

## High habitat invasibility unveils the invasiveness potential of water frogs

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**Abstract** Determining the invasibility of habitats by alien species is crucial for understanding their spread potential, the habitats the most at risk and to implement adequate management actions. This is urgent for introduced taxa that show high invasion potential across broad geographical scales. We here assess these processes in invasive *Pelophylax* water frogs which are widespread colonizers across Western Europe and for which the invasibility of habitats remains to be quantified. Specifically, we used hierarchical occupancy models in a Bayesian framework to identify local- and landscape-scale features that can enhance occupancy of the most common invasive water frog, the marsh frog (*P. ridibundus*), in southern France. Water frogs were highly detectable and showed high occupancy across the invaded landscape. The invaders expressed a very broad habitat tolerance for both local- and landscape-scale variables while their invasion was facilitated by the occurrence of deep, permanent ponds with abundant aquatic vegetation and high sun exposure. Cross-validation showed a good transferability of models across space. The high invasibility of a wide range of habitats by *Pelophylax* water frogs is alarming and unveils their invasiveness, contributing therefore to explain their success of invasion over broad geographic scales.

**Keywords** amphibians · habitat invasibility · invasive alien species · invasiveness · *Pelophylax ridibundus* · water frogs

## Introduction

Among the plethora of introduced species, only a small number successfully establish and disperse, crossing environmental barriers and then extending their invasion ranges outside their natural limits of distribution (Blackburn et al. 2011; van Kuijk et al. 2021). This capacity to become invasive is facilitated by a number of species-specific traits, such as fast body growth, high fecundity, high competitive or predatory abilities, dispersal adaptation, anti-predator defense and broad ecological preferences (Alpert et al. 2000; Pyšek and Richardson 2008). Therefore, these features determine the vulnerability of a habitat to the establishment and spread of invasive alien species (IAS) (Alpert et al. 2000; Vicente et al. 2010). Knowing the invasibility of habitats, that means their likelihood to be occupied by invaders within a region where the invasion has reached stability, is pivotal to assess the invasiveness of IAS (Pyšek and Richardson 2008), to identify the environments that are most at risk and to evaluate the amount of territory that is susceptible to invasion (Alpert et al. 2000; Louppe et al. 2021), and to provide targeted guidelines for management (Gehring et al. 2020; El-Barougy et al. 2021).

In this rapidly changing world, our understanding of invasibility of habitats relies on the correct identification of habitats suitable for IAS. Species distribution models have greatly improved our understanding of biological invasions and allowed invasibility assessment at multiple scales, from the microhabitat to the global scale (Gallien et al. 2010; Zimmermann et al. 2010). However, many distribution models have limited transferability due to niche shifts of IAS (Early and Sax 2014), inclusion of too many predictors that do not directly affect target species (Rödder et al. 2009; Petitpierre et al. 2017) and failure to correctly consider spatial processes (Veloz 2009; Gallien et al. 2012). The Bayesian framework is particularly suitable to build hierarchical models that simultaneously consider multiple processes, such as models determining species detection and occupancy while incorporating spatial processes (Britten et al. 2021; Falaschi et al. 2021). However, these approaches have been rarely used in the framework of invasibility (Pukk et al. 2021).

Aquatic water bodies, such as ponds, are particularly vulnerable to invasions (Cox and Lima 2006; Céréghino et al. 2008; Strayer 2010). Teleost fishes, crayfishes, amphibians, insects and plants are increasingly introduced into these habitats, highly contributing to the massive decline of aquatic organisms, particularly amphibians (Bucciarelli et al. 2014; Kraus 2015; Nunes et al. 2019; Falaschi et al. 2020). Biphase species, such as anurans, have a high invasion potential; they can disperse over land and colonize isolated ponds (Shine 2010; Measey et al. 2017; Van Wilgen et al. 2018). Distribution models help predict their invasion risk at global levels (Ficetola et al. 2007; Rödder et al. 2017). However, finer-grained analyses are needed to understand how local aquatic features and terrestrial landscapes influence the invasibility of both aquatic and terrestrial environments over large networks.

*Pelophylax* water frogs are cryptic invaders in many European countries (Dufresnes et al. 2017). The most widespread taxon, the marsh frog (*Pelophylax ridibundus*), native to Central and Eastern Europe, was introduced multiple times in Western Europe for ornamental and culinary reasons where it is currently spreading broadly (Dufresnes et al. 2018), and recognized as harmful invaders of aquatic ecosystems in many countries (Holsbeek et al. 2008; Dubey et al. 2014; Pagano et al. 2001; Pille et al. 2021). Invasive water frogs can eliminate the genome

of native *Pelophylax* species through hybridogenesis, raising concerns about the preservation of the genetic integrity of native taxa (Dufresnes and Mazepa 2020). Nevertheless, the persistence of native species after water frog invasions suggests that the ecological divergence between native and invasive *Pelophylax* species is causing ecological isolation (Leuenberger et al. 2014). The strong morphological similarity of *P. ridibundus* with native or other *Pelophylax* heavily limits the number of field-based ecological studies on this IAS in its invaded ranges. Previous research has helped understanding some differences in habitat use between invaders and native conspecifics in natural populations, particularly across contrasting environments, such as lotic and lentic waters (Pagano et al. 2001). However, a more integrative understanding at both fine and coarse grain levels is needed to evaluate the invasibility of habitats and to predict the invasion potential.

