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Invasion Dynamics of the Alien Amphibian *Xenopus laevis* in France: Perspectives for Management

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ABSTRACT

Background: Invasive alien species (IAS) are recognised as pervasive drivers of global environmental change and pose significant threats to socio-ecosystems worldwide. Although much attention is focused on prevalent IAS, the oversight of species that are still contained and approaching critical invasion thresholds raises concern. In this context, scientific support to implement effective and spatially informed management strategies is critically needed.

Aims: Our study focuses on the African clawed frog, *Xenopus laevis*, a concerning IAS projected to undergo a substantial expansion in Europe.

Materials & Methods: Using a comprehensive analysis of three distinct datasets, our study aimed to document newly colonised sites and provide an up-to-date overview of the current distribution and invasion dynamics of *X. laevis* in France.

Results: Our results revealed recent colonisation of new sites within the established range of the species and the continuous progression of the invasion front at a rate of 1.2 km per year. This annual progression currently translates to an expansion of approximately 400 km² per year in the predicted distribution range of the species.

Discussion: Emphasising the urgent need for proactive management, we recommend measures encompassing prevention, early detection and rapid responses to invasion, delineated across three strategic zoning levels.

Conclusion: Immediate and coordinated efforts are imperative to anticipate and mitigate the considerable socio-environmental impacts associated with this species in the future.

1 | Introduction

Biological invasions are recognised as one of the five primary drivers of global environmental change (Díaz et al. 2019). Socio-ecological systems experiencing biological invasions incur significant threats from invasive alien species (IAS) including impacts on biodiversity with, for example, native species loss

(Bellard, Cassey, and Blackburn 2016; Bacher et al. 2023) and on human well-being (Jones 2017) through an exacerbation of disease risks (Chinchio et al. 2020). The worldwide economic costs induced by IAS for societies, including annual expenditures on damage loss, repair and management efforts, were estimated at \$162.7 billion in 2017 (Diagne et al. 2020). These costs quadruple every decade (Bacher et al. 2023), being currently

Alain Pagano and Clément Harmange are co-first authors.

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comparable with the economic impact of natural disasters (Turbelin et al. 2023). Therefore, managing IAS invasions has become a decisive issue for many countries, pressing societies to prevent or reduce social-ecological impacts.

To prevent or mitigate the negative impacts of IAS on social-ecological systems, a hierarchical process has been proposed. The strategy ranges from prevention of new introductions, eradication of newly established species (Jones et al. 2016; Robertson et al. 2019), to spatial containment and/or population control programmes (Simberloff et al. 2013) considered as a possible alternative approach when IAS populations are widespread and their complete removal is not possible anymore (Braysher 1993). Prevalent IAS have received significant attention and funding in countries experiencing invasion (e.g., Lowe et al. 2000). However, some unnoticed and still-contained alien species that may be on the verge of reaching an uncontrollable invasion stage have remained neglected, although the costs of inaction or delayed action may outweigh those of early intervention (Ahmed et al. 2022). Early intervention is therefore critical to contain potential IAS spatially, safeguard ecosystems and reduce their economic costs, by preventing the establishment of populations, anticipating uncontrolled spread and mitigating potentially devastating impacts in the future.

In Europe, several invasions of anuran amphibians raise concerns for aquatic biodiversity and the integrity of native freshwater ecosystems. For example, these include invasions by the American bullfrog *Aquarana catesbeiana* (Johovic et al. 2020) and the water frog *Pelophylax ridibundus* (Pille, Pinto, and Denoël 2023; Dufresnes et al. 2024). The current study focuses on the African clawed frog *Xenopus laevis*, native to South Africa and recognised as one of the most detrimental invasive amphibian species (Measey 2016). For instance, *X. laevis* is known to reduce the reproductive occurrence (Lillo, Faraone, and Lo Valvo 2011) and the species richness (Courant et al. 2018a) of native amphibian species. It has successfully established populations on four continents following accidental and deliberate introductions related to scientific use and pet trade (i.e., Asia, Europe, North and South America: Measey et al. 2012). In western France, *X. laevis* was introduced at the Lieu-dit Fronteau, in the village of Bouillé-Saint-Paul in the 1980s (Fouquet 2001), although the accurate date is still debated. Indeed, two different dates and scenarios exist in the literature regarding the release of the first *X. laevis* into nature: The first reports the first capture of the species in 1981, and the second mentions a putative release of several individuals in 1996 when the commercial laboratory supplier closed (see Measey et al. 2012). Whatever the scenario, the species has spread over a substantial part of three *Départements* (i.e. French administrative units) Maine-et-Loire, Deux-Sèvres and Vienne (Measey et al. 2012; Courant et al. 2018a). Although the spatial distribution of this alien species might be relatively limited in France at first sight, recent studies have demonstrated its high capacity to overcome new environmental conditions (Wagener, Kruger, and Measey 2021; Kruger et al. 2022) suggesting a tremendous invasion potential. As a result, *X. laevis* has been recognised as an IAS and is being added to the list of invasive species of European Union concern (European Union 2022).

Anticipating the management of this species becomes urgent, as climate change scenarios predict that 8%–38% of Europe may be suitable for the establishment of the species (Ihlow et al. 2016). However, data on its distribution and invasion dynamics are sparse and site-dependent. For instance, despite being primarily characterised as exclusively aquatic (Measey et al. 2012), reports of overland dispersal distance of *X. laevis* vary greatly, from 40 to 2000m (Measey 2016). Estimates of the invasion speed also show significant discrepancies, ranging from 0.5km/year overland in bocage landscapes to 1km/year through aquatic routes in France (see Fouquet and Measey 2006; Grosselet et al. 2006), and up to 3.1–5.4km/year in Chile (Lobos and Jaksic 2005). Given that dispersal ability is one of the main drivers of invasion success (Wilson et al. 2009), providing accurate and up-to-date estimates of the distribution and invasion dynamics of the species is critically needed to inform and implement efficient, spatially explicit management strategies.

