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# One frog to rule them all: Wide environmental niche of invasive marsh frogs induces large co-occurrence patterns with native amphibian prey in ponds

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## Abstract

Invasive alien anurans are introduced worldwide in freshwater ecosystems where they can have a strong impact on native organisms such as amphibians. The risk for natives is dependent on the degree of niche overlap and co-occurrence in pond breeding sites. In the present study, we focused on alien marsh frogs (*Pelophylax ridibundus*) that are invading nationwide areas in Western Europe and which prey on both caudates and anurans. We assessed aquatic habitat preferences, pond use and environmental niche overlap between invasive populations of marsh frogs and five species of native amphibian prey of the Larzac plateau (southern France). Due to their large environmental niche, marsh frogs have become the most ubiquitous amphibians in the area. Occupancy models revealed that they had aquatic habitat preferences (e.g. water depth and aquatic vegetation) similar to most species of native amphibians. This resulted in a large overlap between the environmental niche of the invader and its potential prey. The frequent coexistence in ponds therefore exposed native species to predation risk and other potential disturbances caused by marsh frogs. Altogether, these results highlight on the risks posed by such opportunist invaders for native amphibians that occur in their wide invasion range.

## Keywords

Niche overlap · Habitat preferences · Invasive alien species · Occupancy models · Predation risk · Water frogs

## Introduction

Freshwater habitats are highly sensitive to biological invasions, and many have been colonized by invasive alien species (Cox & Lima, 2006; Strayer, 2010). Once settled, invasive alien species can have various types of interactions with native species such as predation, competition, disease transmission or hybridization (Kraus, 2015; Nunes et al., 2019; Falaschi et al., 2020). These new pressures can negatively impact native species and communities, sometimes leading to population decline or even extinction (Ricciardi & Macisaac, 2011; Gallardo et al., 2016).

Among the diversity of invasive taxa in freshwater ecosystems, anurans have attracted much attention because of their wide invaded ranges worldwide (Kraus, 2015; Measey et al., 2016). Introduced anurans often exhibit a wide generalist and opportunistic diet, feeding on a wide range of native organisms that are essential to freshwater ecosystem functioning (Courant et al., 2017; Pille et al., 2023). This predation often includes native caudates and anurans at varied stages of their life cycle (Silva et al., 2011; Boelter et al., 2012; Jancowski & Orchard, 2013; Measey et al., 2015; Courant et al., 2017; Bissattini et al., 2019; Oda et al., 2019; Pille et al., 2021). In addition, introduced anurans can also be responsible for non-lethal effects affecting the fitness of native amphibians (Kats & Ferrer, 2003; Bucciarelli et al., 2014; Nunes et al., 2019). Consequently, native species of amphibians can be disrupted at the population or community level in the invaded range of introduced anurans (Li et al., 2011; Lillo et al., 2011; Richter-Boix et al., 2013; Bucciarelli et al., 2014; Courant et al., 2018; Falaschi et al., 2020).

One possible approach to assessing the potential risk faced by native species is to model the environmental niche of invaders and to quantify the overlap with the invaders. Because biological invasions by amphibians can occur on a large continental scale, most previous studies used mainly remote sensing data such as climatic layers to assess environmental niche and to predict the potential threats to many species (Ficetola et al., 2007; Ihlow et al., 2016; Becerra López et al., 2017). However, modeling of the environmental niches on a finer scale of the biological interactions between invaders and native species is needed to fully assess the potential impact on native amphibians. Indeed, most amphibians rely on freshwater bodies for breeding purposes and ponds are therefore privileged places for interactions in amphibian communities (Semlitsch et al., 1996). Pond networks can exhibit heterogeneity along multiple habitat parameters that influence breeding site selection by amphibians (Strijbosch, 1979; Werner et al., 2007). However, due to their generalist traits, the most successful invasive anurans often exhibit a wide environmental niche, enabling them to colonize a large diversity of freshwater bodies (Denoël et al., 2022). As a consequence, invasive amphibians may largely co-occur with native species, therefore increasing the risk of impacting their populations.

Marsh frogs (*Pelophylax ridibundus* [Pallas, 1771]) are the most widely introduced amphibians in the Palearctic (Dufresnes et al., 2024). They originate from many places (in particular in South-Eastern Europe, Turkey and the Middle-East; Dufresnes et al., 2024) and are now found across entire countries, including Belgium (Holsbeek et al., 2010), France (Pagano et al., 2001; Dufresnes et al., 2017a, 2017b), and Switzerland (Dufresnes et al., 2018), and have become a concern in other countries such as Italy (Bellati, 2019; Bruni et al., 2020) and the United Kingdom (Zeisset & Beebee, 2003). Many studies have underlined their impact on sister taxa through hybridization (e.g., Holsbeek et al., 2010; Kolenda et al., 2017). Another work highlighted the potential negative impact of water frogs on populations of native amphians (Roth et al., 2016), whereas some recent papers have alerted about the risk of predation on native amphibians, including vulnerable species of newts and anurans (Pille et al., 2021, 2023; Fuento & Deso, 2023). However, no study has estimated the risk for native amphibians from an ecological niche and co-occurrence perspective.