To identify the factors promoting the invasibility of habitats by alien *Pelophylax* water frogs, we assessed the relationships between occupancy and habitat features in Larzac, Southern France. Water frogs were historically absent in this landscape (Gabrion 1976; Geniez and Cheylan 2012; J. Gabrion, pers. comm.). *P. ridibundus* was introduced at the end of the twentieth century in Larzac and has since expanded across the whole landscape (Dufresnes et al. 2017; Duret et al. 2022), where it preys on multiple native species (Pille et al. 2021). Specifically, we aimed to (A) determine the level of invasion in the area (i.e. proportion of aquatic patches invaded) and (B) identify the ecological factors promoting the invasibility of habitats considering features of the breeding patches (ponds), landscape composition and connectivity, as incorporating multiple scales is recommended for a clear understanding of distribution patterns (Denoël et al. 2019; Cox et al. 2021). Several factors could favor occupancy by invasive *Pelophylax* through different processes as shown in water frogs and other amphibians: (1) deep ponds could offer shelter and (2) have less probability to dry, thus offering a permanent habitat for adults and allowing tadpoles to complete development until metamorphosis (Buskirk 2003); (3) large ponds could host more resources (Hoffmann et al. 2015); (4) aquatic vegetation could provide shelter and increase food resources (Bounas et al. 2020); (5) complex natural substrate of ponds could provide shelter and resources (Zamora-Marín et al. 2021); (6) sun exposure could allow basking and benefit pond productivity and tadpole growth (Halverson et al. 2003; Ficetola and De Bernardi 2004); (7) the presence of fish could affect the survival of tadpoles (Buskirk 2003). At the landscape scale, (8) high pond density should facilitate connectivity (Bounas et al. 2020; Vimercati et al. 2020); (9) forests, despite serving as shelters for terrestrial life in various stages could negatively affect connectivity (Wells 2007; Cordier et al. 2021); (10) areas with more human settlements can benefit invasive frogs (Wang et al. 2021). Testing the role of these potential processes in explaining water frog occupancy will help assess the invasion risk by this alarming alien species, thus improving our global understanding of the complexity of invasions across aquatic and terrestrial environments.