The aim of the study is to provide a new assessment of the invasion dynamics of the African clawed frog in France. Our main objective was to quantify the probability of species occurrence as a function of the distance from the initial introduction site testing whether the last estimates of the invasion speed of 1km/year in France published in 2006 are still valid (see Fouquet and Measey 2006; Grosselet et al. 2006). Based on the data we collected and gathered, we assessed invasion dynamics considering two competing published scenarios (i.e., 1981 or 1996) of the species release into nature. Identifying the scenario most likely to have driven the observed invasion dynamics is crucial for providing accurate estimates of the species' invasion speed. This should allow delineating the current invasion front, a strategic area for prioritising management efforts to (1) closely monitor the invasion dynamics in the expected expansion zone and (2) implement control programmes for the spatial containment of the species. If the introduction event at the origin of the invasion occurred in 1981, the species would have spread over 43 years to reach the current invasion front. The slope in the relationship between dispersal distance from the introduction site and time since introduction is expected to be moderate. Conversely, if the invasion had been driven by the introduction event that occurred 15 years later (i.e., in 1996), the invasion speed would have been faster, which should result in a steeper slope.

2 | Methods

2.1 | Study Area

The study area is located in Western France, in the region of the initial and main invasion site: the Lieu-dit Fronteau (47°01'52.4"N 0°18'02.4"W) in the village of Bouillé-Saint-Paul (Fouquet 2001). It partially covers the three French *Départements* of Deux-Sèvres, Maine-et-Loire and Vienne, which are located in the area of expansion of the invasion (MNHN and OFB 2024). It should be noted that the species has also been detected sporadically in several isolated other locations in France, far from the main area of invasion. Specifically, it was found in South-Western France near Bordeaux (about 200km from the introduction site) in 2016, Toulouse (about 400km from the introduction site) in 2019 and in Northern France near Lille (about 470km from the introduction site) in 2019 (Inventaire National du Patrimoine Naturel 2023; MNHN and OFB 2024).

2.2 | *X. laevis* Data

Occurrence data of *X. laevis* were compiled from three distinct datasets, encompassing data collected between the years 2000 and 2023. This resulted in a total of 354 sampling sites, of which 152 (42.9%) confirmed the presence of the species. The first dataset consisted of unpublished capture data collected by the authors in April–July during the years 2002, 2004, 2005, 2008 and 2023. Sampling sites were strategically selected at the periphery of the established range of the species based on previous studies and extended to encompass surrounding areas where the species had not previously been recorded. This allowed us to investigate the potential spread of the invasion. Maps of ponds and waterbodies (lentic ecosystems) were used to select sampling sites locally, using GIS. Sampling was conducted at each site using one standard submerged funnel trap (40 × 23 × 23 cm with 4-mm mesh diameter and an entry diameter of 6.5 cm, RedFish), equipped with floats to prevent the drowning of individuals. The trap was set during one night per year and baited with dry cat food. A total of 71 sites were sampled during the study period, of which 48 (67.6%) confirmed the presence of the species. The second dataset consists of eDNA surveys conducted by Vimercati et al. (2020) in 2017 on 234 sites selected in both the core area and periphery of the species distribution. The species was detected in 55 (23.5%) of these sites. The third dataset originates from the National Inventory of Natural Heritage (MNHN and OFB 2024). It consists of 163 occurrences (no absence data available) recorded in 2000, 2008, 2013 and from 2017 to 2022 from 49 sampling sites. It should be noted that in this dataset, the geographic coordinates correspond mainly (i.e., for 34 out of 49 sites) to the centroid of the sampled municipalities rather than to the coordinate of the specific sampling site (distance municipality centroid–border: min = 1.7 km ± 1.4; max = 4.7 km ± 2.1). Overall, these less accurate data represent 9.6% (i.e., 34 of the 354 sites sampled) of all the sites sampled. To account for the influence of these less accurate data on the results, statistical analyses (see below) were repeated excluding these data and presented in the Supporting Information. Our study is based mainly on capture data, for which we can reasonably assume there were no false detections. The protocol applied for eDNA detection of *X. laevis* (i.e., in 36% of all the 152 sites where the species was detected) has proven not to return any false positives, whether tested on control ponds located outside the colonised range of the species in western France or on negative PCR controls (Secondi et al. 2016). Additionally, one out of 12 PCR replicates was sufficient to detect the species in all ponds where its presence had been confirmed by capturing two to 358 adults (i.e., at densities as low as one individual per 100 m²; Secondi et al. 2016). This suggests that eDNA false detections are unlikely and that the nondetection of the species would indicate that the species was genuinely absent during the sampling period.

2.3 | Statistical Analyses

2.3.1 | Occurrence of *X. laevis*

First, we assessed the distance between the site of introduction and each sampling site. For each sampling site, we assigned a value of 1 if the species had been detected, or 0 if it had not. For sites sampled several times (17 out of 354 sites, i.e., 4.8%), we

assigned a value of 1 if the species had been detected at least once, or 0 if it had never been detected. Then, we modelled the probability of occurrence of *X. laevis* with the distance from the introduction site (Fronteau, Département des Deux-Sèvres, France) using a generalised linear model (GLM, binomial, logit link) and a likelihood ratio test (i.e., χ^2).

