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Review

The alien marsh frog cocktail: Distribution, causes and pathways of a global amphibian invasion

Mathieu Denoël [a,*], Christophe Dufresnes [b,*]

[a] Laboratory of Ecology and Conservation of Amphibians (LECA), Freshwater and Oceanic Unit of Research (FOCUS), University of Liège, Belgium

[b] Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE-PSL, Université des Antilles, 55 rue Buffon, CP 51, 75005 Paris, France

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ABSTRACT

While some biological invasions are well documented globally, others, more cryptic, are often underestimated despite multiple local warnings. This is the case of the marsh frog (*Pelophylax ridibundus* sensu lato), a Palearctic anuran amphibian distributed from Western Europe to Central Asia. Marsh frogs have been introduced into many European countries, where they pose threats to biodiversity, yet an integrative understanding of their invasion is lacking. Therefore, we combined diverse bibliographic sources with recent DNA barcoding to determine the extent and diversity of invasions in Europe and substantiate the causes and pathways of introductions. We document alien frog populations across 167 sub-regional administrative areas in 19 European countries, corresponding to nine phylogeographic lineages originating from three continents. Introduction pathways from the Balkans and the Pannonian Plain, Anatolia and the Levant coincide with the history of live frog imports into Europe, which involved the trade of hundreds of millions of individuals. Introductions were mainly associated with the consumption of frogs' legs, but also with ornamental, educational and research purposes. While some introductions date to the 18th century, most took place in the second half of the 20th century and new cases continue to emerge. Altogether these results show that the marsh frog is a widespread and complex invasive amphibian species in Europe, and ranks among the most worrying amphibian invaders in the world. Our assessment calls for the immediate ban on the commercial import of live water frogs, especially to prevent new lineage combinations in invaded areas, a Pandora's box that, if opened, could further boost the species' invasive potential.

1. Introduction

Biological invasions are one of the major threats to biodiversity, causing declines at species and community levels in most ecosystems worldwide (Pyšek et al., 2020). Invasions are typically the result of punctual introductions for single purposes such as food resources (Pringle, 2005), biocontrol for agriculture (Shine et al., 2020) or disease mitigation (Pyke, 2008). Islands and lentic freshwaters have suffered greatly from these invasions due to their limited space and often lack of natural predators or efficient competitors leading to the extinction of emblematic species (Capinha et al., 2017; Doherty et al., 2016; Gallardo et al., 2016). The rate of invasion is particularly high and continuously increasing in Western Europe and North America (Mormul et al., 2022; Pyšek et al., 2020). Due to their widespread patterns and the number of taxa and environments affected, biological invasions cause huge economic costs which are becoming higher than those of natural hazards (Turbelin et al., 2023).

Amphibians are a class of vertebrates with more than eight thousand species, many of which threatened by invasive alien species (Bucciarelli et al., 2014; Falaschi et al., 2020; Nunes et al., 2019). However, they are themselves also often introduced outside their native range (Capinha et al., 2017; Kark et al., 2009), where they can have multiple impacts, including on other amphibians (Kraus, 2015; Shine, 2010). The most famous amphibian invader, the cane toad *Rhinella marina*, was introduced in many places, especially Australia, from South America for "pest" control, where it continues to expand rapidly over large areas (Shine, 2018). Other species have also been introduced and recognized as top amphibian invaders: the American bullfrog *Lithobates catesbeianus* (Ficetola et al., 2007), introduced from North America for the food industry, and the African clawed frog *Xenopus laevis*, released and escaped

* Corresponding authors.
E-mail addresses: Mathieu.Denoel@uliege.be (M. Denoël), christophe.dufresnes@mnhn.fr (C. Dufresnes).

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from laboratories where it was used for research and teaching experiments, and as a resource for early pregnancy tests (Measey et al., 2012). While these few species have received a lot of attention and research, the diversity of amphibian invaders is actually much higher (Van Wilgen et al., 2018).

Broadly distributed from Western Europe to Eastern Asia, Eurasian water frogs of the genus *Pelophylax* are involved in multiple, largely overlooked invasions (Dufresnes et al., 2024b). Due to their overwhelming diversity (e.g., ~40 mitochondrial phylogeographic lineages currently delimited into 12 species by Dufresnes et al., 2024b; see also Frost, 2025), the morphological similarities between native and alien taxa, and thus their non-distinction in most wildlife mapping and monitoring programs, the geography and history of *Pelophylax* invasions have remained elusive. However, there has been a growing body of evidence (Dufresnes et al., 2017; Dufresnes et al., 2018; Holsbeek et al., 2008; Ohst, 2008; Plötner et al., 2015), particularly in recent years, that indicates that we may be facing a complex, global amphibian invasion (Bellati et al., 2023; Demay et al., 2023; Dufresnes et al., 2024a; Dufresnes et al., 2018; Jelić et al., 2022; Papežík et al., 2024). In particular, Dufresnes et al. (2024b) identified globally the presence of 14 lineages among alien invaders, most of them from the marsh frogs, *Pelophylax ridibundus* (Pallas, 1771), also known as the lake frog and under its previous classification *Rana ridibunda*. Such a high diversity for exotic populations parallels the tremendous diversity of the native populations of *P. ridibundus*. The species experienced a complex biogeographic history across its vast distribution (from Western Europe to the Himalayas) within the last millions of years, during which it diversified into at least 18 named or unnamed phylogeographic lineages e.g., *P. r. kurtmuelleri*, *P. r. bedriagae*, *P. r. cypriensis*, *P. r. cerigensis*, *P. r. caralitanus*, *P. r. persicus*, *P. r. terrentievi* and other lineages now labeled *P. r.* cf. *ridibundus* following Dufresnes et al. (2024b).

Several studies have highlighted the risk of genetic pollution and gametic exclusion caused by these alien water frogs to related species of the genus *Pelophylax* (Bruni et al., 2020; Dufresnes and Mazepa, 2020; Holsbeek and Jooris, 2010b; Pagano et al., 2003; Quilodrán et al., 2015). Although not much documented, species replacements have been observed in some invaded areas, and this seems particularly alarming for native *Pelophylax* species (Demay et al., 2023; Litvinchuk et al., 2020; Pilliod et al., 2012). Marsh frogs have a very broad ecological opportunism which leads them to occupy a large variety of aquatic habitats and therefore to exhibit a high spatial and temporal overlap with local native populations in pond environments (Denoël et al., 2022; Pille et al., 2021, 2025). This similar use of habitats and the continuous presence in water or at the water-land interface of waterbodies is particularly worrying as it exposes a large variety of native amphibians to predation pressure. Although many native species are expected to persist with marsh frogs, it is likely that their abundances may be affected through multiple direct and indirect processes. Particularly, some species such as treefrogs, which are endangered profitable prey may be particularly affected (Pille et al., 2021). In addition, marsh frogs compete with native species for space use and can harass local anurans, what may ultimately alter their fitness (M. Denoël, pers. obs.). Finally, water frogs can be a vector of diseases which may affect other amphibians (Jakóbik et al., 2024; Kok, 2001). The marsh frog invasions are therefore a multi-facet concern for (amphibian) biodiversity, but there is a lack of understanding of their distribution, causes, pathways and origins, preventing a global overview of the situation, which is necessary to raise awareness among biogeographers, stakeholders, and national and international policy makers.

In the present study, we provide an integrative overview of the global invasions of marsh frogs in Europe, by quantifying the number of invaded areas and the associated diversity of alien lineages, and by cumulating multiple lines of evidence to retrace their geographic origins, chronology, and proximate causes. Specifically, we compile available data associated with the introductions of marsh frogs, including overlooked knowledge from the local literature (e.g. reports of introductions and pathways in distribution atlases) with recently published molecular data from invaded and native territories in Europe, Asia and North Africa (Text A1: Methodological approaches). In doing so, we aimed to emphasize the complexity and significance of the global invasions of marsh frogs, and call for the same consideration and research efforts as given for handling and studying other major global amphibian invaders. Last but not least, our approaches illustrate the complementarity of local sources of knowledge with those of molecular tools to provide a more accurate and exhaustive understanding of invasion patterns and processes, so conservation challenges can be addressed more efficiently.