## **Material and Methods**

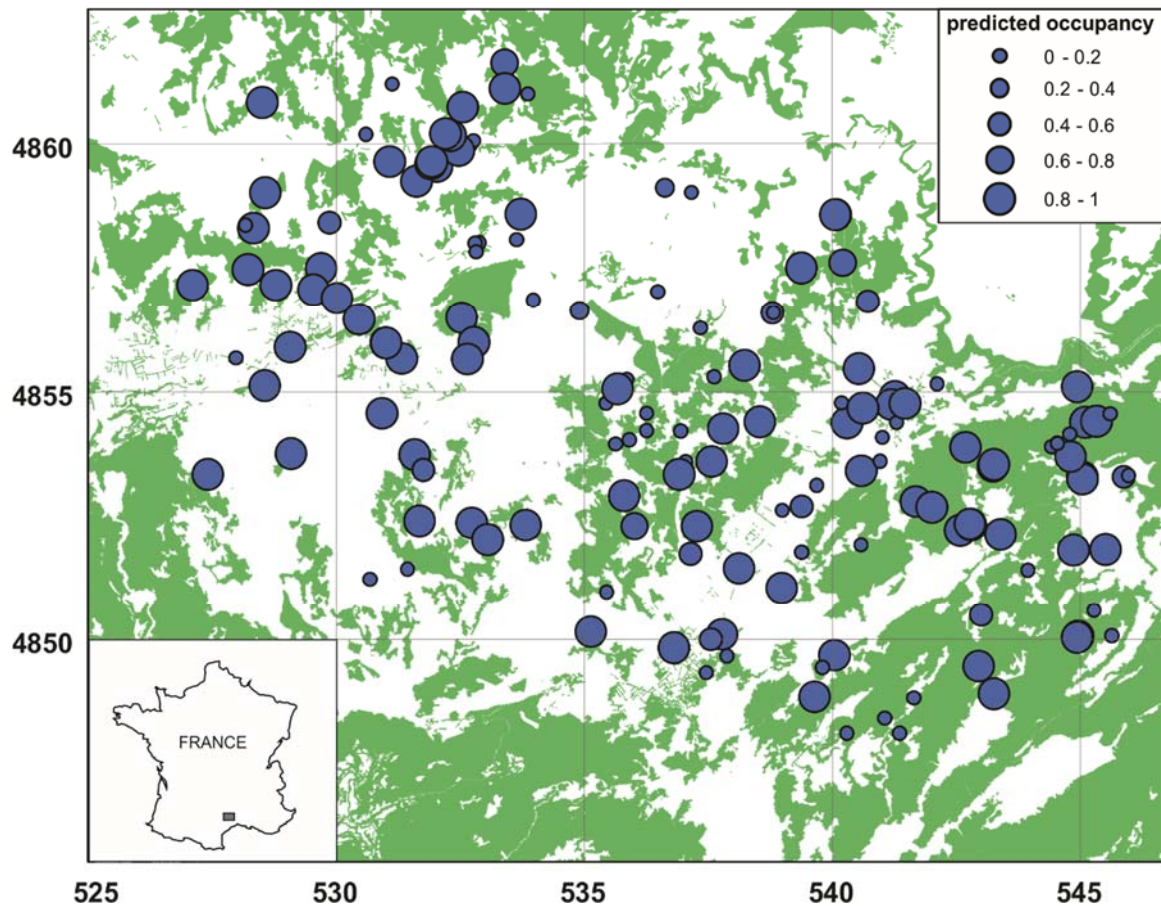
### ***Study area and species***

We focus on *P. ridibundus* water frogs in the Larzac karst plateau (Hérault Department, France). The area is mainly composed of forests and traditionally managed open landscapes. It hosts both natural and artificial ponds and lacks streams and water connections between ponds (Denoël and Ficetola 2014; Duret et al. 2022). Genetic analyses have identified water frogs in the study area as *P. ridibundus* (Dufresnes et al. 2017), a species also named *Pelophylax fortis* in Europe, according to debated nomenclatural revisions (Dufresnes and Mazepa 2020), but the traditional taxonomic assignment is used here until a decision is taken by the code of nomenclature. Two lineages have been identified in the study area, namely, the Balkan marsh frog (*kurtmuelleri* lineage) and the marsh frog (*ridibundus* lineage), which are both of non-indigenous origin (Dufresnes et al. 2017). We consider them a single taxon (*P. ridibundus*) because they show limited phylogenetic divergence, are morphologically cryptic, have unclear delineations, and have the potential to hybridize (Dufresnes et al. 2017; Speybroeck et al. 2020). In order to focus only on the invaded area by marsh frogs, we delineated for the present study a minimum convex polygon (MCP) based on known presence of molecularly identified *P. ridibundus* frogs. We extended this MCP by a 2-km buffer to account for typical dispersal movements (Smith and Green 2005). In this way, we focused only on the invasibility of the habitats within the invaded range, and avoided issues potentially related to habitats that are not colonized because of dispersal limitations (Godsoe 2010).

### **Sampling**

We conducted 578 visual surveys across 159 ponds to determine the occurrence of *P. ridibundus* (Fig. 1). This specifically consisted of 334 and 244 visual surveys performed across 140 and 119 ponds in the studied area in 2019 and 2020, respectively. We took efforts to sample nearly all the ponds in the area, which encompass a broad range of aquatic and terrestrial conditions (Fig. 2). Each pond was surveyed an average of 2.39 (SE: 1.27) in 2019 and 2.05 times (SE: 1.08) in 2020. The surveys were performed between May 2 and July 22 in 2019 and between June 1 and July 21 in 2020 (i.e. day of the year 122 to 203; which is during the peak of the activity period of frogs in ponds: Geniez & Cheylan 2012). Fieldwork was a bit more constrained due to covid restrictions in 2020. Surveys were conducted during daytime (9h02 to 19h14), as water frogs are long-term aquatic residents that are active during the day and easily spotted at either the water surface or the edge of the water body. We determined occurrence in a standardized way: we first checked the entire water surface and its immediate border from a distance with binoculars (Swarovski EL 10x42) to avoid any escape before our arrival. We then walked slowly toward and then around the pond for close-range visual observation.

For each pond, we quantified seven pond-scale features (maximum water depth, water surface area, percentage of aquatic vegetation, type of substrate [natural versus artificial], sun exposure, fish presence, and water permanence) and three landscape-scale features (number of ponds, proportion of forests, and proportions of buildings within 1000 m of each focal pond; the 1000 m buffer is the typical dispersal distance of the target species) (See Suppl. Text S1 for details on the data collection for each variable and the introduction for justification of choice of the variables).



**Fig. 1** Distribution of the studied ponds and occupancy probabilities of ponds (blue circles) by invasive *Pelophylax ridibundus* water frogs (Bayesian static occupancy model). Background (green): forest (BD Topo, open licence, Institut Géographique National, France). Grid: Universal Transverse Mercator (km) (drawn in ArcMap 10.5).