We then used the R function ‘predict’ to calculate predicted values for the probability of *X. laevis* occurrence as a function of distance from the introduction site. These predictions were used to spatialise the probability of occurrence of the species by means of probability isolines, which materialise lines of equal probability of occurrence of the species. The resulting map was produced using QGIS (Quantum GIS Development Team 2022).

2.3.2 | Invasion Dynamics of *X. laevis*

We analysed the progression of the invasion front as the dispersal distance from the introduction site as a function of the time elapsed since the introduction. Firstly, we selected sites where the species had been observed at least once. For sites sampled several years and where the species had been detected more than once, we considered the year of the first report of the presence of the species, which indicates the earliest detection of the species at the given site. Secondly, for each year of sampling, we calculated the maximal dispersal distance of *X. laevis*, that is, the distance between the site of introduction and the furthest sampled site where the species was detected in the given year.

Before testing whether time since release had a significant effect on the dispersal distance of *X. laevis*, we first had to test temporal autocorrelation in our time series. We used an autocorrelation function for irregular time series (i.e., allowing for missing data in the time series) on the dispersal distance from the introduction site to identify the time lag after which the non-autocorrelation assumption was confirmed at a 95% confidence level (Shumway and Stoffer 2011). No temporal autocorrelation was detected in our data set (Figure S1).

We run two distinct linear models with the dispersal distance from the introduction site as the dependent variable and the time since introduction, considered as the delay (in years) from either 1981 (model 1) or 1996 (model 2), as the independent variable. Since the introduction site (Fronteau) is used as the reference for calculating dispersal distances and the year of introduction (either 1981 or 1996) for calculating time since introduction, the y-intercepts of the models were set to 0 as the dispersal distance from the introduction site was 0 m in year 0. A null model was also run, considering no relationship between the dispersal distance from the introduction site and time since introduction. Recognising that the invasion dynamics (i.e., the relationship between distance from the introduction site and time since introduction) might exhibit non-linear patterns, we additionally tested, for each year of introduction (i.e., 1981 and 1996), curvilinear (i.e., second-order polynomial models: models 3 and 4, respectively) and exponential relationships (i.e., on the log-transformed y: models 5 and 6).

Finally, to identify the most plausible scenario for the introduction event (1981 or 1996) at the origin of the observed invasion

dynamics, we used a model selection based on Akaike's information criterion corrected for a small sample size (AICc) (Burnham and Anderson 2002). The Akaike model weights (ω_i) were calculated as support for each model, and the weights of each competing model were contrasted with the best model (i.e., the model with the lowest AICc value) by calculating the evidence ratio (Burnham and Anderson 2002). Competing models with a difference in AICc (ΔAICc) < 2 were considered equivalent. All candidate and null models were considered in the model selection. Given that the exponential models have different (i.e., log-transformed) values for the dependent variable, the model selection process was conducted separately for these models.

To spatially represent the invasion front predicted for 2024, we used the R function 'predict' to obtain the predicted dispersal distance (\pm 95% and 99% confidence intervals) from the best model (see above). The resulting map was produced using QGIS (Quantum GIS Development Team 2022).

All analyses were performed using R software (R Core Team 2022).

3 | Results

3.1 | *X. laevis* Occurrence

Based on the ponds sampled, the probability of occurrence of *X. laevis* decreased with increasing distance from the introduction site ($\chi^2=30.459$; $df=1$; $p<0.0001$; Figure 1). This result remained consistent when the less accurate data reported at the spatial resolution of the municipality were excluded from the analysis ($\chi^2=24.682$; $df=1$; $p<0.0001$). Model predictions indicate that the probability of detecting the species in a pond decreased from 0.70 (\pm 0.05 SE) at 2 km from the introduction site to 0.10 (\pm 0.04 SE) at 70 km (Figure 2). Thus, the probability of detecting *X. laevis* in a pond located 21 km from the introduction site is 0.50 (\pm 0.03 SE; Table S1) suggesting that half of the ponds may be colonised by *X. laevis*. This probability drops to 0.20 (\pm 0.04 SE) for a pond located 52 km from the introduction site (Figure 2) suggesting that one out of five ponds would host the species (Table S1).

3.2 | Invasion Dynamics of *X. laevis*

The maximum dispersal distance of *X. laevis* from the introduction site increased with time, whether considering the 1981 ($F=40.564$; $df=1$; $p<0.0001$; Figure 3A) or the 1996 introduction event ($F=30.676$; $df=1$; $p=0.0001$; Figure 3B). However, model selection indicates that the best statistical support was obtained when modelling the relationship between dispersal distance and time since introduction as linear, considering the 1981 introduction event (AICc = 301.78; Adjusted $R^2=0.753$; Table 1). These results remained consistent when the less accurate data reported at the spatial resolution of the municipality were excluded from the analyses (see Table S2).

