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INVESTIGATING THE STATUS OF BRITAIN'S LOST FROGS: PROSPECTS FOR REWILDING

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Apologies to anyone missed from this list. All errors are my own.

Contents

List of Figures

List of Tables

Foreword

There are just seven species of amphibians generally accepted as native in the UK: smooth, palmate, and great crested newts, common and pool frogs, and common and natterjack toads. For several decades much effort has been spent in the survey, monitoring and conservation of all these species, but attention is now turning to include those we have lost within historical times, spurred on by the realisation that humans have modified nature – often to its detriment – for a very long time and, consequently, repairing ecosystems to a more natural state is favourable to conservation goals. Thus, a movement to 'rewild' Britain's landscapes has emerged, to tackle the ever growing loss of biodiversity from these shores. This exciting project explores the relatively recent demises of moor frogs, agile frogs, and tree frogs in Britain, set amidst this movement.

Fossil and/or documentary evidence at least for the first two is clear; these are native animals which reached these shores before the formation of Britain as an Island. While the history of tree frogs is more circumstantial, at least partly because this tiny, delicate frog does not fossilise at all easily, the historical records for its past presence are far more perspicuous.

If suitable habitats in Britain can be found or created, reintroductions look possible for these species. Indeed, vast habitat restoration efforts are underway, and many look profitable for our amphibians. Extensive studies in Europe where these three amphibians exist, have used scientific analyses to define their habitat requirements, which can be used as a prerequisite to searching for possible translocation sites in Britain.

Provision of habitat is one aspect, another is the persuasion of government agencies to support and accept these frogs. There is a general case for bringing back animals lost to Britain at least partly as a result of human activities, which has developed compounding support especially within this decade. More important, however, are the consideration and consequences of climate change. While the UK has always likely been within the required climate envelope of these three species, it will only become more suitable as temperatures continue to rise. Re-establishing populations in Britain will therefore improve the global conservation prospects for all of them, especially if deterioration occurs elsewhere in their European ranges.

Reintroductions of amphibians can enjoy great success. Water frogs (*Pelophylax* species) have a long history of introduction in Britain. However, suspicion that a population of pool frogs *P. lessonae* in Norfolk was native led to creation of a working group in the 1990s to investigate evidence for this suggestion. On the basis of fossils, call characteristics, written records and genetic studies, it was established that the Norfolk frogs were indeed longstanding *Brits*. Sadly, just as this discovery was made, the last of the frogs croaked it due to habitat change. On the back of this, a successful attempt to reintroduce Swedish pool frogs to managed habitat in Norfolk followed, including releases at the much improved site of the recently extinct population. So far, so good. It would be fascinating to see these other '*lost British frogs*' in the wilds of the countryside in the future.

Professor Trevor Beebee, August 2025

1. Executive Summary

This Winston Churchill Fellowship Report is intended to be a 'status review' of frog species that have long been discussed as extirpated from Britain. The questions I wanted to answer were as follows:

- What does the available literature say about these species in Britain and north-west Europe?
- What ecological features differ between the visited study states and Britain?
- Are these discrepancies as a result of a natural or human cause?
- Can they explain why Britain has lost up to four species of amphibian prior to the Industrial Period?
- If so, could a reintroduction of some or all of the frog species be deemed feasible and appropriate?

Subsequently, after not only lengthy research and travel abroad but also over 5 years of captive study of these species, the key findings are:

- There are a small number of native amphibians, presumedly now extinct, whose former presence in Britain is largely unappreciated. These are the moor frog, the agile frog and the European tree frog.
- There is direct archaeological evidence for the former presence of moor frog and the agile frog, and strong historical evidence for the former presence of the European tree frog.
- These losses are explained by extensive human processes prior to, or during, the industrial period. This constitutes a loss of up to 40% of amphibian species within historic times.
- Abundant frogs (regardless of species) are key features in any ecosystem, supporting a wide range of other vertebrate species of reptiles, mammals and birds.
- Rewilding projects with a focus on ecosystem restoration provide both the space and habitat for the potential recovery of a diverse array of native amphibians in the UK and their recovery is strategic toward the rebuilding of functioning ecosystems that support abundant wildlife.
- Both wetland restoration and frogs engage people of all ages in nature. Tree frogs in particular will play a critical part in engaging a young audience in the future of the natural world.
- Helping to direct some of the conservation communities' attention towards looking deeper into the historic past can improve the ecological integrity of restoration programmes and solve key environmental issues of modern times.

2. Introduction

As ectothermic animals, the geographic distribution of amphibians is closely linked to climatic conditions (Guisan & Thuiller, 2005; Duarte, et al., 2013; He, et al., 2024), with the highest diversities of amphibian species being found broadly in the tropics, due to their sublime conditions and history of stability through the Pleistocene (Jenkins, et al., 2013; Pimm, et al., 2014; Brown, 2014). In the temperate regions, climate is an even more pronounced bio-geographic determinant, as there is only a brief window of suitable conditions for critical events such as reproduction, larval development, metamorphosis, and maturation (Proios, et al., 2024; Henle, et al., 2008; López-de Sancha, et al., 2025).

Like many other taxa, modern assemblages of European amphibians are the result of some 2.6 million years of climatic upheaval; cold glacial periods, followed by warm interstadials, drove-out and advanced the ranges of amphibians, respectively (Holman, 1998; Beebee & Zeisset, 2008; Yalden, 1980). Consequently, a clear division of amphibian-species richness can be observed between the 'glacially disturbed' northern Europe and central/southern Europe; the latter having higher levels of amphibian diversity (Sillero, et al., 2014; Rage, 1997). Southern and central Europe's longer periods of favourable climate, both annually and throughout the Ice Age, can explain this distribution (Araújo, et al., 2008; López-de Sancha, et al., 2025).

As a consequence, Britain – situated in northern Europe and at the whims of austere Pleistocene oscillations – has traditionally been assumed to be naturally depauperate in amphibians (Holman, 1993; Rage, 1997; Yalden, 1980). The presence of only six cold-hardy species has been interpreted as a consequence of the island's limited window for colonisation: a brief ~3,000-year period of land connection to mainland Europe before the inundation of Doggerland (Hoebe, et al., 2024; Smith, 1969; Gleed-Owen, 1998).

Because ecological awareness in Britain did not generally emerge culturally until the later stages of the Industrial Period, the amphibians observed as 'naturally occurring' at that time were assumed to be the only ones with the required hardiness to colonise the country (Holman, 1993; Smith, 1969). However, Britain's ecosystems, landscapes and biota have been modified by people for millennia, with ecological degradation accelerating particularly over the past 1000 years, culminating in the country becoming one of the most nature-depleted nations (Rackham, 1986; Yalden, 2002; Burns, et al., 2023). While the exact number of lost native species is unknown, at least 492 species have become extinct in England since the 1st century AD, according to a 'conservative estimate' (Natural England, 2010; McKie, 2010). Around 162 of those species have been lost since 1500 (Hayhow, et al., 2019). It is therefore unreasonable to uncritically accept the post-industrial assemblage of amphibians as fully natural. A more plausible scenario is that some species have been lost over this period and that this loss has largely gone unrecognised (Snell, 2015).

In the 1990s, a population of the warmth-loving Pool frog *Pelophylax lessonae*, living on Thompson Common in Norfolk, garnered special initial interest by herpetologists Charles Snell and David Billings (Billings, pers. comm., 2023). Pool frogs (and its hybridogenic allies, such as the edible frog *P. esculentus* and marsh frog *P. ridibundus*; together the 'water frogs') have been widely introduced to Britain from Europe from the Victorian period onwards, causing confusion over the origin of this population (Wycherley, 2003; Snell, 1994; Buckley, 1986). However, unlike introduced water frogs, this Norfolk colony had more external and behavioural similarities with recently discovered Scandinavian pool frogs (Clark, 1998), prompting a hypothesis that the British and Nordic populations are more closely related to each other than to continental pool frogs. This would render these 'northern clade' pool frog populations as a rare colonists from after the end of the last Ice Age, native to Britain and therefore in dire need of protection (Snell, 1994; Beebee, et al., 2005).

Several lines of investigation were undertaken to determine the status of the pool frog in Britain, including genetic analysis, bioacoustic studies, and – of particular relevance to this study – archaeological and archival research. The latter efforts not only yielded conclusive evidence towards the pool frog's native status (see Buckley & Foster, 2005; Gleed-Owen, 2000; Kelly, 2004), but also revealed that three additional frog species once inhabited Britain and became extinct prior to the industrial era (Raye, 2017; Snell, 2015; Snell, 2006).

From an archaeological perspective, remains of the moor frog *Rana arvalis*, agile frog *R. dalmatina*, (and pool frog) have been recovered from a range of deposits, supporting their status as native species (Hibberd, 1991; Gleed-Owen, 1998; 1999; 2000; 2021; Snell, 2015). In addition, authors from the medieval to early modern periods reference multiple frog species to varying degrees of clarity, with particularly compelling descriptions of the European tree frog *Hyla arborea* as a native component of the British fauna (Raye, 2017; in prep. & pers. comm., 2025). These species are therefore referred to collectively as *Britain's lost frogs.*

Taken together, the evidence indicates that Britain may have lost up to 4 out of its possibly 10 native amphibians, including the pool frog, in the last 1000 years – constituting a 40% potential loss in batrachian diversity. This decline would represent one of the most severe contractions of a vertebrate group in Britain (Burns, et al., 2023), yet this decline of biodiversity has been overlooked (Snell & Evans, 2006; Snell, 2015).

In the early-2000s, the acceptance of pool frogs as native to Britain led to a shift in their conservation status from being considered an unwanted alien species to the most imperilled amphibian in the British Isles (Beebee, et al., 2005). However, by this time, the wild population had already dwindled to extinction. In response, a reintroduction was launched in 2005 to bring the species back to a carefully managed and confidential site in Norfolk, in close proximity to the frogs' last stronghold (Buckley & Foster, 2005). Because the final British pool frog had died in captivity in 1999 under the care of Charles Snell, the reintroduction relied on genetically similar stock sourced from Sweden (Billings, pers. comm., 2023). To date, the effort has been considered a success; since 2015, pool frogs have once again been seen – and heard – at their historic home on Thompson Common (King, et al., 2021).

Reintroductions of amphibians, like the pool frog, have been largely successful and are likely to become an increasingly useful tool in restoring populations in our evermore fragmented landscapes (Smith, et al., 2020; Carter, et al., 2016). However, as a group they are one of the most neglected species when it comes to ecological restoration and rewilding initiatives (Stark & Schwarz, 2024).

EUROPEAN TREE FROG

Hyla arborea

MOOR FROG

Rana arvalis

AGILE FROG

Rana dalmatina

Figure 1: to scale (A4) adult female and June-aged tadpole representatives of Britain's Lost Frogs. © Jack Perks Wildlife Media / Celtic Rewilding Ltd, 2025.

2.1 The Fellowship Project

While the story of the pool frog is rightly celebrated – not only for challenging the status quo in conservation but also for facilitating the recovery of a lost species – very little attention has been paid to Britain's other extirpated anurans. This is despite a burgeoning interest from professionals, the public and encouragement from government agencies to assess possible lost-natives as part of conservation decision making (ARC Trust, 2021; Barkham, 2021; Cockburn, 2021; Horton, 2021). Therefore, this report is intended to constitute a 'status review' of these species under DEFRA's (2021) *Reintroductions and other conservation translocations: code and guidance for England*.

Species extinctions which occurred in Britain prior to the Industrial Revolution have long been dismissed as irrelevant in regards to our modern ecology and its conservation (Sykes, 2015; Jackson & Hobbs, 2009). This is likely due to strains on resources and the effect of shifting baseline syndrome resulting in an 'apathetic' oversight (Pierrel, 2022). However, the reality that our ecosystems are deeply rooted in the past, and that those past ecologies have been changed extensively by people long before even the industrial period, has become largely accepted thanks to recent discoveries and successful new practices. Stemming from the introduction of agriculture during the Neolithic (c. 4100 BC) when small bands of hunter-gatherers transitioned into large, settled, agrarian societies, human activity has profoundly altered ecosystems across the Britain, resulting in landscape-scale habitat change and the loss of many species (Woodbridge, et al., 2013; Whitehouse & Smith, 2010; Rackham, 1986). Consequently, acknowledging the extent of past human influence highlights the importance of reassessing nativeness and conservation baselines through a deeper temporal lens (Lemoine & Svenning, 2022).

Ecosystem restoration and rewilding projects seek to incorporate the reintroduction of said species; those that would otherwise be present were it not for human impact. So, determining whether a species was lost due to anthropogenic pressures is therefore critical (Crees & Turvey, 2015). To dismiss a possible native on the basis of weak or incomplete evidence would mean Britain's ecosystems could lack a vital component for their proper functioning and be forever impoverished (Polak & Saltz, 2011; Stark & Schwarz, 2024). This is akin to a detective hastily ruling out murder as a cause of death, without a thorough investigation: fundamentally it risks overlooking a human-caused disappearance while undermining the integrity of the entire process. In conservation, as in justice, failing to properly examine the role of human agency risks drawing false conclusions with real-world consequences. That is why this report seeks to analyse these species and their absence to a degree rarely performed for amphibians or indeed many species at all.

I have been greatly influenced by the works of 21st century naturalists such as Derek Yalden and Oliver Rackham, who both exemplified the value of integrating field observations with scientific literature to address retrospective ecological questions. In their publications, they drew on field studies and personal observations from the UK and analogous habitats in Europe, to infer aspects of Britain's past environments and species composition. In combination with over half a decade's experience of keeping each species in captivity, this approach has been adapted to this study of frogs. Therefore, this Sir Winston Churchill Fellowship Project seeks to address key knowledge gaps by researching the historical presence of these forgotten British frogs, understanding their ecology in similar respective locations, exploring why they are now absent from Britain, and assessing whether they could form a part of Britain's natural fauna, once again.

2.1.1. Literature Review

Comprehensive research was conducted into each species' biology, ecology, native status, habitat preferences, and likely causes of extinction in Britain. The scope was to read as much relevant material as possible on each species for each country visited, and of course Britain, in the six months leading up to the field visits. This would help to thoroughly inform the observations I would make on the ground.

2.1.2. Field Visits to Analogous European Environments

The presence of agile frog, European tree frog and moor frog in Britain place them at the north-western edges of their distributions[1] (Sillero, et al., 2014). Conservation and reintroductions at such places can be somewhat challenging. This is because the species as the is at the end of its physiological and ecological envelope. These so-called edge effects, result in a species' habitat requirements being more specific, as only particular environs can meet the demands of a population under the marginal conditions found at such liminalities (Edgar & Bird, 2005). As ectotherms, this effect is more pronounced for reptiles and amphibians (Section 2). Even species common in, say, human modified habitats of southern Europe, are often much more sensitive to the same environmental disturbance in the northern reaches of their range (Corbett, 1989; Birbele, et al., 2024; Dufresnes, et al., 2013). This vulnerability is compounded by the genetically uniform nature of amphibian populations across northern Europe, resulting from the now recognised phenomenon that genetic variation progressively diminishes as species colonised territories increasingly distant from their Ice Age refugia in southern Europe, with a more rapid advance producing greater genetic depletion (see Section 5.2 for more). In contrast, a species core range is where the conditions that it is most adapted to prevail and thus a higher density of the species can be expected, usually with greater genetic diversity too.

At the same time, range edges can be a rather abstract concept, as often experimental or informal introductions of a species well beyond their 'natural range' can result in populations that persist for some time. Examples include the trial introduction of sand lizard *Lacerta agilis* to the Isle of Coll, Scotland, and the accidental introduction of Aesculapian snakes *Zamenis longissimus* to Colwyn Bay, Wales, both occurring around 300-400km north-west of the nearest natural populations (Corbett & Tamarind, 1979; Major, 2024; Sillero, et al., 2014). Therefore, it may be sensible to consider that current species distributions are maybe more flexible than previously thought, and an interplay of factors facilitate a species' presence, some of which

[1] These species would have likely had a restricted distribution in Britain tied to the habitats they rely on.

have been altered by the impacts of humans, throughout history, and some of which are likely to be continually modified into the future (Lemoine, 2021; Cooper, 2025).

Such investigations may provide valuable insights into both the ecological constraints influencing the modern distribution of these frogs, and the factors that may have contributed to their extirpation from Britain. Therefore, it makes sense to visit the current north-western range edge of each of species to see their habitat preference and maybe illuminate possible reasons for their modern absence. This will also allow for an understanding of some of the conservation challenges each of the species faces when under these marginal conditions.

Following on from a research period of this north-western region, the author travelled to countries with climates, land-use patterns, population densities, and ecological histories comparable to the UK, where these species still persist. These included (in order of visitation):

- Denmark, for agile and tree frog.
- Germany, for moor and agile frog.
- Netherlands, for moor, agile, and tree frog.
- Belgium, for tree and moor frog.
- France, for moor, agile, and tree frog

2.1.3. Engagement with Experts

Establishing contacts with a range of experts on each of these species has been vital. I consider the term ‘expert’ to be broad and a largely undefinable term, other than that the person in question has had a notable or particularly long involvement with a species or habitat. Therefore, I have consulted with enthusiasts, restoration ecologists, amphibian breeders, NGO groups, zoologists, civil servants, species historians, habitat managers, and geneticists. Contacts have been made largely through those that have authored publications on each species, but many experts have also been referred to me. The majority of communication has been in person, however due to time constraints some interviews have had to been undertaken via online video call as well.

An obvious barrier to understanding specific, technical knowledge is language. I am very fortunate that my European colleagues are extremely fluent in English; I am forever indebted to their patience and articulation. In the same vein, much of the regionally specific literature on each species is often in the native language, however online document translation tools are accurate and readily available. The experts were also able to guide me to specific publications and vastly contributed to the efficient production of this document.

2.1.4. Proposed Habitat Restoration and Reintroduction Methodology Approach

A specific interest was to see projects or initiatives where these species have been recovered. This may be habitat that has been restored to favour one of the frogs, or where a direct reintroduction has occurred or is in process. From this, I could understand the complexities of habitat restoration, including financing and necessary scale, while direct reintroduction methodology can be adapted to a British context. Sharing experience of keeping and breeding these species in captivity for conservation purposes is also valuable.

2.2 Conservation in Britain

Britain has been ranked one of the most nature depleted countries on earth, with 1 in 6 species currently threatened with extinction (Burns, et al., 2023), and many animals already extirpated from these isles (see Section 2.3). While post-WWII advances in industrial agriculture and urban sprawl are so often blamed for this, many of these declines in habitat or species stem from Neolithic to preindustrial processes. This conclusion, however, has only emerged as mainstream within the last decade (Tree & Burrell, 2023; Monbiot, 2013; Macdonald, 2020). Britain is not just so nature-depleted now, but has been for such a long time – often because of the effects of being an island. This isolation can have its benefits for biodiversity, however in Britain's case, this worked to a largely opposite effect:

- Firstly, founder populations of Holocene arrivals (Section 2) were likely small, due to rapid expansion from glacial refugia, resulting in poor genetic diversity of many edge of range species (Lyons, 2024). Low genetic diversity oftens relates to increased susceptibility to habitat change (Sjögren, 1991; Birbele, et al., 2024).
- If a species became extinct, unless it could fly or tolerate salt-water, it would never recolonise naturally.
- Being a limited landmass, Britain's major rivers are proportionately scaled much smaller than continental ones, therefore being that much easier to straighten, canalise and drain peripheral wetlands. For example, the mouth of the River Great Ouse is 1/6th the width of the Scheldt, a fairly small river by European standards.

From a societal perspective, being an island produces an interesting relationship between people and natural resources. For instance:

- The isolation of islands has been associated with greater social stability relative to mainlands (Veenendaal, 2018). This relative stability often facilitates large-scale land conversion, reclamation, and capital-intensive agricultural projects, as the reduced likelihood of invasion or regime change enhances the prospects for secure monetary returns: as seen in the private investor financed drainage schemes (Ash, 2017; Hoffman, 2014).
- An Island has to be self sufficient to a degree and cannot rely as much on costly imports as continental countries. This meant that land was used much more heavily for domestic production, such as for timber and food.
- Britain was the first country to industrialise in the late 18th and early 19th centuries, which meant it experienced the ecological costs of industrial growth before conservation concepts existed (Cocker, 2019; Macdonald, 2020).

As an example, wetlands are Britain's most manipulated habitat with perhaps the most famous case being the draining of the English Fens, where all of the above factors converged (Gerlach, 2014). In modern times these vast works have been described the countries "greatest ecological disaster" with perhaps up to 3,160 species lost from the area prior to the late 20th century (Rotherham, 2013; Mossman, et al., 2012). Among the notable animal species that disappeared primarily due to drainage (some of which have since shown signs of recovery) are the black tern *Chlidonias niger*, spotted crake *Porzana porzana*, Savi's warbler *Locustella luscinioides*, black-tailed godwit *Limosa limosa*, palmate newt *Lissotriton helveticus*, burbot *Lota lota*, mole cricket *Gryllotalpa Gryllotalpa*, large marsh grasshopper *Stethophyma grossum*, large copper butterfly *Lycaena dispar*, swallowtail *Papilio machaon* and orache moth *Trachea atriplicis* (Rotherham, 2013; Gleed-Owen, 2000; Benton, 2012). Of particular relevance to this study, the pool frog failed to persist even as a relict population within the Fens, surviving only in glacial pingo pond systems in nearby Breckland, despite historical records implying it being a fenland specialist (Buckley & Foster, 2005; Kelly, 2004; Natural England, 2010). The last known fen-dwelling pool frogs survived in a small remnant of undrained reedbed at Fowlmere Fen near Cambridge until 1847, when the site was drained for agricultural purposes, leading to the final loss of the population (Kelly, 2004).

Although rudimentary legal measures did emerge during the Early Modern Period to preserve certain species, such as the common crane *Grus grus* and red deer *Cervus elaphus* from unfettered hunting or harvesting (by the lower classes) (Raye, 2023), conservation in the modern sense only truly developed in the late nineteenth century with the establishment of organisations such as the Royal Society for the Protection of Birds (RSPB) and the National Trust. At that time, conservation largely consisted of protecting small remnants of cultural habitats from increasing agricultural and industrial intensification, pursued primarily as a scientific curiosity or hobby (Cocker, 2019). Nevertheless, many important habitat sites were indeed preserved, and without those early efforts, Britain would almost certainly be even more biologically impoverished than at present.

During the 20th century, conservation began to shift in focus and was arguably taken more seriously, influenced in part by the growing, environmentalist movement. Works such as Rachel Carson's *Silent Spring* (1962) played a pivotal role in raising awareness of human impacts on the natural world. However, some of the greatest losses to Britain's biodiversity occurred in the post-war period. In the effort to 'Dig for Victory,' vast areas of habitat were lost, and subsequent advances in agricultural technology accelerated the intensification of nearly all unprotected land (Tree & Burrell, 2023). This intensification was chronic to the point that even culturally created, semi-natural habitats such as species-rich meadow declined by over 95% (Environment Agency, Chief Scientist's Group, 2022). These declines have continued into the 21st century: between 2016 and 2023, the proportion of species in Britain threatened with extinction increased from 1 in 10 to 1 in 6 (Hayhow, et al., 2016; Burns, et al., 2023).

As a consequence of this extensive degradation, virtually all remaining biodiverse habitats are now afforded some form of protection. However, these protected areas alone are insufficient to sustain a functioning ecological network and the ecosystem services on which society depends (Lawton, et al., 2010; Burns, et al., 2023). Britain's biodiversity intactness stands at 41%, far short of the planetary boundary of 90% and the worst of the G7 (Hayhow, et al., 2019). The only feasible path to restoring a viable and resilient natural environment is through large-scale ecological restoration, rebuilding ecosystems from the ground up. As outlined in the *Lawton Nature Report*, this requires an approach that is "bigger, better, and more joined up" (Lawton, et al., 2010).

2.2.1 Rewilding in Britain

It is against this backdrop that the growing movement of *rewilding* has emerged. Originating as an American concept in the 1990s, rewilding has made its way across the Atlantic to Britain in the 2010s, and subsequently hybridised with the similar Dutch concept of *new-nature*, conceiving a form of ecological restoration appropriate for a densely populated and heavily modified island (Bulkens, et al., 2015; Tree & Burrell, 2023; Jepson & Blythe, 2020). Rewilding is difficult to unanimously define (Carver, et al., 2020), but is broadly a form of mass ecosystem restoration, incorporating many interventions – including species reintroduction – to remove/reverse previous and adverse human influence on nature, "until [nature] can take care of itself" (Rewilding Britain, 2024).

To date, rewilding has been largely met with huge support and success. From a global perspective, the 2020s have been marked by the UN as the decade of Ecosystem Restoration and a global commitment to protect over 30% of land by 2030. Specifically in Britain, over 180,000 ha of land are in an active state of rewilding, as reported by Rewilding Britain's Network which is growing at a rate of 20,000 ha per month (King, pers. comm., 2025). There is also increasing Government support for these efforts, through funding and legislation such as the Environment Act, 2021 (which supports the return of formerly native species). Research is also showing promising signs of rewilding in boosting rural economies and providing employment (Rewilding Britain, 2021), while independent polling has revealed that 4 out of 5 Britons support the idea of rewilding and a substantial 82% want to see the reintroduction of extinct species (YouGov, 2022; YouGov, 2020).

It is therefore no surprise that species reintroductions have been popular and many have been successful, incorporating a variety of taxa, across all major groups (Carter, et al., 2016). Conservation translocations are carried out under a wide-range of rationales, expanded fairly recently to include the novel practices of assisted colonisation and ecological surrogacy (Gaywood, et al., 2023; DEFRA, 2021). Amphibians are particularly suitable to translocations where they are needed, as their low-dispersal capability, small home ranges and often specialised habitat choice make them threatened in our fragmented and highly modified landscapes (Carter, et al., 2016). As mentioned in Section 2, the pool frog is now one of growing number of species that are being actively reintroduced to Britain.

An increasingly common theme among rewilding initiatives, particularly species reintroductions, is the recognition that restoring nature often requires looking further back into the ecological past. Conservation has long been hindered by the concept of *shifting baseline syndrome*: a phenomenon whereby environmental degradation becomes progressively normalized within society (Pierrel, 2022). This occurs because ecological loss has unfolded over timescales far exceeding individual human lifespans or even recorded history (see Section 2.3) leading each generation to unknowingly accept a progressively diminished natural environment. Rewilding seeks to challenge this temporal myopia. For instance Dutch ecologist Frans Vera (2000) proposed the use of feral cattle *Bos taurus* and ponies *Equus ferus caballus* as proxies to the vast herds of prehistoric grazers, such as aurochs *Bos primigenius* and tarpan *Equus ferus ferus*, a concept now widely implemented on rewilding projects (Tree & Burrell, 2023; Jepson & Blythe, 2020). In addition, the idea that beavers, hunted to extinction in the Middle Ages to Early Modern Period in Britain, are vital to the health of riparian habitat and that translocation could help recover rare invertebrates, birds and amphibians – was seen as either irrelevant or a radical concept prior to the late 2000s (Woodroffe, 2005; Brazier, et al., 2020).