In this study, we aimed to measure the degree of co-occurrence in ponds and the environmental niche overlap between alien marsh frogs and native species of amphibians. Our goal was to assess the risk for native pond-breeding amphibians to be exposed to invasive alien marsh frogs during their aquatic phase. To this end, we conducted visual encounter surveys of alien marsh frogs and native amphibians in an area historically devoid of water frogs (*Pelophylax* genus): the Larzac plateau in southern France (Gabrion, 1976). Following multiple introductions in the late 20th century, populations of alien marsh frogs have now been established at high densities throughout this area (Denoël et al., 2022; Duret et al., 2022), where they are considered to exert a negative impact on native amphibians because of predation (Pille et al., 2021, 2023). Due to the broad tolerance of marsh frogs to various aquatic habitat parameters (Denoël et al. 2022) and to the shared preferences by pond-breeding amphibians for some habitat features, we expected wide overlaps between the aquatic ecological niche of the invader and the respective ones of the native species. This hypothesis stands also with the fact that marsh frogs can coexist with some newt and anuran species in their native range (M. Denoël, pers. obs.). Therefore, we did not expect a complete or nearly-complete exclusion of native amphibians, as it has been documented with fish (Denoël et al. 2019), including in the study area (Denoël & Ficetola, 2014). In addition, we expected variation in the respective overlap with each of the native species due to their ecological preferences (Geniez & Cheylan, 2012).

## Methods

### Study sites and species

The study area is located in the Hérault and Gard departments, on the Larzac karst plateau in southern France (43°48’ N to 43°54’ N; 3°21’ E to 3°33’ E; Fig. 1). The landscape is dominated by open and traditionally managed lands as well as forests constituted of supra-Mediterranean assemblages (Durand-Tullou, 1959). This area has many ponds that are not connected through water connections such as streams. Ponds host various native anuran and caudate species, which use them for breeding purposes (Cheylan & Geniez, 2012). In this study, we focused on the species that were prevalent in the diet of invasive marsh frogs (Pille et al., 2021) and for which we had enough data to be included in the analyses: the mid-wife toad (*Alytes obstetricans* [Laurenti, 1768]), the Mediterranean tree frog (*Hyla meridionalis*, Böttger, 1874), the common parsley frog (*Pelodytes punctatus* [Daudin, 1802]), the marbled newt (*Triturus marmoratus* [ Latreille, 1800]) and the palmate newt (*Lissotriton helveticus* [Razoumoky, 1789]). Long-term studies from the 1970s indicated the absence of marsh frogs, as well as other species of *Pelophylax* water frogs, on the Larzac plateau (Gabrion, 1976; Gabrion, pers. comm.). However, marsh frogs were introduced recently and were still scarce in the early 2000s (M. Denoël, pers. obs.). Exhibiting high locomotor and physiological performances under the climatic conditions of the area (Padilla et al., 2023), marsh frogs have now colonized most of the plateau (Denoël et al., 2022). Genotyping indicated that the alien invaders were the marsh frogs *P. ridibundus* including the cryptic *ridibundus* and *kurtmuelleri* lineages which originate as far from the study location as Southeastern Europe (Dufresnes et al., 2017a, 2024). No native populations of *Pelophylax* have been detected in the studied area, which is a plateau limited from the lowlands by Seranne mountain in the south-east (Demay et al., 2023). We focused our surveys on the invaded range of invasive marsh frogs by computing a minimum convex polygon (MCP) on ponds where marsh frogs were molecularly identified. The MCP was extended by a 2 km buffer to account for dispersal movements (Smith & Green, 2005), therefore avoiding pond areas potentially not colonized by marsh frogs (Godsoe, 2010).

