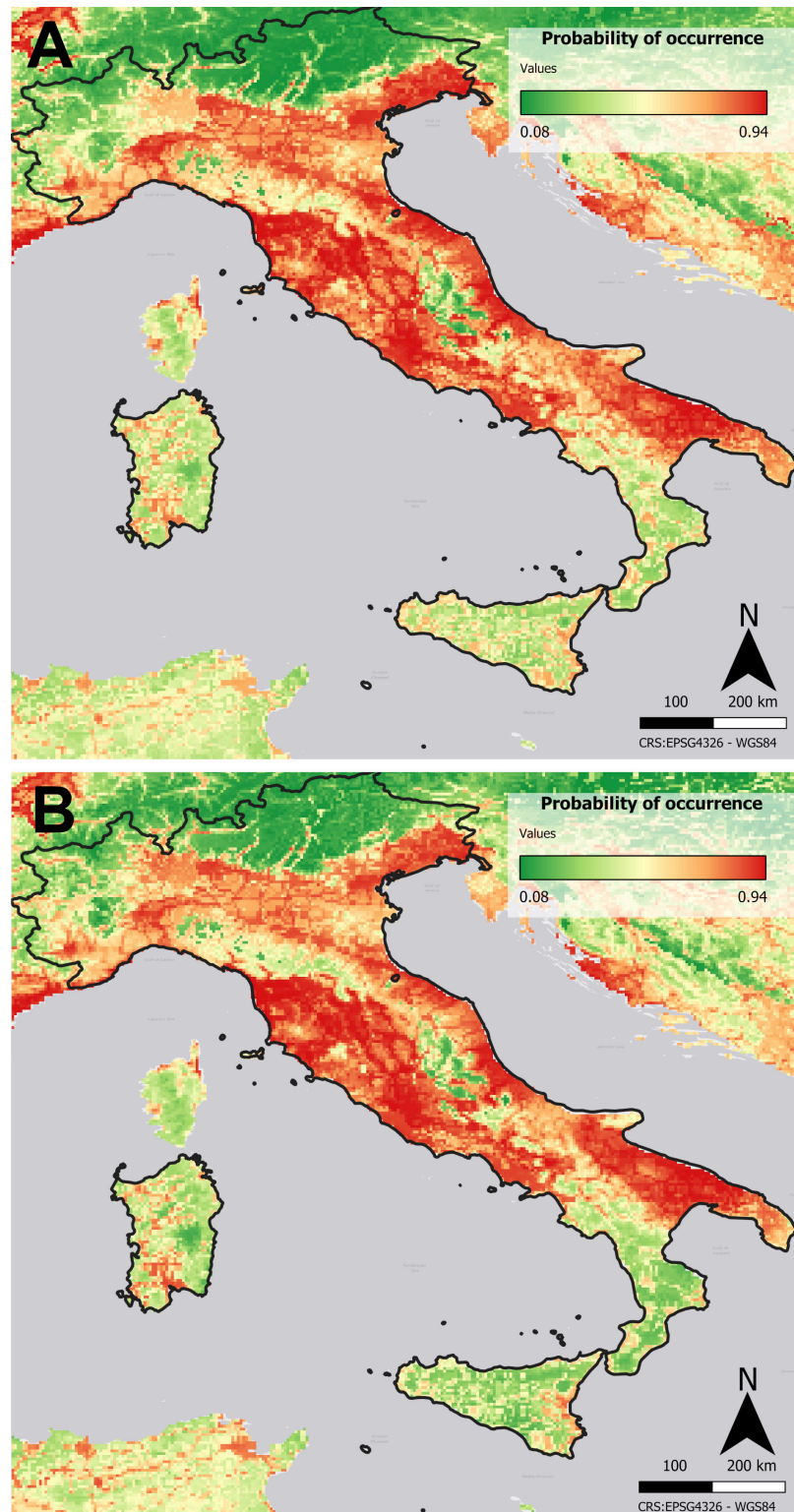


Figure 4. Predicted distribution of *Ludwigia* spp. in Italy. A) Model 1, B) Model 2. Occurrence likelihood is indicated by different colours.

indicating that the detected spatial autocorrelation was not due to the bioclimatic and human footprint factors of our dataset, but to other co-varying environmental and ecological processes that drive the distribution of species, which were not included in the present model (Supplementary material File S3).