2. Patterns of alien distribution in Europe

2.1. Large invasions outside the native range

Alien marsh frogs extensively colonized several parts of the European continent, with introductions occurring both outside and inside the limits of their global native range (Fig. 1a). Altogether, these invasions have been substantiated in up to 19 European countries, covering at least 62 regions and 167 sub-regional administrative units (e.g. provinces) (Table 1; Fig. 1b; Table A1; see Table A2 for the local names of the administrative units in the invaded countries). Although already important, these numbers may underestimate the extent of the invasions, as it only includes the cases presented in publications.

Alien marsh frogs have invaded almost the whole of France (Geniez et al., 2012), all of Belgium (Holsbeek and Jooris, 2010a; Percsy and Percsy, 2007; Percsy and Percsy, 2013), and large parts of Switzerland (Dufresnes et al., 2018; Grossenbacher, 1988), Liechtenstein (Kühnis, 2002) and Italy (Bellati et al., 2023; Bressi, 2006b). They are also present in Luxembourg (Proess, 2003; Weigand et al., 2022), the western tip of Slovenia (Bressi, 2006a), the Netherlands (Felix et al., 2012), Germany (Mayer et al., 2013; Ohst, 2008) and Austria (Grabher et al., 2015). In the north range margins along the Baltic Sea, introductions also occurred in Latvia (Borkin et al., 2002), Estonia (Raanap, 2006), Russia (Milto et al., 2022) including the Kaliningrad enclave (Litvinchuk et al., 2020), and southern Finland, where it has since disappeared (Terhivuo, 1981). Introduced marsh frogs have also been locally reported in Spain (Arano et al., 1995), and potentially within their native range in Croatia (Jelić et al., 2022).

Apart from the mainland, invasions were also reported on large remote islands, such as England (Lever, 1980; Wycherley et al., 2003; Zeisset and Beebee, 2003), Sardinia in Italy (Bellati et al., 2019), and the smaller Gozo island in Malta (Papežík et al., 2024). They were also spotted in several islands in the Mediterranean Sea (Levant Island, France: Tankovic and Riviere, 2023), the Atlantic Ocean (Oléron Island, France: Dussoulier and Grosselet, 2002), the North Sea (Ameland Island, The Netherlands: Bergers and Luitjen, 2009; Sheppey Island, UK: Lever, 1980), and in the Baltic Sea (Christiansø Island, Denmak: Fog et al., 2019), including islets at the mouth of Neva River in the Gulf of Finland (Milto et al., 2022) (Fig. 1a).

2.2. The geographical limits of the invasion

Within or at the boundaries of the native range, identifying genuine vs. introduced marsh frogs populations can be tedious without a molecular assessment or historical data (Günther, 1996). The combined analyses of distribution and alien haplotypes helped to refine the western limit of the continental native range as running from the Rhine valley to Istria, in Croatia (Fig. 1a). The limits in Germany and in the Netherlands are not clear. The northern limit of native marsh frogs is thought to run across Lithuania and Belarus (Milto et al., 2022), implying that populations further north are allochthonous, but the exact limit remains unclear (Fig. 1a).

At both the western and northern limits, competing scenarios for the alien versus native status of some of the populations have been