Overall, the growth of rewilding is sure to produce dividends for both the natural environment and the benefits people derive from it. Already in the Netherlands, where similar practices have been implemented for over 50 years, biodiversity declines have slowed down (van Veen, et al., 2010), while in the UK success is already being reported from a range of sites including the now-famous Knepp Estate, one of the only places where nationally rare species like turtle doves *Streptopelia turtur*, nightingales *Luscinia megarhynchos* and purple emperor butterflies *Apatura iris*[2] are increasing (Tree & Burrell, 2023). Looking to the future, rewilding will have to acknowledge the role of climate change in specific interventions such as reintroductions, and investigate and employ novel techniques such as assisted migration (Carver, et al., 2020; Gaywood, 2024).

2.3 Historical Context

Britain's lost frogs likely became extinct prior to 1800 AD (see Sections, 3.6, 4.6 and 5.6). As such, it is important to consider the historical backdrop amidst pre-industrial Britain when concerned with the natural environment, extinctions, and amphibians, in order to frame these species within their period of demise. There is a certain halcyon idolisation of this particular time, before great urban centres, industry, and complex global trade, suggestive of a period where people existed in harmony with a thriving nature. Nothing could be further from the reality. At this point in time, people had dominated every area of the UK for over 4,000 years, modifying the environment to exactly suit their needs (Monbiot, 2013; Macdonald, 2020). The British landscape that we see today – from the highest peaks, to the lowest of the river valleys – is the product of millennia of intensive human engineering (Rackham, 1986; Raye, 2023; Rackham, 2015; Yalden, 2002).

Understanding the social and economic drivers of this habitat change driven by human use is vital in uncovering the threats that these animals would have historically faced. Framing these threats against modern observations and studies helps to discern possible factors (anthropogenic or otherwise) for the loss of Britain's frogs. One thing to note is that this time period, roughly one thousand years from circa the 8th century to the 18th (henceforth referred

2 Also helped by climate change.

to as MA/EMP), is a huge proportion of Britain's history, full of temporal complexity and cultural nuance fuelled by advances in technology, agriculture and society at large. It is all too easy to generalise, so it should be said that this section is by no means exhaustive. I therefore default to many, brilliantly in-depth works which draw on wildlife and the environment within society of these times, and which referred to regularly, such as Raye's (2023) *The Atlas of Early Modern Wildlife*, and Hoffman's (2014) *An Environmental History of Medieval Europe* and of course the works of the equally brilliant Oliver Rackham and Derek Yalden.

While the MA/EMP represents such a substantive duration for historians, it must be said that ecology functions on much greater timescales (see Section 2.2.1). Any species which has reached Britain by its own agency during the Holocene (the last 11,700 years) and become resident, is regarded as native, even under the most conservative definitions (Natural England, 2025; Crees & Turvey, 2015). These ten centuries carry much environmental significance; representing a time of great change, in leading toward the burst of industrialisation that occurred across Europe post-1750 (Rackham, 1986). Changes on a landscape scale were beginning or already well into effect, such as the creation of the planned countryside as part of the Inclosure Acts, the great drainage projects of the Thames Valley, the Fens, Humber and Somerset Levels, Romney Marsh and others, extensive peat cutting efforts, and the dwindling of forest to something like just 5% of the landcover (Rackham, 1986; Rotherham, 2013; Rackham, 2003). Ultimately, this period represents a great change from small-scale subsistence farming to commercial agricultural entities, with at least three million acres of commons passing into private ownership for 'improvement' around 1760 (Cocker, 2019). Indeed, agricultural reclamation and improvement had reached all of Britain by the 17th century and been so successful that by the end of the Early-Modern Period further intensifications were largely unnecessary (Rackham, 1986).

Hand-in-hand with landscape changes, a great faunal turnover was taking place. Species like the wolf *Canis lupus*, beaver *Castor fiber*, wild boar *Sus scrofa*, Eurasian lynx *Lynx lynx*, common crane *Grus grus* and spoonbill *Platalea leucorodia*, became extinct, while many others, such at the wildcat *Felis silvestris*, capercaillie *Tetrao urogallus*, pine marten *Martes martes*, red-kite *Milvus milvus*, great bustard *Otis tarda*, golden and white tailed eagles *Aquila chrysaetos* and *Haliaeetus albicilla* were heavily contracting in range due to widespread persecution (Yalden, 2002; Yalden & Albarella, 2009; Gerlach, 2014; Raye, 2021). There were also new-comers to these isles, such as common carp *Cyprinus carpio* and rabbit *Oryctolagus cuniculus,* introduced by humans (O'Connor & Sykes, 2010). There is no evidence that people introduced frogs for any particular reason, prior to the early 19th century (Beebee, et al., 2005; Kelly, 2004; Gleed-Owen, 2000).

It would be totally remiss not to mention the Little Ice Age (LIA): a misnomer as this was not a true global Ice-Age, but an ill-defined period when cultural works and historical records suggest a time of cold weather in the north Atlantic during the MA/EMP. Purportedly, the LIA is a time when famines became more common in Europe. When reviewing the latest research, it reveals that the LIA was not a period of unremitting cold, but a period when severe winters became much more common, skewing the average temperature overall (Owens, et al., 2017; Parker, et al., 1992; Wanner, et al., 2022). These frogs live elsewhere in Europe where winter temperatures are significantly colder than Britain's: they are far more affected by cooler summers that reduces larval development and maturation (see Section 7) (Snell, 1985a). One example is the Central England Temperature series that has scientifically tracked and recorded temperature from 1659, in the middle of the LIA to the present, and has found that summer temperatures were not greatly depressed during this timespan (Lockwood, et al., 2017). What cold weather trends did occur could have actually been exacerbated or even caused by vast land use changes (e.g., epidemics in the Amazon leading to afforestation on previously anthropogenically cleared land) or mass population losses (e.g., massacres of Genghis Kahn) (Ruddiman, 2003; Pongratz, et al., 2011).

While great social changes were beginning to take place, trying to understand the specific ecology of this time can be utterly trying. To begin with, literacy rates, while beginning to increase, did not exceed 10-25% for males for this period and published material by volume, was trivial in quantity when compared with later periods (Rigby, 2003). Regular famines, and epidemics such as the Black Death, reaped society of its resources and people. Calorie production was probably the largest driver of social behaviour of this time, leaving little time for meaningful study or documentation (DeWitte & Slavin, 2013; Spencer, pers. comm., 2025). As such, environmental awareness was not at all a feature or aspect of medieval life, and therefore almost never percolated into publications of the time (Hoffman, 2014).

Consequently, Britain lacked the cultural conditions for meaningful documentation of the natural world during the Middle Ages (Hoffman, 2014). This only changed when food production per capita generated a surplus so that attention could turn to studies considered 'trivial,' such as the categorisation of fauna and flora, maybe sometime in the 17-18th centuries (Hoffman, 2014; Mokyr, 1990). Ironically, the very intensification of farming, particularly through wetland drainage, was both the precondition for and the destroyer of the landscapes that that are the objects of conservation interest today (Pryor, 2019; Rotherham, 2013; Ash, 2017).

As such, many species were discovered later than one might expect. For example, the fen raft spider *Dolomedes plantarius*, wasn't described as a British species until 1956 (Lake, et al., 2020). As Waller (1994) observed, because of extensive human-modification, documentary evidence from after these drainage projects "…for the occurrence in Fenland of plants and animals…can be of little value when trying to determine the nature of the pre-drainage vegetation of the basin." It is agreed that MA/EMP authors and early naturalists were mainly concerned with those species which were huntable, edible or a nuisance and to some extent species with certain ethereal or religious characteristics – but not species of benign use (Raye, 2025; Raye, 2023).

2.3.1 Native Frogs as a Subject of Study in Britain

While there was definitely an interest in frogs from pre-modern authors, such as in superstition and witchcraft – the 'Toadmen of East Anglia' being an interesting example (Norfolk Records Office, 2023) – and some authors would contemplate their status in Ireland and other islands, this was not always on the level deemed suitable to reliably discern species (Raye, pers. comm., 2025). There seems to have been a broad cultural aversion to them as unholy, possibly poisonous creatures and so even educated authors didn't want to study them in detail or spend much time differentiating these hard-to discern species (bar the tree frog) (Raye, 2023; Thompson, 2014; Clark, 1994). Even Linnaeus regarded them as *abhorrent* animals, due to their "cold body, pale colour, cartilaginous skeleton, filthy skin, fierce aspect, calculating eye, offensive smell, harsh voice, squalid habitation, and terrible venom" (Linnaei, 1758; Snell, 2006). Linnaeus wasn't alone. To give two specifically British examples:

- Thomas Pennant (1769), the Welsh Naturalist wrote of the toad as "[t]he most deformed and hideous of all animals...its general appearance is such as to strike one with disgust and horror."
- John Morton, the English Cleric and Naturalist, was uninterested in discerning types of amphibian; "whether there are distinct Species of Toads with us, I am not so well assured, having never yet had the Hardiness of meddling with them so far" (Morton, 1712).

These naturalists were not alone in their hatred for these animals, with Pennant (1769) exclaiming "[t]he prejudice against this class is almost universal". To put this in perspective, we have no records or any accounts that describe likely sand lizards (e.g., lizard with green flanks), despite them being a bulky, visible species with a striking male breeding colour (Raye, pers. comm., 2025), nor any for the smooth snake *Coronella austriaca*, although this species is secretive. Despite this, tree frogs seem to have been especially interesting to physicians for believed medical properties (see Section 5.2). The other two lost frogs, however, are inconspicuous and hard to differentiate from the common frog.

We have to remind ourselves that much of the work done by these early naturalists was at a time when biological understanding was extremely crude. Common beliefs of the first half of this period included spontaneous generation (for e.g., frogs from mud) and the belief that extraordinary animals like unicorns, basilisks, and phoenixes were real. Nature was thought to be balanced and unchanging and there to conform to peoples needs; any apparent changes were temporary or due to divine intervention (Thomas, 1983). Additionally, much of the great drainage projects of the 1600s took place well before Linnaeus' concepts of classification came about – a frog was just a frog (Rotherham, 2013). We can see that even after the publication of *Systema Naturae,* Pennant (1771) missed the pool frog while touring the fens, despite making note of loud calling frogs (Kelly, 2004). Also, it wasn't until 1796 that Georges Cuvier established the theory that species could become extinct – no one could believe that God would see one of his holy creations disappear (Faria, 2012).

It is therefore no surprise that in Britain the recognition of herpetofauna occurred late in the categorisation of wild animals; the sand lizard, natterjack toad *Epidalea calamita* and smooth snake were noted in 1804, 1835, and 1859 respectively (Snell, 2006; Beebee, et al., 2009), while the common and widespread palmate newt *Lissotriton helveticus*, was discovered to be a British species in 1843 and debate even rattled on for a further decade as to whether it represented a distinct species from the common newt (Billings, 1985; Inns, 2009). This is despite many of these species being described to science, elsewhere in Europe, several decades prior to their detection in Britain. It is quite pertinent then that the agile frog and moor frog weren't formally described to science until c. ~1839 and 1842 respectively and it was debated as to whether they even represented separate species even into the 20th century (Fitzinger, 1832-1841; Nilsson, 1842; Boulenger, 1897; Clark, 1994). Many countries didn't record these two species until sometimes half a century or more after their formal descriptions (see Sections 3.3 and 4.3 for more). Consequently, it is not likely that the agile and moor frog would have been differentiated on a species level from the common frog, at least before their demise in c.1750-1800, and especially given "frogs [were] poorly recorded" at that time (Raye, 2017; 2023; Sections 3.2 and 4.3). Moreover, due to widespread landscape change, species like the pool frog were already by considered a very rare animal in Britain by c. 1800 (Kelly, 2004).

These fundamental knowledge gaps, historically scuppered by disinterest, aversion and superstition, continue into modern times, however, probably fuelled by other factors. For instance, two populations of Norfolk natterjacks were not scientifically noted until the 1960s while one of the largest populations wasn't recorded in north-west England until 1993 (Kelly, 2004), not forgetting that despite debate for over a century, the pool frog really wasn't formally regarded as a native species until the 1990s, with the discovery of archaeological remains as a key determinant of its native status (Kelly, 2004; Beebee, et al., 2005).

2.4 Archaeological Context

There has been (and still is) a large disconnect between zoo-archaeology and the fields of ecology and conservation, with many archaeologists unaware of the potentially meaningful input they could bring to the better functioning of conservation and ecosystem restoration (Sykes, 2015; Grace, et al., 2019), despite archaeological evidence having the advantage of providing certainty, unlike historical evidence which can drift between fact and fiction in pre-industrial texts (Quinlan, pers. comm., 2025). Nonetheless, historical sources are valuable in offering context about how people interacted with a species or its habitat (Raye, 2023). Ideally, determining native status should draw on both types of evidence, though this can be challenging when dealing with small, delicate, and largely inconspicuous species (Yalden, 2002).

There are numerous taphonomic biases within archaeology. Holocene remains are practically always found within the context of human activity, where construction features such as post holes, foundation trenches, or storage pits can act as inadvertent traps. Once an animal falls into such a feature, rapid sediment deposition may lead to its preservation (Clarkson, et al., 2025). However, inherent biases are presented with this; for instance, synanthropic[3] species may be disproportionately represented, while species capable of climbing or leaping out of such pitfalls are less likely to become entrapped and preserved (Gleed-Owen, 2021).

To date, only two certain subfossils of the pool frog have been described (Beebee, et al., 2005) and this is to be expected: water frog subfossils are much rarer than brown frogs within deposits, despite occurring in high densities in certain habitats (Schouten, 2022). Additionally, as noted in Section 2.3, neither sand lizards nor smooth snakes have historical records of their

[3] Associated with people.

presence prior to the 19th century and in addition, they have no (definitive) Holocene subfossil record either (Gleed-Owen, 2021; Gleed-Owen, 1998). Nonetheless, all of these are regarded as firmly native, their collective poor or absent fossil record being a result of their remote habitat choices away from human settlement (Gleed-Owen, 2025).

To this day, frogs are some of the least studied taxa within the recent zoo-archaeological record due to time constraints as well as a lack of interest, specialists and resources (Bisbal-Chinesta, et al., 2020). Because of a general disinterest, many archaeological sites from the past have unfortunately used >5mm sieves to process material, meaning that tiny frog bones would simply pass through the sieve to be discarded as spoil without anyone taking notice (Gleed-Owen, 2025). Still, the evidence hence forth discovered in Britain is some of the best in Europe (Lenders, pers. comm., 2025). This is largely due to Chris Gleed Owen's (1998) landmark PhD titled *Quaternary herpetofaunas of the British Isles*. This 550 page study was the first of its kind to categorise the recent history of amphibians (and reptiles) specifically in Britain by using fossil evidence. However, limited published work has been conducted since the early 2000s.

Figure 2: the approximate location of the Chopdike Drove archaeological site near Gosberton, Lincolnshire, where archaeological remains of moor, agile, and pool frogs were recovered, as described by Gleed-Owen (2000). Intensive human modification during the MA/EMP has entirely erased all above-ground evidence of the original landscape. When these amphibians were extant, the area would have formed a vast wildland comprising carr woodland, peat bogs, and extensive reedbeds that supported large fauna such as wolves, wild boar, beaver, common crane, and humans. In contrast, the landscape today consists of expansive and 'ecologically bankrupt' arable fields.

3 Agile frog, *Rana dalmatina*

3.1 Introduction

Figure 3: an adult male agile frog, photographed near Køge, Denmark. © Henrik Bringsøe, 2025.

<table>
<tr><td>General Appearance</td><td colspan="3">Very uniform colouration between individuals; yellow or brown base colour, with minimal black flecks; almost always a ‘V’ behind the eyes on back; pale undersides; large overall adult size; athletic appearance; males go dark in breeding season</td></tr>
<tr><td>Size (S-V length)</td><td>6.5-8cm</td><td rowspan="2">Terrestrial Habitat (in NW Europe)</td><td rowspan="2">Light and damp deciduous woodland; sunny, grassland glades</td></tr>
<tr><td>Breeding time</td><td>February-March</td></tr>
<tr><td>Call</td><td>Underwater ‘rog, rog, rog’</td><td rowspan="2">Breeding/larval habitat</td><td rowspan="2">oligo-mesotrophic ponds adjacent to woodland</td></tr>
<tr><td>Larval period</td><td>March-August</td></tr>
<tr><td rowspan="2">Egg mass</td><td rowspan="2">Grapefruit size; below surface; attached to vegetation/sticks</td><td>Preferred pH</td><td>5-8</td></tr>
<tr><td rowspan="2">Conservation Status</td><td rowspan="2">VU (SE); Pre-warning list (DE) ; LC (FR)(DK)</td></tr>
<tr><td>Life span</td><td>7 years</td></tr>
<tr><td>Differentiation from other frogs</td><td colspan="3">The heal extends beyond the snout; tympanum the same size as eye; dark face mask does not extend below the ‘throat line’; white sometimes faintly mottled underside; long and pointed snout; dark leg bands; fainter and uniform colouration; red coloured toe-joints</td></tr>
</table>

The agile frog is so-called due to its ability to leap in rapid bounds of up to 2m (Dufresnes, 2019). This adaptation may have been inherited from a common ancestor similar to its closest relatives, the stream frogs (*Rana iberica*, *R. italica*, *R. graeca*) which require powerful legs for fighting water currents within their riparian habitat (Bringsøe, pers. comm., 2025). The agile frog, however, is not considered a riverine species, but a species of varied topography, that uses ponds as its place of breeding (Speybroeck, et al., 2016; Arnold & Burton, 1978). Their leaping ability must be a useful trait in predator avoidance and navigation within the woodland understory they inhabit (Holman, 1998).

While the majority of European countries refer to the agile frog along the lines of its athletic ability, some named it after its appearance, such as the Czech "skokan štíhlý" meaning "slim jumper", or the Swedish, "långbensgroda" translating to "long-legged frog", while others still have named it in regards to its ecology. Its Hungarian name refers to its habitat, calling it "erdei béka" which simply translates to 'wood frog'. Indeed, the Author observed this species almost solely within or around wooded areas.

Interestingly, the agile frog is the only lost frog to still persist within the British Isles – on the Channel Island of Jersey, where it has faced almost complete extinction. Luckily, this eventuality was thwarted by conservation efforts from a range of organisations (Inns, 2009). It has already experienced extinctions and local declines in northern Europe due to habitat change, suggesting that in these regions it is endangered (Racca, 2004).

3.2 Status in Britain

Table 1: Holocene fossil occurrences of the agile frog.

Age	Description	Location	Source
Early Middle Ages	*Rana cf. dalmatina*	Chopdike Drove, Lincs.	(Gleed-Owen, 2000)
Early Middle Ages	*R. dalmatina cf.*		(Gleed-Owen & Lenders, priv. data)

The agile frog is represented by three subfossils all from a site representing the Middle Ages in Lincolnshire (Gleed-Owen, 2000; Lenders, pers. comm., 2025). While a small level of doubt was asserted over the diagnosis of these fossils at the time of publishing (potentially representing a moor frog instead) (Gleed-Owen, 2000), on-balance and reanalysis Gleed-Owen (2025) is confident that these do indeed represent the agile frog. The same level of doubt was assigned to the pool frog ilium, which became key evidence as part of the native status investigation. Furthermore, the author compared the scientific sketch within Gleed-Owen (2000) with modern agile and moor frog ilia provided by Statens Naturhistoriske Museum and Celtic Rewilding (from natural mortality over the years of keeping the species). The author's opinion is that these do represent agile frogs rather than another *Rana sp*.

As a predominantly terrestrial woodland species, it can be presumed that agile frogs do not readily die within places conducive to sub-fossilisation – such as settlements, which are usually sited in cleared areas – and its jumping ability also likely aids in escaping would-be pitfall traps (Gerlach, pers. comm., 2025). It is also worth noting that no agile frog fossils have been found in Denmark, Sweden or Jersey, where it is native, and that generally, the species is the rarest brown frog in archaeological deposits in northern Europe (Bangsgaard, pers. comm., 2025).

Figure 4: modern ilium of R. dalmatina provided by Statens Naturhistoriske Museum, Copenhagen.© Daniel Klingberg Johansson / SNM, 2025.

Species distribution models in combination with genetic analysis, suggest that the species was likely one of northern Europe's later arrivals during the early Holocene and by extension Britain. Other than within Italy, the agile frog is genetically homogenous, suggesting a fast, postglacial expansion from southern refugia into northern regions (Vences, et al., 2013). Ecologically, the species probably followed the emerging communities of oak-hazel-elm; a mid-late successional stage habitat (Böhme, 1999).

The agile frog is on the Great British Red List of Threatened Species (JNCC, 2023; Foster, et al., 2021) and is classed as a "native species lost" in Natural England's *Lost life* (2010) report. Therefore, it has been included in various metrics assessing historical species extinctions (Hayhow, et al., 2019) and further investigation is recommended (Dunford & Berry, 2012; ARC Trust, 2021). There have been no known introductions of this species to mainland Britain. It is very rare in captivity.

3.3 Species History

The agile frog was described late in the categorisation of Europe's fauna, by Fitzinger in c. 1839, having being overlooked for a long time due to its inconspicuous breeding habits, practically inaudible call, preference for remoter habitats, and complete likeness to the common frog (see Figure 5) (Hachtel & Grossenbacher, 2013; Raye, 2017). Although in the same genus as the common frog, the two species cannot interbreed. Its species name, *dalmatina*, is derived from Dalmatia, a historical region along the Adriatic coast where the species was first collected. This association likely did little to aid its recognition outside southeastern Europe. Northern occurrences were missed by Boulenger (1897) and the agile frog was not formally recorded in Denmark until 1892 or in Sweden until 1907. The full Scandinavian range of the species was only mapped in 1946 (Bringsøe, 2025; Ahlen, 2013). Elsewhere, the species was similarly late to be recognised: it wasn't discovered in Poland, for example, until 1987 (Rybacki, 2008) and continues to be discovered in new places, especially in eastern Europe (Mołoniewicz, 2022; Mołoniewicz, et al., 2021; Hachtel & Grossenbacher, 2013).

Given this history, it is highly unlikely that the agile frog would have been detected as a resident of mainland Great Britain prior to the Victorian Period. The case in Jersey supports this: first recorded there in 1908 by the naturalist Joseph Sinel, the frogs were misidentified as common frogs. Only with Frazer's *The Reptiles and Amphibians of the Channel Isles and their Distribution* (1949) were they correctly re-identified as agile frogs.

Figure 5: the frog that baffled experts. This common frog caused quite a stir, sharing diagnostic features with the agile frog. In the end, a genetic test was the only way to absolutely determine the species.

3.4 Habitat Choice

3.4.1 Terrestrial Stage

Throughout its European range, the agile frog is closely associated with woodland habitats (Ficetola, et al., 2009) and is also considered a mid elevation species (Speybroeck, et al., 2016; Nečas, et al., 1997). The species association with higher elevation may be circumstantial: woodland clearance generally began in the lowlands of Europe and finished or escaped destruction in the uplands. The exception to this rule is Britain (and Ireland), which began clearing upland forests since the Bronze Age (2400-740 BC) or the agile frog just prefers the climate found in these areas (Rackham, 1986; 2015; van Delft, pers. comm., 2025)

While in southern and central Europe the species may have a looser association with a particular forest type, in northern Europe they are tied to deciduous forests with a complex woodland understory in order to foster the correct climatological conditions for terrestrial frogs, especially juveniles/metamorphs (Corbett, 1989; Nečas, et al., 1997). This means at their most northerly reaches in southern Sweden, they inhabit old hazel-oak woodlands, with significant elements of swamp forest and marshes (Nyström, et al., 2013). This is because the bare spring canopies of these woodlands allow for adequate sunlight penetration through to the ground. In addition, the combined effects of the structure of the forest and the very wood of the trees both removes excessive wind and collects and retains heat; together forming a mild spring microclimate (Ahlen, 2013). Therefore, the species is incompatible with coniferous or clear-cuts in these regions (Nyström & Stenberg, 2010). Light grazing of these habitats is thought to be beneficial, creating a varied microtopography and understory (Ahlen, 2013).

Sweden has retained a significant cover of broadleaf woodland throughout the Holocene, when compared to the UK (O'Dwyer, et al., 2021). What deforestation and/or conversion to coniferous forest that did occur is probably responsible for the agile frogs modern day distribution there (Snell, 1985a).

Just slightly south in Denmark, agile frogs display a slightly broader range of occupied habitats when compared to Sweden, including quite open environments and also mixed broadleaf-coniferous woodland (Bringsøe, 2025). The species connection to wooded habitats is still shewn however with "the shorter the distance to a forest, the larger the breeding population at a pond" observed throughout the country (Kjær, et al., 2023). Agile frogs also benefit from damp grassland glades and rides through forest, so long as they retain moisture. They use these as foraging places (Bringsøe, 2025). Agile frogs in maritime climates certainly can persist within open habitats – but this is only where the common frog is absent – such as on the dunes, coastal heathlands, shrublands, and grasslands of Jersey (Racca, 2004; Inns, 2009). One element which seems to determine which species of brown frog dominates, is the overall dryness of the landscape and the distance between the breeding place in the spring, and the appropriate summer terrestrial habitat (Kjær, et al., 2023). The agile frog displays a competitive edge in woodlands, and dryer environments with greater distances from wet areas to their forested summer lodgings (Fog, 2024).

Of the European brown frog species, the agile frog is possibly the least synanthropic: as to be expected from a woodland species, it generally doesn't thrive in modified habitats such as in agricultural land or gardens. Numerous translocation projects to such habitats have failed for these reasons (AmphibiaWeb, 2025a; Inns, 2009; Riis, pers. comm., 2025; Bringsøe, pers. comm., 2025). The species has suffered more modern regional extinctions, such as in Luxembourg and Belgium (Corbett, 1989).

Hibernation likely takes place on land, amongst deadwood and leaf litter, and lasts from November to January.

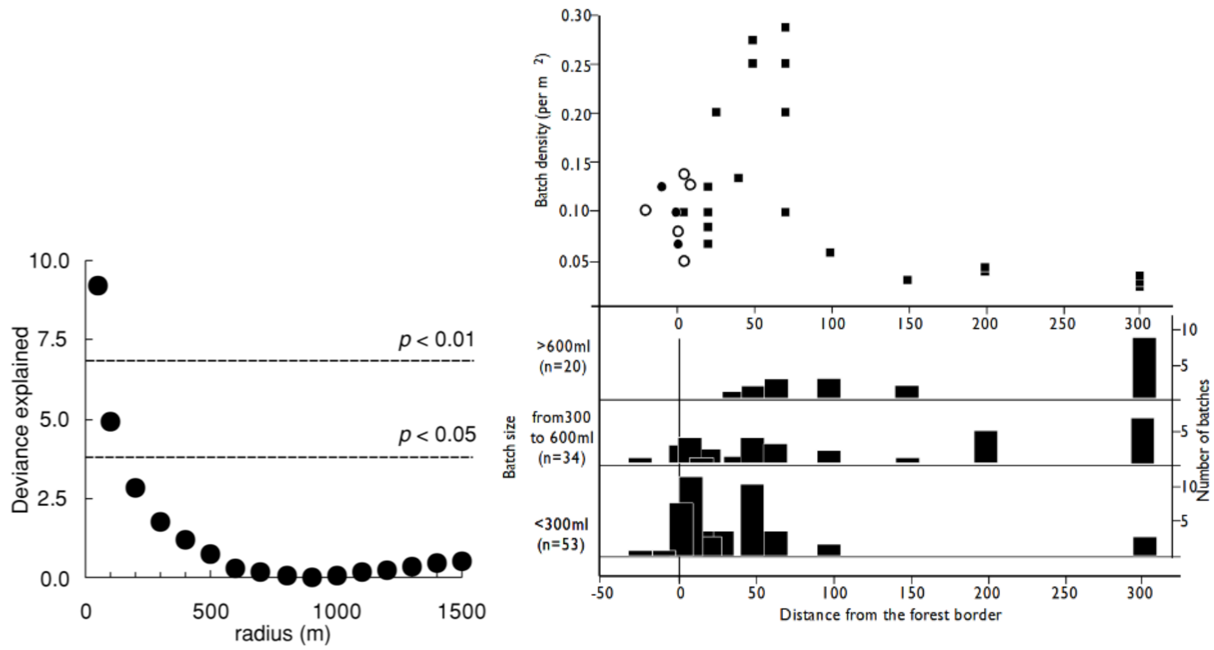


Figure 6: left, the negative relationship between distance from forest and the presence of agile frogs taken from Ficetola, et al. (2009), right, the negative relationship between the number of spawn clumps with increasing distance from the forest edge, taken from Ponsero & Joly (1998).