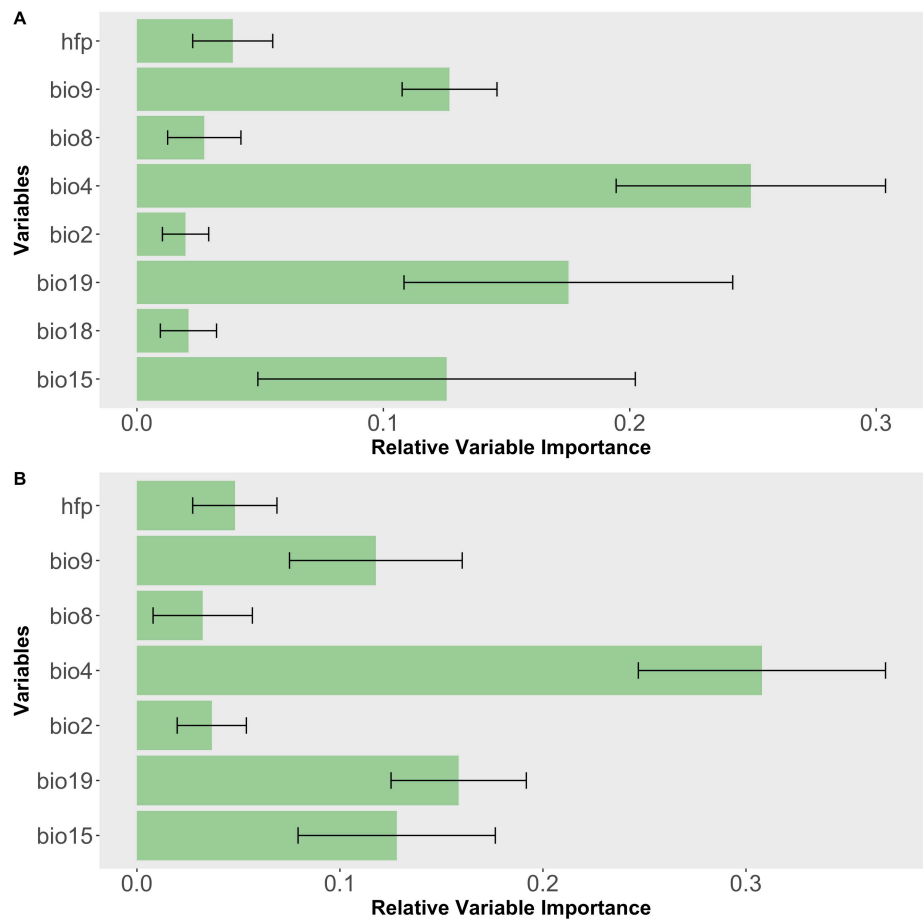


Figure 5. Relative variable importance of predictors in Model 1 (A) and Model 2 (B). hfp (human footprint layer), bio2 (mean diurnal range), bio4 (temperature seasonality), bio8 (mean temperature of wettest quarter), bio9 (mean temperature of driest quarter), bio15 (precipitation seasonality), bio18 (precipitation of warmest quarter), bio19 (precipitation of coldest quarter).

Land use in predicted areas

The main land use in the areas with invasion likelihood > 0.8 were non-irrigated arable land both for Model 1 (41,495 km² accounting for 41% of the total covered area) and Model 2 (23,407 km², 39% cover) and complex cultivation patterns (12,665 km², 12% cover for Model 1 and 8,284 km², 14% cover for Model 2). Broad-leaved forest appeared as a suitable area as well with 12,650 km² and 12% of cover for Model 1 and 6,215 km² and 10% for Model 2. In Model 1 predictions, 1,456 km² (1%) of land use areas with invasion probability > 0.8% were CLC aquatic habitats (namely rice fields, inland marshes, salt marshes, coastal lagoons, water bodies and water courses), whereas in Model 2 predictions they accounted for 752 km² (again, 1%) in these areas. According to Model 1 and Model 2, respectively, aquatic habitats covered 592 and 225 km² in the Continental biogeographic region, and 547 and 456 km² in the Mediterranean one. Overall, aquatic habitats represented only 1.15% of all land cover predicted with > 0.8 probability of occurrence. The overall area with invasion likelihood > 0.8% was higher in Model 1 than in Model 2 (101,482 km² for Model 1 and 59,311 km² for Model 2), and the