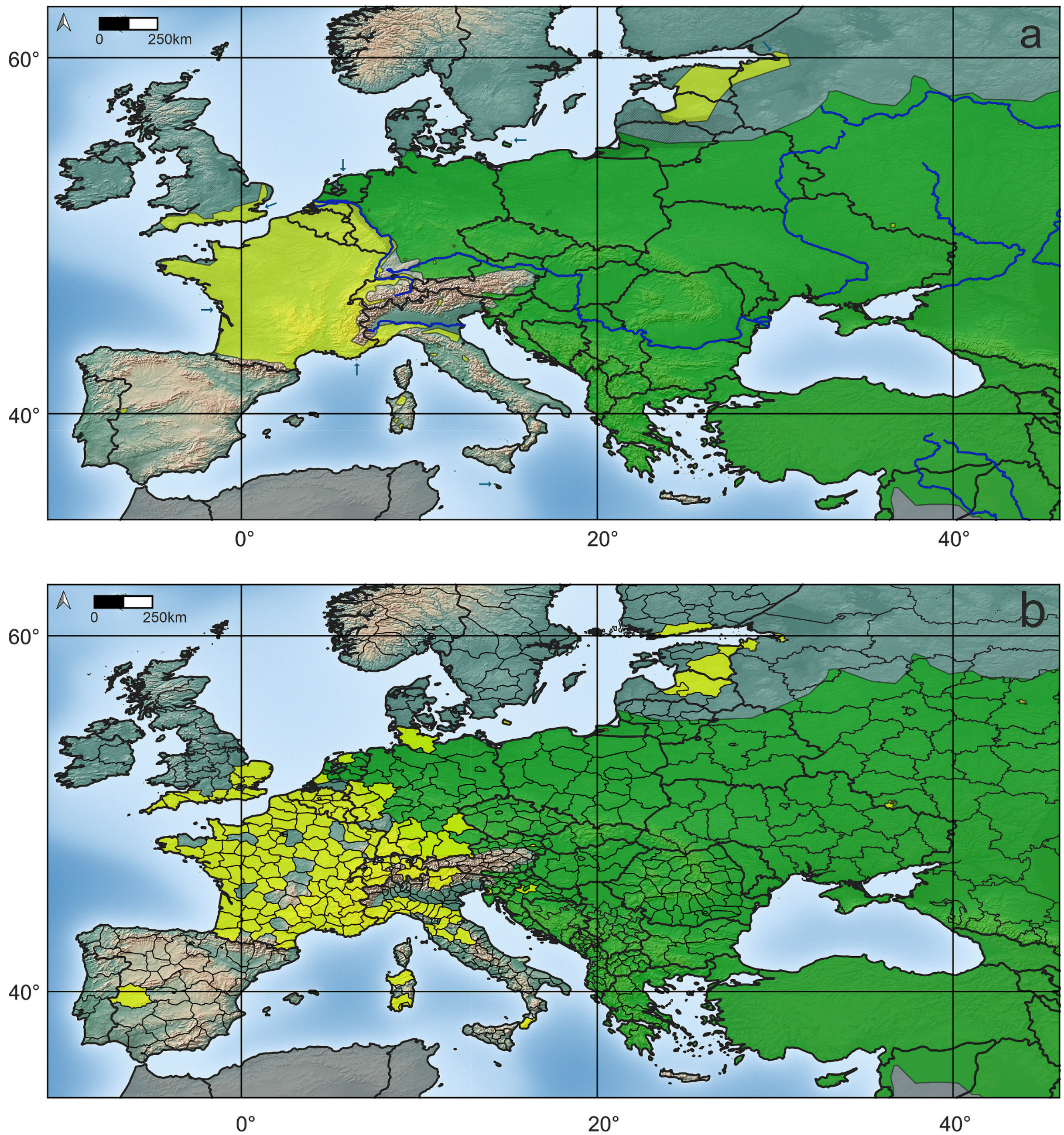

Fig. 1. Native (green) and alien (yellow) distribution ranges of marsh frogs (*Pelophylax ridibundus*) in Europe: (a) approximate boundaries of ranges, (b) invaded sub-regional administrative units. The native area outside of Europe is also shown within the limits of the map. Dash dark areas emphasize unclear limits. Black arrows point to small invaded islands. The populations in Finland are considered extinct. Major rivers are shown by blue lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hypothesized. On the one hand, the presence of southern haplotypes in northern countries may stem from post-glacial expansions northward (Litvinchuk et al., 2020) from the genetically-rich Balkan refugia (Dufresnes et al., 2024b). On the other hand, some of these populations may be the consequences of human-mediated dispersal. For instance, in the northern populations of Kaliningrad (Russia), the presence of two distinct mitochondrial lineages, of Balkan and Anatolian origins, is consistent with introduction events (Litvinchuk et al., 2020). The latter hypothesis is also suggested by the very old records of translocations in the same oblast (see Section 2.4) (Milto et al., 2022) as well as introduction records documented in nearby Estonia (Raanap, 2006) and Latvia (Borkin et al., 2002), and by the observation that multiple lineages within the same ponds are the hallmark of marsh frog introductions elsewhere (Bellati et al., 2023). However, marsh frogs are known from an isolated Baltic island, Bornholm (Rybacki and Fog, 1995) where they might be natural relics, hence the northern range of *P. ridibundus* may be a mixture of persisting native and recently introduced alien populations. The native status of the Bornholm population is pending confirmation (e.g., by a genetic study), however, especially since historical introductions were documented in a nearby island (Fog et al., 2019). In France, the national and regional atlases, local knowledge, and genetic analyses, all suggest that marsh frogs should be considered native only in the Rhine valley near the German border, from where they may have penetrated slightly deeper into the country (Geniez et al., 2012; Ohst, 2008; Pagano et al., 1997; Parent, 1981; Vacher, 2010), even though a wider natural range is sometimes given (IUCN SSC Amphibian Specialist

Table 1
Distribution and lineage diversity of alien marsh frogs (*Pelophylax ridibundus*) in Europe.

Country	N_1	N_2	Mainland	Island	Report	Range	Lineages
Austria	2	2	*		*[a]	Mixed	
Belgium	3	11	*		*	Out	*kurt, rid,* cf *rid F, bed*
Croatia	1	1	*			Mixed	*kurt*[d]
Denmark	1	1		*	*	Mixed[c]	
Estonia	2	2	*	(*)	*	Out	*kurt, rid*
Finland	1	1	(*)		*	Out	
France	12	75	*	*	*	Mixed[c]	*kurt, rid,* cf *rid C*
Germany	5	13	*		*	Mixed	*kurt, rid*
Italy	10	25	*	*	*	Mixed	*kurt, rid,* cf *ridB,D,F,K, bed*
Latvia	2	2	*		*	Out	*kurt, rid*
Liechtenstein	1	1	*		*	Out	
Luxembourg	1	1	*		*	Out	cf *rid F*
Netherland	3	3	*	(*)	*	Mixed	*kurt or rid*
Malta	1	1		*		Out	cf *ridB*
Russia	5	5	*	*	*	Mixed	cf *rid G,K*
Slovenia	1	1	*		*[b]	Mixed	
Spain	1	1	*		*	Out	
Switzerland	6	11	*		*	Out	*kurt, rid,* cf *ridK*
United Kingdom	4	10	*	*	*	Out	

Notes: N1, N2: number of regional and sub-regional administrative regions per country; Mainland/Island: presence on the mainland and island of each country, respectively (*): extinct; Reports: direct (non genetic) evidence of introduction (*proved, but *[a]: suspected/out of range, *[b]: report in nearby Italy); Range, out: no marsh frogs are native in the listed country, mixed: both native and alien marsh frogs are found in the country ([c]: possibly only aliens); Lineages (following Dufresnes et al., 2024b): *kurt (kurtmuelleri), ridib (ridibundus),* cf. *ridib (cf ridibundus), bed (bedriagae); kurt*[d]: alien origin to be confirmed (Croatia). For further details and references, see Table A1.

Group, 2023; Litvinchuk et al., 2020). Several arguments cast doubt on the natural occurrence of marsh frogs in eastern France, and consequently, in France as a whole. First, DNA barcoding reported alien lineages in this area, including from lineages that could not have come by themselves due to their distant origin (Dufresnes et al., 2018) (see Section 3 and Table A1). Second, marsh frogs were considered rare in the area five decades ago (first records in Petite Camargue Alsacienne, in Haut-Rhin Department: Baumgart, 1982; Brodmann, 1979). Third, these early observations coincide with the first recorded introductions and the development of piscicultures (Brodmann, 1979). Fourth, the closest populations in nearby Germany, Switzerland and Luxembourg were shown to have an allochthonous origin according to their exotic genetic diversity and specific reports of introductions (Dalbeck et al., 2001; Dufresnes et al., 2018; Jäckel et al., 1996; Ohst, 2008) (Table A1). The presence of alien marsh frogs in eastern France is therefore most likely due to direct introductions and dispersal from the introduced populations of neighboring countries (and vice-versa for expansions eastwards: Ohst, 2008). Whether marsh frog populations in France are natural (Vacher, 2010) or exogenous has profound consequences for conservation – the misassumption that *P. ridibundus* is native in eastern France creates a conservation paradox, since it confers a national protection of this invasive species, thus hindering management actions.

2.3. Cryptic introductions within the native range

Several introduction events within the native range of marsh frogs have been suggested by DNA barcoding, namely the presence of genetic variants that are otherwise known only from geographically distant and/or disconnected populations (Table A1). Examples of such introductions are found in Germany (Mayer et al., 2013; Ohst, 2008). Unexpected haplotypes, particularly from *P. r. kurtmuelleri*, were also found in several central and eastern European countries (for instance in Croatia, Poland and Ukraine: Dufresnes et al., 2024b; Jelić et al., 2022; Kolenda et al., 2017; Litvinchuk et al., 2020). As highlighted above, such patterns must, however, be interpreted with caution, as they could also reflect dynamic biogeographic processes, namely refugial hybridization followed by past range expansions, during which genetic variants may be carried over significant distances and short time scales. While such explanation is reasonable for some populations (Dufresnes et al., 2024b), human-assisted dispersal appears a more parsimonious hypothesis elsewhere, particularly in Germany, where introductions have been documented (Dalbeck et al., 2001; Jäckel et al., 1996; Sowig et al., 2007). In Poland, the introduction hypothesis finds some support in records of live fish importation from the Balkans (Kolenda et al., 2017). Short-distance translocations have also been reported from nearby countries, such as in Trieste (north-eastern Italy), with *P. r. kurtmuelleri* frogs originating from Istria (north-western Croatia) (Bressi, 2006b), and suspected in Vienna (Austria), with marsh frogs originating from other eastern Austrian localities (Grillitsch, 1990). In fact, introductions suspected on the basis of unusual patterns of genetic diversity are most likely only the visible part of the iceberg, and many more populations or individuals considered natives may be of alien origin. Accordingly, the most widespread marsh frog lineages, notably *P. r. ridibundus*, are genetically unstructured across their vast ranges (Ohst, 2008), thus reducing the diagnosticity of DNA barcoding markers to distinguish populations inhabiting different regions. For instance, the same mitochondrial haplotypes are sometimes found across thousands of kilometers (Dufresnes et al., 2024b), which implies that any translocations within the corresponding area cannot be detected, and that narrowing down the sources of introduced populations bearing these haplotypes are impossible without a better phylogeographic resolution. To this end, the implementation of multilocus approaches (e.g., additional mitochondrial markers, genome-wide loci) with fine-scale sampling represents a promising research direction.