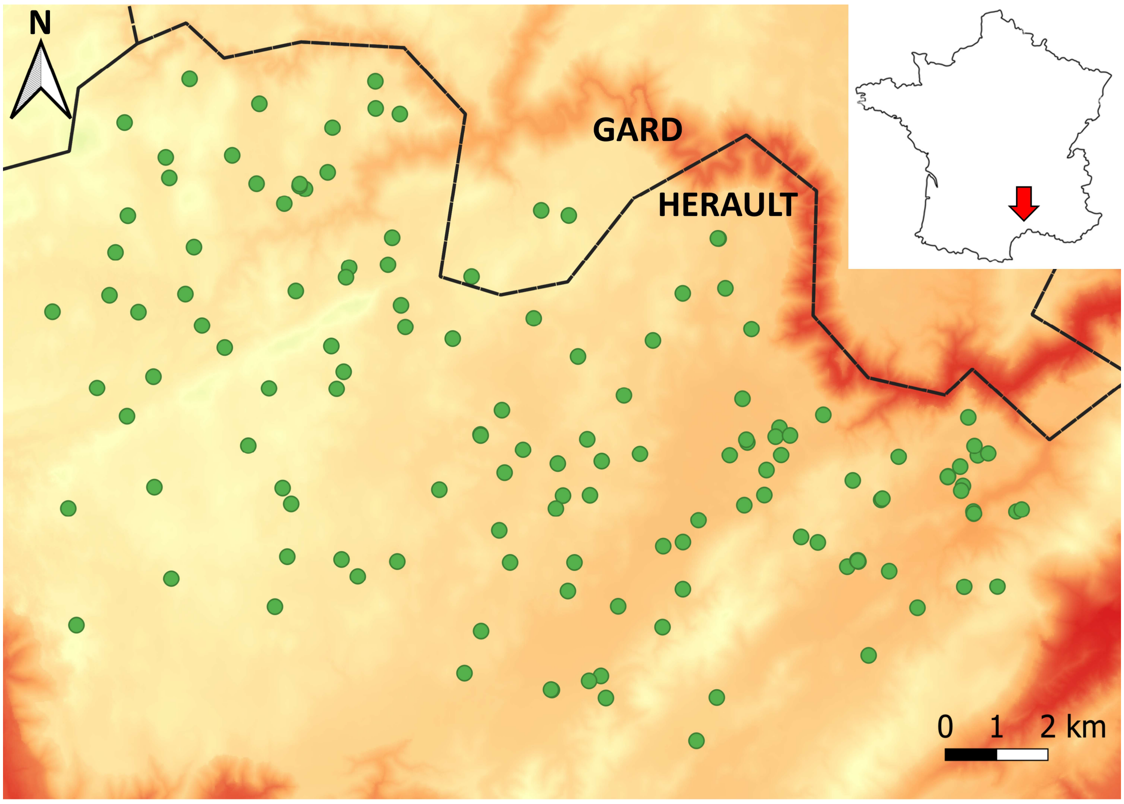

**Fig. 1** Localization of the surveyed ponds (green dots) on the Larzac plateau. The insert map shows the study area in France. Higher altitudes are indicated in light yellow and the lower altitudes in dark orange.

## Sampling

### *Amphibians detection*

Visual encounter surveys were conducted during repeated day-time and night-time visits to maximize detection (Petitot et al., 2014). All development stages (eggs, larvae and adults) were considered. During day surveys, amphibians were visually detected on the water surface or along the shoreline using binoculars (Swarovski EL 10 × 42). By night, amphibians were detected using headlamps. During both the day and night surveys, we walked slowly around the ponds to detect terrestrial individuals on the shores and immerged individuals. The amphibian communities were assessed by conducting 799 visual encounter surveys (440 by day and 359 by night) across 140 ponds in 2021 and 2022. The surveys extended from April 1 to July 21 in 2021 and from April 14 to June 14 in 2022 to cover the breeding period of amphibians (Geniez & Cheylan, 2012). Ponds were visited on average 3.46 (SE: ± 0.17) and 2.74 (SE: ± 0.15) times during day-time and night-time, respectively.

*Habitat features*

During each survey, we assessed four habitat gradients (i.e., continuous variables): maximum pond depth (m), water surface area ($m^2$), proportion of submerged macrophytes (%), and proportion of sun exposure (%),as well as three binomial habitat factors: pond substrate (i.e., natural versus artificial), water permanence (permanent versus temporary, i.e. not retaining water during the whole study period) and presence of fish (absence versus occurrence of either *Carassius auratus* [Linnaeus, 1758]*,* *Gambusia holbrooki* Girard, 1859*,* *Salmo truta* Linnaeus, 1758 or *Rutilus rutilus* [Linnaeus, 1758]). The maximum pond depth was measured using a graduated stick at the deepest point of the ponds. Water surface area was computed from measurement of pond dimensions using laser measures (GLM 250 VF, Bosch). The proportion of submerged vegetation (most typical species: *Groenlandia densa* Fourreau, 1869*, Potamogeton crispus* Linnaeus, 1753*, Ranunculus aquatilis* Linnaeus, 1753*,* and *Chara* sp. Linnaeus, 1753) was determined visually by estimating the percentage of submerged macrophytes (*sensu lato*) covering the total surface area of ponds. Sun exposure was assessed by measuring the percentage of tree cover in the 5-m buffer around the center of each pond.

Statistical analyses

*Occupancy models*

The habitat preferences of the introduced marsh frogs and native amphibians were assessed by performing Bayesian static occupancy models with binomial error distributions for each species separately. The seven habitat parameters (pond depth, water surface area, proportion of submerged vegetation, proportion of sun exposure, type of substrate, water permanence and presence of fish) were tested as explanatory variables. The variables were not strongly correlated (all $|r| < 0.49$; Supplementary Table S1). “Site” random effects were also added to consider the non-independence of the multiple surveys at the same ponds in the ecological sub-model. The day of the year and day/night condition were considered as covariates of detection probabilities. All variables of occupancy and detection probabilities were standardized with a mean of 0 and a standard deviation of 1.