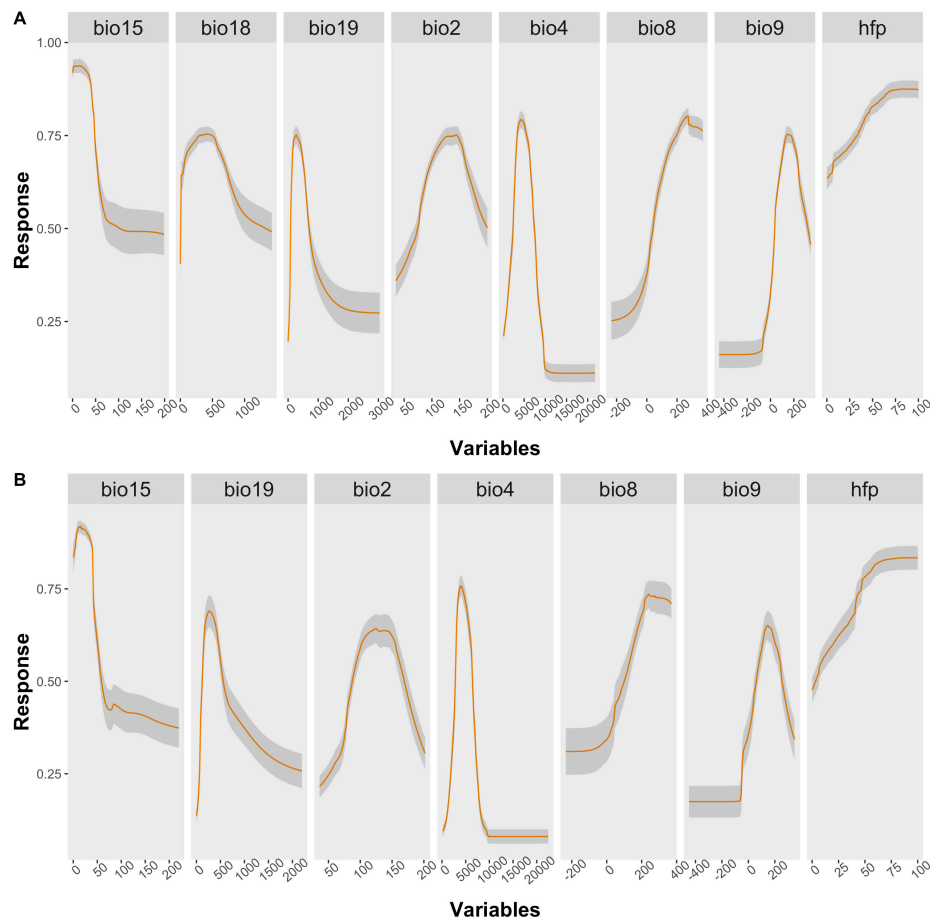


Figure 6. Response curve of *Ludwigia* spp. occurrence likelihood to the variables used as predictors for Model 1 (A) and Model 2 (B). hfp (human footprint layer), bio2 (mean diurnal range_°C), bio4 (temperature seasonality_°C), bio8 (mean temperature of wettest quarter_°C), bio9 (mean temperature of driest quarter_°C), bio15 (precipitation seasonality_%), bio18 (precipitation of warmest quarter_mm), bio19 (precipitation of coldest quarter_mm). Temperatures and precipitation are 10x.

Table 1. Performance of the e models evaluated by AUC (Area Under the (ROC) Curve), Sensitivity, Specificity, TSS (True Skill Statistics) and ccr (Correct Classification Rate) for each modelling algorithm and overall mean: SVM (Supported Vector Machine), RF (Random Forest), BRT (Boosted Regression Trees) and MARS (Multivariate Adaptive Regression Splines). Mean values and SD (standard deviation for 5 replications of 5-fold cross-validation runs).