2.4. Timing of introductions in invaded countries

The oldest records of marsh frogs outside their range that were clearly associated with introductions are from the northern margin of the range, namely in the 18th century in St-Petersburg (Milto et al., 2022), 1925 in Estonia (Raanap, 2006), in the 1930s in Finland (Hoogesteger et al., 2013), 1935 in the United Kingdom (Smith, 1949) and 1950 in Denmark (Fog et al., 2019) (Fig. 2). In Central Europe, the oldest records likely date to 1920 – later confirmed in 1951 – in Switzerland (Grossenbacher, 1988), from the end of the 19th century in eastern Austria (Grillitsch, 1990), in the 1980s in western Austria (Kühnis, 2002), and since the 1970s in Germany (Jäckel et al., 1996). In Southern and Western Europe, the earliest introductions are from 1941 in Italy (Lanza, 1962), in the 1960s in Britany, France (Pelloté et al., 2019), in the 1970s in other regions of France, notably Pays de la Loire

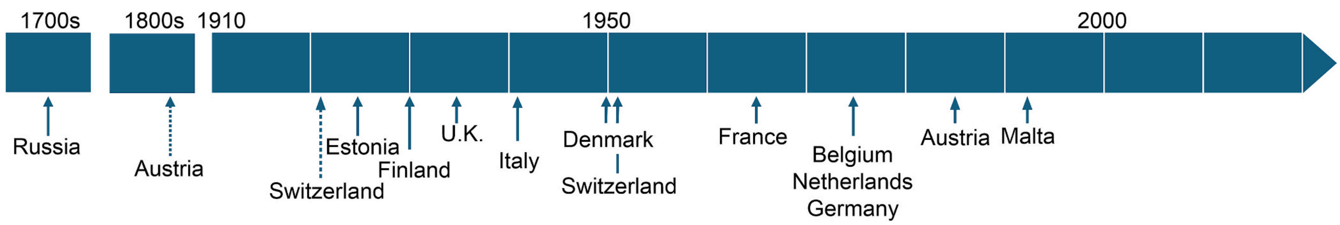

Fig. 2. Chronology of the first reported introductions of marsh frogs (*Pelophylax ridibundus*) in European countries. Interrupted and full arrows refer to presumed and confirmed initial introductions, respectively.

(Bonhomme, 2022), Grand Est (Grange, 1995), Provence Alpes Côte d'Azur (Dusoulier and Swift, 2012) and Occitanie (Demay et al., 2023), as well as in Belgium before 1975 (Parent, 1997), and in the Netherlands (Hoogmoed, 1975) (Fig. 2). New introductions continue to be reported in the 1980s in France, notably in Auvergne – Rhône Alpes (Duget and Joly, 2015) and Normandie (Barrioz et al., 2015). It is likely that many of the first introductions were reported later than the initial releases or escapes, and the timeframe mentioned above should therefore be interpreted cautiously, especially when the exact date of introduction was not documented. In particular, large commercial frog imports started before some of the first wild findings of marsh frogs (see e.g. Section 3.1), and the latter were likely to have been overlooked given the morphological similarities between the introduced and native species. The introduction in Malta may be more recent, namely from the early 1990s (Sciberras and Schembri, 2006). New regions continue to be the object of introductions, with the first records detected as recently as the early 21th century, such as in various parts of Italy (Bruni et al., 2020; Razzetti et al., 2010).

2.5. *Passing through the environmental filters: successful establishment and dispersal*

The wide allochthonous distribution of marsh frogs across thousands of invaded sites through many countries reflects their successful establishment (Fig. 1b; Table 1). Soon after the colonization of new sites, local population sizes can become high in favorable habitats (Duret et al., 2022). As a result, marsh frogs often become the most abundant *Pelophylax* in some invaded areas, e.g., in Belgium (Percsy and Percsy, 2009). The continuous current distribution is thus the result of hundreds of introduction events followed by natural dispersal (Fig. 1a). For example, in Switzerland, the invasion range now links both edges of the suitable lowland areas (Swiss Plateau, from Geneva to St-Gall) although it was seemingly initiated by a few spatially distant introductions (Dufresnes et al., 2018). In other parts of the invaded range, reports are consistent with a rapid expansion within a few decades or even a few years following the first introduction events, as e.g., in France (Demay et al., 2023; Denoël et al., 2022), Italy (Bressi, 2006b) and Austria (Grabher et al., 2015). In the Herault part of the Larzac plateau in southern France, the species colonized more than 100 ponds (i.e. 63 % of available ponds) throughout the landscape just from a few starting points in a couple of decades (Denoël et al., 2022).

Despite this general trend of expansion, some declines have also been reported among introduced populations, all in the northern edge of the range, e.g., in the UK (Lever, 1980) and northwest Russia (Milto et al., 2022). The species even seems to have disappeared from Finland in the decades after its introduction (Hoogesteger et al., 2013). Marsh frogs are also considered extinct from one island in the Netherlands where they had been previously introduced (Bergers and Luitjen, 2009).

The invasion of marsh frogs was promoted by their broad ecological opportunism (Denoël et al., 2022; Padilla et al., 2023; Pille et al., 2023; Pille et al., 2025). In the Larzac plateau in southern France, where water frogs were historically absent, marsh frogs have acclimated to all types of available freshwater habitats within a couple of decades, with a preference for deep, vegetated and sunny ponds (Denoël et al., 2022). Such preferences, particularly water depth, have been cited as possible resource partitioning with other native *Pelophylax* species (Leuenberger et al., 2014). However, changes in habitat characteristics following human modifications of the landscape have often favored marsh frogs over native water frogs (Demay et al., 2023).

3. Multiple origins of introductions and lineages

Comparisons of the genetic diversity between invaded and native ranges highlighted the involvement of multiple mitochondrial haplotypes and lineages in the invasions. In their recent overview of the phylogeography of Palearctic water frogs, Dufresnes et al. (2024b) reported no less than nine alien lineages of marsh frogs in Europe (Table 1). Their taxonomy is however unsettled, and these lineages received various designations in the literature, which renders correspondence sometimes difficult. Following the taxonomy and terminology of Dufresnes et al. (2024b), invasive lineages include ***P. r. ridibundus*** from Central, Eastern and South-Eastern Europe, ***P. r. kurtmuelleri*** from the western and southern Balkans, ***P. r. bedriagae*** from the Levant, and six closely related lineages referred to as ***P. r.*** cf. ***ridibundus*** B (sometimes considered as the subspecies ***P. r. caralitanus***, in southern Turkey), C (from eastern Turkey to Iran), D (south western Turkey), F (the northern half of Turkey), K (sometimes referred as the Cilician west populations in Adana Province, central southern Turkey) and G (from eastern Ukraine to the Urals) (Fig. 3).

Considering invasions at a sub-regional scale (e.g., provinces) for which barcoding was available (i.e., 61 areas), the most frequent lineages confirmed across invaded areas are *kurtmuelleri* (61 %; excluding eastern European populations where the native vs. introduced status is unclear; see above), *ridibundus* (51 %), the lineages regrouped under cf. *ridibundus* (46 %) and *bedriagae* (8 %) (Fig. 4; Table A1). The cf. *ridibundus* lineages, which are not always discernable depending on the DNA barcode used (27 sub-regions in total), could be further distinguished for 19 sub-regions, which are occupied by cf. *ridibundus* F (10 sub-regions), K (5 sub-regions), C (3 sub-regions), B (2 sub-region), D (1 sub-region) and G (1 sub-region). Again, these numbers under-represent the diversity of the invaded ranges, since only a small proportion of exotic populations has been genetically barcoded (Fig. 4; Table A1). For example, only 36 % of the geographic areas hosting confirmed marsh frog introductions have been clearly assessed by molecular surveys. Moreover, the barcoding effort is greatly variable between regions (Fig. 4; Table A1). For instance, genetic data are available for most of the invaded provinces of Italy (21 out 25; where altogether 7 different lineages have been detected), and the invaded cantons of Switzerland (9 out of 11). In contrast, there is a significant deficiency of DNA barcoding data in countries like France, where marsh frogs were genetically clearly identified in only 11 out of the 75 invaded departments (Fig. 4; Table A1). A broad scale molecular survey is also missing in the United Kingdom (Fig. 1a, b). Strong regional biases are also flagrant within some countries such as Belgium, where genotyping is available for the five Flemish provinces versus only for one in Wallonia (Fig. 4; Table A1). Such DNA barcoding surveys should ideally quickly follow the first alerts raised by local reports, to better link introductions with pathways and exports (see hereafter).