Occupancy models were run following the parameterization proposed by Denoël et al. (2022). Vague priors were used to run all models (Guillera-Arroita et al., 2019). Three Markov chains Monte Carlo (MCMC) for 400,000 iterations were run for each model. The first 300,000 iterations were discarded as burn-in. We used a thinning interval of 100 to obtain 1,000 posteriors in each chain. Trace plots were used to assess chain convergences, and MCMC chains were run until Rhat values <1.1 were obtained (Brooks & Gelman, 1998). Bayesian static occupancy models were run using the “nimble” package (de Valpine et al., 2017) in the R environment (R Core Team 2023).

### *Co-occurrence and environmental niche overlaps*

To compare the overall occupancy rate of marsh frogs and each species of native amphibians, we performed bootstraps (10,000 repetitions) on odd ratios comparing their respective observed occupancy in the 140 ponds. The cumulative occupancy of marsh frogs was considered larger to that one of native amphibians if the 95% confidence intervals of odd ratios were larger than one. The environmental space for niche assessment was determined by computing a principal component analysis (PCA) of the seven pond features (scaled variables) on all ponds (available environmental space). This bidimensional available environmental space (first two axes of PCA) have been fractioned into a 100 × 100 cell grid to apply a kernel density function that smoothed the densities of occurrence for each species. Similarities in the environmental niche were assessed by pairwise comparisons of grids between invasive marsh frogs and each species of native amphibians in the available environmental niche using Schoener's D (Schoener, 1970; Broennimann et al., 2012). This index was bounded between 0 (no overlap) and 1 (complete overlap). To compute the fraction of the environmental niche of each native amphibian that overlapped the environmental niche of marsh frogs, we followed the procedure proposed by Fourcade et al. (2017). First, the grid of density of occurrence was transformed into estimated presence or absence data. To do so, we used the lowest density value associated with any of the input occurrences as the threshold for transforming each cell of the grids into binary scores. We then computed the area of the environmental niche (i.e., the number of cells with positive occurrence) for each species respectively. The fractions of the environmental niche overlapped by the marsh frogs were then calculated. Niche overlaps were computed using the "ecospat" package (Di Cola et al., 2017) in the R environment (R Core Team 2023).

## **Results**

### Occupancy models

For *P. ridibundus*, the 95% credible interval of one variable did not cross zero (positive effect: pond depth), against five for *H. meridionalis* (positive effect: submerged aquatic vegetation cover, pond substrate, sun exposure and pond depth; negative effect: introduced fish), four for *P. punctatus* (positive effect: sun exposure and pond surface area; negative effect: introduced fish and pond depth), two for *A. obstetricans* (positive effect: sun exposure; negative effect: introduced fish), two for *L. helveticus* (positive effect: submerged aquatic vegetation cover; negative effect: introduced fish) and three for *T. marmoratus* (positive effect: submerged aquatic vegetation cover and pond depth; negative effect: introduced fish). For *P. ridibundus*, the vegetation cover also tended to have an important effect as its 95% credible intervals barely crossed zero but not its 90% credible intervals. The other variables varied across species, yet with tendencies in the same direction as marsh frogs, particularly for sun exposure in anurans such as *H. meridionalis, P. punctatus* and *A. obstetricans* which showed preference for sunny ponds. All native species of amphibians avoided ponds invaded by alien fishes (Fig. 2, Supplementary Table S2).