Estimates of the best model indicated an invasion speed of 1.205 km (\pm 0.189 SE) per year (Table 1). This suggests that the predicted invasion front for the species in 2024 is approximately

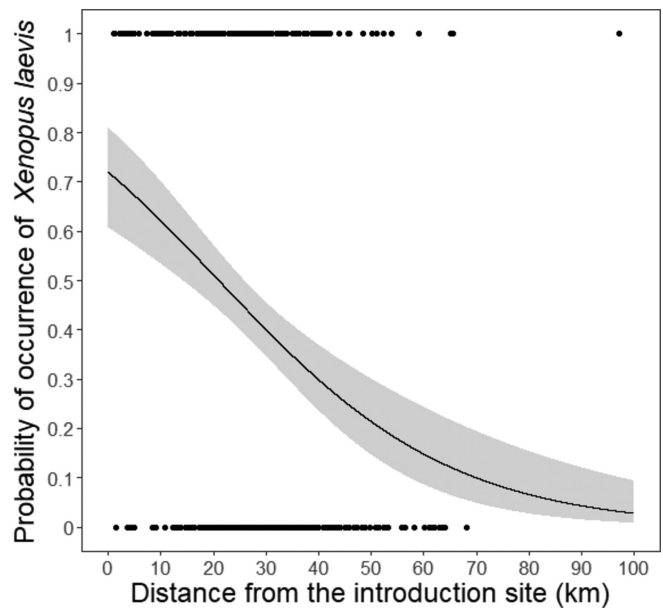


FIGURE 1 | Predicted probability of occurrence of *Xenopus laevis* (solid line) as a function of distance (in km) from the introduction site (Fronteau, Département des Deux-Sèvres, France). The grey envelop represents the 95% confidence interval.

51.8 km from the introduction site (95% CI = 34.1–69.5 km; 99% CI = 27.0–76.7 km) (Figure 4).

4 | Discussion

Our study aimed to document newly colonised sites and provide an updated overview of the invasion dynamics of *X. laevis* in France. Our results clearly indicate the colonisation of new sites within the established distribution range of the species and the progression of the invasion front at a rate of 1.2 km/year, updated upwards compared with previous studies in France (Fouquet and Measey 2006; Grosselet et al. 2006). This supports the hypothesis that the invasion is continuing to progress in France. Although many countries face the challenge of prioritising invasion management with insufficient baseline data (McGeoch et al. 2016), our study provides an updated baseline estimate of the invasion speed and established range of the species that should support management in France.

4.1 | Established Distribution Range

Our results showed that within the established range of *X. laevis*, the sites monitored for 25 years without any evidence of the species (Lesbarrères et al. 2010; Pagano, unpublished data) have recently been colonised, in 2023. Additionally, sites sampled using eDNA protocols in 2017 that had not detected the species (Vimercati et al. 2020) have been colonised 6 years later. These findings suggest that the invasion continues to progress in France, potentially leading to population densification within the established distribution range of the species. This pattern contrasts with the reduction of populations of *X. laevis* observed after an initial spread in South Wales (Measey et al. 2012). Further quantification and monitoring