		AUC		Sensitivity		Specificity		TSS		ccr	
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Model 1	overall	0.979	0.009	0.948	0.019	0.944	0.018	0.892	0.029	0.946	0.015
	SVM	0.981	0.006	0.949	0.014	0.956	0.010	0.904	0.016	0.952	0.008
	RF	0.990	0.003	0.964	0.012	0.959	0.014	0.923	0.016	0.962	0.008
	BRT	0.971	0.006	0.929	0.016	0.929	0.015	0.858	0.015	0.929	0.007
	MARS	0.975	0.005	0.948	0.017	0.933	0.011	0.881	0.017	0.940	0.009
Model 2	overall	0.986	0.008	0.961	0.015	0.954	0.019	0.915	0.027	0.958	0.014
	SVM	0.989	0.002	0.964	0.009	0.963	0.007	0.928	0.008	0.964	0.004
	RF	0.996	0.001	0.976	0.008	0.975	0.007	0.951	0.008	0.976	0.004
	BRT	0.978	0.005	0.956	0.012	0.936	0.014	0.891	0.012	0.946	0.006
	MARS	0.981	0.002	0.949	0.014	0.942	0.015	0.891	0.010	0.945	0.005

predicted area was larger in the Mediterranean than in the Continental biogeographic region in both models, whereas the prediction in the Alpine biogeographic region was very low (Figures 7, 8, Table 2).