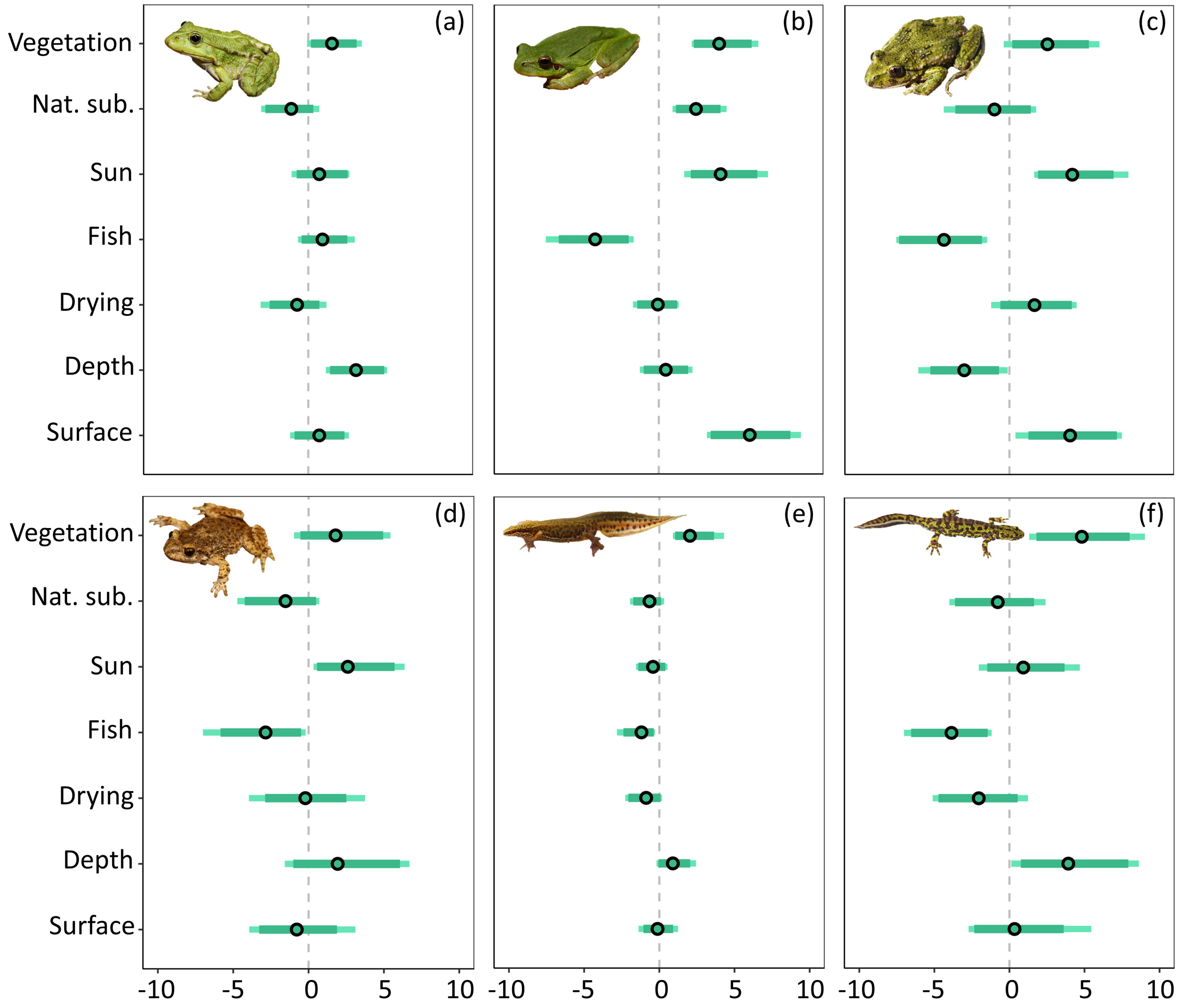

**Fig. 2** Mean, 90% (dark green) and 95% credible intervals (light green) of estimates of pond parameters according to occupancy models, respectively, for each species: (a) *P. ridibundus*, (b) *H. meridionalis*, (c) *P. punctatus,* (d) *A. obstetricans*, (e) *L. helveticus* and (f) *T. marmoratus*. Vegetation = proportion of the pond surface area covered by submerged aquatic vegetation; Nat. sub.: natural substrate; Sun = proportion of the pond surface area directly exposed to sun exposition; Fish = presence of introduced fish; Drying = drying of pond during summer; Depth = pond depth; Surface = surface area of ponds.

Invasive marsh frogs were observed in ponds during the entire study period with very large detection probabilities (>0.8; Supplementary Fig. S1). The overall detection probabilities of all species of native amphibians were lower than for marsh frogs (Supplementary Fig. S1) but increased during the night (Supplementary Table S3). Detection probabilities decreased with the day of the year for *P. punctatus* and *L. helveticus* but this effect was important only for *P. punctatus* (Supplementary Table S3; Supplementary Fig. S1). The opposite trend was observed for *P. ridibundus*, *H. meridionalis*, *A. obstetricans* and *T. marmoratus* but the increase in detection probabilities was important only for *P. ridibundus* and *T. marmoratus* (Supplementary Table S3; Supplementary Fig. S1).

## Co-occurrence and environmental niche overlap

Invasive marsh frogs were observed in more ponds than the native species of the Larzac plateau (*H. meridionalis*: odds ratio = 2.48, 95% CI: 1.55 to 4.05; *P. punctatus*: odds ratio = 1.71, 95% CI: 1.06 to 2.83; *A. obstetricans*: odds ratio = 7.91, 95% CI: 4.71 to 14.69;; *T. marmoratus*: odds ratio = 3.79, 95% CI: 2.32 to 6.47; Table 1), except *L. helveticus*, which was found in statistically similar proportion to marsh frogs in ponds (odds ratio = 1.39, 95% CI: 0.83 to 2.22). Marsh frogs have colonized very large proportions of ponds used by native species. The first two axis of the environmental PCA explained 30.5% and 19.2% of the total variance of the available environmental niche respectively. Schoener's D comparisons showed large similarities in the environmental niches of invasive marsh frogs and native species (Table 1). The environmental niche of marsh frogs was strongly similar to that of *H. meridionalis, P. punctatus* and *L. helveticus* (Schoener's D > 0.80). They also showed partial similarities with those of *A. obstetricans* and *T. marmoratus*. Almost the entirety of the environmental niche of native species was overlapped by marsh frogs (Table 1; Fig. 3).