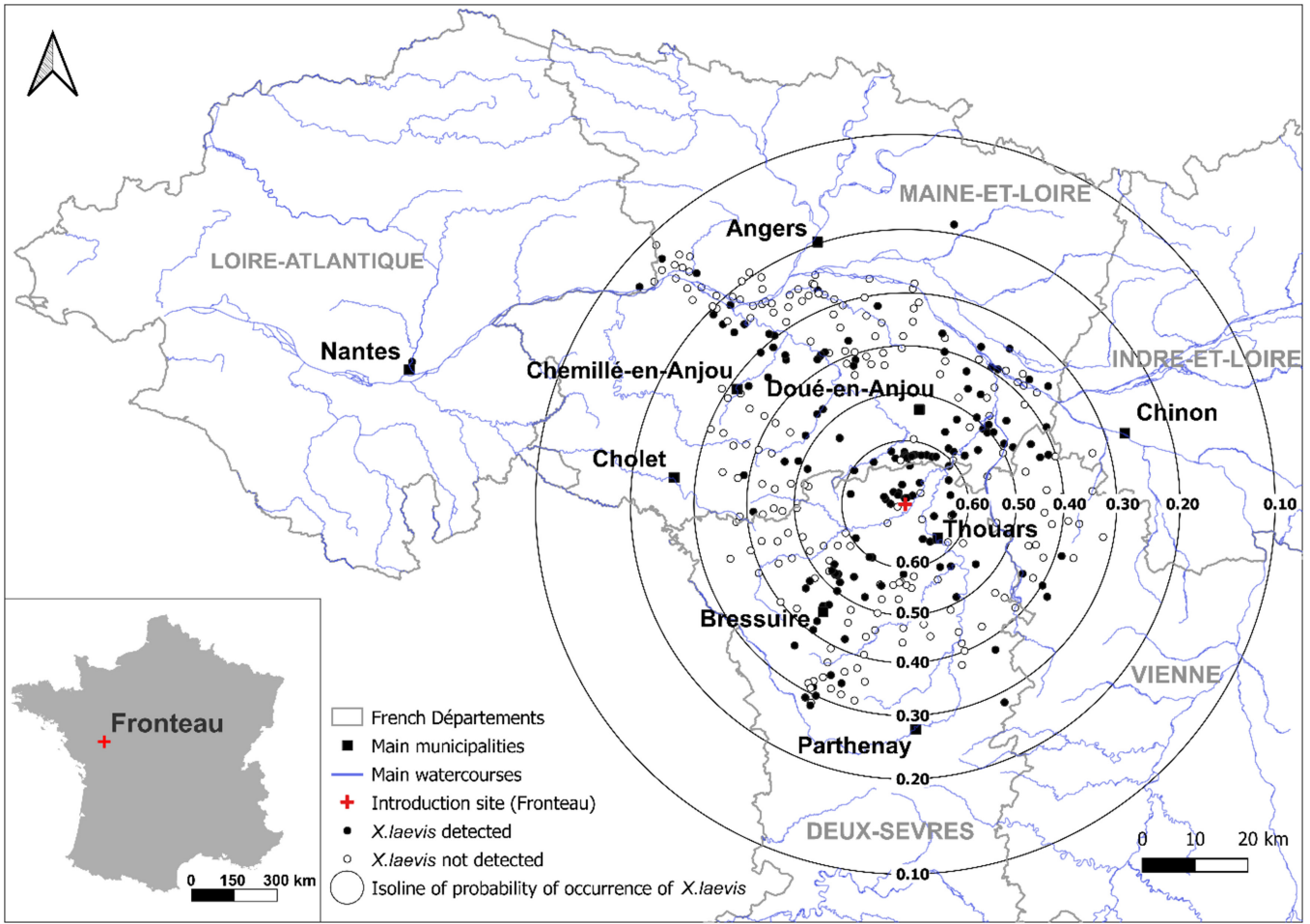


FIGURE 2 | Spatial distribution of the sites sampled in western France where *Xenopus laevis* was detected (black dots) or not detected (white dots). Black circular lines represent the isolines of probability (from 0.60 to 0.10) of species occurrence, with the respective probability indicated in bold font. See Table S1 for details.

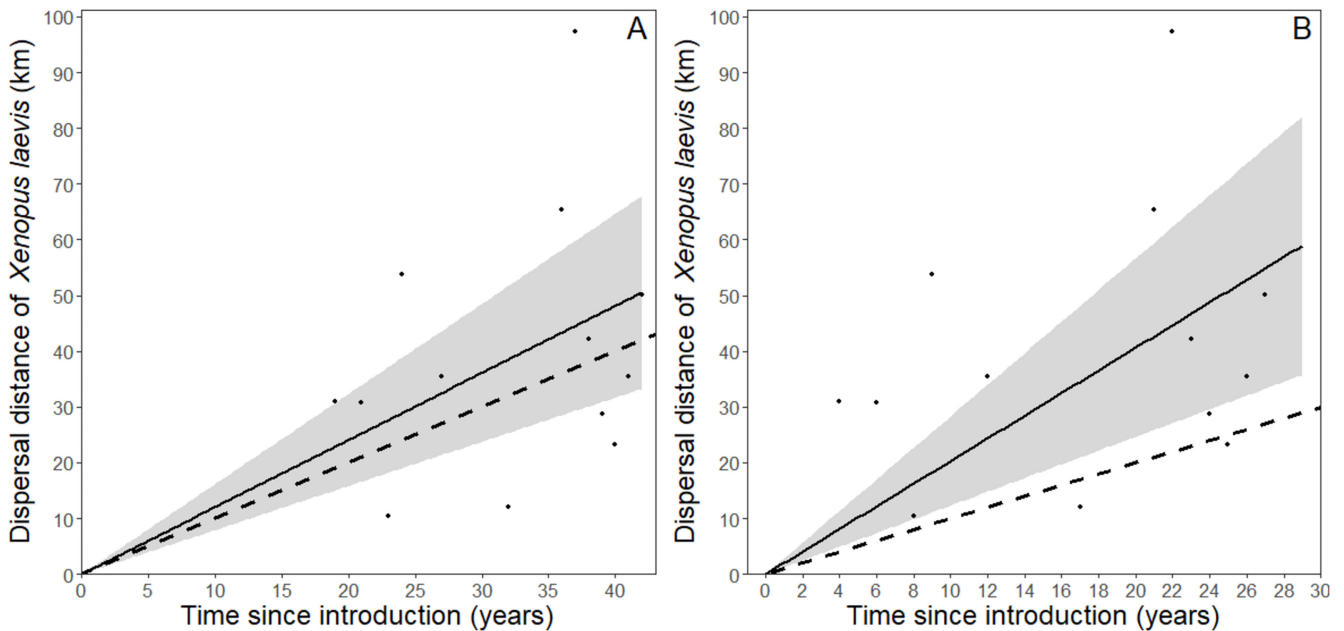


FIGURE 3 | Predicted relationships (solid lines) between dispersal distance (in km) of *Xenopus laevis* from the introduction site (Fronteau, Département des Deux-Sèvres, France) and time since introduction (in years). Time since introduction was considered from 1981 (A) or 1996 (B), based on Measey et al. (2012). The grey envelopes represent the 95% confidence interval. The dashed lines represent the expected invasion dynamics based on the estimated dispersal of 1 km/year suggested by Fouquet and Measey (2006).

TABLE 1 | Statistical support for models testing the effects of time since introduction on the dispersal distance of *Xenopus laevis* from the introduction site (Fronteau, Département des Deux-Sèvres, France). Time since introduction is considered as the time (in years) since the introduction event of 1981 or 1996, based on Measey et al. (2012). Three types of models, including linear (models 1 and 2), curvilinear (i.e., second-order polynomial models: models 3 and 4) and exponential relationships (i.e., on the log-transformed y : models 5 and 6), were tested. Given that the exponential models are based on different (i.e., log-transformed) values for the dependent variable, the model selection process was conducted separately for these models (i.e., 5 and 6). The selection process was based on Akaike's Information Criterion corrected for small sample size (AICc). The number of parameters (K) is presented together with model weights (ω_i), log-likelihood values (LL) and differences in AICc (Δ AICc) in respect of the model with the highest statistical support. The best candidate model appears in bold. The estimates (in meters) \pm SE and the adjusted R^2 of the models are indicated.