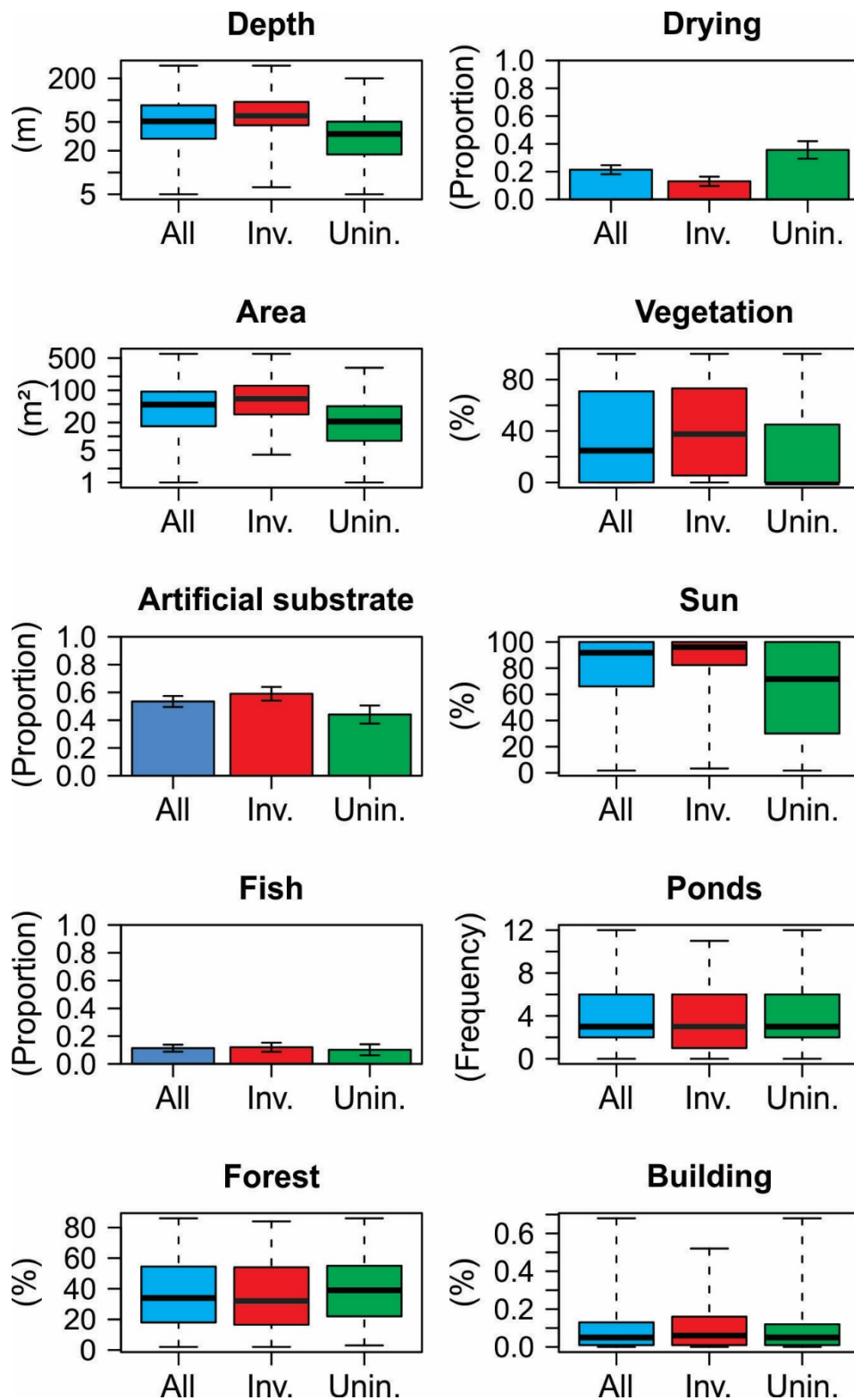
### *Statistical analyses*

We used data from both years to build static occupancy models with binomial error distribution within a Bayesian framework to identify habitat features associated with invasibility by water frogs. Occupancy models are hierarchical models that simultaneously consider ecological and observational processes in order to correct biases in parameter estimates due to false absences. Such models also allow the calculation of reliable estimates of the overall species occupancy across a landscape and of the relationships between species and environmental features (Kéry and Royle 2016). In all the models, we assumed that the date of the survey (expressed as day of the year) and hour could influence the detection probability of frogs due to their phenology and behavioral habits, both traits being also possibly temperature dependent. As a consequence, day of the year and hour were considered as covariates of detection probability. Data from a subset of observations confirmed that temperature was correlated with the day of the year (Pearson correlation coefficient,  $r = 0.64$ ,  $P < 0.001$ ). We tested ten variables representing our *a priori* hypotheses at the local scale (pond features) and landscape scale (Fig. 2; Suppl. Text S1) on the occurrence of water frogs; these variables were regarded as covariates of occupancy

probability. Preliminary analyses confirmed the absence of strong collinearity between the occupancy covariates (all  $r < |0.7|$ ; see Suppl. Table S1). Pond area and water depth were log-transformed to avoid skewed predictors. All variables were then standardized with mean = 0 and standard deviation = 1 to allow comparison of effect sizes and reduce convergence time. To estimate average occupancy separately for the two years of the study, we added a year random intercept. Additionally, we added a “site” random effect to take into account the non-independence of surveys performed at the same site in different years.

To evaluate the necessity of integrating a spatial term, we checked potential autocorrelation of model residuals in the non-spatial model by calculating Moran’s I in both years. Following Wright et al. (2019), we defined residuals of occupancy as  $r_{i,p} = z_{i,p} - \psi_{i,p}$  where  $r_{i,p}$  is the residual at site  $i$  and for the posterior  $p$ ;  $\psi_{i,p}$  is the probability of occupancy;  $z_{i,p}$  is the latent occupancy state, defined as  $z_{i,p} \sim \text{Bernoulli}(\psi_{i,p})$ . Subsequently, for each posterior, we calculated Moran’s I value using the EcoGenetics R package (Roser et al. 2017), obtaining a distribution of Moran’s I values at different distances. We considered Moran’s I as significant if its distribution did not overlap zero at any distance. To further test a possible advantage of accounting for unmodelled spatial autocorrelation, we run additional models including a spatial autoregressive term. This variable was calculated on the basis of an intrinsic Gaussian conditional autoregressive model (Banerjee et al. 2014). Intrinsic conditional autoregressive (ICAR) models are used to integrate spatially correlated random covariates; they perform well, showing an excellent capability to identify relationships between species distribution and environmental variables with complex spatial structures (Beale et al. 2010). The adjacency matrix used in the ICAR model had a truncation distance of 2.1 km, which is the minimum distance needed to connect all the study sites. The model integrating the spatial autoregressive term did not include the site random effect. Additionally, we ran a simplified model without the detection component, to evaluate potential differences in the estimated effect of occupancy covariates due the inclusion of detection probability.