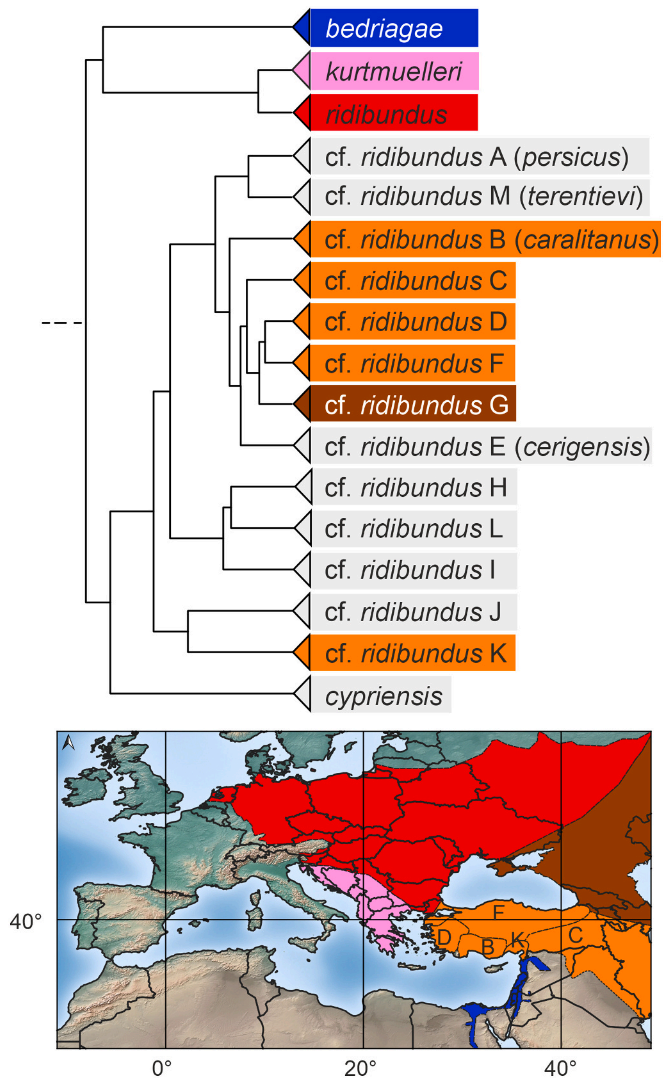

Fig. 3. Evolutionary relationships and native distributions of the invasive marsh frog (*Pelophylax ridibundus*) lineages: (a) Mitochondrial DNA-based phylogenetic tree (adapted from Dufresnes et al., 2024b) and (b) simplified approximated respective ranges. Parapatric areas consist of a mix of several lineages (see Dufresnes et al., 2024b).

3.1. From South-Eastern Europe: the Balkan and Pannonian origins

The largest reported exports of *Pelophylax* to European countries originate from the former Yugoslavia, which began exporting in 1928. Within 41 years of record, at least 6312 tons of live water frogs, corresponding to more than 100 million individuals, were exported, with a peak of 420 tons/year reached in 1976 (Ljubisavljevic et al., 2018). These frogs were initially shipped mainly to France, and since 1977, to Italy (93 % of exports), with the remainder being distributed to Austria, Germany, Belgium, Denmark, Greece, Great Britain, Romania, and Switzerland (Džukić et al., 2003) (see also Section 3.4.; Fig. 5). Regional data showed that more than half of the Serbian counties were harvested for water frogs in the 1990s, with the highest rate in Vojvodina in the Pannonian Plain, while the south and south-west of the state seem to have been unaffected (Džukić et al., 2003). No records of harvest exist in Kosovo, at least until the end of the 20th century. The second major exporter was Bulgaria, with up to 281 tons/year in 1971, mainly from heavily harvested areas in the regions of Plovdiv, Pazardzhik, Jambol, and Sofia (Beshkov and Nanev, 2006). Among others, Bulgaria exported to Switzerland (Honegger, 1978). In addition, Greece and Albania exported live marsh frogs to France (Dubois, 1983), while Turkey exported to Switzerland (Dufresnes et al., 2018). Albania typically supplied the Italian market with figures for Europe overall reaching 14–57 tons/year in the period 2012–2022 (UNEP-WCMC, 2023). Hungary started to export live frogs in 1933 but its main exports were between the 1950s and 1974, reaching 100 to 130 tons of water frogs, including live *P. ridibundus*, harvested in the Pannonian Plain every year to France, Switzerland, Italy and Germany (Tóth et al., 2023) (Fig. 5), and exports to Poland have also been mentioned (Dubois, 1983). While most of water frogs exports correspond to marsh frogs, which are larger and thus have a higher commercial value, other water frog taxa, such as *P. esculentus* and *P. shqipericus* were also included (Altherr et al., 2022; Ljubisavljevic et al., 2018; Tóth et al., 2023).

The presence of the Balkan lineages *P. r. ridibundus* and *P. r. kurtmuelleri* (Table 1; Fig. 4) are thus consistent with the records of Balkan and Pannonian exports (Fig. 5). Accordingly, newly founded populations carrying *kurtmuelleri* mtDNA occur in Italy (Bellati et al., 2023; Bisconti et al., 2019), including Sardinia (Bellati et al., 2019) and also in France (Dufresnes et al., 2017). Specimens of Balkan ancestry have also been found in diverse populations in the Rhine and Ruhr valleys in Germany (Ohst, 2008). More generally, both lineages are exceedingly found across multiple Western European locations that were associated to known introduction events (Dufresnes et al., 2024b), including some from the Balkans for which historical records exist. In Italy, marsh frogs were introduced in the north-western province of Imperia, from Albania (Lanza, 1962), and are now spreading westward towards the French border (Oneto et al., 2021), as well as eastwards (Falaschi et al., 2018). Introductions from Bulgaria, which appears naturally inhabited by a mix of *ridibundus* and *kurtmuelleri* haplotypes (Fig. 3), have been documented in South Holland in the Netherlands (Hoogmoed, 1975) and in Flanders in Belgium (Jooris, 2002). Escapes from frogs originating from the Balkans were also mentioned in Switzerland (Kühnis, 2002). Minor trade also had major impacts, as shown by the first invasion in the UK, which was initiated by 12 frogs captured in Hungary (Puky et al., 2005). Their descendants are now found throughout southern UK, in parallel to additional introductions (Lever, 1980), which should motivate a formal investigation to determine their exact extent and diversity.

3.2. The Eastern European routes

Several exports of frogs were documented in Eastern Europe. The Volga Delta, which discharges in the Caspian Sea, has been a frequent harvest area for the frog trade within Russia (Litvinchuk et al., 2020). Ukraine exported from Crimea up to 56 tons of frogs annually in 1974–1980 (Kuzmin, 1999). Some of the introductions in Kaliningrad and surrounding areas could have come from other parts of Russia, although it has not yet been substantiated (Litvinchuk et al., 2020). The marsh frogs imported in St-Petersburg supposedly came from southern Russia, which is consistent with the occurrence of the lineage (cf. *ridibundus* G). As multiple introduction events occurred all over the eastern current range of *P. ridibundus*, such as in Kazakhstan and Siberia (Kuzmin, 1999), it is not unlikely that it also contributed to some undocumented translocations elsewhere within Europe.