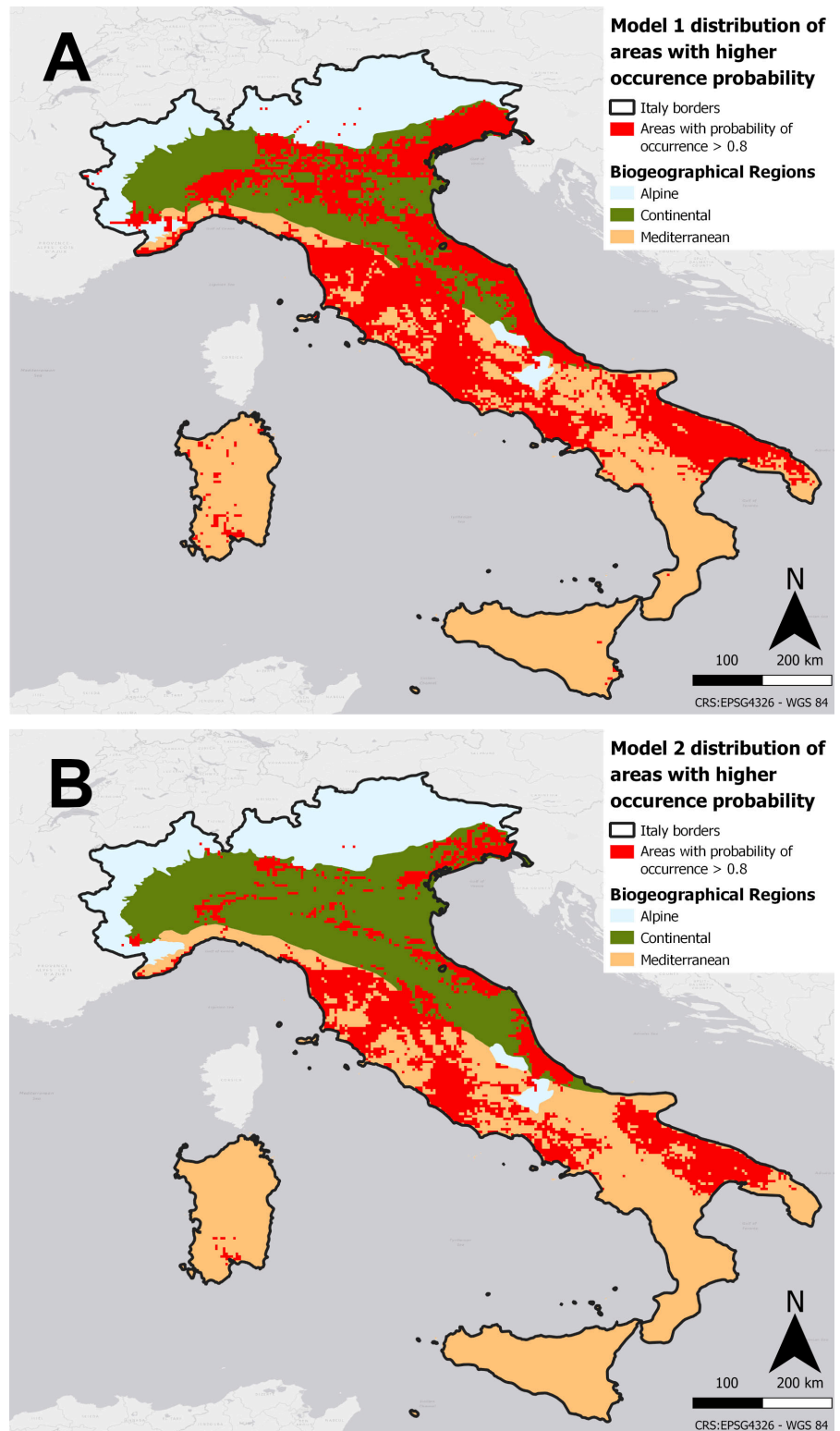


Figure 7. Predicted suitable areas of Model 1 and Model 2 (with likelihood > 0.8) in each biogeographic region in Italy.

Discussion

The long history of introduction and management of *Ludwigia hexapetala* and *L. subsp. montevidensis* in France—where these species are shortlisted among the most invasive species—provides lessons and clear examples of

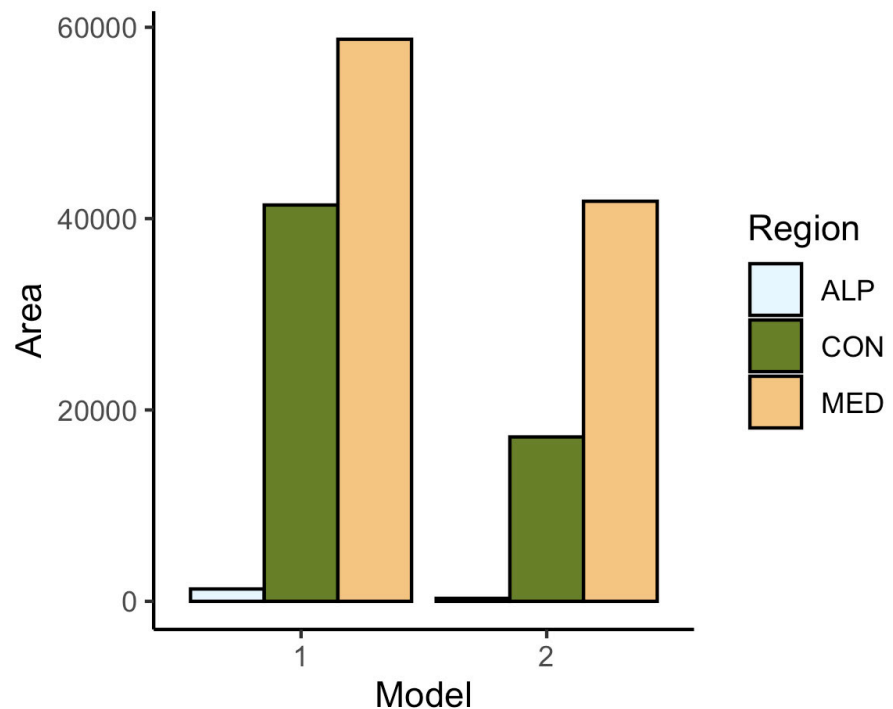


Figure 8. Locations of new records of *Callinectes sapidus*. Previous records in the Iberian Peninsula are shown in panel A (blue circles). The nearest location where *C. sapidus* was known previously is shown in panel B (blue circle). New records of *C. sapidus* are shown in panel C (2017) and panel D (2018) (red circles). Sampling locations without *C. sapidus* captures in this study are shown with white circles. For details see Supplementary material Table S1.