| Candidate models | Dependent variable | Independent variable | K | AICc | Δ AICc | ω_i | LL | Evidence ratio | Estimate \pm SE | Adj. R^2 |
|-------------------|---------------------------------|--|----------|---------------|---------------|-------------|----------------|----------------|-------------------------------------|--------------|
| Model 1 | Dispersal distance | Time₁₉₈₁ | 2 | 301.78 | 0 | 0.59 | -148.29 | | 1.205 \pm 0.189 | 0.753 |
| Model 2 | Dispersal distance | Time ₁₉₉₆ | 2 | 304.49 | 2.71 | 0.15 | -149.64 | 3.88 | 2.033 \pm 0.367 | 0.695 |
| Model 3 | Dispersal distance | Time ₁₉₈₁ + Time ₁₉₈₁ ² | 3 | 304.81 | 3.03 | 0.13 | -148.07 | 4.55 | | |
| Model 4 | Dispersal distance | Time ₁₉₉₆ + Time ₁₉₉₆ ² | 3 | 304.91 | 3.13 | 0.12 | -148.12 | 4.78 | | |
| Null model | Dispersal distance | — | 1 | 318.14 | 16.37 | 0.00 | -157.89 | 3586.74 | | |
| Null model | Log (Dispersal distance) | — | 2 | 28.65 | 0 | 0.61 | -11.73 | | | |
| Model 5 | Log (Dispersal distance) | Time ₁₉₈₁ | 3 | 30.93 | 2.28 | 0.20 | -11.13 | 3.13 | | |
| Model 6 | Log (Dispersal distance) | Time ₁₉₉₆ | 3 | 30.93 | 2.28 | 0.20 | -11.13 | 3.13 | | |

of population abundances or densities would be needed to corroborate this hypothesis.

An unexpected result is the nondetection of the species at many sites within the established range, including in recent surveys (2017, 2023) conducted close to the introduction site (< 25 km). Although the eDNA protocol applied in Vimercati et al. (2020) has proven capable of detecting the species at densities as low as 1 individual per 100 m² (Secondi et al. 2016), we cannot exclude the possibility that the species was missed in some sites where the population density was lower or in sites sampled using other methods such as captures, which typically have lower detection rates. To estimate and maximise the detection rate, future studies should consider conducting three sessions of one-night capture between May and September, combined with complementary methods (e.g., landing net, visual observation using spotlights and eDNA; see Merlet et al. 2022a, 2022b).

Additionally, abiotic environmental characteristics, including morphological (e.g., water body size, depth and hydroperiod) and physico-chemical conditions (e.g., temperature, pH, O₂ and turbidity), are recognised as pivotal drivers influencing habitat use by amphibians (e.g. Pagano et al. 2001). Specifically, water quality was previously found to influence the survival of the study species, which was negatively correlated with nitrogen and phosphorus concentrations (Kapfer, Sandheinrich, and Knutson 2007). Further studies, focusing on the established range of the species, are critically needed to understand the effect of abiotic variables on the establishment success of the species when present in the surroundings. This should help identify conditions suitable for the establishment, predict the probability of occurrence and determine which water body is most at risk of being colonised, thereby informing spatially explicit management strategies (Venette et al. 2010). Secondly, consideration of biotic variables (e.g., amount of organic matter and prey as a proxy of food availability, population densities of amphibian species as potential competitors or fish as potential predators) (West 2018; Montaña et al. 2019) is essential to understand both the drivers of species establishment and its potential impacts on native aquatic ecosystems.

4.2 | Invasion Dynamics

After an initial spread, invasive species may exhibit exponential expansion (Hui and Richardson 2017), stabilisation or reduction in their distribution range, as observed for *X. laevis* with local population extirpations in South Wales (Measey et al. 2012). A non-linear (i.e., curvilinear and exponential) trend might thus have been expected in the invasion dynamics. However, our results suggest a contrasting trend in France, with a continuous, linear progression of the invasion. Linear invasion dynamics have already been documented, particularly in species with constrained dispersal abilities, such as aquatic or semi-aquatic species that primarily spread through river networks. Examples include the expansion patterns of the quagga mussel *Dreissena rostriformis* in Europe (Hui and Richardson 2017) and the invasive cane toad *Rhinella marina* in Australia (Phillips et al. 2007). However, although linear relationships may effectively describe invasion dynamics over short-term periods, they