3.3. From non-European origins: the Anatolian and Levantine routes

Turkey continues to over-harvest its water frog populations, mostly for the international trade (Çiçek et al., 2021), and it was accordingly ranked as the third non-EU country to supply the EU frog leg market over the 1999–2009 period (Altherr et al., 2011). Hundreds of tons of frogs, including live specimens (up to 648 tons in 2012) are exported annually, mainly to France, Switzerland and Italy, but also to Spain (Auliya et al., 2023; Dubois, 1983; UNEP-WCMC, 2023) (Fig. 5). Switzerland for example imported 450,000 live frogs/year from Turkey (Altherr et al., 2022). This Turkish connection is well illustrated by the genetic diversity of Belgium (Holsbeek et al., 2008), Italy, including Sardinia

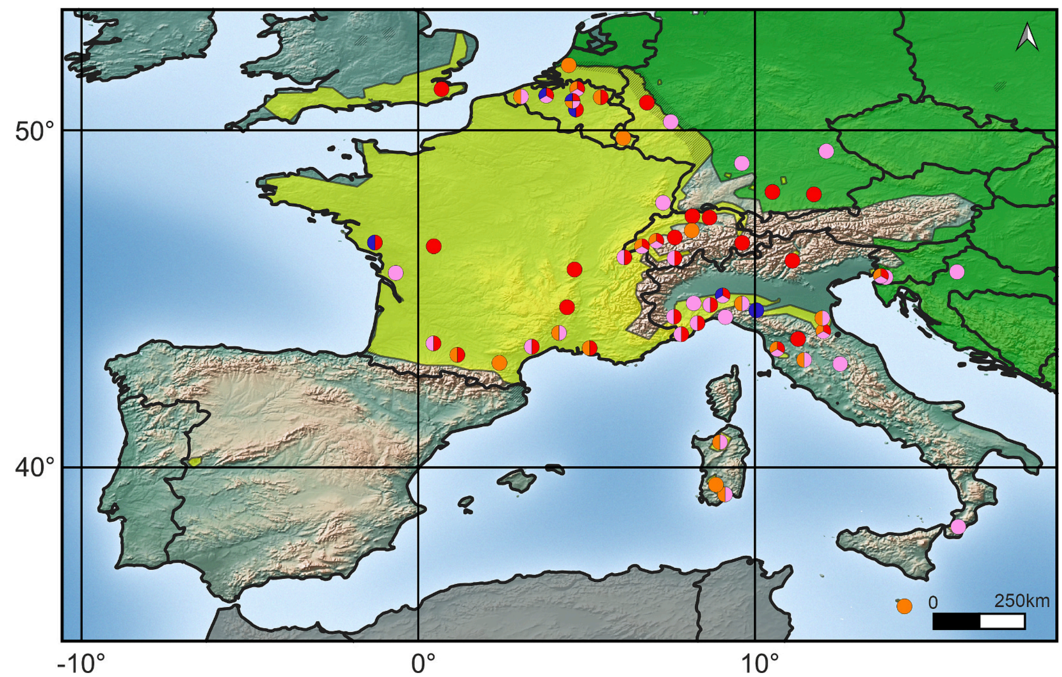

Fig. 4. Geographic origin of alien marsh frog (*Pelophylax ridibundus*) populations in Western and Central Europe. The pie charts are positioned in the invaded subregional units (e.g. provinces), with their colors illustrating the areas of origins, which are inhabited by different lineages, namely the western and southern Balkans (pink; *kurtmuelleri*), Central/Eastern Europe (red; *ridibundus*), Anatolia (orange; cf. *ridibundus*), and Egypt/Levant (blue; *bedriagae*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

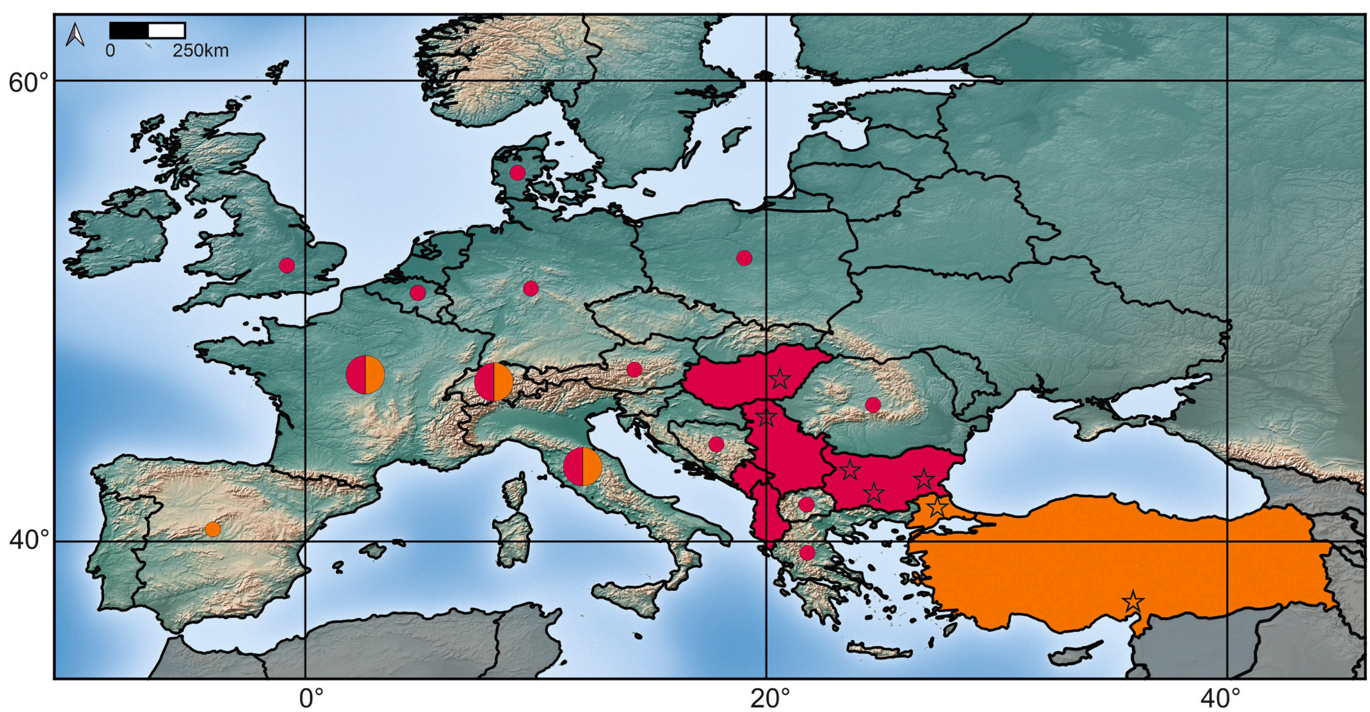

Fig. 5. Main exports of marsh frogs (*Pelophylax ridibundus*) from the Balkans, the Pannonian plains and Turkey into European countries, colored in respect to their corresponding lineages: *ridibundus/kurtmuelleri* (dark pink); cf. *ridibundus* (orange). The pie charts represent the countries of destination (larger symbols represent the main exports). The stars represent the main harvested areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Bellati et al., 2019, 2023), Luxembourg (Weigand et al., 2022), Switzerland (Dufresnes et al., 2018), France (Dufresnes et al., 2024b), Kaliningrad (Litvinchuk et al., 2020) (Figs. 1a, b, 4, 5). Out of the nine marsh frog lineages, five are either endemic or partly distributed in Turkey (*P. r.* cf. *ridibundus* B, C, D, F and K) (Fig. 3). In particular, one third of the frogs annually collected in Turkey (estimated to 17 millions of large individuals) solely come from the Seyhan and Ceyhan deltas in the south-eastern province of Adana (Çiçek et al., 2021) (Fig. 5). This area is inhabited by a phylogeographic lineage unique to the northern Levantine coast (*P. r.* cf. *ridibundus* K), but which is now also found thousands of kilometers away in several areas of Italy (including Sardinia; Bellati et al., 2019, 2023), Switzerland (Dufresnes et al., 2018) as well as in Russia, near the Ukrainian border (Dufresnes et al., 2024b) (Fig. 1a, b). If it represents a sustainable introduction, the latter, which was detected opportunistically (Dufresnes et al., 2024b) may be worrisome as it could threaten the native *Pelophylax* communities inhabiting the Eastern European plains. For instance, Ukraine, which is home to well-studied hybridogenetic populations (Mezhzherin et al., 2023; Suriadna et al., 2020), seems to have so far been spared of alien marsh frog invasions. Given the high levels of Turkish exports, it is likely that the Turkish lineages may continue to spread across European populations.