3.4.2 Breeding and Aquatic Stages

Agile frogs spawn the earliest out of all the frogs in northern Europe, often while there is still snow on the ground or ice on the breeding ponds, typically anytime from January to April (Riis, 1997). The peak spawning period occurs when temperatures of 6-10 ºC are reached and often ceases before it exceeds 15 ºC (Ward & Griffiths, 2015). In Denmark and Sweden, the present distribution of the species is in areas with a coastal influence, where the risk of late-night frost is low (Riis, pers. comm., 2025). They spawn in larger and deeper ponds, averaging about a third of a hectare in size (Bartoń & Rafiński, 2006; Ahlen, 2013). Unique among north European amphibians, they can use shaded waters as part of woodland pond networks, even at their most northern occurrences (Ahlen, 2013; Nyström, et al., 2013). Suitable breeding ponds must be nearly permanent yet free of fish and ideally form part of a broader wetland complex where occasional droughts introduce some ephemerality (Bringsøe, 2025; Riis, pers. comm., 2025).

It has been shown that the numbers of spawn clumps drastically decrease with increased distance from forest edges (see Figure 6). Therefore, agile frogs prefer ponds either within glades or within 100m of woodland edges (Fridolf, 2014; Ponsero & Joly, 1998).

Males call from underneath the water's surface letting out a practically inaudible 'rog, rog, rog'. Females join the males in the water where they subsequently deposit their eggs, simultaneously with the release of the males' sperm, in the middle or bottom of the water column, clumped around some vertical vegetation like reed stalks or twigs. This spawning behaviour differs when compared to the other brown frog species. This is one of the reasons beavers have been shown to create benefits for the agile frog, through the provision of submerged woody debris in the form of dams, lodges and vast quantities of discarded 'feed sticks,' but also through the creation of important warmer microclimates through the thinning of the canopy (Hartl, 2024; Campbell-Palmer & Rosell, 2022).

As the eggs develop and reach 2-3 weeks in age, and presumedly the weather improves, the clump detaches from the twig or stalk and floats to the surface and spreads slightly (Bringsøe, 2025). Here, the top layer of eggs dries and hardens, forming a 'magnifying layer' which warms up the rest of the clump. Once the eggs hatch, at about 1 month in age, the emerging ~6mm long tadpoles feed on the remaining jelly, before dropping to the bottom of the pond, to develop within the silty detritus (Riis, pers. comm., 2025).

As the tadpoles grow larger, they become very capable of swimming, but seemingly stay in the deeper parts of the water, clustering around submerged algae and aquatic plants like hornwort *Ceratophyllum demersum*, where as the other brown frog species seem to actively seek out the warmest or shallowest parts of a given waterbody. Captive experience has shown that their tadpoles are the most susceptible to excessive heat, compared to the other species of frog found in northern Europe (Whitehurst, pers. comm., 2025). Agile frogs have the longest development time of any frog in northern Europe, commonly emerging from the water as froglets in mid-July to mid-August, totalling a development period of 4-6 months. As to be expected from such a development time, tadpoles and emerging froglets are significantly larger than the other brown frogs. Because of the length of time where an aquatic habitat is needed, a long hydroperiod is critical (Racca, 2004).

3.5 Field Observations

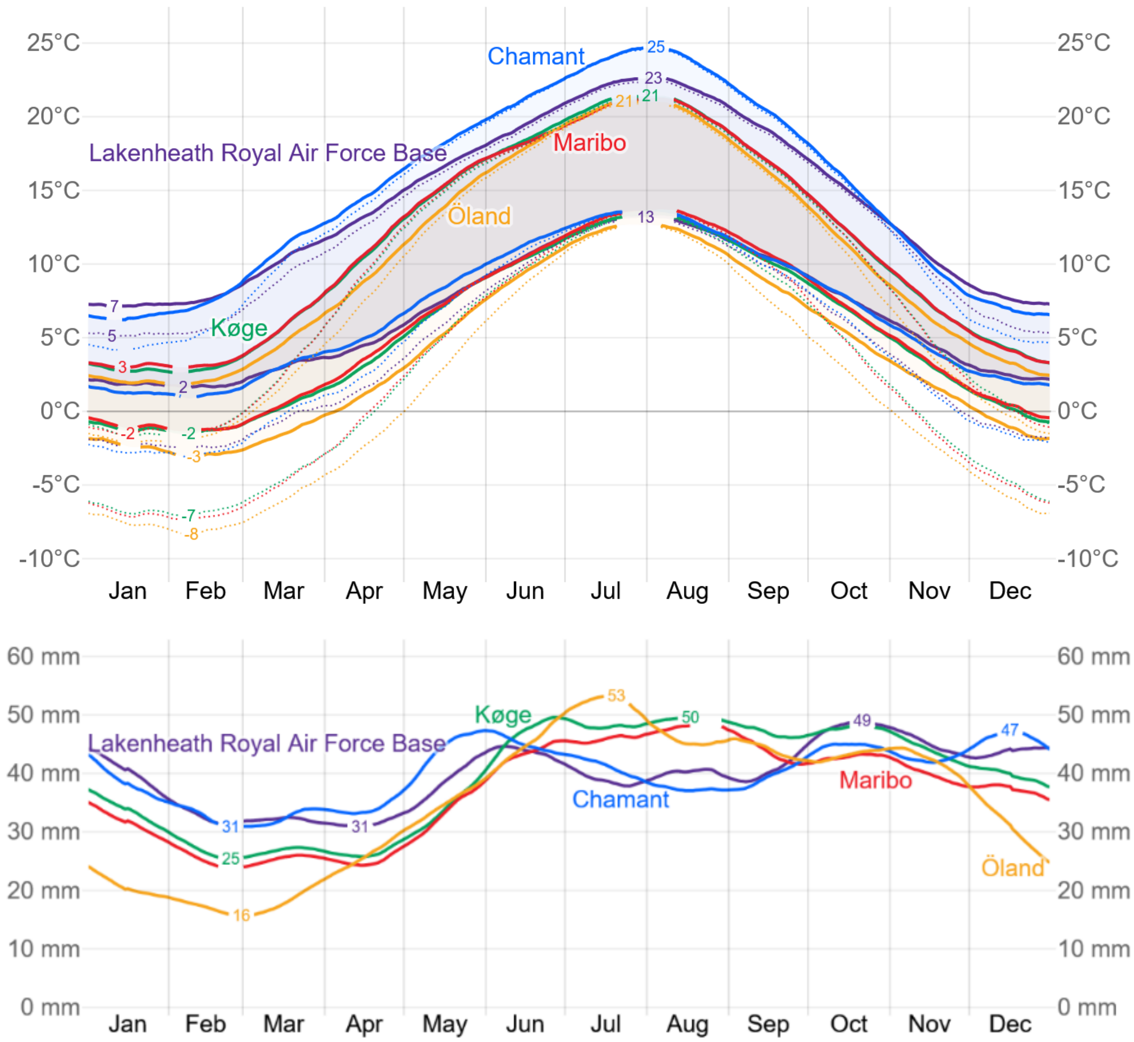


Figure 7: upper: average high and low temperature of some of the visited and mentioned sites compared with climate data from RAF Lakenheath, East Anglia. Lower: average monthly rainfall of each site and RAF Lakenheath.

After Diebel (2025a),[© WeatherSpark.com](https://weatherspark.com).

3.5.1 Woodland Sites

(05/07/2025) Around Køge Ridge, in Sjealland, Denmark, a contiguous block of 230 ha of mainly deciduous (beech *Fagus sylvatica*, sycamore *Acer pseudoplatanus*, oak *Quercus sp.* and hazel *Corylus avellana*) forest, meadows, ponds, swamps, and stream floodplain of the Køge River, harbours a healthy population of agile frogs. I met with Henrik Bringsøe, renowned Danish field herpetologist, who has studied these agile frogs for decades. We visited in rainy conditions, with a temperature of around 17ºC and 4 agile frogs were seen of various ages. Notably, newly metamorphosed froglets were emerging from one of the primary breeding ponds (see Figure 8).

Figure 8: upper: the main breeding pond for the agile frog. The trees in the background shade it quite significantly. Lower: a baby agile frog recently emerged from the above pond.

Figure 9: habitats where the agile frog was encountered. Upper: a damp woodland ride, where adults were foraging. Lower: dense woodland with a well developed ground flora.

Figure 10: woodland tracks like the above provide good opportunities to spot agile frogs as they rather like the ease of movement of open ground but still remain within leaping distance of vegetation. Lower: Henrik Bringsøe photographs an adult on a track, note the camouflage within their woodland home.

(02/07/2025) Søholt Storskov, near Maribo, Denmark, is an 800 ha "renaturation" project financed and conducted by the Aarge V. Jensen Naturfond, inspired by the Knepp Wilding Project (see Section 2.2.1). The area is 1134 ha, including three large glacial lakes totalling 359 ha, 610 ha of forest, and the rest being comprised of mainly arable land, now in the process of reversion to meadow, wood pasture and scrub (Aarge V. Jensen Naturfond, 2025). Within the 610 acres of woodland at Søholt, agile frogs will occur in densities of about 15 adults per hectare, indicating a total breeding population size of ~10,000. I met with Niels Riis, one of the leading researchers who studied the fundamental biology of the agile frog in the 80s and 90s. Riis has subsequently dispelled many myths (like that they hibernate underwater) and has been fundamental to the recovery of the species in Denmark. He is now leading the project at Søholt Storskov and many other nature recovery sites. We went to see the current habitat occupied by agile frogs and how many of the interventions could benefit the species recovery in the area.

Figure 11: a male agile frog encountered right at the start of the day in the middle of a beech forest

Figure 12: two examples of woodland ponds used as spawning places for the agile frog.

Figure 13: upper: Niels Riis surveying for agile frog tadpoles using a dipnet within a restored pond in a woodland glade. Lower: an agile frog tadpole (right).

Figure 14: upper: woodland habitat used by the agile frog. Lower: a female agile frog found in well-lit and dense grassland within the forest.

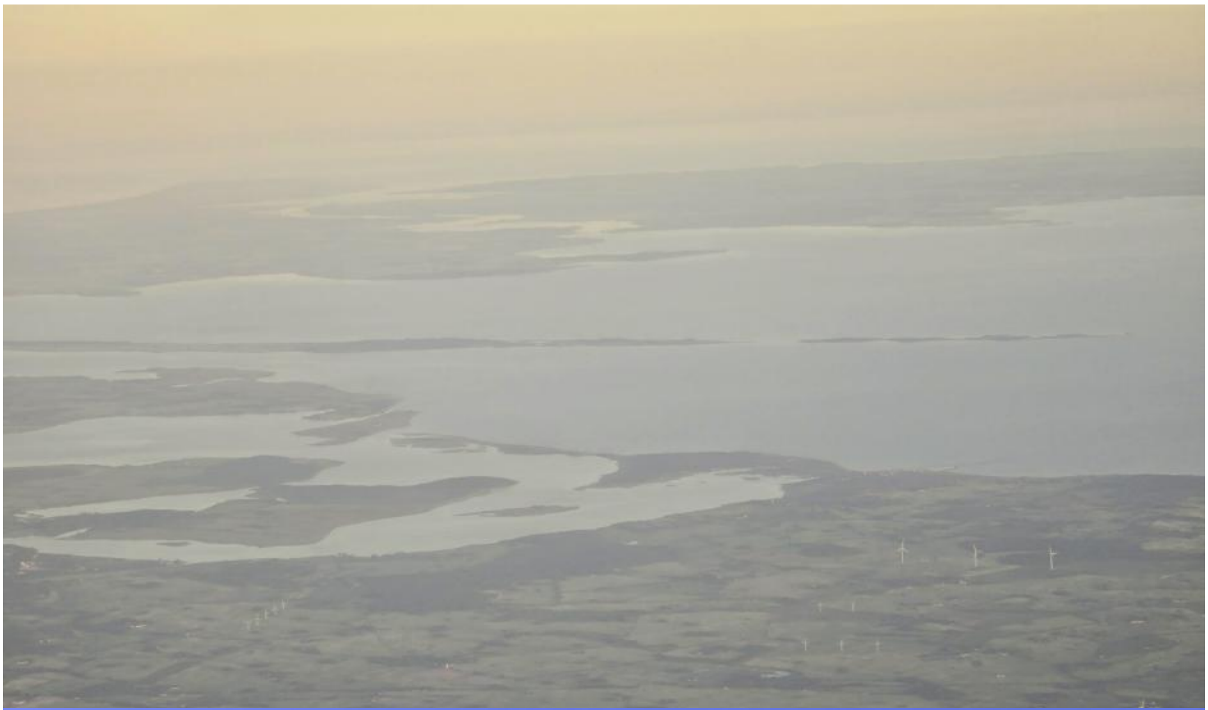
Figure 15: new habitats for the agile frog. Upper: a 3 year old pond, dug adjacent to agile inhabited woods. It has been used, however, the presence of fish heavily impacts on tadpole numbers. Lower: introduction of low-intensity extensive grazing, not specifically for agile frogs but sure to benefit them.

(02/08/2025) Just outside of Paris there are a number of huge, state-owned forests. One of these is Forêt Domaniale d'Ermenonville at 3,319 ha in size. The agile frog population seems substantial, with over 30 seen within about an hour, although these were all newly metamorphosed juveniles. The forest is varied, with open areas of heath, and dense willow scrub. It is a mixed, broadleaf and conifer woodland due to its use as a plantation. While the underlying substrate is sand, the well-developed understory provided a humid microclimate.

Figure 16: the varied quality of Forêt Domaniale d'Ermenonville.

3.5.2 Other Sites

(03/07/2025) Knudshoved Odde, near Neder Vindinge, Denmark, is a 15-kilometer-long peninsula jutting out northwest into Smalandsfarvandet. Just over half of the peninsula is comprised of protected or important habitats, totalling a connected 485 ha block. Much of this area is covered in open grasslands and wet meadows, dozens of shallow ponds, forest, and wood pasture. However, much of these habitats are in the process of restoration as part of the LIFE Clima-Bombina project, helping to create pond habitats for the fire-bellied toad *Bombina bombina*. 17 of the 19 native Danish reptiles and amphibians are found here, including the agile frog, although none were seen due to the warm weather (28ºC). The interesting part of this site is just how open it is, in contrast to the typical habitat choice of the agile frog. That is not to say that the area is devoid of woodland, a contiguous block of 182 ha does exist at the eastern end of the site. The area does not appear to provide optimal conditions for common frogs, likely due to its overall dryness despite coastal influence. This is attributed to the lack of topsoil depth, with the substrate consisting primarily of sand. Agile frogs are able to cope with drier conditions better than the common frog, hence their persistence here.



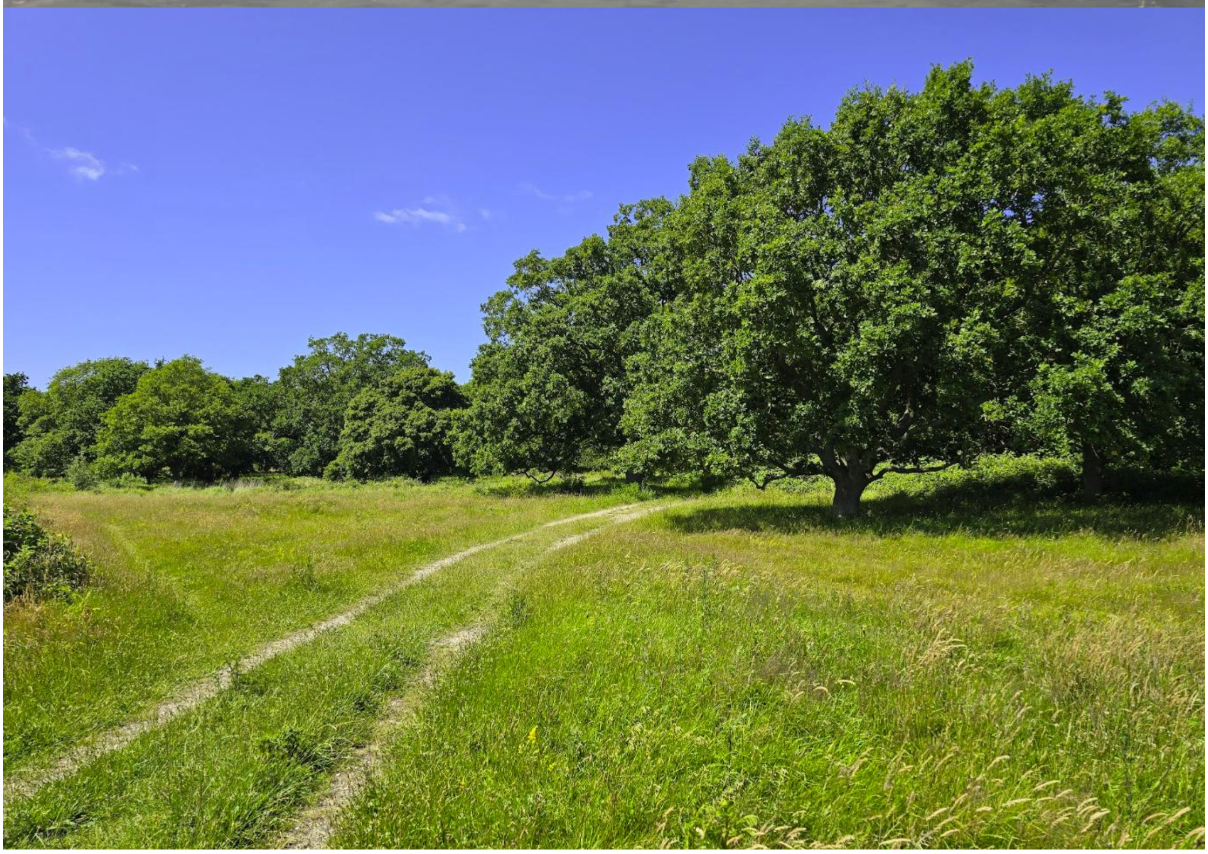


Figure 17: upper: Knudshoved Odde (peninsula seen in the middle of the photograph) as seen from the Plane on the flight out to Denmark! Lower: wood pasture at Knudshoved Odde.

Figure 18: habitats on Kundshoved Odde. Upper: breeding pond for the agile frog. Lower: light open woodland with a dried pond.

(11/07/2025) The woodlands surrounding the towns of Vledder and Noordwolde, along the Drenthe and Friesland border, support a population of introduced agile frogs, occurring outside the species' current range. The nearest native populations lie more than 250 km to the south and east. As a breeding habitat, the agile frogs use ice-rink lakes, which are substantial in size, but are crucially allowed to dry out every year, preventing the persistence of fish. These frogs are thought to originate from a biologist's garden in Vledder, where a variety of animals were kept, and were later released either intentionally or accidentally (Wennekes, pers. comm., 2025).

Today, the frogs inhabit a connected woodland network of over 500 hectares, likely established after World War I and varying in suitability for the species. The population appears to be expanding, suggesting that *R. dalmatina* is more ecologically flexible than its modern distribution implies.

This outlying population may hint at a formerly broader native range for the agile frog in the Netherlands. Historical woodland clearance likely led to its disappearance: by 1850, forest cover in the country had fallen to just 1% (Groenewoudt, et al., 2022), although the species may not favour the flat topography the Netherlands. The species' current persistence in Vledder and Noordwolde has been enabled by post-industrial forest regrowth and replanting.

Figure 19: damp woodland inhabited by agile frogs near Vledder.

Figure 20: upper: the dried up ice-rink used by the agile frog as one their breeding locations. Lower: a juvenile agile frog found at this site © Stefan Wennekes, 2025.

3.6 Extinction

Interestingly, populations of the agile frog inhabit numerous (but not all) islands in southern Scandinavia, including Öland in Sweden and a large proportion of Denmark's archipelago, such as Bornholm, Sjælland, Lolland, and Fyn (Figure 7) – some of which were visited by the author. These islands, due to their northern latitude and coastal influence, experience summers with either peak temperatures either identical to, or 1–2 °C cooler than, much of southeastern England (Diebel, 2025a). While incidental human introduction (in transported hay for example) can maybe explain some occurrences between closely situated islands, genetic studies and computer modelling demonstrates that the agile frog has withstood climatic fluctuations for at least the past ~8,000 years, in the region as a whole (see Section 7) (Riis, pers. comm., 2025; Vences, et al., 2013; Mołoniewicz, 2022).

Recent works on mapping the suitable climatic distribution of the agile frog in Britain reveal that the species is quite suited to this climate and shows an ability to cope with a deterioration in mean temperatures exceeding 1ºC (See Section 7; Lyons, in prep.). When these models are considered alongside field observations, it becomes clear that the Little Ice Age alone is too simplistic an explanation for its demise (Gleed-Owen, 2000). While the LIA would have contributed towards the vulnerability of the agile frog, on balance, wide-spread woodland clearance during the MA/EMP and competitive exclusion by the common frog are the most plausible explanations for the species' extinction, as suggested by Gleed-Owen (1998) and Riis (1988); largely giving rise to the disjunct geographic distribution of the agile frog observed in northern Europe today (Sillero, et al., 2014). At the northern edge of its range in particular, the species is highly intolerant of clear-cut forest (Ahlen, 2013). While Roman activity did not result in large-scale deforestation (Hoffman, 2014), by the Middle Ages forest cover in Britain had reached a historic low – possibly falling below 5% – as shown by pollen analysis and historical records (Yalden, 2002; Rackham, 2015).

Modern UK woodland cover sits at 13% of landcover, but only 1.9% of landcover is 'natural' forest (Global Forest Watch, 2025). Much of Britain's woodlands, seemingly of ancient appearance, are in fact secondary growth habitat which have sprung up or been planted after or during the Middle Ages (Rackham, 1986). These woodlands can and do lack several typical ancient woodland species while giving the appearance of continuously forested areas (Swallow, et al., 2020). What little forest did remain during the MA/EMP was enclosed, excluded from livestock, and drained in the fashion of wood-banking: ditching woodlands in the belief that improved drainage would help trees to grow (Rackham, 2015; Rackham, 1986). Respectively, these practices would have both removed the necessary light grazing of woodlands and the damp and humid areas that agile frogs require (Ahlen, 2013; Meek, 2018).

It may seem implausible that such a small creature could be extirpated so early from Britain as a result of forest clearance, but even mammal species which are unaffected by woodland drainage, such as the hazel dormouse *Muscardinus avellanarius* and yellow-necked mouse *Apodemus flavicollis*, display curious British distributions as a result of both ancient forest clearance and patterns of countryside management predating the 1700s, while the red squirrel *Sciurus vulgaris* was almost lost completely due to the former (Yalden, 2002). Species of longhorn beetle in the *Cerambycidae* family have either dis-contiguous ranges or are altogether extirpated from the UK, along with many other forest-dependant insects (Twinn & Harding, 1999; Gerlach, 2014). Plant species have also suffered severe losses since the Middle Ages, with many ancient woodland species extinct or heavily contracted in their distributions (Natural England, 2010; Rackham, 2008).

If we consider the agile frog's reliance on two habitats often heavily modified by humans – light, damp woodland for its terrestrial phase and wetlands with slight shade for breeding – it becomes clear that the relentless exploitation and change of use of these habitats, combined with the particular vulnerabilities of an ectotherm, could create a multi-century synergistic process driving the decline of the agile frog (as observed in other parts of Europe) (Corbett, 1989).

However, if woodland clearance was a key driver of the agile frog's extinction in Britain, it raises the question of why the species has survived in Denmark, where forest cover declined to as little as 2–3% (Fritzbøger, 1992). The answer centres on competitive exclusion by the common frog, a dominant ecological generalist well-adapted to the cool, maritime climates of northern and western Europe and capable of exploiting a wide range of habitats, including anthropogenic ones (van Buskirk & Arioli, 2005; Muir, et al., 2014; Vences, et al., 2013; Snell, 2015; Bartoń & Rafiński, 2006; Carrier & Beebee, 2003). In northern and western Europe, by contrast, the agile frog is relatively specialised, with a strong dependence on light woodland habitats (see Section 3.4.1) (Vences, et al., 2013; Fridolf, 2014; Bringsøe pers. comm., 2025), The removal of this habitat in Britain would therefore have forced agile and common frogs into direct competition in open landscapes, where the ecological flexibility of the common frog provided advantage.

In Denmark[4], where seasonal temperatures are more stable and rainfall is relatively low, the agile frog is able to maintain viable populations by spawning earlier in spring when cold weather inhibits the common frog, hence their distribution is seemingly tied to coastal areas where late frosts are unlikely to occur (Riis, 1997; pers. comm., 2025). This allows larval recruitment to occur simultaneously, despite interspecific competition and the longer larval developmental time of agile frogs (Riis, 1988; Hartel, 2005). In addition, the agile frog can also exploit breeding sites surrounded by drier terrain, less favourable to its competitor (Fog, 2024; Kjær, et al., 2023). In Britain, however, the cool maritime climate provides no such advantage. The common frog is capable of spawning as early as December, and high year-round rainfall reduces the availability of warm, dry habitats where the agile frog might otherwise succeed. As a result, competitive pressure on the agile frog following woodland clearance in Britain would have been much greater than in other parts of its range.

The persistence of the agile frog in northern France, including regions such as Hauts-de-France, Normandy, and Brittany, despite similar maritime conditions, highlights the role of land use. During the MA/EMP, more than three times as much woodland was retained in France in comparison to Britain (Birot, 2015) and the fossil record also confirms the species historical presence in this region too (Arbogast, et al., 2010). In contrast, widespread woodland clearance

[4] Denmark also offers nearly 5 times as many ponds per hectare than Britain (EPCN, 2008).

in Britain removed much of this critical habitat forcing agile and common frogs into the same open habitats. In maritime environments these conditions favour the generalist common frog, leading to competitive exclusion of the agile frog. This process is comparable to the displacement of the natterjack toad by the common toad, where vegetation succession alters habitat conditions to favour the latter (Vos, et al., 2007; Bardsley & Beebee, 1998).