**Table 1** Observed (naïve) pond occupancy by amphibians of the Larzac plateau and overlaps with marsh frogs. Total is the cumulated occupancy of each species, with the percentage (%) of ponds in which each species has been detected at least once on the Larzac plateau. *n* is the number of ponds where native amphibians co-occur with marsh frogs, with an indication of the percentage of occupied ponds that are invaded by marsh frogs. Niche similarity is expressed as Schoener's D (0 to 1), and niche overlap is the fraction of the environmental niche of each native amphibian that is overlapped by marsh frogs.

| Species | Occupancy | | Co-occurrence with marsh frogs | | Niche similarity | Niche overlap |
|---|---|---|---|---|---|---|
| | Total | % of ponds | *n* | % of occupied ponds | Schoener's D | % |
| *P. ridibundus* | 93 | 66.43 | – | – | – | – |
| *H. meridionalis* | 62 | 44.29 | 53 | 85.48 | 0.81 | 96.83 |
| *P. punctatus* | 75 | 53.57 | 53 | 70.66 | 0.84 | 91.42 |
| *A. obstetricans* | 28 | 20.00 | 25 | 89.29 | 0.47 | 100.00 |
| *L. helveticus* | 82 | 58.57 | 64 | 78.05 | 0.85 | 92.93 |
| *T. marmoratus* | 48 | 34.29 | 42 | 87.50 | 0.68 | 99.70 |

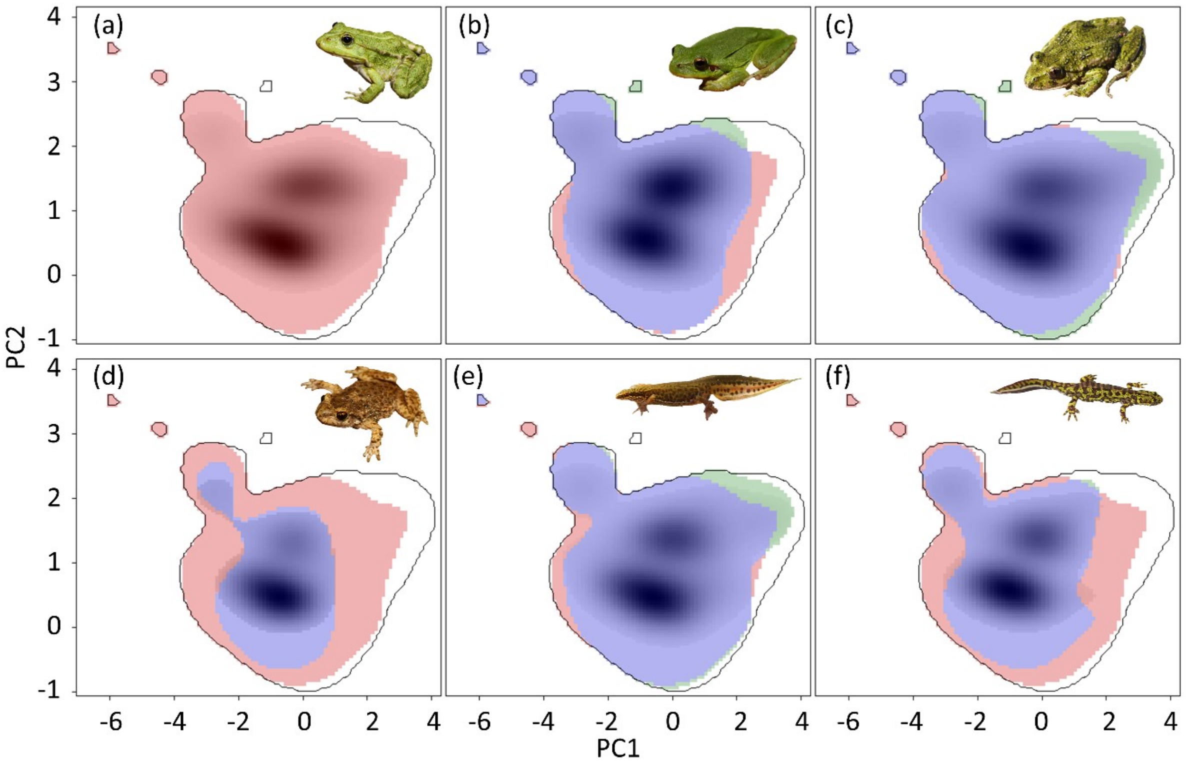

**Fig. 3** Density of occurrence in the environmental space (PCA on ponds parameters) of (a) *Pelophylax ridibundus* and each species of native amphibians: (b) *Hyla meridionalis*, (c) *Pelodytes punctatus*, (e) *Alytes obstetricans*, (f) *Lissotriton helveticus* and (g) *Triturus marmoratus*. Red and green areas are part of the environmental space that are used by *P. ridibundus* and each species of native amphibian respectively, without overlapping. Blue areas are fractions of the environmental niche of each native species overlapped by marsh frogs. Black external lines represent the environmental space available in the ponds of the studied area.

## Discussion

By comparing the pattern of occupancy of alien invasive marsh frogs and potential prey species of native amphibians, this study has provided an overview of the risk in terms of co-existence patterns. More specifically, the analyses highlight the respective habitat preferences and model the multivariate environmental niche of the native and invader species. These results support the hypothesis on the large habitat tolerance of the invader which may lead to potential interactions such as predation risk (Pille et al., 2021) in a large variety of environmental conditions and, therefore on the whole diversity of native species (here, amphibians).