what the situation could be in Italy (both ecologically and economically) if no timely measures are adopted (Dandelot et al. 2005; Dutartre et al. 2007; Thiébaud 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 to 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. *montevicensis* has apparently overcome *L. hexapetala* in number of occurrence records and might be more fit than the latter in expanding its range and in ecological resilience in Italy. This fitness can be associated with the generally more temperate climate in the native range (temperate vs. subtropical in *L. hexapetala* –

Table 2. Land use in areas predicted by Model 1 and Model 2 with likelihood > 0.8. Corine Land Cover code (CLC code) and area (km² and %) occurring within each land use type are indicated. Values in bold cover > 50% of the area.

CLC code	Description	Model 1		Model 2	
		km ²	%	km ²	%
111	Continuous urban fabric	855	0.84	691	1.17
112	Discontinuous urban fabric	4819	4.75	3085	5.20
121	Industrial or commercial units	1850	1.82	1281	2.16
122	Road and rail networks and associated land	114	0.11	92	0.15
123	Port areas	46	0.05	30	0.05
124	Airports	129	0.13	109	0.18
131	Mineral extraction sites	243	0.24	147	0.25
132	Dump sites	29	0.03	22	0.04
133	Construction sites	17	0.02	10	0.02
141	Green urban areas	55	0.05	43	0.07
142	Sport and leisure facilities	133	0.13	92	0.16
211	Non-irrigated arable land	41495	40.89	23407	39.47
212	Permanently irrigated land	398	0.39	257	0.43
213	Rice fields	335	0.33	104	0.18
221	Vineyards	3065	3.02	2279	3.84
222	Fruit trees and berry plantations	1193	1.18	834	1.41
223	Olive groves	5518	5.44	4249	7.16
231	Pastures	904	0.89	449	0.76
241	Annual crops associated with permanent crops	488	0.48	362	0.61
242	Complex cultivation patterns	12665	12.48	8284	13.97
243	Land principally occupied by agriculture with significant areas of natural vegetation	6230	6.14	3144	5.30
244	Agro-forestry areas	53	0.05	1	0.00
311	Broad-leaved forest	12650	12.47	6215	10.48
312	Coniferous forest	676	0.67	383	0.65
313	Mixed forest	1435	1.41	851	1.43
321	Natural grasslands	825	0.81	0	0.00
322	Moors and heathland	2	0.00	438	0.74
323	Sclerophyllous vegetation	829	0.82	381	0.64
324	Transitional woodland-shrub	2314	2.28	979	1.65
331	Beaches dunes sands	229	0.23	117	0.20
332	Bare rocks	14	0.01	2	0.00
333	Sparsely vegetated areas	632	0.62	258	0.43
334	Burnt areas	59	0.06	25	0.04
335	Glaciers and perpetual snow	106	0.10	64	0.11
411	Inland marshes	111	0.11	57	0.10
412	Peat bogs	35	0.03	20	0.03
421	Salt marshes	218	0.21	116	0.20
422	Salines	406	0.40	297	0.50
423	Intertidal flats	280	0.28	113	0.19
511	Water courses	0	0.00	0	0.00
512	Water bodies	26	0.03	22	0.04
521	Coastal lagoons	855	0.84	691	1.17
522	Estuaries	4819	4.75	3085	5.20
523	Sea and ocean	1850	1.82	1281	2.16
TOTAL		101482	100	59311	100

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).