Historical patterns on the Channel Islands reinforce this narrative. The agile frog, once present on both Jersey and Guernsey, disappeared from Guernsey but has survived on Jersey, albeit perilously (Frazer, 1989; Jee, 1972; Guernsey BRC, pers. comm., 2025). Retaining ~1.7 times more natural forest than Guernsey (Global Forest Watch, 2025), Jersey's woodland cover has provided a buffer against extinction. Additionally, Guernsey hosts a native population of the common frog, so the loss of woodland likely eliminated habitat for agile frogs without offering refuges free of competition. The remaining Jersey population(s) survived in suboptimal habitats, notably the tiny dune system of Ouaisné, a drier and more open biome than their preferred continental habitats but persisting nonetheless because the common frog is absent.

In summary, the decline of the agile frog in Britain appears to result from the combined effects of widespread woodland clearance and the subsequent competitive exclusion by the generalist common frog both at the larval and terrestrial phases. While agile frogs can persist in open maritime habitats in the absence of the common frog, their woodland-specialist ecology and reliance on early breeding give them little advantage where both widespread woodland clearance and common frogs dominate. This satisfyingly explains their survival in scattered populations in northern Europe as well as their total loss from Britain.

Experience elsewhere (see Section 3.3) suggests that agile frog most likely perished prior to the 19th century, or it possibly clung on, until becoming a casualty of the late-industrial revolution of agriculture (c. 1900) (Natural England, 2010; McKie, 2010).

3.7 Reintroduction

Fortunately, extensive work has already been completed on the captive raising and reintroduction of the agile frog specifically on Jersey, allowing a project on the British mainland to draw from the successes and failures of techniques implemented and evaluated there (Gibson & Freeman, 1997). As an aside, re-establishing the species on mainland Britain would help to improve the status of the species in the UK as a whole, while also making the agile frog more resilient to climate threats overall (Dunford & Berry, 2012). Jersey is a small island with very limited habitat where quite intensive hands on management will always be required to maintain the population there (Racca, 2004; Ward & Griffiths, 2015; Gibson & Freeman, 1997).

As a woodland frog, it is possible that the agile frogs' diet of many detritovorous invertebrates could be shewn to improve the carbon storage capacity of forest soils; a hypothesis worthy of investigation and has been shown with European salamanders (Laking, et al., 2021).

3.7.1 Notes on Method [5]

Such a project should first begin with selecting a number of suitable sites. From the preliminary SDM data, this is likely an area in south-east England (Lyons, in prep.). A desk-based study should be performed to narrow down potential sites to a few candidate release locations. The habitat should include in excess of 50 ha of varied and complex woodland, and a similar amount of grassland and scrub, with at least a dozen suitable, fish-free ponds within or directly adjacent to said woodland (Riis, pers. comm., 2025). On-site surveys, carefully comparing these candidate locations with studied areas in Europe should be undertaken. It is likely that the agile frog, even when restored, would be a restricted species in Britain but its effects on the common frog should be investigated throughout the reintroduction (Cooper, pers. comm., 2025).

Outside of Italy, the agile frog is genetically homogenous, with the populations found in northern and western Europe grouped within the same haplotype (Vences, et al., 2013). Taken together with local adaptations to climate, the founder stock should be sourced from wild populations in northern France, Germany, or Denmark. Ideally either egg or subadult life stages are to be collected, but this should be decided on balance of a disease risk analysis (eggs are possibly the most bio-secure option) and assessment of the most optimal transport method (Cracknell, pers. comm., 2025). A group representing ~60 unrelated animals should be assembled, ideally as part of a 1:1 sex ratio. If eggs are the preferred option, from 20-30 different clumps should be harvested (each spawn clump represents two different adults).

The subsequent breeding groups of agile frogs should be raised under optimal semi-outdoor conditions to a point where they can breed, in an appropriate captive facility. In the wild, agile frogs can reproduce in their third year, but this can be as short as the second year in captivity. The animals should undergo a hibernation period when they are adults, either naturally within built hibernaculum in outdoor vivaria, or artificially using a temperature controlled cooling chamber.

In early spring, as temperatures slowly begin to climb, the adult agile frogs should start to show signs of breeding. The males will turn a dark grey colour (Figure 21), and the females will head towards water. In the interests of maintaining genetic diversity, it is recommended that care is taken to ensure not one or a few males dominate, possibly even separating individual pairs out in temporary enclosures to spawn independently. Sticks or canes should be added to the water to allow the frogs a surface to attach their eggs. The subsequent spawn (with its sticks) should be collected and transferred to small plastic tubs and carefully labelled to keep track of progeny lines.

The spawn should be allowed to hatch, and the tadpoles develop until they are mobile and capable of free swimming. At this point, they can be sucked up with a pipette, counted, and distributed to large containers (plasterer's baths are an ideal choice) at a density of 1-1.5 tadpoles per litre. These containers could be housed with a well-ventilated polytunnel or

[5] This section is not exhaustive. Before any reintroduction should take place, it is recommended that a follow up report be written to formally set out an agreed-upon methodology that considers all aspects including but not limited to legal, welfare, veterinary and resourcing implications.

similar, to speed up the development process. This could be part of a recirculating aquaculture system. The tadpoles should be raised through the spring and summer until they begin to sprout prominent back legs, feeding them on an appropriate diet and undertaking the necessary water changes. When 10% of the tadpoles develop four legs, they can be carefully released into suitable ponds at the reintroduction site.

Per site, the aim should be to release at least 1-3,000 tadpoles per annum for three years. After that period, it is suggested to thoroughly survey the ponds (using the method demonstrated by

Figure 21: upper: an outdoor vivarium for keeping up to 20 agile frogs at Celtic Rewilding. Note the surrounding green mesh to keep the inclined-to-leap frogs safely contained. Lower: agile frogs in amplexus in a separate tank.

Riis in Figure 13) for signs of breeding to ascertain whether the release at a particular site has been successful. If little or no signs of breeding are detected, a further release for one more year maybe permitted, whereby the survey should be repeated in the spring following release, and the spring a year after that. If no evidence of reproduction is again recorded, that particular site should be abandoned or an exit strategy implemented.

Figure 22: a recirculating aquaculture system as used at the Research Institute for Nature and Forest, Brussels, to raise many different species of amphibian.

4 Moor frog, *Rana arvalis*

4.1 Introduction

Figure 23: a male moor frog displaying its blue mating hues © Celtic Rewilding 2025.

<table>
<tr><td>General Appearance</td><td colspan="3">3 morphs (typica, maculata, striata); brown or creme to reddish base colour, with lots of black spotting on sides and dorsum; often a light stripe runs from snout to the vent; 3 pale undersides; small overall adult size; males sometimes blue for a few days in spring</td></tr>
<tr><td>Size (S-V length)</td><td>4.5-7cm</td><td rowspan="2">Terrestrial Habitat (in NW Europe)</td><td rowspan="2">Peat bogs; expansive wet heath; oligotrophic fens</td></tr>
<tr><td>Breeding time</td><td>March</td></tr>
<tr><td>Call</td><td>Surface chicken like ‘cluck’</td><td rowspan="2">Breeding/larval habitat</td><td rowspan="2">Oligotrophic; acidic shallow expansive wetlands</td></tr>
<tr><td>Larval period</td><td>March-August</td></tr>
<tr><td>Preferred pH</td><td>4.5-6</td><td rowspan="2">Conservation Status</td><td rowspan="2">CR (FR); EN (NL, DE)</td></tr>
<tr><td>Life span</td><td>7 years</td></tr>
<tr><td>Differentiation from other frogs</td><td colspan="3">The heal extends to the eyes; tympanum 2/3 size of eye; white underside; short, pointed snout; fainter and uniform colouration; metatarsal tubercle is large and hard</td></tr>
</table>

When most British ecologists first hear of the moor frog, they often assume a species which prefers upland habitats, because of Britons’ modern use of the term ‘moor’. In Britain, ‘moorland’ is used to describe areas of hilly or mountainous country dominated by largely acidophilic plants. With old-language terms like "morass", "mere", "meer", "marr" and "marsh" serving as etymological cousins, both the (modern) European and old-English uses for moor are broader, using the word to mean a "tract of swampy waste land", not at all restricted to higher ground but also applied to lowland bog (Online Etymology Dictionary, 2025). It is a testament to the extreme destruction of lowland peat bogs in Britain that, as this habitat became less familiar to people, the term 'moor' migrated uphill, being applied to the surviving upland areas where peat-loving plant communities persisted, resembling in part the lowland form that had largely vanished.

Therefore, the moor frog's namesake is that of the habitat it is adapted to and what Europeans still refer to as moorland, this being lowland peat bogs, wet heaths, and nutrient poor fens. The moor frog could just as easily be named the mire, bog, or peat frog; all are terms that have a similar meaning and effect. Indeed, the species is ecologically and physiologically adapted to lowland peaty habitats. As such, its range comfortably correlates with the extent of lowland peatlands in Europe, especially in the north and west (Figure 24).

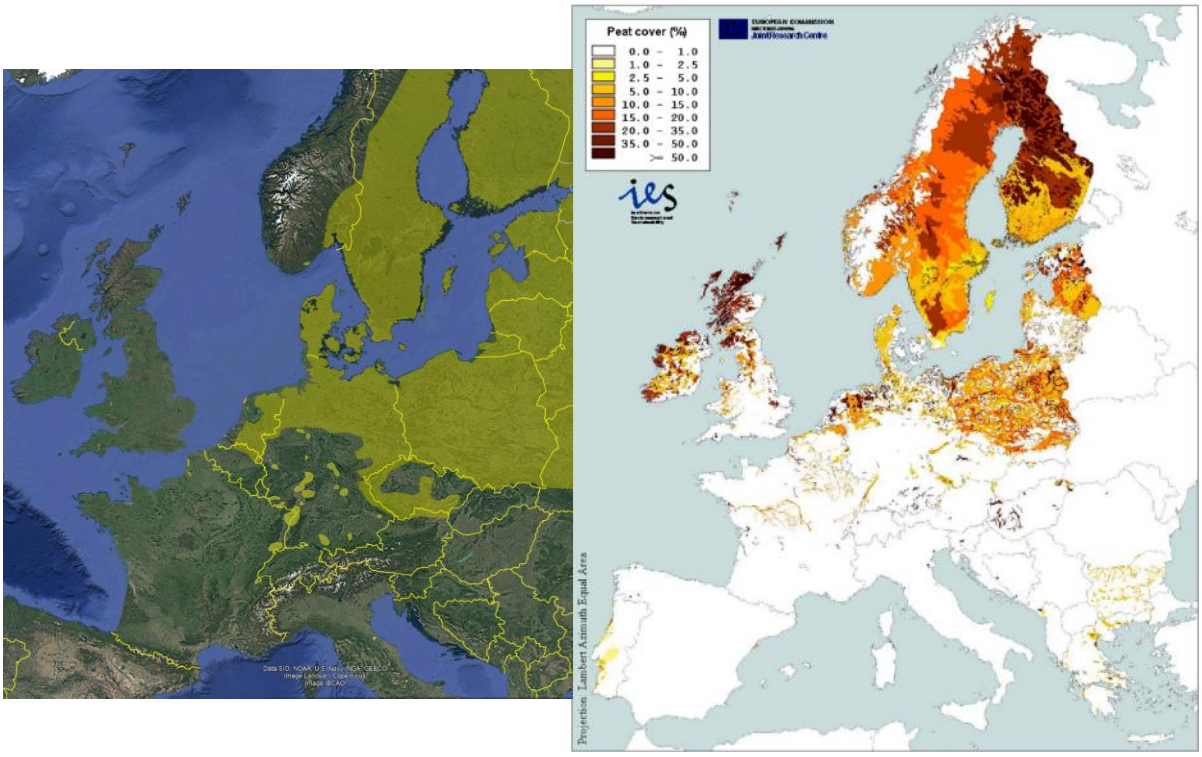


Figure 24: left, the distribution of Rana arvalis ssp. arvalis (taken after Figure 25) in northwest Europe, compared to the distribution of peatland in Europe, right, after Montanarella, et al. (2006).

Figure 25: the distribution of R. arvalis in NW Europe. Current (yellow), Holocene historic (red), uncertain (transparent red). Adapted from Glandt, 2008; Vacher, 2019; Dolmen, 2008; Godin, et al., 2008; Burmeister, 2015; Roček & Šandera, 2008; Blain, et al., 2019; Godin, et al., 2008; GBIF.org, 2025; Clicnat.fr, 2023; RAVON, 2025; Lyons, in prep.; Meßlinger, pers. comm., 2025. Distribution records for R. a. wolterstorffi have been excluded.

4.2 Status in Britain

Table 2: Late Pleistocene/Holocene fossil occurrences of the moor frog in Britain

Age	Description	Location	Source
Middle Palaeolithic	*Rana arvalis*	Swanton Morley, Nf.	(Gleed-Owen, 1998)
Middle Palaeolithic	*R. arvalis*	Shropham, Nf.	
Late Pleistocene	*R. arvalis*	Greenlands Pit, Esx.	(Holman, 1998)
Early Holocene-Neolithic	*R. arvalis cf.*	Milton Hill Cave, Som.	(Gleed-Owen, 1999)
Early Roman	*R. arvalis*	Rectory Farm, Lincs.	(Gleed-Owen & Lenders, priv. data)
Roman	*R. arvalis cf.*	Mount Pleasant, Lincs.	
Roman	*R. arvalis*	St. Clare Street, Ldn.	(Hibberd, 1991)
Early Middle Ages	*R. cf. arvalis*	Chopdike Drove, Lincs.	(Gleed-Owen, 2000)
Early Middle Ages	*R. arvalis*	Hay Green, Nf.	
Early Middle Ages	*R. arvalis cf.*	Chopdike Drove, Lincs.	(Gleed-Owen & Lenders, priv. data)
Early Middle Ages	*R. arvalis*	Hay Green, Nf.	
Early Middle Ages	*R. arvalis*		

Archaeological evidence of the moor frog in Britain occurs continuously from the Pleistocene through to the 9th century, qualifying the species as a firmly native component of British fauna (Holman, 1998; Gleed-Owen, 2000; Natural England, 2025). All subfossil finds are from England, represented by 11 sites where the remains of the species have been recovered, widely distributed across the country. This recent archaeological record can be regarded as remarkable by international standards. For instance, France and Belgium are represented by just one fossil each (Arbogast, et al., 2010; Blain, et al., 2019).

With some populations tolerating body temperatures as low as -16C^{o}, the moor frog is the most cold-enduring anuran known from Europe (Voituron, et al., 2009; Berman, et al., 2020). Coupling this fact with the fossil evidence from late Pleistocene and early Holocene transitional assemblages suggests that the species could have lived amongst the steppe-like conditions of glacier-free southern England/Doggerland (Gleed-Owen, 1998; Holman, 1998). The vast majority of the species range occurs within tundra, steppe and boreal ecoregions (Glandt, 2008), while notable populations occur within remnant 'mammoth steppe' environs in the Altai Republic, and around Lake Baikal, Russia (Kuzmin, et al., 2009). This surely attests to its ecological flexibility to live within these habitats, which occurred in abundance across southern-England and the North Sea at the end of the last Ice Age, as well as its preference for peaty wetlands in temperate climes (Bhagwat & Willis, 2008; Van Geel, et al., 2024).

It is clear that the species survived the Ice-Age in a variety of separate locations, including a northern refugium (Bhagwat & Willis, 2008). Clade 'AI 1-2', which now occupies north-western Europe, has a high genetic diversity for which genetic drift could be explanation (Babik, et al., 2004; Knopp & Merilä, 2009). Therefore, all of these lines of evidence suggest *Rana arvalis* certainly represents a very early colonist to Britain and northern Europe at a time when woolly mammoth *Mammuthus primigenius*, rhinoceros *Coelodonta antiquitatis* and cave lion *Panthera spelaea* prowled across the steppes (Böhme, 1996).

While the fossil evidence ceases around the 9th century, a tantalising historical record from the 18th century extends the presence of the species further (Raye, pers. comm., 2025). John Morton, in *The Natural History of Northamptonshire* (1712) wrote about frogs:

"as to colour; some of a lively green, others a livid [bluish], *others of them yellow, and others in colour exactly like a toad, but in magnitude, in shape, and in the manner of the motion, they agreed, and were all of them frogs."*

Livid is an old-English term for a blue-grey colour and perfectly describes the mating hues of the male moor frog. This record is quite surprising, because elsewhere in Europe the species has a history of remaining largely unnoticed (Poboljšaj, et al., 2008). In the Netherlands, there are no known historical accounts of 'blue frogs' or the like, prior to the 19th century (Lenders, pers. comm., 2025).

The moor frog is classed as a "native species lost" in Natural England's *Lost life* (2010) report and as part of Red List Assessments of Britain's amphibians (Foster, et al., 2021). There have been limited reports of an unconfirmed, presumed extinct population of the species to Lakeview fishery and Leicester University Botanic Garden, Leicestershire (Heaton, 2018). The association of the species with these man-made habitats suggests this is an introduction, if not confusion with the common frog. The species is very rare in captivity.

4.3 Species History

The moor frog is an inconspicuous, unassuming frog, readily proven difficult to detect, due to its secretive habitat use, preference for asynanthropic habitats (expansive bogs), quiet mating call, resemblance to the common frog and extremely short reproductive period (Clicnat.fr, 2023). Although the two species cannot interbreed, moor frogs at their range edges are 'almost impossible' to visually segregate from common frogs (Snell & Evans, 2006). It was therefore named late in the description of Europe's fauna, being missed by the prolific rounds of Scandinavian taxonomic description by Linnaeus, only scientifically assigned by Swedish zoologist Sven Nilsson in 1842. At the time, Nilsson was unsure as to whether the species occurred outside Scandinavia, and there was debate throughout the 19th and 20th centuries as to whether the species was distinct enough to even be considered separate from the common frog (Clark, 1994). In Sweden, the species remained little studied throughout the 19th and 20th centuries, until the late 1970s, when mapping of the species' geographic range began (Elmburg, 2008).

The species was described as a Norwegian species in 1875, and a Dutch species in 1897 (Dolmen, 2008; van Delft & Creemers, 2008). *Rana arvalis* was missed by prominent French naturalists of the 1800s and only recorded in 1915 in places where it is now absent (Clicnat.fr, 2023). Between the 1920s and 1990s, the species was thought to have been lost to wetland drainage until it was rediscovered in some isolated fenland in north-east France in 1999 (Mergeay, et al., 2020; Vacher, et al., 2008). Since then, more westerly, coastal populations were discovered as recently as 2011-2014, while other unknown populations are likely to exist elsewhere in the region[6] (Mergeay, et al., 2020; Godin, et al., 2008; Vacher, 2019). It is no mystery why this species went unnoticed for so long, not least due to its aforementioned secretive nature, but also due to patterns of land ownership in the areas it occupies, and the preservation of large, inaccessible peaty wetlands for hunting (Mergeay, pers. comm., 2025; Blondel, pers. comm., 2025). Experience elsewhere reinforces the species secrecy. In Slovenia, historical records for the moor frog prior to the 20th century were rare or ambiguous, with the only conclusive records for its presence in the country coming from the 1960s, despite it being common and widespread (Poboljšaj, et al., 2008).

There are generally two accepted subspecies of moor frog; the nominate, ssp. *arvalis* and the central European *wolterstorfii*. On the grounds of biogeographical and morphological differences, this study has excluded the *wolterstorfii* subspecies as they represent an evolutionary significant unit (Dufresnes, 2019; Rafiński & Babik, 2000).

4.4 Habitat Choice

Figure 26: the captive moor frogs at Celtic Rewilding are always found hiding under objects in shallow areas of water, they only venture from these places to feed at night. The author is holding up a bark-flat, revealing a female moor frog underneath.

Unlike the other two species of frog mentioned in this report which have easily defined terrestrial and aquatic habitat preferences, this distinction is not as clear cut in the moor frog: the species is considered the most damp and water-dependent species within the brown frog group, breeding in the same places that it lives (Nečas, et al., 1997; Kauri, 1970; Glandt, 2008).

[6] Detection of environmental DNA is now being employed to further map its true distribution in France.

In captivity, it exhibits notably water-seeking behaviour, showing a clear preference for shallow areas of water with ample hiding opportunities (see Figure 26) (Whitehurst, pers. comm., 2025). This strong reliance on water restricts the species' terrestrial range to damp, water-rich landscapes, typically found in flat, lowland regions (Lyons, in prep.) where groundwater is high and seasonal drying of the soils is consequently limited (Speybroeck, et al., 2016; Elmburg, 2008; Šandera, et al., 2008; Puky & Schád, 2008; Tvrtković & Kletečki, 2008). Therefore, these conditions are the classic parameters for paludification[7] (see Figure 24) on top of which specialised habitats develop[8] (Montanarella, et al., 2006).

It is therefore no surprise that across northern and western Europe, moor frogs are primarily associated with peat soils (Figure 24), including sandy-peat mosaics, while being notably absent from calcareous or clay-rich topsoil (van Delft & Creemers, 2008). Their distribution is strongly correlated with lowland, acidic peatlands, especially raised bogs and heathland mires, reflecting a clear case of ecological niche specialisation. These acidic environments tend to exclude the common frog, whose larvae are less tolerant of low pH. Moor frogs, by contrast, have tadpoles adapted to acidic waters, allowing them to exploit a narrow niche between minimal competition from the common frog (<pH 6.5), and outright death from overly acidic conditions (<pH 3.8-4.5) (Rä Sänen, et al., 2003).

The common frog, by comparison, is a dominant ecological generalist with broad physiological tolerance (Vences, et al., 2013). It shows little specialisation in habitat selection and is capable of exploiting a wide variety of aquatic environments, from flooded meadows to artificial ditches, temporary puddles, and ornamental ponds (Vos, et al., 2007; Bartoń & Rafiński, 2006; Carrier & Beebee, 2003). This flexible approach enables it to thrive in both natural and quite heavily modified agrarian landscapes, although it has still faced historic declines from the intensification of agriculture (Shoard, 1980). In contrast, the moor frog is never encountered in agricultural areas as they can't be maintained in farmland ponds (Loman, 2004; Loman, 2008).

In a small number of cases, Moor frogs are also found in alkaline peat fens, such as those in northeastern France. Even in these alkaline sites, it is obvious that they populate these sites much less densely – these are not totally optimal habitats. At such a site in France, Benjamin Blondel (pers. comm., 2025), responsible for the reserve, remarked that the individual we observed was the first he had seen in several years (Section 4.5.2). Here, niche partitioning is less defined by pH and more by habitat structure and lack of fish presence. Moor frogs breed in expansive, shallow wetlands that provide suitable thermal gain and space for larval development. These systems differ from those favoured by the 'opportunistic' common frog which can exploit disturbed breeding habitat like vehicle ruts. Importantly, moor frogs are largely intolerant of fish, which prey heavily on their eggs and larvae. However, the oligotrophic nature of alkaline fens results in low fish biomass and diversity, reducing predation and enabling moor frog populations to persist (Lake, et al., 2020). The lack of nutrients probably also dampens the vigorous nature of tadpoles of the common frog, which have special

[7] Peat formation.
[8] It goes without saying that moor frogs are totally intolerant of fires.

Figure 27: upper: a beaver dam in Torfowisko Wielkie Błoto, Poland, which has pushed water laterally over land for 200 metres to form a wetland used by moor frogs. Middle: the resultant spring-time wetland formed from the lateral flow of the water from the beavers' dam. These shallow and extensive peaty-quagmires provide exceptional opportunities for moor frogs. Indeed, many were sighted here, with the males calling and beginning to turn blue. Lower: a female moor frog making her way to the waters' edge.

physiological adaptations to profit from nutrient and therefore food rich waters (Ruthsatz, et al., 2019).

In Belgium, one population (around Zonhoven) survives in a modified landscape within a series of failed fishponds originally established for aquaculture (now fish-free). While this might suggest some degree of habitat flexibility, historical landscape analysis reveals that these sites were once heathland and bog, with small fragments still present today (Mergeay, et al., 2018). These remnants must be just enough to maintain the moor frog's specialism, but the populations are small and genetically vulnerable (Mergeay & Van Howe, 2013). Their presence is likely down to chance, persisting more due to historical contingency than current habitat suitability. These frogs are effectively stranded in a suboptimal niche, and their continued presence reflects legacy effects, rather than a displaying more varied habitat choice (Van Doorn, pers. comm., 2025).

Moor frogs are one of the most commonly recorded amphibians found exploiting beaver-created wetlands, with an exceptional ability to rapidly colonise new ponds constructed by beavers (Trakimas, 2008; Vehkaoja & Nummi, 2015). As mentioned, moor frogs are intolerant of fish and so the increased habitat heterogeneity created by beavers allows moor frog larvae to avoid predation more effectively (Campbell-Palmer & Rosell, 2022). In ‘wilderness areas’, moor frogs and beavers are largely sympatric, with this ecosystem engineer facilitating optimal habitats for the species at all its key life stages (see Figure 27). Beavers transform linear environments – such as ditches – into structurally heterogeneous habitats and increase the complexity of ecotones (Jepson & Blythe, 2020). These processes have been shown greatly benefit the moor frog which has a preference for bog-edge habitat (Remm, et al., 2018). In Finland, moor frogs are rarely ever recorded from waterbodies not modified by the action of beavers (Vehkaoja & Nummi, 2015). In addition, low-density grazing of cattle is beneficial to the species, creating microtopography in the form of light poaching of the ground (van Delft & Creemers, 2008)

During spring, moor frogs spawn in expansive shallow water, often the result of winter flooding, usually between March and April. The eggs take a few weeks to develop and hatch; with the resultant tadpoles taking 3-5 months to grow into froglets. They hibernate from October until February/march, likely within bushy thickets (Blondel, pers. comm., 2025).

The moor frog is regarded as a local species, which often occurs in small, isolated pockets of habitat (van Delft & Creemers, 2008). This increases the vulnerability faced by the species to habitat change, which fragments populations and reduces gene flow as has been observed in genetic studies (Vos, et al., 2001). It is very sensitive to the artificial lowering of the water table (Corbett, 1989). The conversion of natural flood plains to agriculture, drainage and canalisation of rivers, removing the necessary seasonal lateral flow of water for breeding, has caused regional extinctions in areas such as the Netherlands and France (Vacher, et al., 2008). As a result, in western Europe it now only occurs in nature reserves (van Delft & Creemers, 2008).

Sometimes called a ‘continental species’ moor frogs occur in numerous maritime locations, such as southwestern Norway, coastal Denmark and Germany, northern France and Texel and Schouwen-Duiveland in the Netherlands (Dolmen, 2008). Moor frogs also occur past the Arctic

Circle, where they breed as late as May or June and may be active for only a few months of the year (AmphibiaWeb, 2025b; Elmburg, 2008). Moor frogs appear well adapted to the climate of central and eastern England and were unaffected by the LIA, see Section 7. The species is likely to be vulnerable to warming and drying effects of climate change, meaning translocation to cooler areas could be beneficial (Mergeay, pers. comm., 2025).