We used two alternative approaches to assess the predictive performance of our models: the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS). AUC and TSS are threshold-dependent and -independent measures of accuracy, respectively. AUC ranges from 0.5 to 1; values between 0.5 and 0.7 indicate low accuracy, values between 0.7 and 0.9 show good accuracy, and values  $> 0.9$  depict high accuracy (Swets 1988). TSS ranges from  $-1$  to  $1$ ; a value of  $1$  indicates perfect agreement between model prediction and testing data, while a value of  $0$  indicates performance no better than random (Allouche et al. 2006; Cohen 1960). Performance measures for both model types (with and without spatial terms) were assessed using an independent set of presence/absence data for validation. To do so, we run each model type four times, each time excluding 20% of sites (32 sites) closest to the northern/southern/western/eastern borders of the study area. Presence/absence at excluded sites were then used to calculate AUC and TSS values, separately for the two years of sampling. To estimate predicted values of occupancy at testing sites, site or spatial random effects were set to zero, respectively in non-spatial and spatial models. To build maps of occupancy, we used average estimates between 2019 and 2020 if a site was sampled both years.



**Fig. 2** Environmental features of Larzac ponds (All; blue), and those invaded (Inv.; red) and not invaded (Unin.; green) by *Pelophylax ridibundus* water frogs. Bars: means, box-plot: two times interquartile ranges; whiskers: ranges in box-plots, SE in bar plots.

All the models were run with vague priors (Guillera-Arroita et al. 2019). Priors for the intercept and covariate of detection probability (day, hour) were normal with mean = 0 and precision = 0.01; priors for the intercept and covariates of occupancy were normal with mean = 0 and precision = 0.1; the prior for the site random effect followed a normal distribution with mean = 0 and variance  $\tau$ . The  $\tau$  parameter followed a half-Cauchy distribution (Gelman 2006); the prior for the precision parameter of the ICAR model was taken from a gamma distribution with mean = 0 and precision = 0.1. The occupancy models were run in the R environment (R Core Team 2021) with the *nimble* package (de Valpine et al. 2017). For each model, we ran three Markov chain Monte Carlo (MCMC) chains for 400,000 iterations and discarded the first 300,000 as burn-in and sampling with a thinning of 100, obtaining a total of 1,000 posteriors for each chain. Convergence was assessed both visually and by running MCMC chains until reaching Rhat values  $< 1.1$  (Brooks and Gelman 1998).

We tested the goodness of fit of the model with the site random effect with a posterior predictive check, by calculating the Freeman-Turkey discrepancy for real data and data simulated from the posterior distribution (Kéry and Royle 2016).

## Results

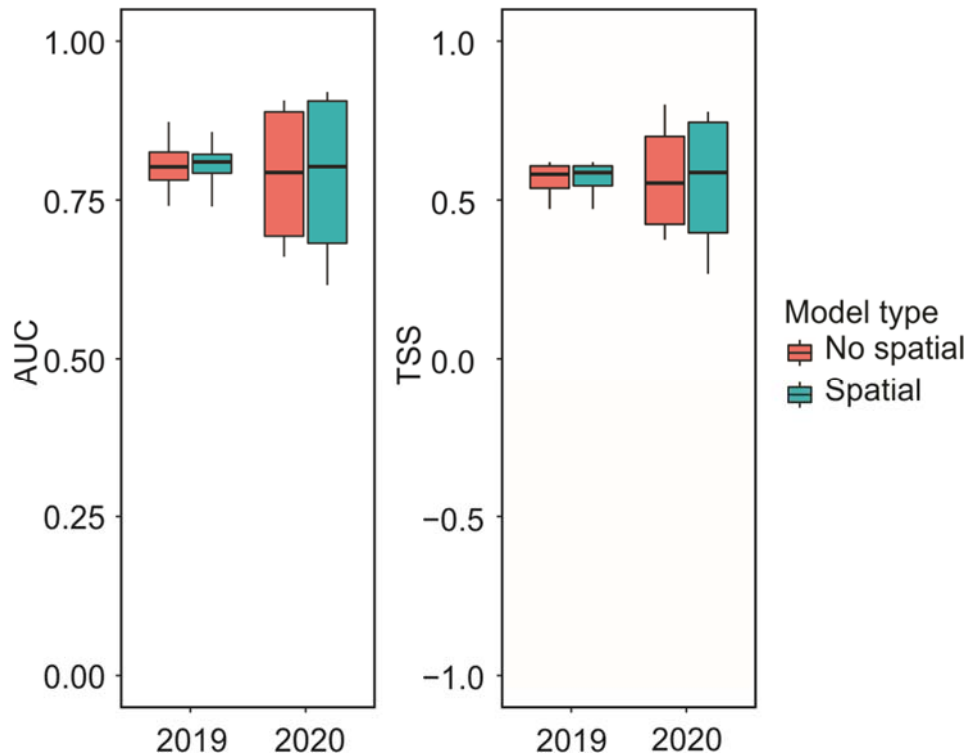
### *Model performance and occupancy predictions*

All models showed good to excellent performance in predicting the testing data, with all mean AUC and TSS values above 0.78 and 0.55, respectively (Fig. 3). Moran's I values for the residuals of the non-spatial model broadly overlapped zero (Suppl. Fig. S1). The inclusion of spatial autocorrelative terms in the models did not significantly improve the predictive performance (Fig. 3). As a consequence, we used the non-spatial model to estimate occupancy (Fig. 1).

The models with and without the detection component showed very similar performance (Fig. 3 and 4; Suppl. Fig. S2). Detection probabilities were very high: average = 91.5% (95% CI = 88.2 – 94.3%). The date of the survey did not show a clear effect on detection probability while the hour showed a negative effect (odds ratio = 1.46; Suppl. Table S2).

Goodness of fit test showed that Freeman-Turkey discrepancies of real vs. simulated data were evenly distributed around the 1:1 line, with a Bayesian  $p$ -value of 0.52, indicating that the model was appropriate to describe the data (Suppl. Fig. S3).