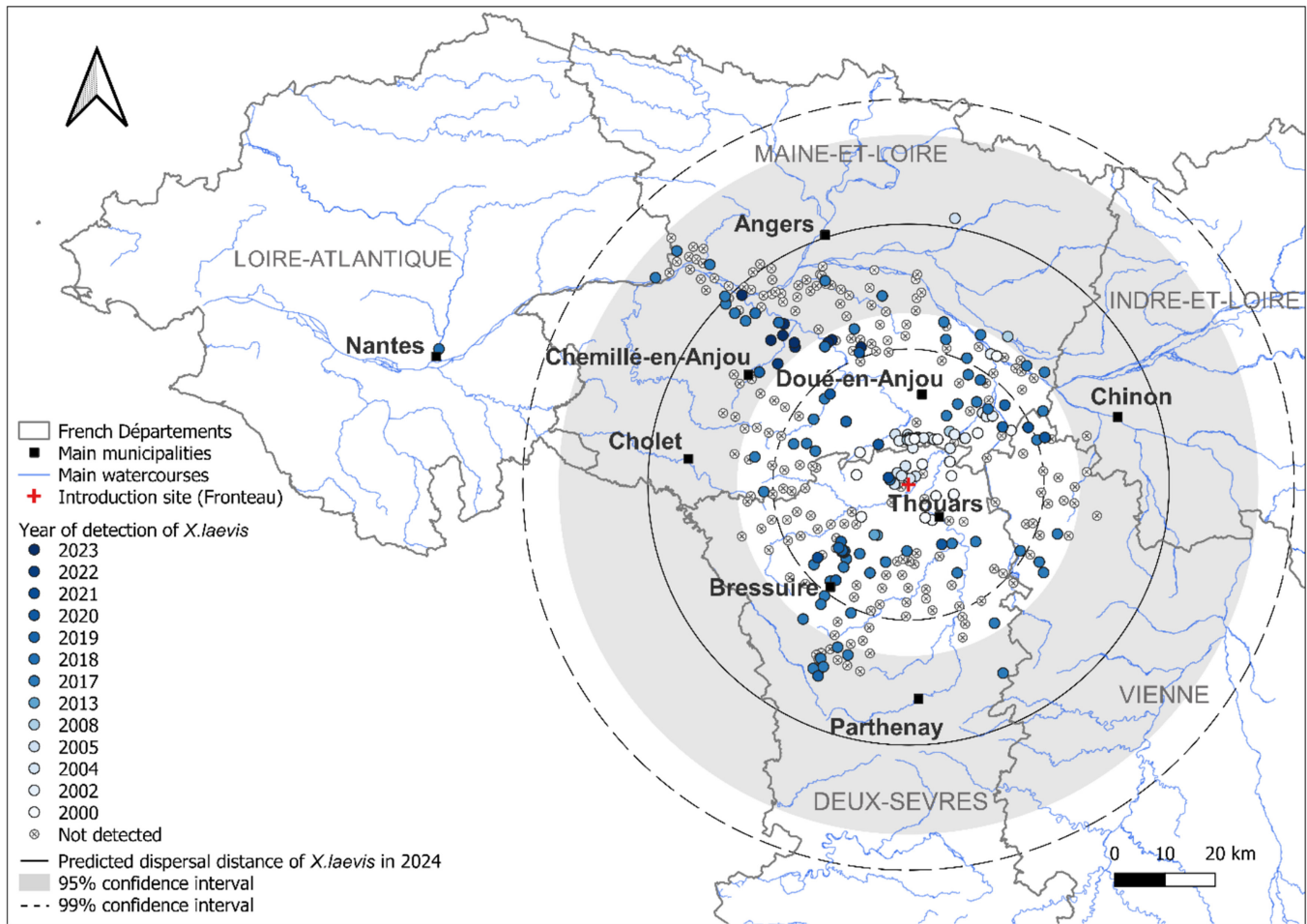


FIGURE 4 | Dispersal distance of *Xenopus laevis* from the introduction site, predicted for the year 2024 (black solid line). The 95% (grey envelopes) and 99% (dashed lines) confidence intervals of the estimated invasion front are indicated.

can be prone to exponential acceleration over the long term (Hui and Richardson 2017). This potential for acceleration poses a threat to the spatial containment of invasions. This emphasises the need for vigilant and systematic monitoring of the invasion to allow early detection of any signs of potential acceleration in the spread of *X. laevis*.

Considering the 1981 introduction event, which is more likely to be at the origin of the observed invasion dynamics (compared with the putative 1996 introduction event; Measey et al. 2012), our results provide an upwardly updated estimate of the invasion speed at 1.2 km/year. This result is consistent with the previously estimated invasion speed of 1 km/year in France (Fouquet and Measey 2006). It supports that there is no observed slow-down in the spread of the invasion and that there may even be a slight increase compared with previous estimates of 2002–2003 (Fouquet and Measey 2006). This emphasises the strong colonisation capacity that *X. laevis* could have, which may extend up to 3.1–5.4 km/year, as reported in Chile (Lobos and Jaksic 2005). In comparison, most amphibian species would typically have dispersal distances of less than 1 km (e.g., 300 m in *Rana dalmatina*, 313 m in *Bombina variegata*, 460 m in *Rana temporaria*, but up to 3.6 km in *Bufo bufo*; Smith and Green 2005), although dispersal may be significantly underestimated in amphibians (e.g., in the cane toad; Phillips et al. 2007). *X. laevis* demonstrates an ability

to disperse at a speed of 0.5 km/year overland in France (e.g., in bocage landscapes; Grosselet et al. 2006) and up to 1 km/year through aquatic routes in France (Fouquet and Measey 2006; Grosselet et al. 2006) and 2 km/year in Wales (Measey 2016). Variations in weather conditions (e.g., in the cane toad; Phillips et al. 2007), landscape structure (including land use, density of linear features such as road and river networks) and the presence of ecological corridors could influence the radial spread and speed of invasion (Ficetola and De Bernardi 2004). Specifically, asphalt and bare soil were found to accelerate the locomotion speed of *X. laevis* in France, whereas grass and leaf litter reduced it, particularly in juveniles (Vimercati, Kruger, and Secondi 2021). Further research on landscape permeability, that is, the capacity of landscape features or land cover to facilitate (e.g., through corridors) or mitigate (e.g., physical barriers) the spread of the species, is critically needed to (1) identify high-risk areas for colonisation and (2) implement landscape management measures, based on land covers or landscape features of low permeability, to slow down the invasion.

4.3 | Implications for Management

The estimated invasion speed locates the invasion front at a distance of 51.8 km (95% CI = 34.1–69.5 km) from the introduction

site. This translates into a predicted established range of about 8400 km², suggesting that eradication has probably become unfeasible. Indeed, although successful eradications of amphibian IAS on a landscape scale have already been reported (e.g., in the American bullfrog in the United States; Kamoroff et al. 2020; Hossack et al. 2023), these instances remain rare. In contrast, intense control efforts have proven ineffective at containing *X. laevis* in Chile, where its estimated range has expanded from 10,432 km² (Measey et al. 2012) to 36,055 km² (Mora et al. 2019).