4.5 Field Observations

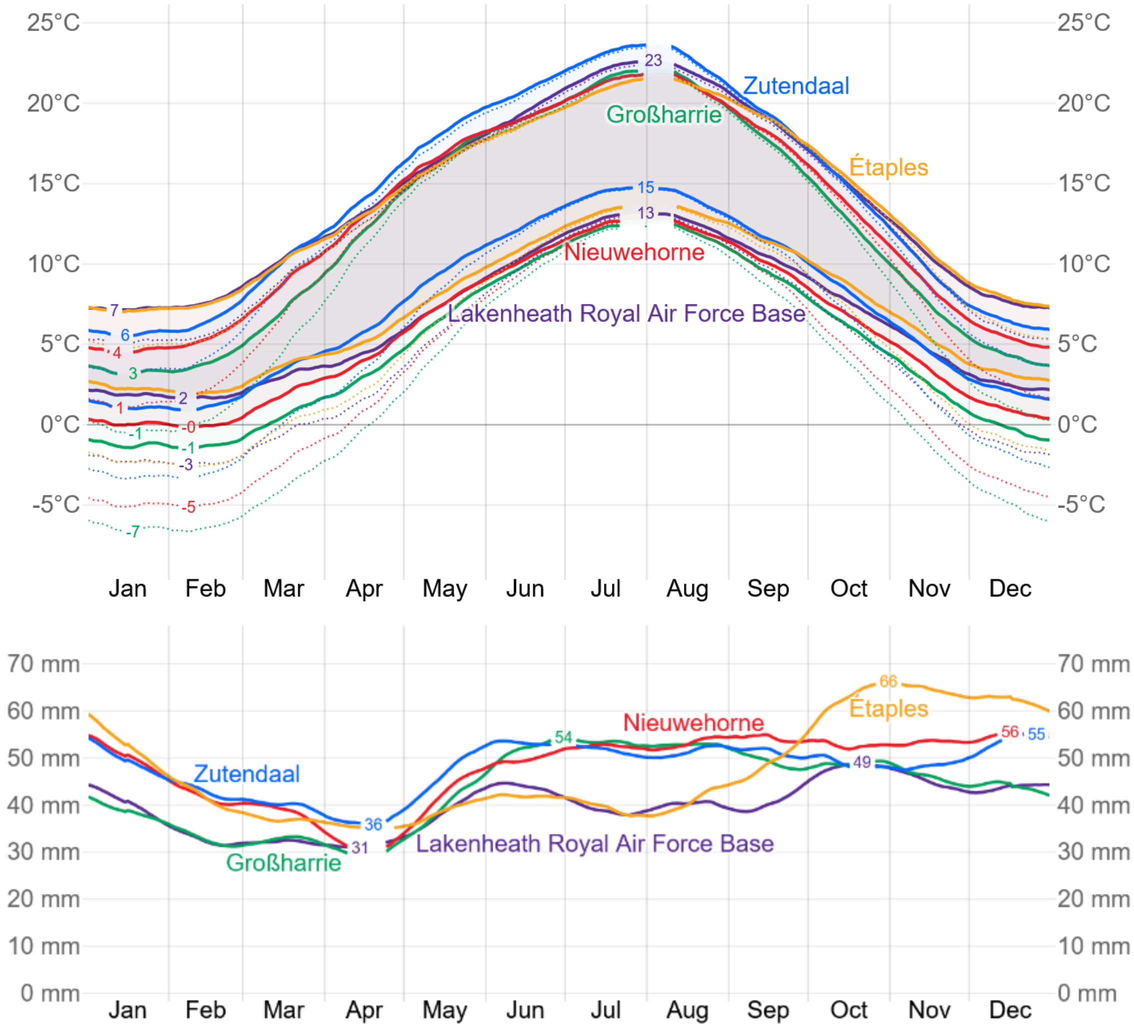


Figure 28: upper: average high and low temperature of some of the visited sites (closest weather stations), compared with climate data from RAF Lakenheath, East Anglia. Lower: average monthly rainfall of each site and RAF Lakenheath.

After Diebel (2025b), © WeatherSpark.com .

4.5.1 Peat Bog Sites

(07/07/2025) At 521 hectares, Dosenmoor, north-east of Neumünster in Schleswig-Holstein, is the largest example of a raised bog in the region, with a large population of moor frog to boot. The vegetation comprises primarily of heather, with notable amounts of low, scrubby birch *Betula sp*. scrub, *sphagnum sp*., cranberry *Vaccinium oxycoccos* and cottongrass *Eriophorum sp.* Smaller patches of purple moor grass were present, but this species was clearly not dominant. Large areas of surface water, dotted with islands of purple moor grass and cotton grass, often surrounded with a thick band of exclusively sphagnum moss were common throughout the moor. On a 4 km walk of the moor looking for moor frogs from the path, 6 amphibians were seen, all of which were *R. arvalis*.

While the majority of the peat has been at some stage drained and cut, a core block of ~65 ha has been spared. It is from this area that all of the moor frogs were seen. This area probably served as the refugia during the worst of the reclamation and peat winning of the surrounding land. The damaged area of the reserve has been undergoing restoration since the 1970s and it is clear that the moor frogs will benefit. One of the restoration techniques observed is the repeated damming of drainage ditches across the reserve. It is very likely that moor frogs will profit from the increased lateral waterflow as a result of this activity (LLUR, 2021).

Figure 29: a likely breeding pool on Dosenmoor for the moor frog.

Figure 30: Dosenmoor. Upper: wet, boggy, sphagnum dominated bog areas. Lower: slightly drier, heather and purple moor grass dominated area.

Figure 31: the complex yet open vegetational structure and abundance of surface water result in the moor frog being so common here.

Figure 32: three examples of juvenile (second year) moor frogs, each representing a different morph. From top to bottom: maculata, typica, striata.

(08/07/2025) Pietzmoor, near Schneverdingen, Germany, is a 260-ha expanse of lowland moorland and bog within the complex of heathland, woodland, and geest habitats known as Lüneburger Heide, located between Hamburg and Hanover in Lower Saxony. Unlike Dosenmoor, this site is dominated by purple moor grass and while it has a greater coverage of open water, it also has larger areas of drier heath and grassland when compared. This site is in effect more swampy and is crisscrossed with boardwalks. In spring, these board walks provide brilliant views of blue moor frogs. The reserve is very popular with wildlife watchers and photographers wanting to observe this phenomenon.

Figure 33: Pietzmoor. Vast, complex and swamp-like tracts of peat bog.

Figure 34: Upper: the promotion of Pietzmoor as a good place to witness the moor frogs breeding blues. Lower: one of the spots where masses of blue males are often seen in spring.

(10/07/202) Delleboersterheide and the bordering Diakonieveen, are nature reserves some 272 ha in size, located near Oldeberkoop in Friesland. Once nourished by the plain of the now-canalised Tjonger River, the reserves are located in what remains of a *beekdallandschap*, or stream valley landscape. This is an area where streams flow through sands left behind by glaciers. Over time, this landscape has developed a mix of wet and dry heathlands, pools, fens, peat grasslands, and river dunes, in addition to glacial features, such as meres and pingos. This type of landscape is regionally common but globally rare and may explain why moor frogs are relatively abundant in the Netherlands, as these landscapes are largely oligotrophic and conducive to peat formation, due to the underlying sand. Additional areas of land are being purchased in order to increase the size of the reserve. There were consequently areas of younger, secondary habitat, of seemingly mesotrophic or eutrophic soils with plant species such as willow *Salix spp*. and bramble *Rubus spp*. being prevalent. It is unclear if the moor frogs are using these areas (It Fryske Gea, 2025).

Figure 35: expansive wet heathland at Delleboersterheide.

Figure 36: a sand ridge sloping down towards an acidic wetland at Diakonieveen. A newly morphed moor frog was seen here but evaded the camera!

(11/07/2025) A similar, albeit much larger landscape is the Nationaal Park Drents-Friese Wold, an over 6,000 ha mix of heaths, shifting sands, stream valley grasslands and large areas of forest. Like Delleboersterheide, much of it is comprised of a stream valley landscape which is quite well preserved amidst the much-drained landscape of the Netherlands. That being said, restoration is in progress to 'rewiggle' straightened water courses, improving lateral flow and increasing the water table. Two moor frogs were seen here during the day, amongst the purple moor grass and sphagnum on the notably damper parts of the Park along with many large marsh grasshoppers (Nationaal Park Drents-Friese Wold, 2025).

Figure 37: two views of Ganzenpoel at Nationaal Park Drents-Friese Wold. Upper: where two moor frogs were sighted in the bottom left of the photo.

(01/08/2025) Neerharerheide is a compartment of 42 ha which is part of the National Park Hoge Kempen, a large plateau formed by the retreat of the glaciers at the end of the last Ice Age, leaving a land expanse of glacial till, mainly comprised of sand. This sand provided the grounds for expanses of heathland and bog to form. I was shown around the site by Loïc van Doorn, a biologist and manager of amphibian captive breeding at the Research Institute for Nature and Forest (INBO). We went to see works completed in 2021 to slow the flow of water from the heathland and improve the available aquatic habitat for species like moor frog.

Figure 38: upper: the results of the works to reduce drainage and improve water levels. Moor frogs have now bred within this site. Lower: the wet-heath portion of Neerharerheide, with the dryer sandy ridge in the background.

(06/06/2025) Kalmthoutse Heide is the one of the oldest nature reserves in Flanders, being protected since the end of World War II. Straddling the border between Belgium and the Netherlands, it is a huge 1,500ha+ area of bogs, mires, inland dunes and forest, adjoining a further 1,000ha+ protected area on the Dutch side. One of the largest and most genetically diverse populations of moor frogs is found here, due to the conservation of landscape-scale habitats (Mergeay & Van Howe, 2013).

Figure 39: upper: view over Kalmthoutse Heide. Lower: the high water table provides expanses of wet bog, and the vegetation structure provides structure ideal for moor frogs.

4.5.2 Alkaline Peat Bog (Fen) Sites

(29/07/2025) Marais de Romaine near Ponthoile, France is referred to by the French as an alkaline peat bog but is best described to British readers as a lowland fen meadow, containing the *Juncus subnodulosus–Cirsium palustre* community. The Fen constitutes a 650-ha wetland area that spiders out around south of Rue and is a rare habitat type in France. This site is undrained, due to its use as a snipe shoot, inadvertently protecting the site from otherwise inevitable 'improvement'. The moor frog was only discovered on the site in 2014, emphasising their cryptic nature, with all evidence pointing to this population being native (Blondel, 2014). All populations of the moor frog in France are wholly confined to peat bogs (Godin, et al., 2008). Interestingly, this population is on an alkaline site, unlike the majority of other cases which are acidic. The geology and climate of this part of France is not at all conducive to the forming of acidic bogs, with the species living on the total edge of its range in western Europe (Blondel, pers. comm., 2025). It's range terminates here, with wetland drainage causing the extirpation of further populations (Mergeay, et al., 2020), although only northern France is wet enough to support the species, which doesn't cope with excessive periods of dryness (Holman, 1998; Poboljšaj, et al., 2008). One juvenile moor frog was spotted, but only briefly, not allowing for a photograph. At the same time over a dozen common frogs were sighted, showing that the two species can co-exist in expansive oligotrophic[9] peat-wetlands (Section 4.4).

Figure 40: a newly created pond for spawning moor frogs. The juvenile was seen close by.

[9] Nutrient poor.

Figure 41: upper; during the winter the whole area floods, forming an irregular and shallow wetland ideal for spawning moor frogs. By summer, the water recedes into depressions, with the tadpoles following. Lower: dense sedge beds provide the humid microclimate required for moor frogs.

4.6 Extinction

In our fossil-fuel powered world, it can be difficult to imagine a time before even rudimentary hydrocarbon fuels, such as coal, were widely exploited for domestic and industrial energy. During the MA/EMP, coal was only gathered on a small scale from exposed coastal seams, rather than extracted from the extensive mines that characterised the later Industrial Revolution (Rotherham, 2009). Instead, many communities turned to peat, a fuel source that was abundant, easy to harvest, and, once dried, capable of producing significant heat. Peat represents the accumulated remains of thousands of years of partially decomposed plant material, and for many rural populations (especially those in treeless or deforested landscapes) it was the sole year-round source of fuel (Rotherham, 2020). Evidence shows that peat has been cut in excess of 2,000 years into the past and continues (on a somewhat controlled scale) into modern times (Rotherham, 2009).

While peatlands are today recognised as very rare and highly specialised habitats, especially at the lower elevations associated with the moor frog, their historical extent was immense (Lyons, in prep.). This former abundance is echoed in artwork, cultural memory, and place names: terms such as "moss", "turf", "mor/more/moor", or "fenn" are scattered widely across the country, in areas where these namesake habitats have not survived (Rotherham, 2009; Cole, 2015). Examples included places such as the Thames Valley, the Trent Basin, the Mersey catchment, and vast stretches of eastern England including the Fens (Rotherham, 2020; Rotherham, 2013).

Modern pollen analyses have revealed the presence of acidophilic and bog-like plant communities in areas where no trace of peat has been detected, including regions of – commonly alkaline – silt fen (Waller, 1994). This demonstrates that ombrotrophic (rain-fed) habitats readily develop independently of the underlying substrate, leading to the inescapable conclusion that present soil type alone cannot be relied upon to determine the former extent of peatlands (Waller, 1994; Godwin, 1978). In reality, Britain's wetlands would have been a completely heterogeneous mosaic of ever changing habitats, even if their homogenous contemporary state doesn't prompt for such immediate conclusions (Pryor, 2005). These habitats were shaped by abiotic processes, chiefly via fluctuating water sources: riverine (minerotrophic) wetlands were typically base-rich and neutral to alkaline, whereas ombrotrophic systems were base-poor and acidic (Rackham, 1986; Lake, et al., 2020), but also biological processes, like the water engineering efforts of beavers and large herbivores like elk *Alces alces* (Brazier, et al., 2020). Consequently, when historical evidence, pollen analyses, and mapping of surviving peat deposits are considered together, it is likely that in pre-Roman Britain, peatlands covered half of the country's land area (Spencer, pers. comm., 2025; Rotherham, pers. comm., 2025).

Today, the picture is starkly different. Peatlands occupy only around 8.5% of England's land area, the vast majority of which lies in the uplands (Kratz, et al., 2025). Lowland acidic peat has been most severely affected: raised bogs have suffered a historical decline of more than 99%, with only about 500 hectares remaining nationwide (BRIG, 2011; Rotherham, 2020). This destruction has been described as "one of the greatest environmental disasters in Britain" (Rotherham, 2009; Rotherham, 2013).

Figure 42: the historical extent of peat digging at Whixhall Moss on the Shrophsire-Welsh border, which indefinenitely began around 1500, with commercial cutting starting from 1650 (Marches Mosses BogLIFE, 2025). Taken from Godwin (1978).

Many previous studies underestimated the true extent of peatland, particularly in said lowland areas (Rotherham, 2020). This has been due to the monumental scale of peat extraction and the fact that, once cut or drained, peat rapidly decomposes and disperses through wind and water, leaving little trace of its former presence (Pryor, 2005). A striking example is the 300 km² area of the Norfolk Broads: it was not until the 1960s that soil coring, combined with historical research, revealed that the lakes and reedbeds were in fact abandoned 14th-century peat diggings, where some 25 million cubic metres of peat was cut and consumed, largely without a trace[10] (Moss, 2001; Rackham, 1986). Similarly, the wholesale destruction of raised bogs in

[10] Within a 45 minute drive of where I write this, the largest lowland peat bog is only around 12 ha in size and it was cut in the 17-18th centuries. This is despite numerous place names and the general geography eliciting widespread presence of this habitat on my home patch in the past.

the Fens during the 17th century erased evidence of the acidophilic flora they once supported. Already by the Victorian period, naturalists were left questioning whether acid-loving plants had ever existed in the region at all (Godwin, 1978).

It is therefore unsurprising that the alteration of vast areas of wetlands has resulted in species of once-common acidophilic plants like cranberry, cottongrass, and the round-leaved sundew *Drosera rotundifolia* disappearing from entire lowland regions like the Fens (Godwin, 1978). Reflecting on this loss of raised bogs and acidic habitats due to human activity, particularly the removal of rare botanical communities[11] and the structural complexity they provide, the prominent 20th-century ecologist Sir Harry Godwin (1978) lamented that it "has quite certainly involved the Fenland extinction of many animals… especially [those] that are specialised to them". His observation is especially relevant to invertebrates. For instance, the fen raft spider became so rare that it was only recorded late on, in 1956, and at just a handful of sites (Lake, et al., 2020). Similarly, the bog bush-cricket *Metrioptera brachyptera* persists in a scattered distribution, while the large marsh grasshopper has been extirpated from entire regions, both outcomes linked to the destruction of wet, peaty habitats (Benton, 2012). As one of the very few British vertebrates specialised to peatlands, the moor frog can be easily envisaged as another of these casualties. Equally telling is the loss of the palmate newt, also associated with peaty wetlands, from large areas where it once occurred prior to modification (Inns, 2009; Gleed-Owen, 2000).

For what peatlands survived the initial onslaught of harvesting, such as those within the Bedford Level of the Fens, the turn of the 1600s would herald the arrival of the most ambitious drainage and land-reclamation efforts the country had ever witnessed (Ash, 2017). Wetlands are the most modified habitat in the UK (Gerlach, 2014), driven by substantial capital investment and supported by imported expertise and workforces such as those of the Dutch engineer Cornelius Vermuyden. By 1750 virtually all of Britain's even semi-natural wetlands had been destroyed through a complex of sea-walls, embankments, drainage canals, sluices, ditches, and wind-powered pumps (Rotherham, 2013; Ash, 2017; Pryor, 2019). Studies have shown that drainage features are completely unsuitable habitats for moor frogs (Remm, et al., 2018; Vacher, et al., 2008). It is estimated that 600,000 kilometres of ditches have been dug across Britain, a length equivalent to circumnavigating the Earth 15 times (Lake, et al., 2020).

Specifically, The Environment Agency (2022) has calculated that 99.7% of lowland fens have been destroyed, while the few fragments of 'relictual' wetlands that do remain, such as the ten or so within the Fens, are far from untouched habitats. Wicken Fen, for example, was both stripped of its peat and largely drained before its designation as a nature reserve in 1899, whereby difficulties around land ownership prevented it from remaining dry for long (Rowell, 1986). While the fens of Woodwalton, Holme, Chippenham, and Fulbourn may have not been themselves internally reclaimed, so pervasive has the surrounding drainage been, that they have become so water-starved, causing their peats to oxidise and shrink, resulting in the

[11] Many fenland plants have really struggled in Britain but are common elsewhere in Europe such as the fen orchid *Liparis loeselii* and Blandow's bogmoss *Helodium blandowii*.

encroachment of trees, displacing wetland and exacerbating this ecological decline further (Rackham, 1986). Virtually all of Britain's remaining fen is threatened by a lack of connection to river systems due to drainage and canalisation (Lake, et al., 2020).

For all of the reasons outlined in Section 4.3, there is a possibility that moor frogs could have survived beyond the end of the EMP, perhaps persisting into the 19th or 20th centuries as suggested by Snell & Evans (2006). In such a scenario, the species would likely have been confined to small, fragmented patches of habitat. Detailed genetic studies in Flanders indicate that the long-term maintenance of a viable moor frog population over a 100-year period requires either ~150 ha of continuous suitable habitat or a network of smaller sites that are well connected, allowing for regular migration between them (Mergeay, et al., 2020; Mergeay & Van Howe, 2013). It is difficult to envisage the species surviving beyond the extensive

Figure 43: comparison of Norfolk and the Fens, UK (Top) with Friesland, Drenthe and Groningen, with habitats broadly suitable for moor frog, circled. At 165km elevation.

Victorian modifications of wetlands, such as the introduction of steam-driven pumps (Ash, 2017; McKie, 2010).

The loss of the moor frog does prompt the question of how the species has managed to cling-on in other, heavily modified regions, such as Flanders and the Netherlands. The short answer is that it has not. As shown in Figure 25, the moor frog has declined across a large area of western Europe, encompassing northern France, Belgium, and Holland, as well as throughout much of central and southern Germany due to peat harvesting and wetland loss (Mergeay, et al., 2020; Vacher, et al., 2008). In addition, it is the Czech Republic's most endangered frog, and threatened in Slovenia, in both cases due to drainage of wetlands (Nečas, et al., 1997; Šandera, et al., 2008). Roček & Šandera (2008) established that the species is absent throughout western Europe because of land use changes which took place centuries ago – therefore the species' extirpation from Britain is consistent with these regional patterns of decline.

From my travels to landscapes still harbouring moor frogs, I have noted some key differences between Britain and the rest of Europe in terms of wetland manipulation and use, which help explain why the species has survived in some areas but been lost in others. Firstly, the UK's insular geography results in relatively small catchment sizes compared to those on the continent (see Section 2.2). For example, the Rhine basin, which debouches via the Netherlands, is roughly 12 times larger than the Thames catchment. This smaller size makes it much easier to manipulate rivers across their entire length and drain the surrounding land. A major contrast lies in drainage practices: in the Netherlands and Flanders, ditches have traditionally been kept wet year-round, whereas in Britain, dry ditches became the norm, maintained through intensive water pumping (Pryor, 2019; van de Ven, 1993). An island also provides an added layer of social stability, allowing for larger and bolder capital drainage works to be implemented without too much worry of invasion, which would thwart profits, such as the huge private-investor led Fenland drainage (Ash, 2017). Additionally, in the Netherlands and Flanders, it seems that a large proportion of land was reserved for sheep grazing, presumedly because of a lack upland areas, whereas in Britain, many wetlands prior to the 16th century were drained in order to convert them from rough grazing land to more profitable to arable production.

Table 3: the threats faced by the moor frog from the Roman era onwards.

Activity	Time Period	Environmental Impact on Moor Frog
Extensive Peat cutting	Pre-Roman era onwards	• Direct removal of critical peaty habitats • Lowered water table reducing wetland extent • Stripping of microhabitat structure and complexity • Over-acidification (egg mortality of over 95% at pH <5)
River embankment	Roman era – onwards	• Removal of lateral water flow, preventing seasonal flooding which maintains extensive wetlands • Lowers the water table at a whole catchment level, vastly reducing wetland coverage • Cuts off the source of water to fens • Removes necessary dynamism in riparian ecosystems
Extinction of the beaver in England	c. 1100s	• Removal of a key habitat 'facilitator' and wetland 'creator/manager' • Desiccation and fragmentation of habitats • Reduction and cover of suitable breeding waters and the damp microclimate needed for terrestrial phase frogs • Damp and open breeding sites lost to succession
Large-scale drainage	1630s	• Total elimination of expansive wetlands used as breeding sites • Loss of humid microclimate essential as refuge and foraging habitat • Peat oxidation, decomposition and subsequent habitat loss
Burning and 'paring' of dried wetlands	1630s	• Stripped the surface of vegetation and peat • Altered moisture retention and water flow, reducing habitat suitability • Likely direct frog death
Liming, 'claying', and 'marling'[12]	Late 1600s	• Destroyed the moor frogs' competitive advantage/specialist niche • Neutralised acidic soils critical for moor frog breeding • Introduced competition with common frog, to which moor frog succumbs
Conversion to arable ploughing and agriculture	Late 1600s	• Removes even marginally useful habitat (such as short grassland) for moor frogs • Lost of even tiny areas of remaining suitable habitats • Likely direct frog death

[12] Marling of land in order to reduce the acidity became a common practice from the 17th century onwards.

4.7 Reintroduction

The loss of the moor frog from Britain acts as a cautionary tale to those conserving the species on the continent and highlights the importance of protecting and restoring temperate wetland ecosystems (Šandera, et al., 2008). The moor frog is particularly special due to its need for peatlands, a strategic biological carbon store which sequesters more CO_2 than any other terrestrial ecosystem (International Peatland Society, 2025). Remarkably, the moor frog appears to be the only British vertebrate which totally depends on peatlands as its habitat. This connection could render the species a mascot in the drive to restore Britain's peatlands. Indeed, the species' brilliantly blue breeding colours offer an enchanting natural spectacle, when entire spring lakesides glow aquamarine. They are also a brilliant food source in peaty, otherwise moderately unproductive habitats, to a suite of predators such as pine marten *Martes martes*, pike *Esox lucius*, hooded crow *Corvus cornix*, and common crane (Elmburg, 2008).

4.7.1 Notes on Method [13]

A reintroduction of the moor frog can be modelled after the brilliant Projekt Moorfrosch which is reinforcing the local population in Baden-Württemberg, Germany, via collecting spawn, head-starting in captivity and releasing the froglets back into the wild (Projekt Moorfrosch, 2025).

While the moor frog's loss has been driven by a dramatic decline in its specialist habitat, there are numerous areas which seem to satisfy criteria found in Flemish studies, mainly that suitable site should exceed around 150 ha in size (Mergeay, et al., 2020). Possible sites with big enough areas of habitat and within the preliminary SDM data and therefore suitable for a reintroduction include but are not limited to:

- Roydon Common, Dersingham Bog, and alkaline fens/broads in Norfolk
- Thorne and Hatfield Moors in South Yorkshire
- Strensall Common, North Yorkshire
- Manchester Mosses in Merseyside and southern Lancashire
- Solway Mosses, Cumbria

A desk-based study should be performed to fully assess the suitability of a range of candidate release locations. Further on-site surveys, carefully comparing these candidate locations with studied areas in Europe should be undertaken.

As an early colonist, British moor frogs would have represented the north-western European lineage AI, likely representing haplotypes A1 and A2. The modern distribution of these haplotypes corresponds to France, Belgium, the Netherlands, Denmark, West Germany and southern Sweden and Norway (Babik, et al., 2004; Knopp & Merilä, 2009). Founder stock

[13] This section is not exhaustive. Before any reintroduction should take place, it is recommended that a follow up report be written to formally set out an agreed-upon methodology that considers all aspects including but not limited to legal, welfare, veterinary and resourcing implications.

Figure 44: the Projekt Moorfrosch raising facility. The polytunnel is where the tadpoles are grown on. Reproduced from Projekt Moorfrosch (2025).

should be obtained from these regions. Ideally, collections should target either the egg or subadult life stages, with the final choice guided by a disease risk assessment (as eggs are likely the most biosecure option) and by evaluating the most practical transport method (Cracknell, pers. comm., 2025). A founding group of approximately 40 unrelated individuals should be established, preferably maintaining a 1:1 sex ratio. If eggs are selected, 20-30 separate spawn clumps should be collected, noting that each clump represents the offspring of two different adults.

The subsequent breeding groups of moor frogs should be raised under optimal semi-outdoor conditions to a point whereby they can breed, in an appropriate captive facility. These enclosures should be very wet and peaty, modelled on bog-gardens (Fremming, pers. comm., 2025). Moor frogs are fairly slow growing, even in captivity, reproducing from their third year. The animals should undergo a hibernation period when they are adults, either naturally within built hibernaculum in outdoor vivaria, or artificially using a temperature-controlled cooling chamber.

In early spring, as temperatures begin to rise, moor frogs should start exhibiting breeding behaviour. Male frogs may turn blue, while females will move towards water bodies. The water provided for them should be shallow, unlike the agile frog. To maintain genetic diversity, care should be taken to prevent one or a few males from dominating the breeding pool. Where possible, individual pairs may be placed in temporary enclosures to spawn separately. Small rafts of floating hornwort should be provided for egg attachment.

Once spawning has occurred, the egg masses (along with some vegetation they have been attached to) should be collected and transferred to small, clearly labelled plastic tubs to keep track of each progeny line. The spawn should be left to hatch, and the tadpoles allowed to develop until they are mobile and capable of free swimming. At this stage, they can be gently collected with a pipette and counted into plasterer's baths – at a density of 1 to 1.5 tadpoles per litre.