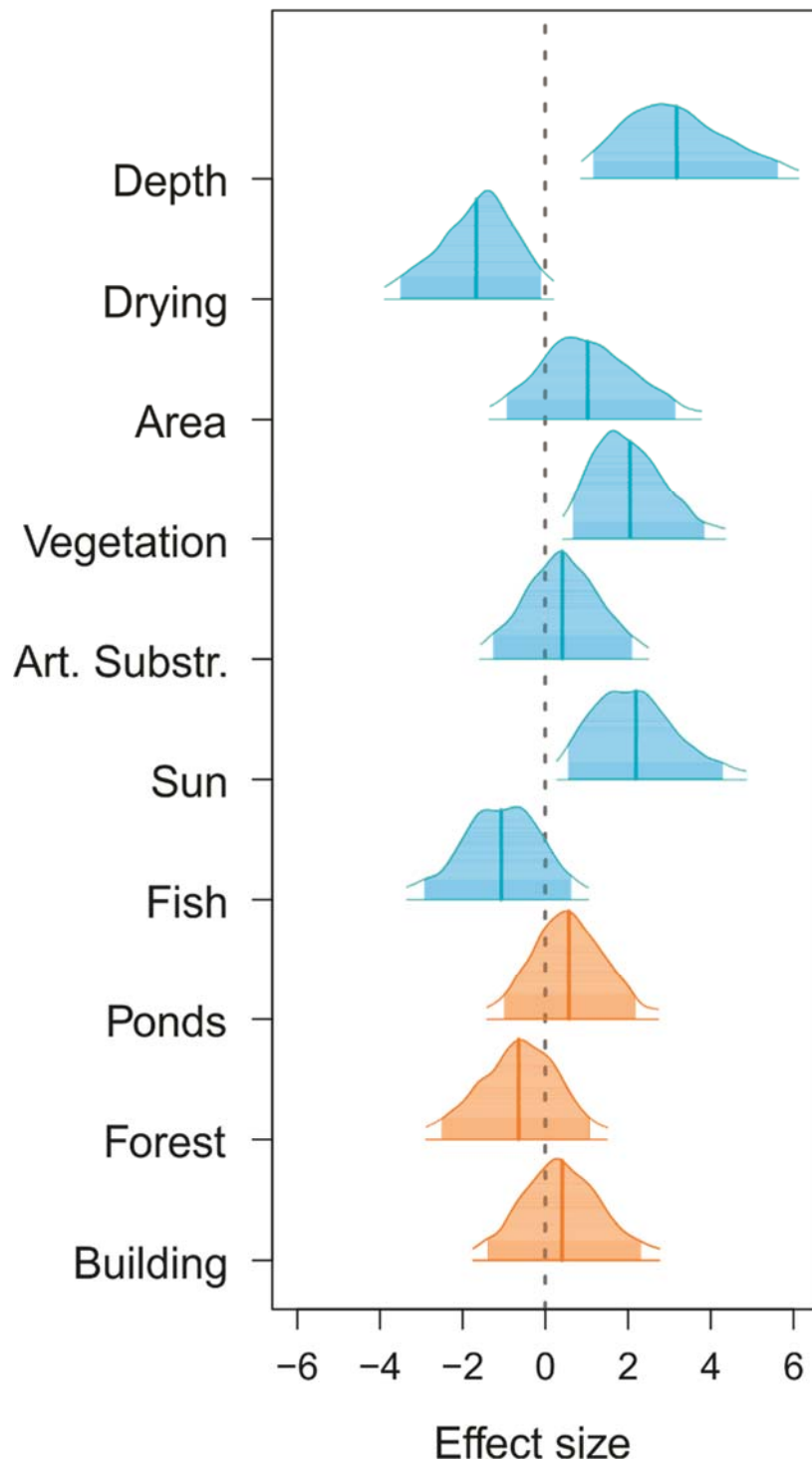


**Fig. 3** Measures of performance of the models depicting the occupancy of habitats in terms of occurrence of invasive *Pelophylax ridibundus* water frogs. Performance was calculated through cross-validation, by running four replicates of the model with 80% data and tested on 20% of the data. Random site: models not considering spatial autocorrelation and with site identity as a random effect; Spatial: models considering spatial autocorrelation. AUC: area under the receiver operating characteristic curve, TSS: true skill statistic. Bars: means, box-plot: two times interquartile ranges; whiskers: 1.5 times interquartile range.