### Ecological niche and invasion success

Marsh frogs have become the most ubiquitous and dominant amphibians in the ponds of the Larzac plateau. This success in invading the diversified ponds in this area can mainly be explained by their generalist traits toward habitat selection. Despite having some habitat preferences toward deep and vegetated ponds, they occurred in a high diversity of ponds. The large tolerance of a high range of environmental features was certainly a clear asset during their invasion (Denoël et al., 2022). In contrast, native species showed a higher preference for some habitat features than marsh frogs as evidenced by the higher size effects of environmental covariates in native than in alien species (e.g. sun exposure for native anurans). As a result, natives were observed in a smaller number of ponds than the invader. Furthermore, despite the fact that all species of native amphibians avoided most ponds invaded by fish, marsh frogs frequently coexisted with these introduced species.

The invasive success of marsh frogs is also reinforced by their generalist and opportunistic feeding strategies, which allow them to use a very diversified spectrum of prey at the air–water interface of most ponds (Pille et al., 2023). This is typically less the case for native species, which feed almost totally on aquatic (newts; Lejeune et al., 2021) or terrestrial (anurans; Cogălniceanu et al., 2001; Kovács et al., 2007) invertebrates. Moreover, marsh frogs are less constrained in foraging as they have a larger mouth than the studied native amphibians which were studied here (Cohen et al., 1993). In the specific context of the Larzac plateau, where no sister species of native *Pelophylax* occurs, these niche differences with other species of amphibians may have facilitated the establishment of marsh frogs. Similarly, the American bullfrogs succeeded in establishing in communities of native amphibians in Texas for the same reasons (Schalk et al., 2018). Therefore, trophic and habitat generalism enable the large potential of marsh frogs to colonize widely non-native areas (see Dufresnes et al., 2024), as has been shown for other successful invaders such as the American bullfrog (Johovic et al., 2020), the African clawed frog (Measey et al., 2012) or the cane toad (Vidal-García & Keogh, 2017).

## Co-occurrence and niche overlaps

Ecological niche overlap between invasive alien species and potentially impacted native species has largely been studied using two essential scales for the assessment of impact risk. While trophic ecology research informed on mechanisms such as predation and competition in targeted sites (Wu et al., 2005; Mohanty & Measey, 2018; Bissattini et al., 2021; Lejeune et al., 2023), spatial ecology modeling gave insight into where native and alien species would meet and therefore interact. For instance, previous research showed large climatic overlaps between freshwater invasive and native anurans, which suggests a possible risk to native species (Escoriza & Boix, 2012; Becerra López et al., 2017; Vidal-García & Keogh, 2017). However, climatic niche overlaps do not necessarily involve site occupancy overlap in ponds because invaders and natives may have contrasting habitat preferences at the local scale.

Several native species showed habitat preferences toward deep, sunny, and/or vegetated ponds. Indeed, submerged vegetation and water depth provide resources and shelters for amphibians (Bounas et al., 2020; Denoël et al., 2022), whereas sun exposure promotes thermoregulation of metamorphosed anurans and boosts tadpole growth (Halverson et al., 2003; Michaels & Preziosi, 2013). In our study area, marsh frogs and several native amphibians exhibited preferences toward these habitat features, which increased co-occurrences between natives and invaders in those types of ponds. On one hand, the preference of native species for highly vegetated habitats may promote their persistence despite the occurrence of invaders (Adams et al., 2011). On the other hand, the shared preferences with marsh frogs suggest that native species are highly likely to meet the invader when they are present in ponds. The risk posed by marsh frogs may therefore be of particular concern. Due to their generalist ecology, marsh frogs occupied 66% of the ponds in the area during the study period, which is more than for each native amphibian species. The high tolerance and similar habitat preferences between the invader and natives translated into high global environmental niche overlaps between them. Therefore, there are therefore only a limited number of habitats devoid of pressure (e.g., predation) from marsh frogs. However, the degree of overlap depends on the characteristics of both local habitats and the associated native species. In their native range, water frogs occupied a large diversity of habitats that were not present in our study area, such as rivers, swamps, floodplains, lakes and ditches (Çiçek & Mermer, 2006; Kovács et al., 2007; Balint et al., 2010; Paunovic et al., 2010; Plitsi et al., 2016). Considering the large non-native range of *Pelophylax* species in Western Europe (Dufresnes et al., 2024), these invasions may be a concern for many native amphibian species. This may not be for all as Cayuela et al. (2013), in studying the co-occurrence between the yellow-bellied toad (*Bombina variegata*) and alien water frogs in small pools bordering rivers, found only low overlaps between the two species. More studies assessing the impact of alien *Pelophylax* frogs should be conducted depending on the local context of invasions.