These containers can be kept inside a well-ventilated polytunnel or similar structure to encourage faster development. This could be part of a recirculating aquaculture system (see Figure 22). Throughout spring and summer, the tadpoles should be fed an appropriate diet and

Figure 45: an outdoor enclosure at Alfons Fremming's amphibian and reptile breeding facility. This enclosure could hold 40 adult moor frogs. Lower: a pair of moor frogs in amplexus within a spawning tank. The male is beginning to turn blue.

their water changed regularly as they grow and begin to develop hind legs. When approximately 10% of the tadpoles have developed all four legs, they can be carefully released into suitable ponds at the reintroduction site. Each site should aim to release a minimum of 1-3,000 tadpoles per year for three consecutive years. Following this period, thorough surveys of the ponds should be carried out to look for signs of breeding and assess the success of the release. If little or no breeding activity is detected, an additional release may be conducted for one more year. Surveys should then be repeated in the spring immediately following the release and again the next year. If no evidence of reproduction is found after this period, the site should be considered unsuccessful and an exit strategy implemented.

Figure 46: upper: spawn removed from a spawning tank and clearly labelled. The tadpoles will stay in here until they are capable swimmers. Lower: a cohort of juvenile moor frogs at a size (c. 20mm snout-vent) that would be appropriate for release.

5 European Tree frog, *Hyla arborea*

5.1 Introduction

Figure 47: an adult male European tree frog, perched on a branch.

<table>
<tr><td>General Appearance</td><td colspan="3">Fairly uniform between individuals, variation due to genetics, temperature or mood; brilliant green base colour, with a line running from the nostril to the iliac region; this line almost always flicks slightly upwards in front of the hind limbs; white undersides; small overall adult size; males possesses a large single subgular vocal sac</td></tr>
<tr><td>Size (S-V length)</td><td>3-5cm</td><td rowspan="2">Terrestrial Habitat (in NW Europe)</td><td rowspan="2">Sun-rich, thorny scrub; preference for deep thickets of bramble</td></tr>
<tr><td>Breeding time</td><td>April-June</td></tr>
<tr><td>Call</td><td>Loud, nocturnal rasping 'quack, quack, quack'</td><td rowspan="2">Breeding/larval habitat</td><td rowspan="2">Shallow, warm, fish-free ponds with amble scrub surrounding</td></tr>
<tr><td>Larval period</td><td>May-September</td></tr>
<tr><td rowspan="2">Egg mass</td><td rowspan="2">Several; up to walnut sized; below surface; wrapped around vegetation</td><td>Preferred pH</td><td>6-8 (?)</td></tr>
<tr><td rowspan="2">Conservation Status</td><td rowspan="2">Largely EN in NW Europe</td></tr>
<tr><td>Life span</td><td>3 years</td></tr>
<tr><td>Differentiation from other frogs</td><td colspan="3">Unmistakable unless for another European Hylid, in that case the only way to discern species is to consult range maps</td></tr>
</table>

With a name containing the word *tree*, it is natural for one to assume that the European tree frog (herein referred to as just tree frog) is a woodland animal. Whilst the species may utilise wooded habitats in southern and central Europe, in the northern reaches of its range, the tree frog is a species of open, sun-drenched habitat, including biotopes such as dunes. It is most commonly associated with bramble, the spines of which presumedly provide protection from predators, with thickets within maybe 100m of water (Arnold & Burton, 1978).

Tree frogs are unlike the other frogs covered in that they actively seek out warmth and tolerate surprising levels of dryness. In fact, their basking provides a physiological advantage to northern climes: they are able to digest food much quicker (Meek, 2011; Snell, 1985b). This enables them to far exceed the growth rate in species like the agile or moor frog. When exceptional summer conditions prevail, tree frogs sometimes attain sexual maturity by the subsequent spring (>1 year) (Marijnissen, pers. comm., 2025).

Male tree frogs are one of the loudest amphibians in Europe, with their call traveling up to 1km away (Speybroeck, et al., 2016). A brilliantly green coloured frog and easily visible in the correct habitat and conditions, the tree frog carries a broad appeal not often encountered with other amphibian species (Dufresnes, 2019; Marijnissen, 2013). Projects to conserve or reintroduce the species have been met with significant interest and appeal.

5.2 Status in Britain

Table 4: historical references to the European tree frog as a native component of British fauna. After Raye (2017).

Text	Author	Date	Evidence of Tree Frog
De differentalis animalium libri decem	Edward Wotton	1552	• '*Rana parva*'
A Treatsie…	Timothie Bright	1580	• 'greene frogges'
Pseudodoxia Epidemica	Thomas Browne	1648	• '*Ranunculus viridis'* • '*Rana arboreus*'
Panzooryktologia	Robert Lovell	1660	• '*Ranunculus viridis*' • 'Frog of the land' • 'green frog'
Pinax rerum naturalium Britannica	Christopher Merrett	1667	• '*Ranunculus viridis*' • 'Dropetes'

A limited literature search for tree frogs in pre-industrial Britain was first carried out by Charles Snell in 2006 and later augmented by Lee Raye. Although natural-history reporting in the early modern period was generally scanty (see Sections 2.3 and 2.3.1), Raye demonstrated that a number of prominent early modern writers listed the tree frog as part of Britain's fauna (see Table 4). For example, Dr Christopher Merrett recorded "*Ranunculus viridis*, the Green Tree Frog" in a work devoted to British species. While several naturalists of this time did not mention the tree frog, only a single source, *Rosa Anglica* (1502), has been interpreted as indicating absence. By way of comparison, numerous authors and distinguished naturalists of the MA/EMP likewise denied the presence of the pool frog in Britain, despite later confirmation of its native status (Snell, 1994). On balance, the weight of the evidence from early modern authors supports treating the tree frog as a resident species in the MA/EMP (Raye, 2023).

Records suggesting the tree frog's absence from pre-industrial Britain can be best explained by the perception of tree frogs as devilish and, the species' ecology and population dynamics (Lenders, 2010). Both the European tree frog and the pool frog exhibit locally abundant, highly variable populations. Each has narrow ecological requirements in northern Europe and experiences cyclical 'boom-and-bust' dynamics (Snell, 2006; Buckley & Foster, 2005; Arens, et al., 2006). On the continent, tree frogs are both vagile and locally restricted, their distribution determined by the availability of specific habitat (Arens, et al., 2006).

Climate-based species distribution models (SDMs) indicate that *Hyla arborea* would likely have occupied a patchy, scattered distribution across south-eastern England during the MA/EMP, reflecting its preference for comparatively warm and dry summers (Dufresnes, et al., 2020; Lyons, in prep.). Perhaps it is pertinent that two of the most important records for the species, Sir Thomas Browne's *Pseudodoxia Epidemica* and Timothie Bright's *A Treatsie…*, were written when the authors lived in East Anglia[14], near to the Brecks and Fens, one of the warmest and most continental areas of Britain (Snell, 2006). Browne (1646), a distinguished polymath of the 17th century, stated, seemingly about British frogs:

> *"I mean the little frog of an excellent Parrat green, that usually sits on Trees and Bushes, and is therefore called Ranunculus viridis, or arboreus"*

At that time, "green frogs" were the accepted vernacular for tree frogs (Raye, 2017; 2023). Similarly, Bright (1580), an imminent physician who championed the use of native, home-grown cures as opposed to imported, exotic ones, cited a medicinal recipe:

> *"And first to begin with Cankers, are cured (if with any medicine) … by the juice of…* [various plants and minerals and] … *greene frogges"*

Taken together, these sources suggest that the tree frog was historically present within Britain's countryside (Raye, pers. comm., 2025). However, Raye (2017; 2023) is unsure as to whether this population constitutes a native or introduced one. To date however, no direct or circumstantial evidence has been detected for the intentional introduction of tree frogs for any particular purpose during the MA/EMP (Raye, pers. comm., 2025; Beebee et al., 2005).

The discovery of Holocene *Hyla arborea* subfossils predating the MA/EMP would support native status but none have yet been recovered (Gleed-Owen, pers. comm., 2025). The apparent absence of tree frog remains from Holocene deposits in England can be largely attributed to

[14] Norwich and Cambridge respectively.

Figure 48: illustration of a tree frog basking on a leaf from The history of four-footed beasts and serpents by Edward Topsell (1658).

taphonomic bias. Not only are tree frog fossils are exceedingly scarce throughout the much longer Pleistocene sequence because of their delicate skeletal structure (Rage & Roček, 2003; Bailon, 1991) but reconstructions of Britain's historic amphibian assemblage (including *Pelophylax lessonae*, *Rana arvalis*, and *R. dalmatina*) are based mainly on subfossils recovered from 'incidental pitfall traps' created by human activity, such as postholes, foundation trenches and pits for 'industry' (Gleed-Owen, 2025; Gleed-Owen, 2000). Incidental pitfalls are the most common feature to preserve amphibians and indeed many other small animals (Clarkson, et al., 2025).

It is obvious that records of this species would be practically absent from such archaeological features; possessing adhesive toe pads, the *Hyla* complex are the most extensive climbers of European anurans even able to ascend glass, vertically (Arnold & Burton, 1978). Amphibian pitfall trapping studies in areas with extant European *Hylids* also corroborate with this line of thought, as this method rarely collects the species (Pabijan, et al., 2023; Pajiban, pers. comm., 2025).

Also, there is no evidence to suggest that tree frogs were used as a food item by people, prior to the EMP; being roughly 1/20th the size of the commonly gourmandised edible frog, they would make for a meagre meal. Therefore, tree frog remains are unlikely to be found in historical refuse, middens or even commensal situations more broadly (Schouten, pers. comm., 2025). For comparison, only a single Holocene sub-fossil has been discovered from the whole of the Netherlands (Schouten, 2016) none are known from Sweden or Denmark, and in France, only 3 sites have recovered sub-fossils despite the species being within its core range and widespread across the whole of the country (Bailon, 1991; MNHN - OFB, 2025).

A similar pattern is observed in water frogs, which constitute only 2.33% of total anuran finds in Germany despite their local abundance (Snell, 2006; Gleed-Owen, 1999). This bias likely arises because water frogs are less terrestrial than brown frogs, rarely undertaking migrations between brumation and breeding sites, and are therefore less prone to accidental entrapment in pits (Snell, 2006; Cooper, pers. comm., 2025).

In light of this poor preservation potential, SDMs provide an important complementary line of evidence. Over the past two decades, SDMs have become increasingly accurate tools for reconstructing past and potential species distributions under various climatic and land-cover

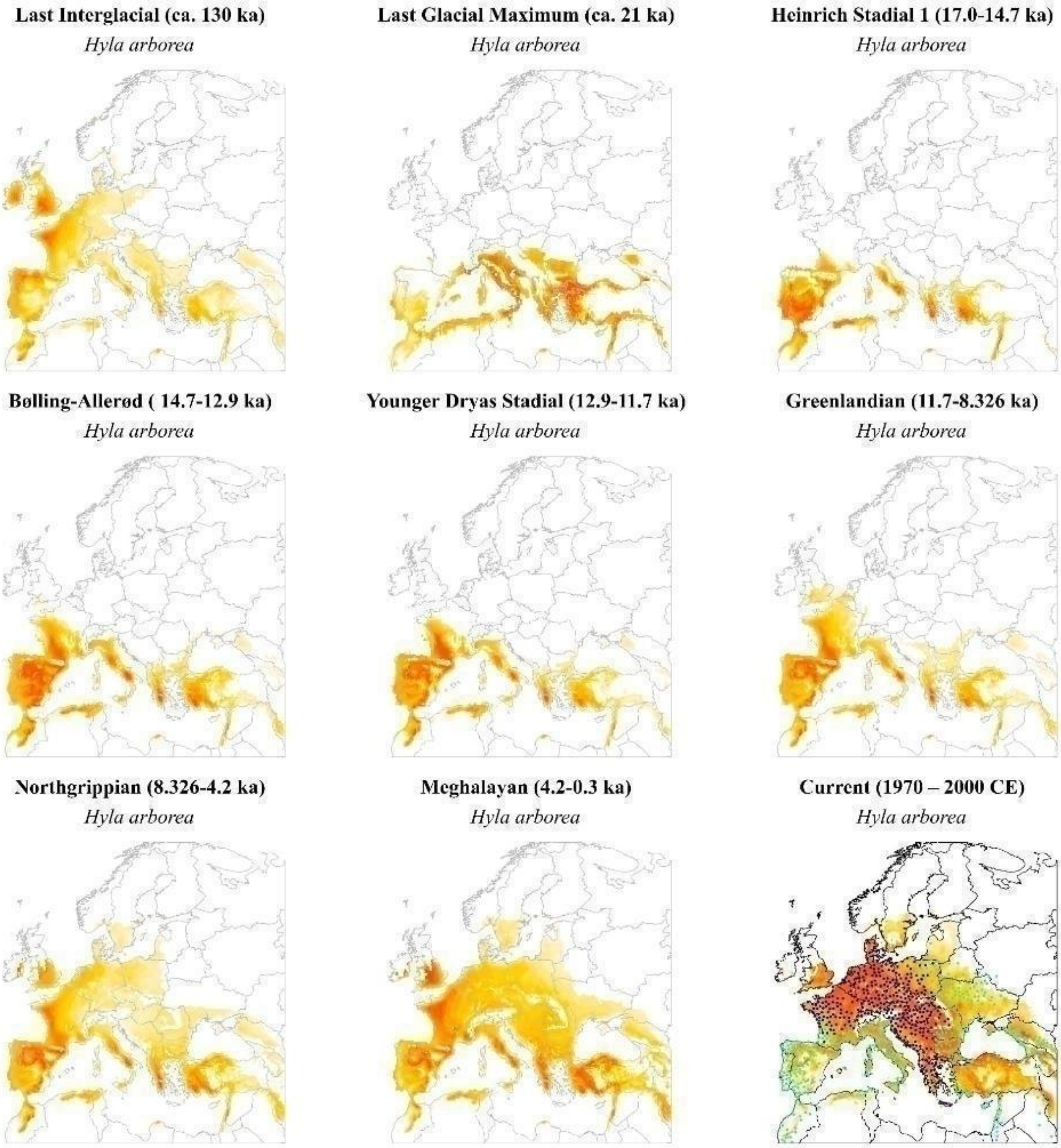


Figure 49: a preliminary SDM of the European tree frog, across Europe, over the last 130k years. Purple points represent H. arborea records used for the model, green points are records of other Hyla sp., not used. Produced by Rhys Lemoine using Maxent via RStudio with climate data from PaleoClim.

conditions (Franklin, 2023). Particularly informative are models simulating the Pleistocene–Holocene transition, when tree frogs could have dispersed into Britain via Doggerland. Dufresnes et al. (2020a) demonstrated climatically appropriate areas of terrain could have existed across the exposed North Sea plain and southern England, indicating that no significant climatic or geographical barriers would have prevented colonisation during this key period. These models are being improved and given great nuance by the likes of Rhys Lemoine and Thom Lyons. Preliminary results from these investigations are given in Figure 49, and show a key window of about 3000 years when colonisation could have occurred (Yalden, 1980). Like the case of the agile frog (Section 3.6), the native presence of the species across many islands in Scandinavia attests to a post glacial expansion prior to the flooding of the North Sea plain and subsequent persistence (Gvoždík, et al., 2015). It is therefore not a extraordinary claim that the tree frog could be a native species, when we consider this in the context of countries sharing paralleled geographic and faunal histories – Sweden being the best example.

Geographically, both Sweden and Britain were formerly connected to continental Europe via land bridges. These were Doggerland in the southern North Sea and the Øresund Strait in southern Scandinavia, which were submerged at roughly the same time following post-glacial sea-level rise, 8000-9000 years BP (Björck, et al., 2008; Hoebe, et al., 2024). As a result, the two countries support almost identical assemblages of temperate species (Snell, 2006; Clark, 1998; Snell, 1985a). Many thermophilic species, such as field crickets, wart-biter crickets *Decticus verrucivorus*, pool frogs and natterjack toads occur on their northern range edge in Sweden and England. The countries also share the same reptile guild, (grass snakes split only recently into two species) a group that is notably thermophilic (Speybroeck, et al., 2016).

From an amphibian perspective, all of Britain's extant and historically recorded species are also present in Sweden, except for the palmate newt. Importantly, this species likely reached Britain before sea levels rose, but not Sweden. This can be explained, maybe due to climatic nuance but primarily by two key factors:

- Poorer colonisation capability. Newts, including the palmate newt, are generally poor dispersers (Isselin-Nondedeu, et al., 2017), both due to their slower mobility and need for mature ponds for breeding (Grundy, pers. comm., 2025).
- Glacial refugium location. Genetic evidence and its westerly modern distribution[15] imply that the palmate newt persisted in a western glacial refugium in the Iberian Peninsula, closer to Britain than Sweden (Burriel-Carranza, et al., 2025).

In contrast, amphibian species present in Sweden but absent from Britain include: fire-bellied toad, green toad *Bufotes viridis*, common spadefoot toad *Pelobates fuscus* and triploid edible

[15] Although out of the scope of this work, it is interesting that the range of the palmate newt ends abruptly in northern Germany. This boundary appears to be influenced by genetic factors. As a species expands northward from a glacial refugium, its populations often become increasingly genetically homogeneous, particularly if dispersal occurs rapidly. Consequently, there seems to be a limit to this process – a "genetic steam" if you will – whereby populations eventually lose sufficient diversity to sustain further expansion (diversity being inversely correlated to distance from refugia). Continued dispersal may only resume once genetic diversity is replenished through mutation, admixture, or secondary contact with other lineages. The same phenomenon has been observed with European tree frogs and likely northern and southern clades of pool frogs.

frogs *Pelophylax kl. esculentus*. All of these species have distinctly eastern distributions. Genetic studies support the idea that these species persisted in eastern glacial refugia (for e.g., around the Black Sea), rather than those in western or central Europe (Fijarczyk, et al., 2011; Dufresnes, et al., 2020b; Crottini, et al., 2007; Dufresnes & Mazepa, 2020). This positioning would have allowed them to reach Sweden before sea levels rose, while preventing their dispersal to Britain.

The European tree frog, by contrast, appears to have persisted in the Balkan refugia (together with for e.g., the European pond turtle *Emys orbicularis* and great crested newt *Triturus cristatus*), located roughly equidistant between Britain and Sweden, making natural colonisation of both regions equally plausible (Dufresnes, et al., 2020a; Sommer, et al., 2007; Wielstra, et al., 2013). Furthermore, in SDMs, Scandinavia is consistently shown to be poorly suited for post-glacial colonisation (at this preliminary scale), whereas Britain and western Europe are, more broadly, depicted as highly suitable (Lemoine, pers. comm., 2025). Also, Fennoscandia was the last region in Europe to be colonised by temperate species (Knopp & Merilä, 2009).

When the aforementioned points are considered alongside species distribution models, they strongly suggest that the European tree frog colonised Britain naturally, among the other thermophilic fauna characteristic of north-west Europe, during the early Holocene (Langton, et al., 2011). It is also worth considering that:

- Tree frogs are the most capable dispersers of the north European frogs (Lenders, pers. comm., 2025). They are able to rapidly colonise new habitat up to 12 km away from ponds they originally metamorphosed from (Vos, et al., 2000; Schuster, 2004; Pellet, et al., 2006). Populations exist in a static or expanding state depending on habitat availability (Marijnissen, pers. comm., 2025). Compare this with the pool frog, which disperses around 25-500m from their breeding ponds in a single season, wherein a they can move at a rate of 300-400m per generation (Wilström, 2018).
- Tree frogs are extremely cold-tolerant, surviving even bodily freezing events (Snell, 1985a), meaning they could tolerate the colder winters of the Holocene transition. They are also largely a pioneer species, inhabiting early successional-stage habitat like young scrub and even coastal dunes, biotopes that would have occurred in abundance across Doggerland (Grosse & Nöllert, 1993).
- The slow-moving European pond turtle made it to Britain after the last ice age (Snell, 2006; Stuart, 1979), migrating across Doggerland and subsequently becoming marooned in East Anglia (Cribdon, 2021). No where in the modern ranges of either tree frogs or pond turtles does the latter exist further north than the former (Speybroeck, et al., 2016). This suggests that *Hyla arborea* likely emigrated as part of the same wave of thermophiles, including agile and pool frogs, and for example sand lizards and field crickets *Gryllus campestris* (Langton, et al., 2011; Böhme, 1996; Gleed-Owen, 1999).

The weight of this circumstantial evidence has led experts like Chris Gleed-Owen (2021) to exclaim that on Doggerland, the tree frog "ought to have been there… [and] could well have got across" to Britain, despite the lack of archaeological evidence. Therefore, some organisations class the species as an extinct native, such as the Wildlife Trust (2025), and the tree frog has been utilised within UK historic biodiversity loss metrics (Natural History Museum, 2019; Hayhow, et al., 2019). It also features on the Red List of Threatened Species for Great Britain (JNCC, 2023).

5.3 Species History

Unlike the other species of frog covered in this work, the tree frog is a conspicuous species: it was a readily observed for an amphibian species, at least throughout the second half of the EMP. It is therefore no surprise that it was first described by Linnaeus (1758) in his *Systema Naturae* and subsequently detected early and described from Denmark in 1782 (Andersen, et al., 2005).

In 1768, the legendary naturalist Gilbert White in his seminal *Natural History and Antiquities of Selborne*, exclaimed that:

> *"Merret, I trust, is widely mistaken when he advances that the Rana arborea is an English reptile; it abounds in Germany and Switzerland."*

In light of this, the Author believes that by this time, the tree frog had already gone extinct (see Section 5.6) with the concept of extinction not permeating into zoological discourse until around 1800 (Faria, 2012). Further to that, Snell (2006) postulated that a long-lasting colony of tree frogs that survived until the 1980s near Beaulieu, the New Forest, Hampshire, could have been native, however, both this population proximity to White's former haunts and hearsay from an anonymous source has revealed that the population was likely introduced (Anonymous, pers. comm., 2022).

As recently as the first half of the 20th century, the tree frog had a more widespread and northerly distribution both in Sweden and Denmark, occurring up to N 56º18', roughly on the same line of latitude as Perth, Scotland. It has been lost from these more northerly locales due to habitat loss; its current range does not fully encapsulate its true ecological tolerance (Edenhamn, et al., 2000). An introduced population occurs even further north, outside of Kungsbacka, Halland County at a staggering N 57º27', which is further north than Loch Ness. Models show that tree frogs were and are currently limited more by vegetation type than climate in southern Sweden; dense woodland, especially coniferous forest, is averse to the species (Snell, 1984; Lemoine, pers. comm., 2025; Corbett, 1989; Kjær, et al., 2023).

The European tree frog experience a rapid post-glacial expansion, however this came at the cost of genetic diversity. This has resulted in northern populations being incredibly susceptible to habitat change, relative to their southern counterparts (Birbele, et al., 2024; Dufresnes, et al., 2013). Therefore, the northern populations are most threatened, with Denmark in particular having witnessed declines of over 95% in the past (Corbett, 1989).

There have been many instances of tree frogs being (re)introduced to Britain, in the post-Industrial Period, starting around 1840, where frog importation became common (Lever, 2009). The origin of these releases must be questioned, as prior to the mid-1990s, it was thought that

Hyla arborea occurred from the Iberian peninsula across to western Asia (Arnold & Burton, 1978). However, thanks to improved genetic sequencing from the mid-1990s it is now know that the European tree frog is not one species but at least 5 (Gvoždík, et al., 2015). The true, 'European' tree frog occurs only through the northern three quarters of France, the Low Countries, Germany and western Poland, north to Sweden and south to Greece. We know that these introductions came from a variety of source locations, so it is unlikely that many were comprised of typical northern frogs[16] (of the type that would have colonised Britain) (Snell, 2006). This probably contributes to why these populations never persisted; there are no known extant populations today.

Dubious origin/hybrid European tree frogs are moderately common in captivity. The northern type is very rare in captivity.

5.4 Habitat Choice

5.4.1 Terrestrial Stage

Of the three species of lost frogs, the European tree frog is the most thermophilic, during its active period of spring and summer. This means that in the cooler climates of northern Europe it relies on relatively specific habitat conditions to achieve its ideal physiological temperature. These conditions are typically found in early successional-stage habitats, particularly open, sun-exposed shrubland and thickets composed of shade-intolerant vegetation (Marijnissen, 2013). Because such habitats are transitional and naturally short-lived, tree frogs have evolved a highly mobile, vagile lifestyle. They readily disperse to avoid areas that have become too densely vegetated through succession and to exploit newly forming shrubland elsewhere in the landscape (Arens, et al., 2006).

Bramble is one of the most commonly used plants as a basking and resting place for tree frogs, in order to regulate bodily water content, temperature and to absorb UVB. In fact, there were only a couple of instances whereby the Author observed tree frogs sitting on another species of plant. On suitable leaves and stems, tree frogs bask in the sun, tightly tucking in their limbs in order to reduce moisture loss. I hereby coin this behaviour *loafing*[17] (see Figure 61). This behaviour is widely observed across many sun-loving tree frog species. An interesting point raised by Kees Marijnissen (pers. comm., 2025), was that maybe the species does use other habitat features as bramble presents a selection bias; it grows to around head height and is easy to look into. Furthermore, Marijnissen has observed tree frogs a dozen metres or more up in large poplar trees, a place the casual observer is unlikely to look.

With the onset of cooler weather around late October or November, tree frogs begin to seek out hibernation sites. These likely consist of log piles and deep leaf cover on the edges of forests or within thickets.

[16] For instance, almost all northern *H. arborea* feature an upward branch to their lateral lines yet photos of the Essex colony lack this trait, suggesting they may be the Turkish tree frog *H. savigni* instead.
[17] Loafing; when domestic cats tuck in their limbs in order to conserve heat.

5.4.2 Breeding and Aquatic Stage

Hyla arborea is the latest of the lost frogs to breed. When nights consistently reach above 8ºC, usually around late-April or early-May, male tree frogs descend on their breeding ponds

Figure 50: upper: clumps of European tree frog spawn, all from the same female. Lower: Feeding tree frog tadpole.

whereby they call nocturnally, with individual tree frogs reaching volumes of ~80 dB (Schneider, 1971; Lukanov & Naumov, 2019). This calling echoes across the landscape in order to broadcast to and attract gravid females, which are usually dispersed over a considerable distance from the breeding waters (Dufresnes, 2019). Spawn is laid in multiple walnut-sized clumps around the pond. The breeding season ceases around June (Carols, pers. comm., 2025).

These breeding ponds are often very shallow with water that becomes warm to the touch (Lever, 2009). Ideally, adult basking habitat should reside close by, but the ponds can vary in maturity, with tree frogs even known to spawn within freshly dug ponds or deeper puddles (Marijnissen, pers. comm., 2025; Carols, pers. comm., 2025).

Seasonal drying of ponds is necessary to reduce the fish load, as tree frog tadpoles are highly susceptible to predation. This vulnerability arises because the tadpoles primarily occupy the pelagic zone and feed at the surface. They appear to consume fine, windblown detritus such as pollen that settles on the water's surface (Whitehurst, pers. comm., 2025). Observations in captivity show that the tadpoles readily respond to crushed larval diet landing on the surface by inverting themselves so that their mouths just break the surface film (Figure 50). Additionally, their eyes are positioned on slight protrusions, which likely provides an enhanced field of view both above and below the water surface (Whitehurst, pers. comm., 2025).