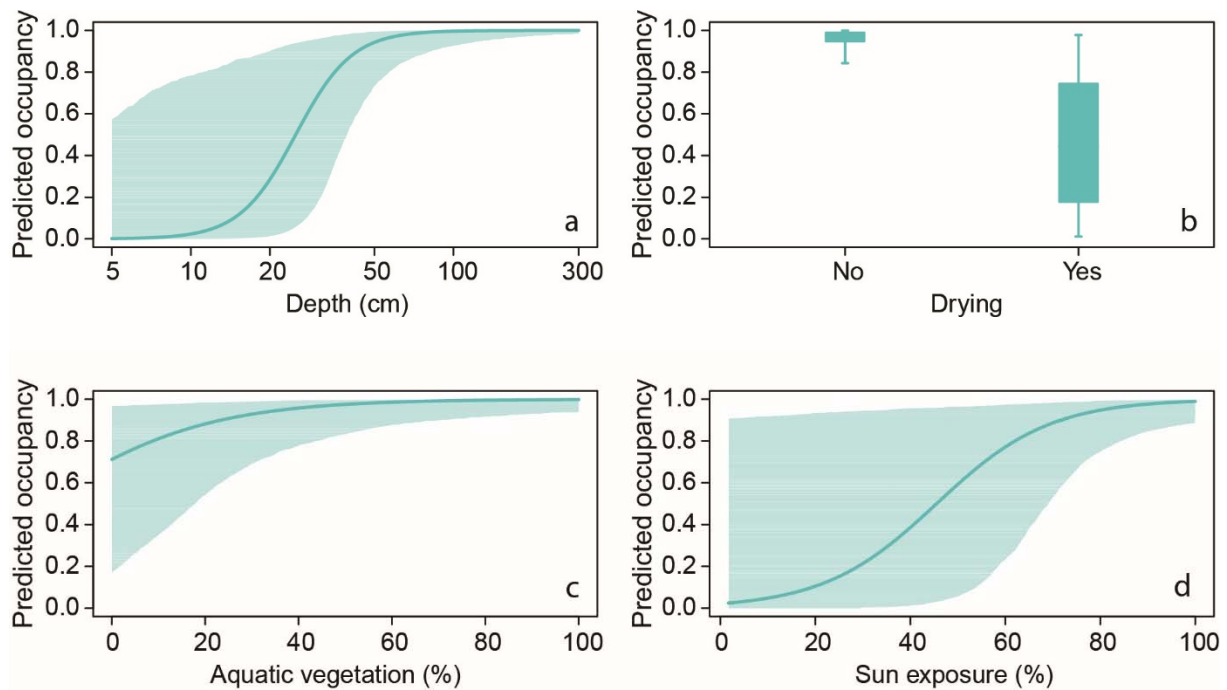
### ***Habitat invasibility***

Invasive marsh frogs were detected in 100 (63%) out of the 159 surveyed ponds (59% of the 140 surveyed ponds in 2019 and 66% of the 119 surveyed in 2020). The average predicted occupancy of ponds was 61.6% (95% CI = 54.0 – 69.0% ; Fig. 1). In 2019, it was 61.3% (95% CI = 53.3 – 69.3) and in 2020 it was 69.6% (95% CI = 61.3 – 77.7%).

Marsh frogs were found in shallow and deep ponds, permanent and temporary, small and large, vegetated and not vegetated, with and without natural substrate, with and without much sun exposure, with and without fish, quite isolated and not isolated from other ponds, in forested and not forested landscapes and in areas with none and much buildings (Fig. 2). Nevertheless, occupancy by marsh frogs was affected by some environmental features, and was particularly high in deep and permanent ponds with high sun exposure and aquatic vegetation cover (Fig. 4 and 5; odds ratio: depth = 22.58, permanency = 5.35; sun exposure: 8.75, vegetation cover: 7.31). The other variables showed no strong effects on invasibility, as shown by the credible intervals crossing zero for each parameter (Fig. 4; Suppl. Table S2). The model built without detection probabilities (Suppl. Fig S3) showed similar results to the model with detection probabilities (Fig. 4).



**Fig. 4** Posterior distributions of parameters related to *Pelophylax ridibundus* water frogs occupancy for both local (blue) and landscape (orange) features, as estimated by Bayesian occupancy models accounting for detection probability. The outlines represent the 95% Credible Intervals (CIs), the shaded areas represent 90% CIs, and the vertical lines denote the mean estimate. The variables are explained in Suppl. Text 1. Art. Subs.: artificial substrate.



**Fig. 5** Relationship between the estimated occupancy of *Pelophylax ridibundus* water frogs in Larzac and the four strongest predictors, as estimated by occupancy models. Conditional regression plots with credible interval for (a) water depth (in log scale), (b) box plots for drying risk (bars: means, boxes: 75% CIs, whiskers: 95% CIs), (c) aquatic vegetation cover, and (d) sun exposure.

## Discussion

Almost all water bodies considered in the analyses showed high occupancy for invasive marsh frogs. This suggests an impressive invasibility of habitats by this IAS, which can explain its fast expansion over Western Europe (Dufresnes et al. 2017) and ranks water frogs among the most successful amphibian invaders (Capinha et al. 2017; Shine 2018; Johovic et al. 2020). Their broad tolerance for a large variety of pond traits and surrounding landscapes as well as their preference for habitats which are considered favorable for native species also alarm for their potential impacts on native communities.

The results are supported by our multiple modeling Bayesian approaches, which all performed well, showing a very good performance in predicting occupancy. Static occupancy models are usually based on detection/non-detection data from a single season of survey across a study area. Performing surveys across multiple years allowed us to take into account the variability of environmental conditions over time and thus alleviate transferability issues (Fourcade et al. 2018; Liu et al. 2020).

Taking into account SAC can affect model results (Domisch et al. 2019; Dormann et al. 2007) and improve their transferability (Dormann et al. 2007; Veloz 2009; Fourcade et al. 2018). However, existing occupancy models only rarely integrate autocorrelative terms, and to the best of our knowledge, this has not been implemented in the framework of IAS. This is

probably related to the difficulty of integrating environmental features and spatial data in the same models. Bayesian models provide a flexible framework that allows the implementation of spatial autocorrelation terms, detection probabilities and habitat features to depict occupancy (Kéry and Royle 2016). In the present study, data were not spatially autocorrelated, likely due to the high occupancy pattern. It was therefore not surprising that adding a spatial term did not improve model prediction in the present case.