South of the Levantine coast, Egypt exported up to 140 tons of marsh frogs in 2000, followed by a steady decrease (Ibrahim, 2013). Marsh frogs were harvested in large lakes close to the Mediterranean coast as well as in the Nile creeks (Ibrahim, 2013). In Vendée (western France), marsh frogs were found near a shop that used to import live specimens from Egypt (Dubois, 1983), and similar imports were documented in Belgium (Kok et al., 2002). The only marsh frog lineage known from Egypt is the Levantine subspecies *P. r. bedriagae* (Dufresnes et al., 2024b) (Fig. 3), which was accordingly reported in Western European countries (e.g., Belgium, France and Italy), in accordance with the provenance of imports (Dubois, 1983; Kok et al., 2002). The imports of this lineage are also probably underestimated, as some shipments from Egypt and elsewhere were shown to be wrongly labeled at least in Belgium (Kok, 2001), thus calling therefore for more controls through DNA barcoding.

3.4. The mismatch: imports into exporting regions

Despite its high quantity of exports, former Yugoslavia simultaneously imported live water frogs from the former Soviet Union (Ljubisavljevic et al., 2018). As emphasized, multiple introductions within and from Russia have been clearly documented (Kuzmin, 1999; Milto et al., 2022), some of them from the heavily harvested Volga delta. After the 1990s, exports of live frogs are known from Serbia and/or Montenegro to Bosnia-Herzegovina, North Macedonia and Albania (Džukić et al., 2003). Conversely, Serbia also imported live water frogs from Bosnia-Herzegovina (Ljubisavljevic et al., 2018) and Belgium re-exported many of its imported water frogs (Altherr et al., 2022). In addition, genetic data suggest an introduction of marsh frogs from the Balkans (*P. r. kurtmuelleri*) in Libya (Dufresnes et al., 2024b).

3.5. Secondary translocations

The local literature helped to further identify trans-national short-distance movements, such as from Switzerland to Germany and possibly also to Liechtenstein (Kühnis, 2002). Many introductions typically involved regional translocations. In Larzac for instance, locals transferred alien frogs from the lowlands to a pond in the plateau, and from there to another lowland area (M. Denoël, pers. obs.). In Belgium, Percsy and Pecsy (2002) reported that alien marsh frogs were moved from garden ponds to other habitats to avoid noise issues. Such local translocations are certainly very common throughout the native and invaded ranges, and in the latter, contributed to the rapid colonization of the species (Bellati et al., 2019). Secondary regional translocations are also illustrated in coastal islands, such as Levant Island (France), where frogs were taken from an invaded mainland area (Tankovic and Riviere, 2023), and in the proximate Christiansø Island from Bornholm Island in Denmark (Fog et al., 2019). Their presence in such islands is therefore not due to over-sea colonization although they do sow some tolerance to brackish water and are found occasionaly in sea shores in other areas (Natchev et al., 2011). In Malta, marsh frogs could have originated from Cyprus or Anatolia (Papežík et al., 2024); as Cyprus was itself home of introductions from Anatolia (Dufresnes et al., 2024a; Plötner et al., 2015), it is difficult to disentangle among the pathways as these populations share the same genetic variants. Similarly, in Spain, the introduced water frogs were reported to possibly come from Italy (Arano et al., 1995), therefore from other introduced populations.

3.6. The cocktail of coexisting alien invaders

Several introduced populations feature different phylogeographic lineages, sometimes co-existing in the same water body, including distinct *ridibundus* haplotypes (Domeneghetti et al., 2013), two lineages (*kurtmuelleri* – *ridibundus*, *bedriagae* – *ridibundus*, cf. *ridibundus* – *ridibundus*) or more (e.g., *ridibundus* – *kurtmuelleri* – *bedriagae* or cf. *ridibundus*) (Bellati et al., 2023). Such mixes either result from independent or successive introductions from multiple sources, or through escapes from breeding facilities where the transit of various specimens converged (Dufresnes et al., 2017; Dufresnes et al., 2018). Rather than distinct co-existing forms, these mixes may represent hybrid swarms, given that the marsh frog lineages involved are closely related and thus genetically compatible (Dufresnes et al., 2024b). Accordingly, studies combining mitochondrial and nuclear loci reported instances of genetic introgression among the distinct genomes involved in the introductions (Dufresnes et al., 2017). By increasing their genetic diversity, genetic introgression could boost the adaptive potential of invasive marsh frogs and propose new allelic combinations that may further destabilize native *Pelophylax* hybridogenetic systems such as *P. lessonae* – *P. esculentus* or *P. perezi* – *P. grafi* (Dufresnes and Mazepa, 2020).

4. Causes and facilitators of introductions

4.1. The food market

The frog leg industry appears a main driver of invasions by marsh frogs (Auliya et al., 2023). Consumption of alien frogs, particularly in Western Europe, implied foreign imports (see Sections 3.1 and 3.2; Fig. 5) (Altherr et al., 2022), especially following decreases in local harvests that coincided with declines of local frog populations (Dubois, 1983), and resulted in changes of the legislation in consuming countries (Ohler and Nicolas, 2017; Dubey et al., 2025). Interest in foreign species was also driven by their larger sizes, and in some countries, only the largest individuals can be harvested (e.g. over 30 g in Turkey), but not in others (e.g., Egypt; Ibrahim, 2013). The imports of water frog for human consumption have recently decreased but remains high, e.g., 800 tons imported from Egypt to France in the second half of the 20th century (Dubois, 1983); also 800 tons from Turkey in the early 2000s vs. 300 tons in 2017 (Çiçek et al., 2021).

Introduced marsh frogs also persist in areas with a long culinary tradition of frog consumption such as Alsace (Baumgart, 1982) and Rhône-Alpes (Duget and Joly, 2015) in France, and Emilia-Romana in Italy (Bellati et al., 2023). Accordingly, the first introductions in Italy supplied local restaurants (Lanza, 1962). In Belgium, residents were seemingly responsible for local introductions or translocations of water frogs in an effort to access larger frogs (Parent, 1984). As importing companies like local vendors sold their products to various restaurants and “fish” shops, the number of potential escape locations significantly increases, resulting in nationwide introductions that remained unnoticed in the many places where the morphologically-similar native frogs were locally abundant (Dubois, 1983).

4.2. Ornamental species in garden ponds

A second major driver of introductions is in the enrichment of private garden ponds with frogs, for ornamental reasons. For instance, the oldest marsh frog introduction, namely in St-Petersburg in the 18th century was the doing of Catherine II, the Russian Empress, because she was fond of their advertisement calls (Milto et al., 2022). Adult frogs or tadpoles were commonly sold as garden pets in many places at the end of the 20th and the beginning of the 21st century, although no quantitative assessments are available. In Belgium, frogs were frequently sold in "garden" shops, such as Brussels, Walloon Brabant and Hainaut, with introduced populations documented nearby some of them (Kok, 2001; Kok et al., 2002; Percsy and Pecsy, 2002). In East Flanders, Belgium, DNA analyses traced the stocks of a frog seller to Egypt, and emphasized their genetic relatedness with specimens released nearby (Holsbeek et al., 2010). Records exist of ponds that were deliberately or accidentally stocked with marsh frogs by their owners, a potentially very common phenomenon in Western Europe (Dalbeck et al., 2001; Jäckel et al., 1996). Besides outdoor enclosures, indoor captive breeding has been reported as well (Michaels and Försäter, 2017) and could thus contribute to escapes. Many introductions might also have been passive, i.e., through the unintentional release of eggs or tadpoles shipped together with aquatic plants purchased from piscicultures or shops where frogs were breeding (Kühnis, 2002).