Tree frog tadpoles develop rapidly, going from a newly hatched tadpole of maybe 7mm to a 15mm limbed froglet within about 2 months. These froglets emerge around late-July until early September whereby they disperse over several kilometres to suitable terrestrial habitat.

5.5 Field Observations

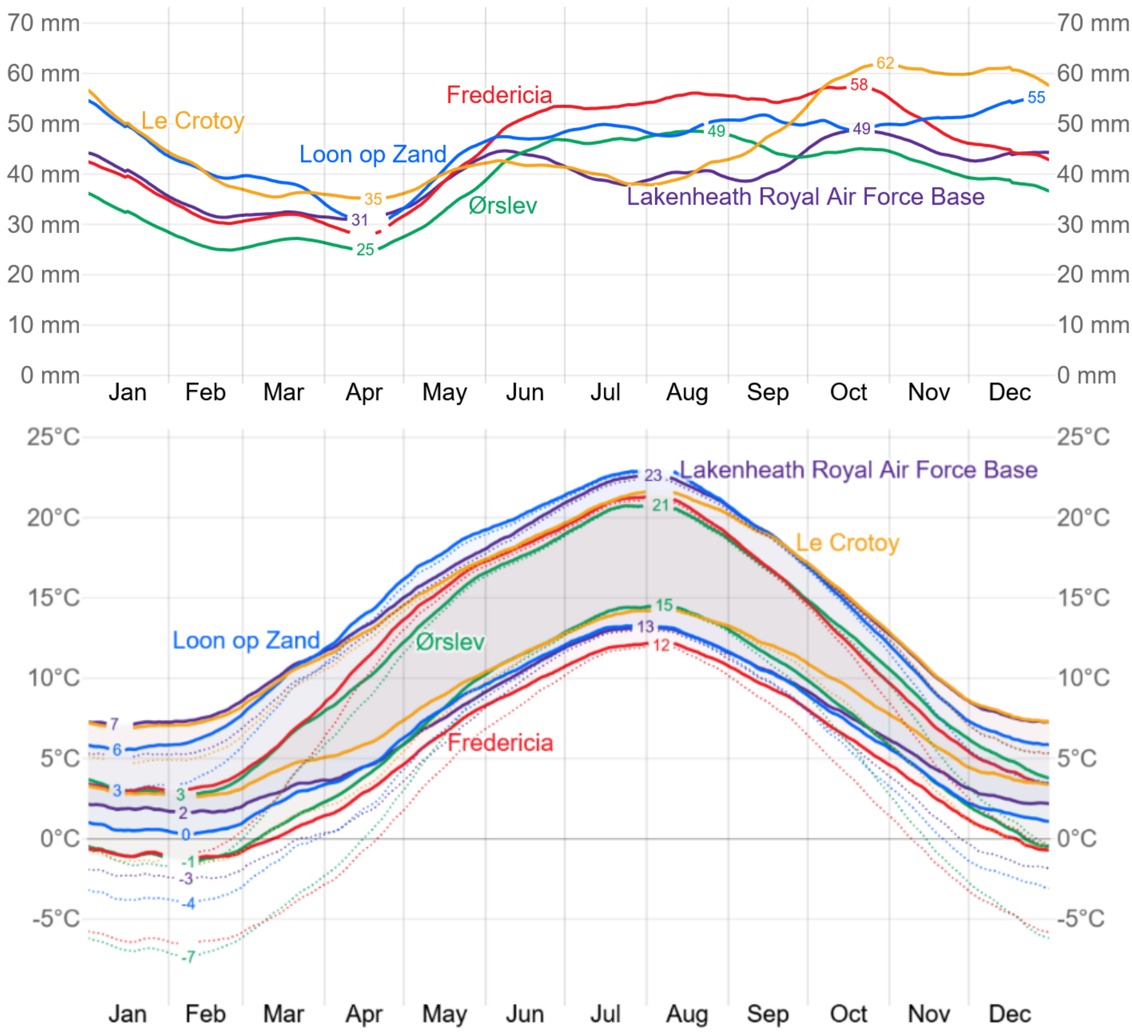


Figure 51: upper: average high and low temperature of some of the tree frog sites (closest weather stations), compared with climate data from RAF Lakenheath, East Anglia. Lower: average monthly rainfall of each site and RAF Lakenheath. After Diebel (2025), © WeatherSpark.com

5.5.1 Shrubland Sites

(03/07/2025) Knudshoved Odde, Denmark, needn't an introduction (see Section 3.5), but in addition to hosting an agile frog population, it also has a population of tree frogs, although none were seen by the Author. The most apparent point that arises from this population is that it is in a very maritime, exposed and windswept location, as the peninsula is just out and is surrounded by the Smålandsfarvandet.

Figure 52: the ponds on Knudshoved Odde are very shallow and have great water quality, hence the presence of water crowfoot Ranunculus aquatilis, which in addition, H. arborea enjoys as a spawning plant.

(04/07/2025) Kulsbjerg Training Area is a 496 ha block of open grasslands, wetlands and ponds, hedgerows and scrub owned by the Danish Armed Forces. The site's use by the military dates back to 1969 when the land was expropriated. Therefore, the landscape has escaped chronic degrees of agricultural intensification, and has reverted back to a wild state, 'managed' by free-roaming cattle and ponies. In 1988, the biologist Kåre Fog proposed reintroducing the European tree frog back to the area, considering that lots of pioneer scrub had formed and ponds could be restored. In the period from 1988 to 1991, a number of ponds were desilted, and opened to the sun, creating a more varied flora around them. Almost 900 tree frogs were released into Kulsbjerg. The release and care of the many ponds has been so successful that where in 1991 there were only 3 waterholes with tree frogs, today there are 22 waterholes occupied. The number of singing males has grown from 4 in 1991 to 230 in 2013.

When I visited this site, the temperature was around 25ºC with just a slight breeze, making for perfect conditions to view tree frogs, if not a little too warm. Over about 3 hours, 6 were seen.

Figure 53: the main breeding pond "Langesoe" for the tree frogs at Knulsberg.

Figure 54: upper: a scrubby bank facing south-east, where tree frogs were sighted. Lower: the excellent camouflage of H. arborea.

Figure 55: Spot the tree frog.

Figure 56: perfect scrubby edge habitat for tree frogs. A number of likely 1 year old juveniles were sighted here.

(06/07/2025) Trelde Næs near Fredericia, Denmark, is a 640 ha peninsula comprised of woodland and protected coastline. Some of the forest is believed to be continuous cover for the last 15,000 years. In one particular glade in the forest, I got a good impression of what the probable prehistoric ecology of tree frogs may have been. In this glade, the open character is maintained by a group of ponies. One could imagine time when northern Europe was much more forested, but disturbance in the form of fire or ungulates could create areas of temporary and open, park-like habitat (Vera, 2000). It is for these instances that the tree frog's apt dispersal capabilities and loud call of the male seem clearly adapted for.

Figure 57: upper: the breeding pond at Trelde Næs. Lower: ponies manage the woodland glade, reminiscent of a time when great herds of wild herbivores would have driven ecological processes and vegetational succession.

(11/07/2025) The same site as covered in Section 3.5.2, the open shrublands surrounding the towns of Vledder and Noordwolde, hold not just a population of introduced agile frogs, but also an introduced population of tree frogs which share the same habitat. Just like the agile frog, the ice-rink lakes are crucially allowed to dry out every year reduce the fish load and are extremely favourable to the tree frog. This process inadvertently replicates rare wetland dynamics not seen in our drained landscapes, when untamed rivers would push out water laterally forming seasonal shallows that would shift and change annually. The Author's visit was well timed; thousands of tree froglets were observed having recently emerged from the water.

The means of introduction of these frogs are thought to be the same as that of the agile frog, via intentional or accidental escapes from a nearby biologist's garden (Wennekes, pers. comm., 2025).

Figure 58: an adult female tree frog sitting on bramble growing at the edge of the ice-rink.

Figure 59: upper: an adult tree frog resting amongst bramble on the shores of the ice-rink. Lower: the ice-rink, which has almost completely dried up.

(12/07/2025) De Brand near Udenhout in the Netherlands, is a 525 ha nature reserve part of the larger Loonse en Drunense Duinen National Park. Since the 1980s an active tree frog restoration project has been taking place in order to save the species from extinction in North Brabant. I was shown around by Kees Marijnissen, who has headed up this project for all that time and Dr Rob Lenders, co-founder of RAVON (the Dutch reptile and amphibian conservation organisation). Kees tracked the decline of the tree frog through the Netherlands in an attempt to reconstruct its past range. He found that despite the species being visible and easy to identify, anecdotal evidence was few and far between. When Kees first started to work on De Brand, there may have been as few as 5-25 tree frogs. Now over 10,000 are estimated to reside within the reserve and they are spreading, fast.

Immediately, ponds were restored in order to create the perfect breeding habitats for the species, as land drainage and pollution had resulted in the loss of the population. The tree frogs now use around 70 restored ponds, with Kees explaining that the ponds must be dug so that they are shallow (Marijnissen, 2013). While initially successful, the growth of the population was slow. This was down to the colony being descended from so few founders. Therefore, after lengthy discussion, a plan was devised with the appropriate permissions to move a number of tree frogs from elsewhere in the Netherlands in order to boost the genetic diversity of the tree frogs. Since this 'genetic supplementation', the numbers of tree frogs have exploded and spread (at around 2km/year) out of the bounds of the reserve and are even occupying domestic gardens and parks.

Many photographers and nature enthusiasts were at the reserve during my visit. Kees informed me that people come from all over Europe to view the tree frogs within the wonderful setting. While there have been conflicts between the conservation of the species and the will of photographers to get the perfect shot, fencing and well displayed information have reduced these impacts. Assumedly, these visitors will also be spending money within the local economy,

Figure 60: the swamp-like character of De Brand.

contributing towards a socio-economic benefits. It was just brilliant to see so many people enjoying these wonderful frogs.

Figure 61: upper; Rob Lenders and Kees Marijnissen search for tree frogs. Note the fence, intentionally erected in order to prevent visitors from trampling the vegetation and disturbing the tree frogs. Lower: a young tree frog loafing in the brambles to the left of the upper photo. Kees explained that when they turn this golden colour it means they have hit their warmest and most optimal body temperature.

Figure 62: upper: grazing by cattle is vital to the maintenance of a healthy tree frog population. Compartments of 2-2.5 ha are stocked with 2 cows in each. Lower: an adult tree frog partially shading itself during the hottest part of the day.

(29/07/2025) Across Hauts-de-France and especially around the Baie de Somme, tree frogs have been somewhat conserved from extensive inland agricultural intensification due to the complex of largely intact dunes and associated habitats. Connectivity seams to be key here, as the species uses different parts of the dunes for different purposes throughout the year. In the height of summer, when I visited, the tree frogs were sticking to the damper environs within the landscape.

Figure 63: upper: the flat, swampy character of much of the landscape of this region. Lower: huge numbers of wading birds, such as these white storks Ciconia ciconia populate this region due to its rich wetlands and abundant prey which includes ample amphibians.

Figure 64: upper: a humid dune slack which seasonally fills with water and hence provides a brilliant breeding habitat for the local tree frogs. Lower: a site close to a village managed by hardy ponies for tree frogs.

(31/08/2025) The importance of clever engagement with the public and especially with the next generation of naturalists is exemplified at Zwin Natuur Park, located right on the north sea cost on the Belgian-Dutch border. Zwin was one of the only places in the whole of Belgium to continually host a population of tree frogs. Therefore, it has served as a strategically important site for the species and display of tree frogs and their habitats to the public. At large, the nature park is wonderful: it is highly accessible and contains many creative ways to convey ecology and conservation in an exciting way. For tree frogs in particular, specially created south facing banks planted with bramble and gorse *Ulex europaeus* are designed in such a way that they are close to paths so the public can easily observe the species. Boardwalks across ponds allow visitors to view their special breeding habitat. In addition, a tree frog trail has been built whereby children can complete an obstacle course and hence 'climb like a tree frog' through some of the very scrub that the tree frogs rest within.

Figure 65: the tree frog trail. Three adult tree frogs were sighted within bramble just to the left of the image.

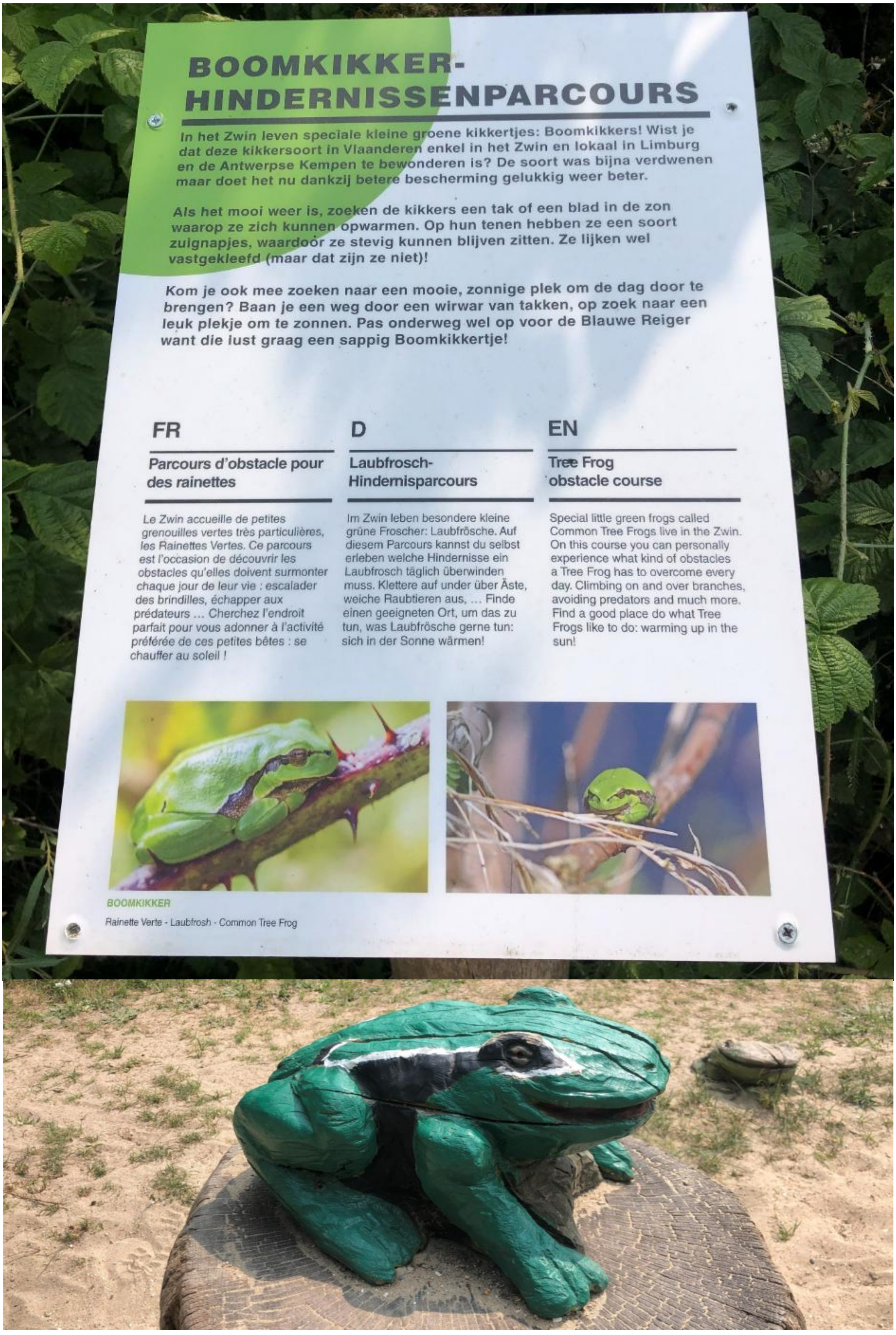


Figure 66: Interpretation and a wooden carving for the tree frog trail.

5.5.2 Active Reintroduction Sites

(16/07/2025) On the outskirts of Marche-en-Famenne, Wallonia, Belgium, the European tree frog is being reintroduced to a specially prepared site. The Author met with Charles Carels, the lead coordinator of Project Tree frog, a partnership between Natagora (the largest Wallon Nature NGO) and a variety of stakeholders including zoos and landowners. From 2022 to 2025 over 3000 juvenile tree frogs have been released into the reserve. In order for releases to result in thriving populations it is imperative to turn out surprisingly large numbers of froglets per annum for up to 4 years. Anything from 1000-3000 froglets is appropriate, but this does depend on the size and nature of the site. Within a year, the males, of the batch first to be released, began to call and successful reproduction was noted in 2024. While the Author was touring the site, three juveniles were spotted, thereby confirming successful breeding for 2025 too.

A couple of key points from this particular visit was the possible importance of tree frogs in the diet of red-backed shrike *Lanius collurio* a bird which perished in Britain during the 1980s due to a lack of prey and suitable habitat and that is currently experiencing lots of interest in the prospects of reestablishment in Britain (Jones, 2023). Also, these tree frogs have shown a propensity to favour newly created ponds, reinforcing their status as a pioneer species.

Figure 67: a 2025 juvenile tree frog observed at the site.

Figure 68: upper: ponds don't need to be large in order to facilitate tree frogs' breeding. Lower: a 2025 juvenile basks on a bramble leaf.

Figure 69: upper: the dense but extensive scrub at the reintroduction site. Lower: the importance of using a low-density of native cattle, to break up dense thickets and provide dung rich in invertebrates, cannot be stressed enough.

5.6 Extinction

It is unlikely that the European tree frog survived much past 1700 (Section 5.3), therefore this species was the earliest of the lost frogs to go extinct. It has been shown in Latvia (albeit with *Hyla orientalis*, formally considered synonymous with *H. arborea*) that the processes of rapid wetland drainage easily destabilises northern populations of tree frogs, resulting in regional extinction (Zvirgzds, et al., 1995; Edenhamn, et al., 2000). Likewise, the Author has calculated that the area occupied by tree frogs in Sweden is now only 2% of their historical distribution (Edenhamn, et al., 2000) and similar declines have also observed in in Denmark (Corbett, 1989).

In addition, the extinction of the beaver has been linked to the loss of numerous populations (Meßlinger, pers. comm. 2025; Scwab, pers. comm., 2023). Without the ecological engineering provided by this rodent, such as the creation of warm, shallow ponds and management of succession for the provision of humid shrubby glades, the thermophilic tree frog can face declines and extirpation (Birbele, et al., 2023; Dalbeck, et al., 2020). The reverse is also true: where beavers have been reintroduced, tree frog populations rebound in a short period of time (Schwab, 2015; Birbele, et al., 2023). The tree frogs' propensity to benefit from disturbed habitats that result in pioneer vegetation communities (Grosse & Nöllert, 1993) is certainly an adaptation from a legacy of living with large herbivores, like beaver, and the habitats those animals facilitate. It is therefore easy to comprehend northern populations of tree frogs struggling under the loss of this keystone, ecosystem engineer.

Figure 70: a beaver created wetland inhabited and used by tree frogs for breeding purposes in Bavaria, Germany. © Ulrich Meßlinger, 2025.

Notably, the ephemeral nature of tree frog breeding ponds have been historically of low importance to people (Spencer, pers. comm., 2025). Ponds for agricultural and domestic use were regularly deepened, desilted and lined with clay in order to make them more useful as permanent sources of water (Williams, et al., 2018). Furthermore, the MA/EMP saw the uptake of fish farming, especially of carp (Raye, 2017). As highlighted, tree frog tadpoles are intolerant of fish, the introduction of which has been responsible for local extinctions and declines in Europe (Brönmark & Edenhamn, 1994). It is therefore no surprise that as a result of historic human processes like these, only 2% of the ponds found in the British landscape today are natural origin (Williams, et al., 2018). This all being said however, the tree frog has the least strenuous habitat requirements of the three frogs, so additional factors must have been in play.

More broadly, the destruction of wetlands (as similarly seen with the moor frog, Section 4.6) results in the fragmentation of populations, which not only restricts genetic flow, but also makes these sorts of environments hitherto more accessible to people (Rotherham, 2013). It is not surprising that species requiring large wetlands, like the little egret *Egretta garzetta*, night heron *Nycticorax nycticorax*, Eurasian spoonbill *Platalea leucorodia*, and common crane, all became extinct in Britain during the 17th century as a result of hunting and egg collection, facilitated by landscape simplification through drainage (Yalden & Albarella, 2009; Bourne, 2003; Stewart, 2004).

Historical sources show that tree frogs were also readily used in Early Modern medicine, both in Britain and to a lesser extent on the continent (Section 5.2) (Raye, 2023; pers. comm., 2025). Their use was promoted initially by Dioscorides, the ancient Greek physician and pharmacologist (Raye, pers. comm., 2025). Later works, such as Lanfrank's (1380) "*Science of cirurgie*" show tree frogs being used as a cure for deafness:

"summe seien þat þe fatnes of grene froggis, þat lyuen among trees; take hem & seþe hem, & gadere þe fatnes of hem & caste in his eere, for þis haþ vertu for to make men heere." [Translation: some talk about the fat of green frogs that live among trees, take them and seep them and take the fat and drop it in the person's ear, for this has the power to make people hear].

Furthermore, within "*...the treasure of pore men*" (Anonymous, 1540), tree frogs are used as a tooth-pulling agent:

To make tethe to fall by themselfe: Take a water frogge & a verte frogge & sethe thē togyder & gader the grece & smere therwith thy go/mes aboute the tothe. [Translation: to make teeth fall out by themselves. Take a water frog and a green frog and boil them together and take the fat and smear it on your gums around the tooth].

This exploitation was likely the major factor pushing the species towards extinction (Raye, 2017), inline with observations of other species. A similar medicinal fad has been observed through the EMP to the 19th century concerning the harvesting and use of the medicinal leech *Hirudo medicinalis*. Bloodletting via leech has been in practice for over 3,500 years, but really began to become an industrialised processes at the end of the EMP, until the trend exhausted wild stocks around 1850 (Whitaker, et al., 2004). At just one hospital in London, over 97,000 leeches were used in treatments in 1832 and 100 million were used every year in France (Whitaker, et al., 2004). As a result of this widespread harvesting, in accordance with widespread loss of wetland habitats, the modern distribution of the species is 'extremely geographically restricted' in Britain, reaching a low of 31 occupied sites in the 1970s[18] (Ausden, et al., 2002).

Furthermore, the total extermination of the Eurasian beaver from the British Isles was in part due to castoreum, a special secretion produced by the animals' castor sacs, which sit within the cloaca at the base of the tail (Campbell-Palmer, et al., 2015; Raye, 2023). This substance was highly prized, as it was used to treat a range of ailments. A rather huge international trade network developed through the EMP solely to facilitate the movement of castoreum to where it was sought and various myths and folklore stories[19] idolised the properties of this substance. Perhaps these treatments were successful too, as castoreum contains salicylic acid, the active compound in aspirin, derived from the willow diet of the beaver (Gow, 2020). Also, similar extinctions have been observed through the Industrial Period when crazes for certain plant species emerged. Probably the most famous example is the lady's-slipper orchid *Cypripedium calceolus* which was over collected and presumed extinct by the start of the 20th century (until a single plant was rediscovered in the Yorkshire Dales) (Plantlife, 2025).

Over-collection as a extinction factor for tree frogs in Britain is also emphasised by the genetics of northern populations. The rapid post-glacial expansion of tree frogs from the Balkan refugium to northern climes came at the cost of genetic diversity and wholly deteriorated the northern populations' resilience to human impacts (Dufresnes, et al., 2013). These impacts, such as over-collection and habitat loss, serve to deplete the genetic diversity of a population, ultimately pushing the species into an extinction vortex, where extirpation becomes inevitable (Birbele, et al., 2024; Dufresnes, et al., 2013). This process played out in the story of the pool frog (Sections 2 and 2.2) whereby drainage efforts and habitat change (no serious collection efforts) caused the population to dwindle to just one site, whereby possible inbreeding caused the final loss (Lyons, pers. comm., 2025). Modern observations demonstrate that even when exposed to the same threats, southern tree frogs (i.e., Balkan area) show considerable resilience when compared to their northern counterparts (edge effects are probably also in play here too) (Dufresnes, et al., 2013).

The loss of the European tree frog from Britain represents an early example of extinction driven by both ecological disruption and human exploitation. Tree frogs are the easiest to catch of the lost frogs, as a keen eye can readily spot them amongst bramble and they only move to dodge a hand at the last moment. Some of the northern populations can be very small, such as Sweden, which at its lowest had maybe less than 3,000 individuals (Snell, 1985b). It is not hard to imagine the removal of even a proportionately small number of fecund females from a population to cause its extinction. Recent tree frog populations have more recently been driven to extinction through over-collection for the pet trade (Corbett, 1989), showing that such pressures do result in extinctions. Therefore, it is most likely that wetland drainage, the loss of

[18] There have been positive signs of recovery since, due to the cessation of harvesting and wetland restoration.
[19] For instance, it was believed that a beaver would bite of its own testicles (at that time the castor sacs were thought to be gonads) in order to be spared death by the hunter.

beaver-created habitats, and collection for medicinal use likely caused its disappearance, compounded by the low genetic diversity of postglacial northern populations. It makes sense to perhaps pursue ancient environmental DNA analysis of sediments in south east England to see if tree frogs are detected, but, as Trevor Beebee (pers. comm., 2025) exclaimed “one can look for evidence for ever”. Ultimately, this species’ story perhaps illustrates how historic land use, trade, and culture have shaped biodiversity change in Britain.

5.7 Reintroduction

Tree frogs serve as an excellent source of an easy-to-catch food source for a variety of predators including owls (Bisbal-Chinesta, et al., 2020) and seemingly the red-backed shrike (see Section 5.5.2). By sunning themselves within bushes, they occupy a space totally different to our other native amphibians. A reintroduction programme for tree frogs could be modelled on successful European initiatives that have bolstered local populations by collecting spawn, head-starting larvae in controlled conditions, and releasing froglets into suitable restored habitat. In a British context it makes sense to hold a captive group of adults, maybe 60 in number.

Perhaps the greatest benefit of pursuing a reintroduction of the European tree frog is the increased resilience it could offer the species as climate change intensifies and drives shifts in the distributions of more southerly or introduced species that may threaten northern populations. For instance, numerous non-native species of tree frog have only been recently detected in the Netherlands through genetic tests (Kuijt, et al., 2023) and hybrid swarms are expected to form when climate change suits a southern species over the northern form (Dufresnes, et al., 2015). By establishing a secure, climatically suitable population in Britain, a strategic buffer could be created against future habitat loss, competition, and disease pressures arising elsewhere in the species’ range. Because the European tree frog historically occurred in Britain (Section 4.2), it poses minimal ecological risk if reintroduced (van Delft, pers. comm., 2025). Assisted colonisation in terms of herpetofauna has been discussed with increasing interest and has been met with high levels of support from British practitioners and herpetologists, but has yet to be trialled (Foster, 2021). A European tree frog reintroduction would represent one of the safest and most scientifically justified applications of this strategy, if a translocation uses best practice and is well-studied. Moreover, demonstrating its viability in Britain would not only enhance the species’ long-term security but also contribute to wider wetland restoration efforts by providing a charismatic species that can help galvanise public and institutional support for habitat recovery.