### ***High habitat invasibility***

Among the traits promoting invasiveness, high ecological tolerance makes invaders highly successful in extending over large geographic areas (Alpert et al. 2000; Vicente et al. 2010; Louppe et al. 2021). The high invasibility of ponds to marsh frogs shows that this species is highly tolerant to various environmental conditions and therefore can invade most habitats at both local and landscape scale. Here, we sampled all kinds of available ponds in the study area (including remote ones), which have a wide range of environmental features, and considered only ponds inside the invaded area after the completion of the invasion. Interestingly, none of the land covers surrounding the studied ponds affected occupancy. This considerably differs from the case of many other amphibian species, where pond availability in the neighborhood or the presence of open versus forest areas typically favors occupancy and dispersal (Cayuela et al. 2020; Denoël and Ficetola 2007; Vimercati et al. 2020). The broad use of aquatic and terrestrial habitat resources also contradicts the view that non-native water frogs may have some habitat requirements that could limit their replacement of native taxa (Leuenberger et al. 2014). Our findings also support the view that marsh frogs stand among the most successful amphibian invaders, such as cane toads (Shine 2010; Shine 2018), bullfrogs (Ficetola et al. 2007; Johovic et al. 2020), and African clawed frogs (Measey et al. 2012).

### ***Predictors of habitat invasibility***

Suitable aquatic and terrestrial habitats favor the colonization of invaders after establishment. Despite their generalist ecology, the occurrence of marsh frogs was favored by some pond features. Invasibility was particularly high in sunny, vegetated, and deep ponds that did not dry. These habitat features are important for many amphibians and often increase occupancy for native species (Rowe et al. 2019; Falaschi et al. 2021; Hamer et al. 2021; Romansic et al. 2021), suggesting that the most favorable habitats for native amphibians are particularly at risk of invasion. Together, these results call for research on coexistence patterns, which may be facilitated by refuges provided by aquatic vegetation, and the complex consequences of invasion on natives (Bucciarelli et al. 2014; Manenti et al. 2020). However, this task is challenging, as invaders may also cause shifts in the composition of invaded communities.

Sunny ponds favor basking, a behavior of water frogs that are often described as thermophilous anurans (Ficetola and De Bernardi 2004), and increase the growth of tadpoles (Halverson et al. 2003). Vegetation promotes the complexity of aquatic microhabitats, can increase the availability of prey (such as insects) and can provide shelter to predators (Briggs

et al. 2019; Hamer et al. 2021). Deep ponds can also give shelter to adults (Duret et al. 2022). Although the depth of ponds is not strongly correlated to drying risk in the studied ponds (see Suppl. Table S1), the deepest ponds are usually permanent. Together, pond depth and a low drying risk allow permanent availability of water, which is essential for water frogs. The tadpoles of water frogs require long periods for metamorphosis, and adults remain in water bodies for even longer periods (Dufresnes et al. 2020; Duret et al. 2022).

Many IAS are more tolerant than native species to anthropogenic habitats, taking advantage of apparently suboptimal habitats during their colonization (Marvier et al. 2004; Wang et al. 2021). Indeed, although introduced teleost fish are detrimental to native amphibians (Denoël et al. 2019; Bounas et al. 2020; Miró et al. 2020; Schmidt et al. 2021), including those in the study area (Crochet et al. 2004; Denoël and Winandy 2015), the marsh frogs in this study have invaded ponds regardless of fish presence. The same pattern was found in another broad-scale amphibian invader, the bullfrog (Rowe and Garcia 2014; Rowe et al. 2019). Similarly, artificial ponds, natural ponds, and areas with varied building cover show similar invasibility by marsh frogs. González-Bernal et al. (2016) found that feral cane toads can thrive better of anthropogenic habitats over shrublands. This suggests that some patterns can be generalized for any invasion and that some invasive species (in our case invasive frog species) can benefit from the same environmental patterns, which have yet to be determined, in light of the invasion syndrome (Novoa et al. 2020).

## Conclusions

The present study pinpoints the high invasibility of habitats by marsh frogs at both local and landscape scales. These frogs' broad ecological tolerance is in perfect concordance with their broad and fast geographic invasion patterns across Western Europe (Dufresnes et al. 2017), suggesting the capacity of this IAS to use most pond environments and their surroundings. Habitat management could help to decrease locally the occupancy by water frogs but potential effects on native species have to be considered (Rowe et al. 2019). Indeed, preferences for the most permanent ponds, well vegetated and sun exposed are also likely to favor some native amphibian taxa as well as other organisms of the studied area (Geniez & Cheylan 2012). Frog removal in target habitats may help locally native species but is likely difficult given the high number of invaded ponds. The difficulties of management along with the broad-scale invasion and the identified predatory pressure on native amphibians (Pille et al. 2021) are therefore particularly alarming. Future research should encompass the long-term impacts of these invaders on native communities, how the spatial niche of invaders and native species overlap at local and landscape scales and what solutions could benefit native species. The recent diffusion of metabarcoding approaches will help target future research on this morphologically cryptic group of amphibians over invaded and native ranges (Dufresnes et al. 2020). Fine-grained, broad-scale phylogeographic studies, such as those using RADSeq approaches, will also help shed light on the origin of IAS (Dubey et al. 2019). Together, these results will enhance our understanding of how the diversity of IAS and invaded landscapes can affect the invasibility of habitats (Maitner et al. 2021) and ultimately depict the invasiveness potential of water frogs and other IAS.

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**Supplementary Information** The online version contains supplementary material

### **Data availability statement**

All data analysed during this study are included in this published article [and its supplementary information files].

### **Declarations**

**Conflict of interest** The authors declare that there is no conflict of interest

**Consent for publication** The authors give consent to publish.

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