4.3. Education and research

A third, largely underestimated source of introductions is the extensive use of live frogs for research and education by many European universities and schools (Kuzmin, 1999; Tóth et al., 2023). The large size of marsh frogs has been cited as one of the reasons for choosing this species for zoological courses or experiments, thus adding multiple potential points of entry by thousands of individuals into non-native ranges (Smith, 1949). Dubois (1983) discussed quantities as high as 10 tons per year for research purposes in France alone. However, the link between marsh frog introductions and research or education in Europe is poorly documented, given the natural occurrence of morphologically similar species, but examples exist at least in the vicinity of universities and research centers as in Germany (Jäckel et al., 1996) and France (Baumgart, 1982; Grange, 1995; Neveu, 1989), as well as Switzerland (C. Dufresnes, pers. obs.).

4.4. Farming

Initially developed to limit the over-harvesting of local wild populations, frog farming has been identified as a source of introductions of alien frogs into the wild, particularly through escapes (Auliya et al., 2023). To avoid such risk and its consequence on local herpetofauna, some authors recommended to prohibit the farming of imported live frogs early on (Parent, 1984). Accordingly, alien marsh frogs have been reported near an unsuccessful farm in Spain (Arano et al., 1995), and escapes from a farm were reported in western Switzerland (Grossenbacher, 1988). Although farming activities continue to subsist, the activity is marginal in Europe (Dufresnes et al., 2018; Parent, 1984). This is the case in France, where the activity is renewing through the engineering of a special race (RIVAN 92) by selective breeding of genitors initially collected in 1980s near Rennes (north-western France), namely from an area where marsh frogs putatively escaped a research laboratory (Evrard and Montfort, 2020; Neveu, 1989). These frogs were chosen for their large size (Neveu, 2009), and two farms exploiting this breed have since opened in the last decade in different parts of France (Drôme, Manche), for a yield of several tons a year (Evrard and Montfort, 2020). Other farming practices may be permeable to escapes, such as in Hungary, where frogs have been stocked in fenced ponds before export (Tóth et al., 2023).

4.5. Fisheries

The passive translocation of tadpoles as part of fish stocking is considered a common source of introductions of marsh frogs in the eastern part of their range, such as in Russia and Kazakhstan (Kuzmin, 1999). In Western Europe, such a situation was documented in Germany (Sowig et al., 2007), and may be more common than currently appreciated. For instance, the unexpected presence of southern marsh frog lineages in Poland and Kaliningrad (see above), might be related to stocking activities relying on fish supplies from the Balkans and the Ponto-Caspian region (Kolenda et al., 2017; Litvinchuk et al., 2020).

4.6. Transit areas

Finally, the ground zero of several regional invasions corresponds to transport hubs, such as Stuttgart airport in south western Germany (Sowig et al., 2007), Zurich airport in northern Switzerland (Grossenbacher, 1988), as well as the train stations of Buchs in Aargau canton, Switzerland (Kühnis, 2002), and of Ljubljana, Slovenia (K. Poboljšaj, pers. comm.), emphasizing the additional role of these transit areas for releases or escapes of frogs transported for the international trade. Other transitional areas, such as companies importing live frogs to produce frog legs locally, have also been suggested as points of releases (Dufresnes et al., 2018).

5. Conclusions

In this review, we have provided arguments as to why the marsh frog *P. ridibundus* must be considered a complex, global-scale amphibian invader. (1) The species has already invaded large areas, including entire countries. (2) Its invasions are the short- and long-term results of hundreds of introduction events, in a minimum of 19 European countries so far, mainly within the last century. (3) These introductions have various causes and pathways, all related to a multi-million live frog global trade such as the frog leg market, the ornamentation of garden ponds and the use in research and education. (4) They involve multiple lineages of diverse geographic origins spanning three continents, with a diversity that may be bolstered by hybridization. (5) The invasions already have significant ecological costs that may worsen in the near future without a strong international response. To establish these elements, cross-referencing of DNA barcoding data with the history of introductions, as reported in the local literature (e.g. distribution atlases and specific reports), provided a comprehensive framework to appreciate the diversity, origin and pathways of these well-established yet still emerging invasions.

Based on the above, marsh frogs should be listed among the most important amphibian invaders worldwide, along with cane toads (Shine, 2018), American bull frogs (Ficetola et al., 2007) and clawed frogs (Measey et al., 2012), which they outmatch in terms of the complexity (origins and causes). At the European scale, the marsh frog is by far the most successful alien amphibian species, at least in its number of occupied regions and countries. All in all, the pervasiveness of marsh frogs fuels the view that Europe is particularly vulnerable to biological invasions (Bellard et al., 2016). These invasions of marsh frogs are not restricted to Europe, however, but also affects Central and Far-Eastern Asian areas including Kazakhstan (Dujsebayeva et al., 2021), Kirghizstan, Siberia (up to eastern Urals at the geographical borders of Europe) and Kamchatka (Kuzmin, 1999; Lyapkov et al., 2018), the extent of which remain to be investigated in details. It is likely that additional invasions may be reported in the near future elsewhere in the Palearctic, pending genetic analyses and herpetological surveys. As such, any new populations, which putatively represent introductions, should call for immediate DNA barcoding, for which reference sequence datasets are now available for the whole Palearctic (Dufresnes et al., 2024b). Moreover, accurate knowledge of the delineated native and invaded areas offer a background to build ecological niche models (ENMs) from which to project the potential distributions of invasive lineages (e.g. Litvinchuk et al., 2024). Recent measures of physiological performance across temperature gradients in marsh frogs may also be useful in this perspective (Padilla et al., 2023, 2024). We are only starting now to appreciate some of the effects of marsh frog invasions on native wildlife communities (see e.g. Pille et al., 2021, 2025), and many aspects remain to be investigated, notably in relation to the nature and diversity of the lineages involved. Of particular concern would be the consequence of introgressive hybridization between distinct lineages in generating genetically more variable and thus potentially more adaptable individuals, which might particularly impact the maintenance of existing hybridogenetic systems (see also Litvinchuk et al., 2020).

In the wake of the early warnings (Arano et al., 1995; Dubois, 1983; Grossenbacher, 1988) mitigating future risks will require to prevent new releases of marsh frogs into the wild and apply rapid responses to newly detected invasions, particularly of additional lineages, which may contribute to invade an even wider spectrum of habitats depending on their ecological adaptability. However, management programs may be realistic only for recently established introductions, or geographically isolated alien populations, such as on islands (see e.g. Tankovic and Riviere, 2023). A key step forward would be to consider marsh frogs or at least all non-European lineages to the list of the most invasive species at the European level (Genovesi et al., 2015) and apply the regulation it implies to ban the (commercial) import and transport of any (live) marsh frogs and more generally water frogs, since *Pelophylax* introductions also involve other species (see Dufresnes et al., 2024b).

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CRediT authorship contribution statement

Mathieu Denoël: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Christophe Dufresnes:** Writing – review & editing, Visualization, Resources.

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Declaration of competing interest

The authors declare no conflict of interest.

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Data availability

Data are provided in Table A1. Barcoding data followed Dufresnes et al. (2024b) and are stored, with links to GenBank at DOI: https://doi.org/10.5281/zenodo.10423702.

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