Urgent action is crucial, as the annual progression of 1.2 km of the invasion front in western France currently translates into an expansion of approximately 400 km² per year in the predicted distribution range (Figure S2). This underscores the potential for significant detrimental effects with each year of delayed action (Ahmed et al. 2022). Furthermore, recent isolated observations of *X. laevis* far from the introduction site—in Bordeaux (2016) and in Toulouse and Lille (2019) (Inventaire National du Patrimoine Naturel 2023)—may indicate an accelerating pace of possible new introductions in the recent years, potentially fuelling the invasion across the national territory. This also applies to other European countries, including Belgium and mainland Italy, where the species has recently been reported (GBIF Secretariat 2023) despite being previously absent or not established (Measey et al. 2012; van Doorn et al. 2022).

Our findings emphasise the importance of a territorialised management of *X. laevis*, focused on three strategic zones. Firstly, priority should be placed on adopting proactive management strategies, including prevention, early detection and rapid responses for containment and eradication at new introduction sites, which have proven to be more cost-effective than reactive responses (Venette et al. 2021; Ahmed et al. 2022). This requires implementing a national surveillance programme for early species detection (Venette et al. 2021; Britton et al. 2023) and developing rapid response strategies for containment and eradication upon detection (Measey et al. 2012). This has proven effective in Spain (Barcelona), where detection of 18 tadpoles in a pond in 2007 prompted an immediate response, allowing *X. laevis* to be eradicated in 10 days (Pascual et al. 2007). In Portugal, an eradication programme implemented 4 years after *X. laevis* was first reported in the wild (2010) has successfully contained the invasion, reduced adult abundances and achieved local extirpations (Moreira et al. 2017; da Bento 2021). Secondly, attention should be directed towards monitoring the invasion dynamics at the predicted invasion front through a long-term programme with standardised protocols (see Merlet et al. 2022a, 2022b). Finally, comparative studies between colonised and noncolonised sites within the established range of the species are needed to (1) identify environmental drivers conducive to successful establishment, similar to studies that have identified suitable habitat conditions for American bullfrog establishment (i.e., increased water depth, floating vegetation and low canopy cover; Fuller et al. 2011; see also Nelson and Piovia-Scott 2022), and (2) assess impacts on native biodiversity, such as shifts in macroinvertebrate communities, reductions in native amphibians' reproduction and species richness caused by *X. laevis* (Lillo, Faraone, and Lo Valvo 2011; Courant

et al. 2018a, 2018b) or decreased density and species richness of native frogs caused by increased American bullfrog density in China (Li et al. 2011). Overall, this should help identify high-risk areas to prioritise management measures for local containment or eradication, concentrating survey efforts on the sites most likely to be colonised and/or severely impacted (Britton et al. 2023; Pili et al. 2024).

This management strategy aligns with French recommendations, which advocate four main actions (Merlet 2022): (1) highly vigilant surveillance to prevent the species establishment, (2) local containment of water catchments as an early detection measure in areas of low population densities, (3) high lethal control pressure applied to each developmental stage (i.e., eggs, larvae, juveniles and adults) in source areas with high population densities and (4) habitat management and restoration to conserve native species. Although the Life CROAA control programme (2016–2022) deemed it unfeasible to implement control measures across the entire established range of *X. laevis* in western France, local efforts drastically reduced the number of captured individuals over 6 years. Similarly, control measures focused on small clusters of American bullfrogs reduced captures from 16,352 individuals per year initially to 156 at the end of the programme (<https://www.life-croaa.eu/>; Société Herpétologique de France 2022).

In conclusion, although spatially informed priority actions are pivotal for achieving effective and timely IAS management (McGeoch et al. 2016), particularly when resources are limited (Bonnet et al. 2023), our study provides a scientific basis for decision-makers and stakeholders to implement regulatory policies for the spatially explicit, integrated management of *X. laevis*. Incorporating spatial considerations into management strategies will allow to optimise resource allocation, prioritising efforts towards high-risk areas (Venette et al. 2021), that is, areas where the probability of invasion is highest or the impact would be most severe (Venette et al. 2010). Spatially explicit management strategies should also facilitate territorialised management by promoting collaboration and coordinated efforts among researchers, decision-makers, managers and local communities. We believe that only such immediate and substantial coordinated efforts will allow to collectively anticipate and mitigate the considerable future costs the species could impose on biodiversity and society (Venette et al. 2021; Bonnet et al. 2023).

Author Contributions

Alain Pagano: conceptualization, investigation, methodology, resources, supervision, validation, project administration, writing – original draft, writing – review and editing. **Clément Harmange:** conceptualization, data curation, investigation, methodology, formal analysis, visualization, writing – original draft, writing – review and editing. **Mariastella Rappoccio:** investigation, resources, writing – review and editing. **Tatiana Colchen:** investigation, resources, writing – review and editing. **Gabriel Combet:** investigation, resources, data curation, visualization, writing – review and editing. **Philippe Chouteau:** investigation, resources, writing – review and editing. **Damien Picard:** investigation, resources, writing – review and editing. **Eléonore Moreau:** investigation, resources, writing – review and editing. **Marco Bartoli:** supervision, writing – review and editing. **Olivier Pays:** conceptualization, methodology, supervision, funding acquisition, writing – review and editing.

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Ethics Statement

Permission to capture and handle amphibians was given by the authority Préfecture Départementale du Maine-et-Loire (Numbers 49/SEEB/CVB 2022–19; 49/SEEB/CVB 2023–27). As an invasive species in France, *X. laevis* is not subject to capture authorisation. All applicable French guidelines for the ethical use of animals in the research were followed.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The dataset analysed during the current study is available in the Open Science Framework repository, <https://osf.io/v7bcs/>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.