## Potential risk for native amphibians

The presence of aquatic alien invasive species can have a more complex impact than simply the removal of native species. For instance, the occurrence of invasive bullfrogs did not influence ponds occupancy by native amphibians (Rowe et al., 2019; Silveira & Guimarães, 2021). However, American bullfrogs, which have similar behavior and ecology to marsh frogs, frequently prey on native amphibians and compete for feeding resources (Wu et al., 2005; Silva et al., 2011; Boelter et al., 2012; Bissattini et al., 2019; Oda et al., 2019). A global review showed that several experimental studies revealed altered behaviors among native species (i.e., reduced activities and foraging; increased sheltering and habitat use alteration), altered growth and decreased survivorship of native amphibians (Kats & Ferrer, 2003). Invasive African clawed frogs also feed on native amphibians (Courant et al., 2017) and impacted their reproduction occurrences in colonized ponds (Lillo et al., 2011). Field surveys also revealed community effects, with a reduced richness of native amphibians in the presence of each species of invasive anuran (Li et al., 2011; Courant et al., 2018). However, despite the fact that the impacts of several invaders are partly known, no study to date has assessed the long-term impacts of invasive marsh frogs on native amphibians.

Although invasive marsh frogs coexist with a large number of native amphibians, there is a need to explore their effects on abundance patterns and potential declines across time. Presence/absence do not inform on abundances and some effects may therefore be missed or under-evaluated. Getting abundance data for whole communities remains a difficult task, as this would typically require the use of dip-netting rather than visual encounter surveys. Finally, the lack of historical measures of abundance before the arrival of marsh frogs and their recent presence makes it difficult to quantify declines. The observed coexistence does not mean that native populations are not affected. The risk is also likely species-dependent, with some species, such as hylids and, to a lesser extent, newts, being highly predated at the adult stage, which suggests a likely effect at the population level over the long-term (Pille et al., 2021). Despite there are no native ranids in our studied area, there were several indicators of the decline of some ranids following marsh frog invasions in the eastern parts of the invaded range (Pilliod et al., 2012).

Another important aspect of co-existence in ponds is temporal patterns. Most native amphibians exhibit different phenologies, frequenting ponds mostly at their larval stage or during their respective breeding seasons (Geniez & Cheylan, 2012). However, the detection probabilities of marsh frogs remained very high, meaning that they were active in the vicinity of ponds during the overall study period. Indeed, marsh frogs spend most of their active period near the shoreline of ponds, either at the water surface or on the shore (Duret et al., 2022; Pille et al., 2023) and are active and feed until overwintering (Paunovic et al., 2010; Geniez & Cheylan, 2012; Bayrackci & Çiçek, 2023). Therefore, native species of amphibians may be exposed to marsh frogs during the entire time they spend in ponds, which is crucial because of aquatic breeding. For instance, a previous study carried out on the Larzac plateau showed that, despite the constant activity of marsh frogs around ponds, predation pressure likely reaches its maximum in April during the peak breeding period of the most ubiquitous native amphibians, such as *H. meridionalis* and *L. helveticus* (Pille et al., 2021). Therefore, in the case of invasive marsh frogs, temporal patterns also indicate a very large overlap and a pronounced risk for native species.

## Conclusions

In recent years, an increasing number of studies have highlighted new identifications of population of alien water frogs across several European countries (e.g. Bellati, 2019; Bruni et al., 2020; Doniol-Valcroze et al., 2021; Jelić et al., 2022; Bellati et al., 2023, Dufresnes et al., 2024). Other works showed their potential to invade many freshwater environments (Denoël et al., 2022; Duret et al., 2022), where they can impact aquatic communities and native amphibians through predation (Pille et al., 2021, 2023) and hybridization, potentially replacing native sister species of *Pelophylax* if present (Holsbeek & Jooris, 2010; Kolenda et al., 2017; Dufresnes et al., 2018; Bruni et al., 2020; Jelić et al., 2022). Furthermore, the results of the present study suggest that many species of native amphibians may share their breeding sites with invasive water frogs, thereby incurring the risk of exposure to negative interactions with invaders. Being dominant at the pondscape scale, invasive marsh frogs may shape the communities of amphibians in invaded areas. The cryptic nature of these invasions has led to an underestimation of their geographical spread and their potential ecological impact on native fauna. Moreover, global warming may have facilitated their current invasions and may further promote new colonization (Padilla et al., 2023). Altogether, these studies provided multiple criteria for considering that the introduced complex of water frogs induces a similar risk as other major invasive anurans in the world such as the cane toads, the bullfrogs and the African clawed frog.

## Author contributions

FP contributed to conceptualization, methodology, formal analysis, investigation, writing, original draft preparation, reviewing and editing the manuscript. LS, AC, PT and CD contributed to formal analysis, investigation, reviewing and editing the manuscript. MD contributed to conceptualization, methodology, funding acquisition, supervision, writing, reviewing and editing the manuscript.

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## Statements and Declarations

### Conflict of interest

The authors declare that they have no conflict of interest.

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### Data availability

Data are available from the corresponding author on reasonable request.

### Supplementary Information

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