Current and predicted distribution

The current distribution of the two species is almost completely confined to northern Italy, apart from a 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 (Figure 2), despite our recent field observations would suggest that they occur more frequently in stagnant waters. In rivers, the habitats that we observed being colonised 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 Apennine have a low probability of being colonised, although the unsuitable mountain area is more extended in Model 2. The altitude peaks predicted by both models (> 2000 m) seem unlikely to be colonized at the moment, but cannot be excluded given the extreme temperatures caused by climate change. A similar presence/absence map of suitable distribution was shown by the SDM model by Rodríguez-Merino et al. (2018), based on WorldClim data and a different human footprint layer for *L. peploides*. The invasion risk of *Ludwigia* spp. appears therefore very high all over the peninsula, although other local factors not considered by our models, like habitat connectivity, water chemical-physical characteristics, competition by other species, increase of drought in lakes and rivers due to climate warming, may deeply influence the ability of the two *Ludwigia* species to persist, reproduce and colonise new environments. Interestingly the risk appears lower in the region Calabria (the tip of the peninsula) and in the two main islands (Sicily and Sardinia). According to the model of Rodríguez-Merino et al. (2018) the risk in these areas is low for *L. hexapetala*, while it is high, like in the rest of the peninsula, for *L. peploides* subsp. *montevidensis*. The human footprint layer used in our study indirectly accounts for some of these factors (introduction pathways, connectivity, water eutrophication) and showed a gradual increase in the occurrence of *Ludwigia* species with the intensification of these factors, as also reported by Bolpagni et al. (2020) and Montanari et al. (2020, 2022) for other invasive aquatic and non-aquatic plants in the Italian territory. Human footprint factors are more uniform among continents than climate, for this reason the importance of these factors may be lower than those of bioclimatic variables in our models. The consequences of the more and more frequent drought events in the Mediterranean region due to climate change are more difficult to predict, for the uncertainty of the middle and long-term climatic projections. However, the area at high altitude predicted by our study could maintain suitable aquatic habitats for the survival and spreading of the two species if drought should intensify in the lowland. Many native hydro-hygrophytes have found a refuge from habitat degradation and land use change in lowland in small artificial lakes or ponds in the hills or low mountains

(Lastrucci et al. 2004; Buldrini et al. 2017; Gigante et al. 2022; Viciani et al. 2022) and a similar migration can be expected for alien species. Evolution of genotypes that are able to resist to rising temperatures and temporary drought can also be expected, as occurred to several plant species that modified their dispersal mechanisms and growth rates to adapt to urban climate (Johnson and Munshi-South 2017).

Water bodies in agricultural land have the highest likelihood of being invaded according to both Model 1 and Model 2. In the areas predicted as suitable by these models, dominant land uses are non-irrigated arable lands (CLC code 211), complex cultivation patterns (CLC code 242) and broad-leaved forests (CLC code 311), i.e. the rural environments typical of Italy at the foot and on the slopes of the Appennine, especially in the Mediterranean bioregion. According to Model 1, aquatic habitats within the most suitable areas cover 1,172 km², 547 of which in the Mediterranean bioregion; according to Model 2, aquatic habitats cover 688 km², of which 456 km² in the Mediterranean bioregion. These values are most likely underestimated as CLC codes do not consider the numerous small water bodies and water courses (ditches, irrigation canals, private or small lakes and water reservoirs) which are present in the agricultural land and could provide habitat and connectivity among other water bodies. Indeed, available land-cover maps may fail to identify the smallest freshwater habitats (≤ 10 ha Bolpagni et al. 2019; CLC Technical Summary, <https://land.copernicus.eu/en/products/corine-land-cover>) due to resolution issues. Although areas with aquatic habitats may appear small, these might be the only water bodies occurring in the Mediterranean region and an invasion by *Ludwigia* spp. in this area might have more serious consequences on biodiversity and economy than in areas where water is more abundant. The two models are consistent concerning the bioclimatic conditions that can predict the distribution of the two species: low seasonal variation in temperature and precipitation, as well as high temperature in the driest period of the year (average ≥ 20 °C) and low precipitation in the coldest period. Temperature seasonality and annual mean temperature were also the main variables in the model by Gillard et al. (2017) explaining invasive *Ludwigia* spp. distribution in the northern hemisphere. 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 conspicuous, although no flowers are produced (Yen and Myerscough 1989): in other words, they would be favoured by a climate similar to that of the subtropical and intertropical regions they come from. According to Gillard et al. (2017), *Ludwigia* spp. would benefit from an average temperature in the warmest quarter > 27.5 °C. Interestingly in the Po valley, where *L. peploides* subsp. *montevidensis* is currently most widespread and abundant, average summer temperatures of 25–26 °C were recorded in the period 1991–2020 (data from the meteorological observatory of Modena).