5.7.1 Notes on Method[20]

Out of the three species of lost frogs, tree frogs present the greatest opportunity for public engagement within a species restoration programme. This was the finding on balance of visiting two captive raising projects, both in Belgium, which employ quite different rearing techniques. Firstly, the Aquarium-Museum of Liège holds around 2000 tree frog tadpoles per year and raises them completely indoors, using large filtered tanks originally used for fish within one of University of Liège's laboratories (Figure 71). A nice public display and exhibit is situated downstairs within the aquarium, allowing guests to view the frogs up close (Figure 72).

Figure 71: the laboratory which holds the majority of the tree frogs raised by the Aquarium-Museum of Liège.

[20] This section is not exhaustive. Before any reintroduction should take place, it is recommended that a follow up report be written to formally set out an agreed-upon methodology that considers all aspects including but not limited to legal, welfare, veterinary and resourcing implications.

Domaine des Grottes de Han is an incredible wildlife park located in Han-sur-Lesse, Wallonia. The park displays native European species, including those which have perished long ago, for instance brown bear *Ursus arctos*, alpine ibex *Capra ibex*, and reconstituted aurochs and tarpan. Since 2021 the park has taken part in Project Tree frog (Section 5.5.2). Initially the park sought to keep the tadpoles outside but this was difficult to manage; the baby tree frogs are apt climbers and hard to catch (see Figure 74 and Figure 75).

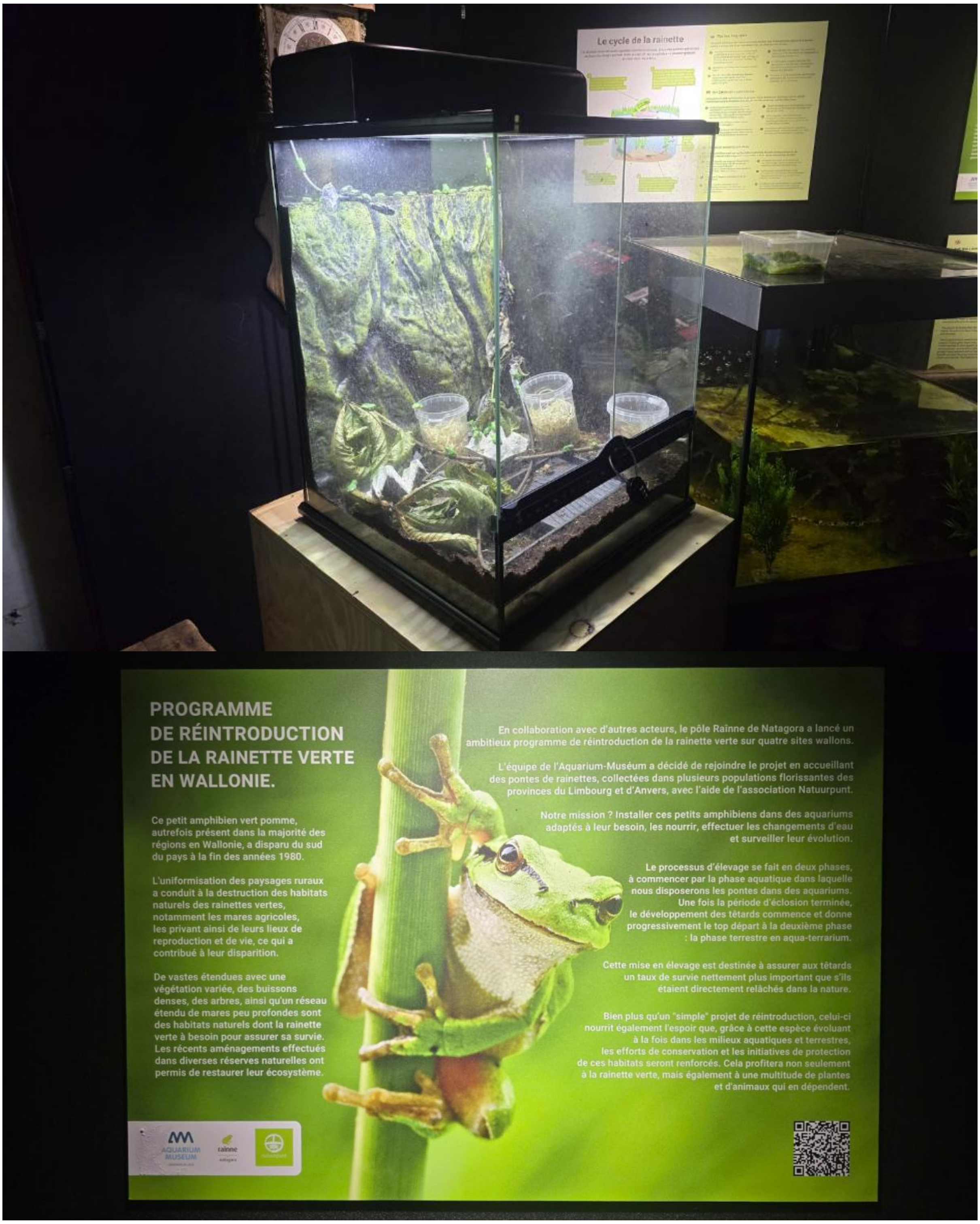


Figure 72: a public display featuring tadpoles and young tree frogs to be released and the associated interpretation.

The genetic lineage of tree frogs historically found in Britain was likely most similar to those found in north-western continental populations today (Gvoždík, et al., 2015; Dufresnes, et al., 2020a). Modern distributions of these lineages span northern France, Belgium, the Netherlands, Denmark, Sweden and north-western Germany (Speybroeck, et al., 2016). Founder stock should therefore be sourced from these regions. Ideally, eggs or subadult stages should be targeted, with the choice guided by a disease-risk assessment, eggs generally posing the lowest risk, and by considerations of transport practicality (Cracknell, pers. comm., 2025). When collecting eggs multiple clutches should be selected, ensuring a broad genetic base without overly impacting donor populations.

To begin with, the European experience shows that any proposed release site should be as well connected as possible, with ample amounts of shrubs, thickets and high quality shallow ponds. 100 ha of high-quality habitat, is probably required, managed by cattle and/or ponies to ensure early-successional vegetation is maintained.

Breeding groups should be raised under optimal conditions until they reach reproductive age. Enclosures are best adapted from greenhouses, not necessarily for the more optimal climate, but for the practicalities of dealing with a very apt climbing frog (Whitehurst, pers. comm., 2025; Fremming, pers. comm., 2025). These greenhouses should provide lots of vegetation (thornless bramble and raspberries being great choices), hibernacula and shallow water for egg deposition (see Figure 73). Tree frogs typically mature quite fast, with some females in captivity breeding in their first or second year. Adult frogs should experience a controlled hibernation period, either naturally in the hibernaculum or through a brumation chamber.

With the arrival of early spring and rising temperatures, tree frogs should become active, but they don't actively breed until the warmer nights of April or May. Males will call frequently at night from elevated perches and from the pond edge, while females will approach the pond when ready to enter amplexus with a male. Provided water bodies must be shallow and rich in emergent vegetation. To maintain genetic diversity, steps should be taken to prevent a small number of males from dominating the breeding. In some cases, pairs may be temporarily isolated to ensure equitable reproduction. Floating vegetation (e.g., hornwort) should be supplied as egg-laying substrate.

Following spawning, egg masses along with associated vegetation should be transferred to individual labelled containers to preserve lineage records. Once hatched, tadpoles should be reared until they become free-swimming and mobile. At this point, they can be carefully transferred into rearing tubs or to an RAS at controlled densities to promote healthy development.

These rearing containers may be housed within a well-ventilated polytunnel or a similar sheltered structure to promote faster larval development. Throughout summer, tadpoles should be provided with an appropriate diet and their water replaced regularly as they grow and begin forming hind limbs. Once approximately 10% of the cohort has fully developed all four legs, the metamorphs can be carefully released into suitable breeding ponds at the reintroduction site. Each site should aim to release at least 1,000 tadpoles or newly metamorphosed froglets per year over a three-year period.

A year after these releases, comprehensive surveys of the ponds should be undertaken to detect calling males, thereby assessing the establishment of a population. If little or no reproductive activity is found within 3 years after reintroduction, a supplementary release may be undertaken for one additional year. Surveys should then be repeated the spring immediately after this final release and once again the following year. If no evidence of successful reproduction is detected after this evaluation period, an exit strategy can be implemented.

Figure 73: an adapted green house used to hold tree frogs.

Figure 74: upper: tadpoles raised in unfiltered plastic tubs at Domaine des Grottes de Han. Lower: transition tanks with just a little water and plants to allow four legged frogs to emerge safely from the water.

Figure 75: upper: screen mesh enclosures provide the ideal environment to raise froglets. Lower: biosecurity is key.

6 Conclusion

6.1 Key Recommendations

A species can be considered native to Britain if it colonised the island and became resident by natural agency. For amphibians, this required dispersal at the end of the last Ice Age, when dry land connected continental Europe to Britain across the North Sea. This project, its thesis, and the pioneering work of British and European colleagues that underpin it, demonstrate that more amphibian species achieved this natural colonisation than those currently present or traditionally recognised as native. Human activity throughout the preindustrial period accounts for their subsequent loss from this island. As a result, up to 40% of Britain's original amphibian species have gone extinct[21] within the last 500 years: a period recognised by the IUCN as both recent enough for these losses to be considered relevant and their reintroduction favourable (Foster, et al., 2021). And ultimately, from a cultural lens, these frogs are as British as Æthelstan, William the Conqueror, Shakespeare or the Tudors.

Key recommendations:

- A detailed reintroduction feasibility study is commissioned, to address further resourcing, legal, biosecurity, and habitat suitability questions.
- More species distribution modelling is conducted to illustrate the range of sites whereby these frogs could be reintroduced together with 'ground truthing' surveys.
- Employ the new technique of ancient environmental DNA detection to help inform species history even further.
- Inform the development of biosecure and scalable captive methods that could raise the necessary number of froglets for successful reintroductions and the sourcing and import of appropriate stock to such a facility.

Subsequently:

- The reintroduction of the agile frog to suitable wet, woodland sites.
- The reintroduction of moor frog to suitable peaty sites.
- More investigation/experimentation with the European tree frog to assess its suitability as a translocation candidate.

It is important to consider that where reintroductions do take place the resources needed to carry out such projects avoid depriving extant natives of conservation measures. Reintroductions of lost species carry such an appeal that funding is often generated outside of conservation circles, however (Dennis, 2021). It is also recommended to pursue reintroductions on rewilding sites, where habitat management is taken on a landscape scale approach, not only offering these species a plethora of habitat opportunities, but also because ecological restoration is no hinderance but central to the business models of such projects.

[21] 4 species, including the pool frog, have gone extinct. 6 species have been continually present from the end of the Ice Age.

Table 5: the reintroduction of the lost frogs set against Natural England's (2025) priorities for species translocations.

Reintroduction Priorities	Agile frog	Moor frog	Tree frog	Justification
The species creates or restores habitats that serve many other species as well as ecosystem functions	✓	✓	✓	All three species are key prey items for a range of predators. Their diets could improve the functioning of soil and detritovorous communities
the species is threatened nationally or globally	✓	✓	✓	Each species is extinct in mainland Britain and threatened in NW Europe
the geographic distribution of a species population is extended	✓	✓	✓	Reintroduction to Britain will broaden their occupied range in Britain, making them more resilient to future threats i.e. climate change
the species is iconic and engages the public and stakeholders in support of packages of wider objectives	✗	✓	✓	Agile frogs would be difficult to discern from common frogs by the public. Moor frogs turn bright blue during the breeding season and can help promote peatlands. Tree frogs are highly emotive and can encourage pond restoration more scrubbiness in the landscape

6.2 Discussion

One of the most striking learnings of studying Britain's pre-industrial past is the sheer, relentless effort people expended to simply survive. This struggle came at a profound ecological cost: nature endured centuries of sustained pressure that ultimately fuelled the rise of the world's first industrialised nation. From the 19th century onward, this pattern intensified on a global scale, with biodiversity loss accelerating dramatically as similar pressures shifted to other regions. The very processes driving habitat destruction today, such as deforestation in the Amazon and Southeast Asia, or the drainage of wetlands like the Mekong Delta, played out in Britain centuries ago, reshaping its landscapes long before present. Crucially, these impacts took place in Britain prior to the development of conservation concepts, so the complete understanding of total losses is unknown.

We are now so fortunate to live in a time when, for example, Britain's remaining peatlands needn't be cut to keep houses warm; when ancient woodland is no longer felled to craft basic necessities; and when modern medicine negates the need for superstition or folk cures, relieving tree frog populations of harvesting for purported remedies.

It is undeniable that the time we now live in has witnessed great human achievements, but this period is proportionately tiny when compared to the gruelling struggle that is rest of human history. The past century could be marked as the first time ever that resource surpluses have enabled a shift in world-view from a solely human-centric to a planetary one[22]. Although, global threats to Earth's ecosystems are likely to intensify in the foreseeable future, the present moment represents a rare crossroads, a point at which informed, decisive action can shift these trajectories for the benefit of both nature and society. The pressures to restore ecosystems for the services they provide, for everything from the economy to the enjoyment of nature, have never been greater. So in Britain, the time for ecological restoration, for rewilding, is *now*.

Ultimately, this work is not only about frogs; it is about offering a broader reflection on the relationship between people and nature in Britain, and what the future of ecological restoration could and should look like. We must acknowledge that modern conservation is not preserving a truly natural species assemblage, nor is it adequately dampening ongoing extinctions. If conservation is to remain effective and resilient, it must adapt by embracing recognition of historical loss in order to withstand the political and social pressures of the present and the decades ahead, in a world dominated by decreasing public spending yet an increasing interest in combating biodiversity loss through rewilding.

At the same time, it must be emphasised that rewilding and species reintroduction should not be about returning to a fixed moment in the past. It is clear that for all the time leading up to the last 1000 years, the three species of frog co-existed in what can be regarded as a 'managed landscape'; an environment already altered by people, to serve their whims, but to some degree dictated by the forces of nature. It is a completely erroneous suggestion that peoples prior to the industrial period were at all harmonious in their use and interpretation of the natural world; this and previous studies have shown that there was never a halcyon, untouched idyll. Britain has no remaining wilderness, and in a densely populated, heavily modified landscape, it cannot be totally recreated. And already, conservation is having to contend with the impacts of climate change and must experiment with adopting novel techniques in maintaining ecological function. In the words of the ecologist Frans Vera (Knepp, 2025): "our world is irrevocably changed…but we can try and create something interesting and valuable with nature, using the components that are left to us."

For the longest time we have been under wrong assumptions over what these said components were, despite a common notion that Britain has always been at the forefront of natural history and conservation (Beebee, et al., 2009). However, this study highlights the paltry extent of current research conducted on Britain's lost species, calling this traditional view into question. Perhaps the default approach – like a crime scene – should be to assume human mediation for lost species and search for evidence to the contrary. The hope is that this method of investigating extirpated taxa through captive study, literature review, and exploration of analogous habitats may be effectively adapted to other habitat-restricted biota that have been

[22] And allowed people like myself to fret about things as small as frogs!

disproportionately affected by land-use change and over-collection, including larger, well-documented beetles, butterflies, and perhaps plant species. Therefore, we can develop a greater understanding of what components are lost to us and could be reinstated, as part of a resilient, future natural (Bird, et al., 1996).

This study and the broader rewilding movement reveals that reintroducing long lost species, quickly become vital tools in combating modern conservation issues. While individually small, amphibians in healthy wetlands form a mighty feast to a whole host of predatory species. Studies are also highlighting that some amphibians help ecosystems sequester carbon by preying on, and thereby regulating, detritovorous invertebrates (Laking, et al., 2021). Perhaps the most neglected, or underutilised benefit in restoring amphibians is social engagement with conservation. These species can garner huge interest[23] and this support can be used to thereby catalyse wetland restoration, one of the earth's greatest carbon sinks (Barkham, 2021; Horton, 2021). Frogs, but especially tree frogs, also have the most brilliant appeal with people, especially children, who help partake in release programmes reinforcing the most vital lessons: to care of the planet and 'put back what has been lost'.

In a time where the world feels increasingly dewilded, progressively tamed and systematically explored, we must hope that significant discoveries for restoring our ecologies lie in plain sight, obscured by the passage of time. The sustained curiosity to look deeper into the past and discover unbeknownst components to repair our ecosystems with, is sure to uncover yet unimaginable benefits for conservation, for humanity, and for the future of all living things.

[23] A recent example is just one video about the European tree frog in Britain posted on Facebook that has attained over 600,000 views.

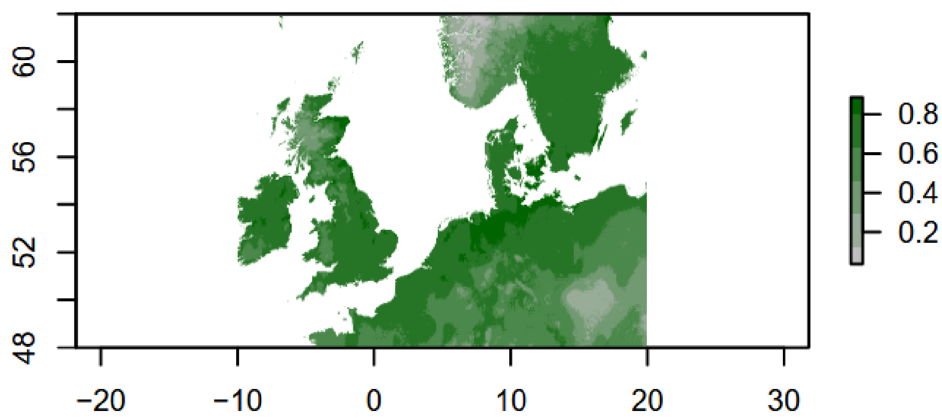
7 Species Distribution Models

The species occurrence data for these *draft* species distribution models (SDMs) was acquired from GBIF.org 2025. This was filtered for records occurring within the study area (latitude 46, 66, longitude -10, 34), with a location to accuracy of 1km and records from Britian were removed as they derive from human introductions. These were then uploaded to R Studio v47. A buffer area of 200km around occurrence points was set to provide a sampling area for background data. This was converted to a spatial raster grid of resolution 30 seconds of a degree over the study area. This resulted in 1384 presence cells and 7151 absence cells for *Rana arvalis*, 796 presence and 2443 absence for *R. dalmatina*, and 603 presence and 2271 absence for *Hyla arborea*.

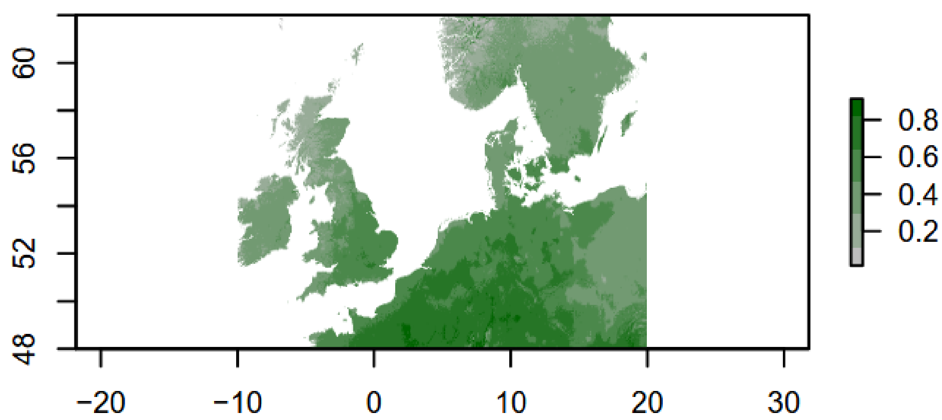
The raster cells were populated with 19 climate variables and elevation data from 1970-2000 from the BioClim climate model. This data was then analysed on R studio using the maxent package v0.1. using all climate variables and elevation as predictors and occurrence points as the response variable. This fitted algorithm was then used to project predicted suitability across the study area resulting in figure X below. Model fit was assessed using area under the IROC curve (AUC) with all results being within 0.7+-0.05. This relatively low predictive power has been put down to the study species being climate generalist and other factors such as habitat contributing more to their distribution than climate. However, the aim of this study is to show that climate is likely not a contributing factor to the speculated extinction of these species in mainland Britain.

The future climate scenario model was obtained from the CMIP6 archive, using the BCC-CSM2-MR global climate model under the SSP3-7.0 scenario for the 2041–2060 period. Data were accessed and downloaded using the geodata R package. The fitted models were then projected onto these climate predictions and plotted in the following figures.

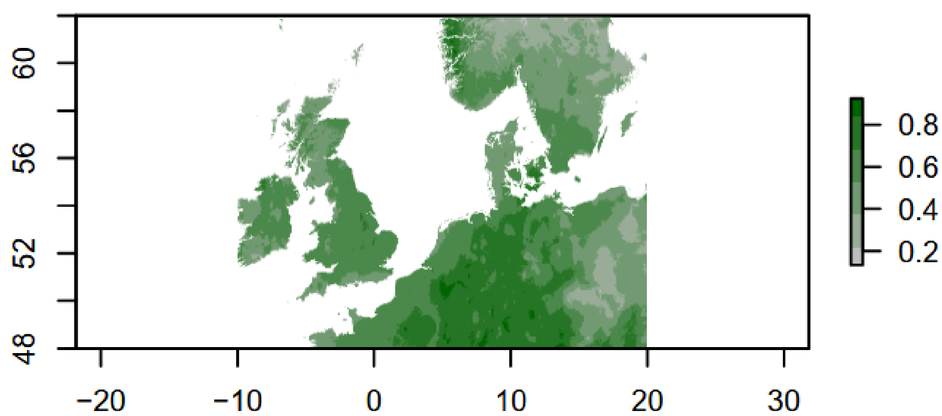
Rana arvalis 1970–2000 MaxEnt

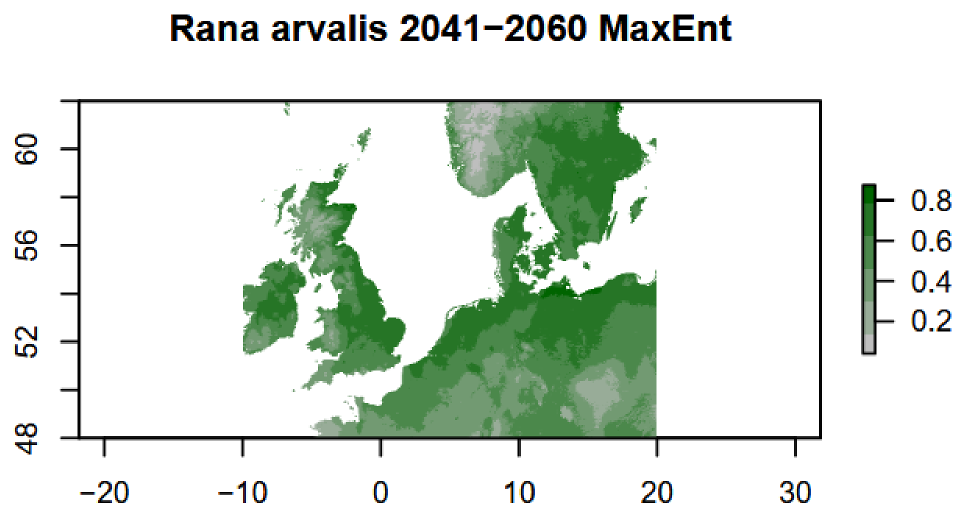


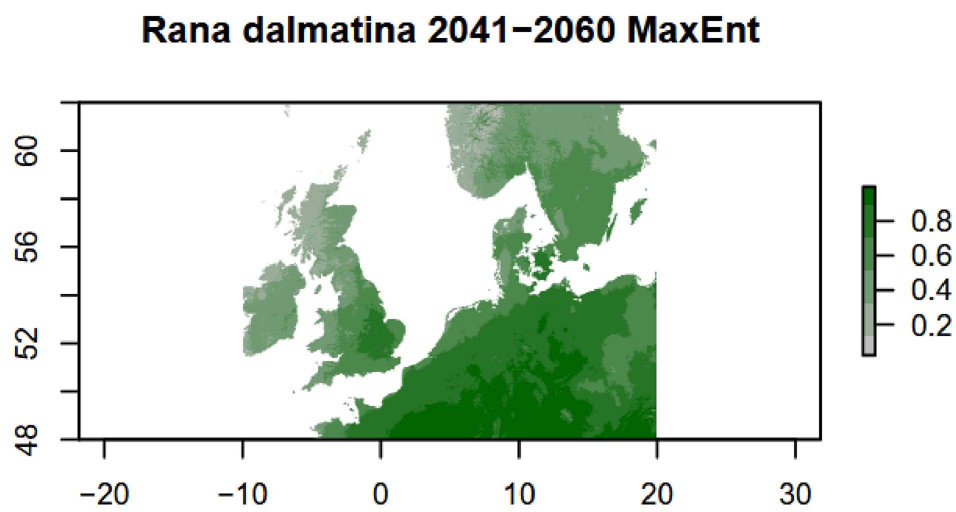
Rana dalmatina 1970–2000 MaxEnt



Hyla arborea 1970–2000 MaxEnt




Rana arvalis 2041−2060 MaxEnt
60
56
52
48
−20
−10
0
10
20
30
0.8
0.6
0.4
0.2


Rana dalmatina 2041−2060 MaxEnt
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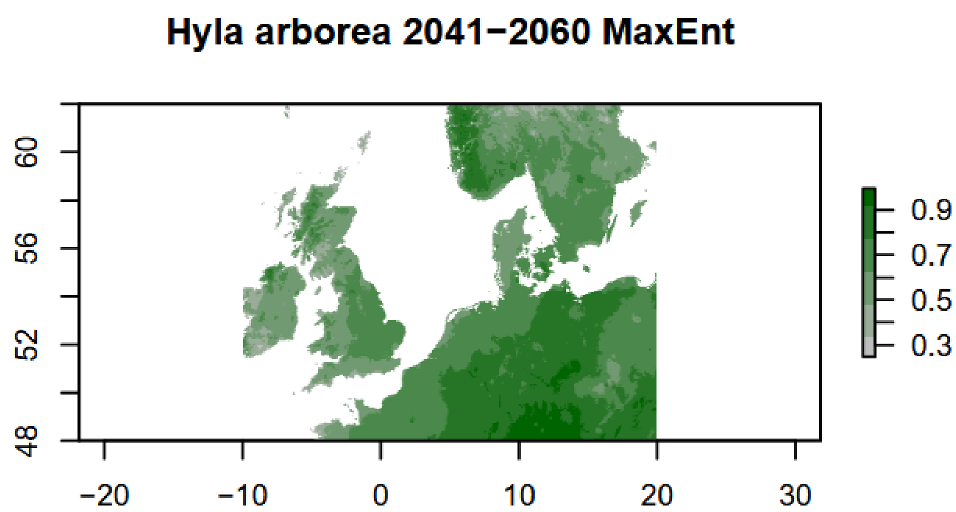
Hyla arborea 2041−2060 MaxEnt
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−20
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0
10
20
30
0.9
0.7
0.5
0.3

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