Precipitation appears to be a factor limiting the occurrence of these species. The occurrence likelihood is highest for low amounts of rain (50 mm) in the coldest period (bio19). Interestingly, 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. Dormancy, regulated by temperature, precipitation and seasonality, is less frequent for herbaceous species in the tropical climate (and especially in tropical rainforests) than in temperate ecosystems (Zhang et al. 2022). Limited tolerance to precipitation during the dormant season (Zhang et al. 2022) can therefore be another trait of tropical and subtropical species adapted to stable climatic conditions and further indicate low evolutionary divergence of invasive from native populations in climatic adaptation. So far, range expansion is therefore most likely driven by climate change, rather than by adaptive evolution occurred in the introduced range. The Mediterranean bioclimatic region, characterised 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. 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 and available habitats in this transition zone (Vennetier et al. 2007; Hernández et al. 2017). In the model of Gillard et al. (2017), the Po Plain has high suitability to be invaded both in the current and in the future scenarios of 2050 and 2070. According to these SDM models, also based on the WorldClim database and the land use datasets of the Global Lakes and Wetlands Database (GLWD), the current distribution of the two *Ludwigia* species would represent only 12.5% of the wetlands that could potentially be invaded in the water bodies existing today in Europe. With this climatic adaptation, under the highest gas emission scenario, *Ludwigia* spp. ranges could shift northwards in Europe and North America and double their extension by 2070, while in their native range in South America the areas of suitable locations are predicted to decrease up to 55% by 2070 (Gillard et al. 2017).

Implications for management

Low tolerance to precipitation in the coldest period has important implications for management, as it suggests vulnerability to water level during a period of time in which the two species are not emerging from the water and are likely dormant in Italy. Wherever water level can be regulated, maintenance of high water level and of wet conditions along the banks, during these cold and/or raining months, 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; Thiébaud and Dutartre

2009; Hussner et al. 2016). The growth of *Phragmites australis* (Cav.) Trin. ex Steud. stands, as well as of other emergent macrophytes, is strongly impaired by water level at the time of emergence, as seedlings and new shoots from rhizome cannot breathe under water (Mauchamp et al. 2001; Widin et al. 2023). The inclusion of both *Ludwigia* species in the European Union black list and the invasion process in Italy are quite recent events, therefore 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, <http://www.lifetib.it>). Therefore, much 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. With all limitations of the models (most likely underestimated distribution of the species, possible misidentification of the species in GBIF, lack of data on the aquatic environment(s) where the two species occur, unpredictable future climatic conditions and human influence, and stochastic evolutionary events), SDMs provided insight into the invasion of *Ludwigia* species in Italy and identified areas where the invasion risk based on the climatic requirements of the two species might be higher. Indeed, risk analysis, monitoring and management of alien plants can benefit from detailed information on the potential distribution and the identity of receptor habitats (Guarino et al. 2021).

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).

Authors' contribution

ADV and BG contributed equally to the manuscript and are to be considered co-first authors. BG analysed the data and drafted the manuscript. ADV reanalyzed all dataset according to the reviewer's comments, 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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Supplementary material

The following supplementary material is available for this article:

Supplementary material File S1. Occurrence records of *Ludwigia hexapetala* and *L. peploides* subsp. *montevidensis* in Italy. http://www.reabic.net/journals/mbi/2024/Supplements/MBI_2024_Gori_etal_File_S1.xlsx

Supplementary material File S2. Occurrence records of *Ludwigia hexapetala* and *L. peploides* subsp. *montevidensis* downloaded from GBIF on 23 August 2022. http://www.reabic.net/journals/mbi/2024/Supplements/MBI_2024_Gori_etal_File_S2.xlsx

Supplementary material File S3. Spatial dependency of Model 1 (global data, 10×10 km grid) and Model 2 (all global data). http://www.reabic.net/journals/mbi/2024/Supplements/MBI_2024_Gori_etal_File_S3.pdf

Supplementary material File S4. Likelihood distribution maps for each modelling algorithm of each model. http://www.reabic.net/journals/mbi/2024/Supplements/MBI_2024_Gori_etal_File_S4.pdf

Supplementary material File S5. Model performance statistics. http://www.reabic.net/journals/mbi/2024/Supplements/MBI_2024_Gori_etal_File_S5.xlsx