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Ecophysiological models for global invaders: Is Europe a big playground for the African clawed frog?

Philipp Ginal¹ | Mohlamatsane Mokhatla^{2,3} | Natasha Kruger^{2,4} | | Jean Secondi^{4,5} | Anthony Herrel⁶ | John Measey² | Dennis Rödder¹

¹Herpetological Section, Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany

²Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

³Rondevlei Scientific Services, Garden Route National Park, South African National Parks, Sedgefield, South Africa

⁴Université de Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, Villeurbanne, France

⁵Faculté des Sciences, Université d'Angers, Angers, France

⁶Département Adaptations du Vivant, MECADEV UMR7179 CNRS/MNHN, Paris, France

Correspondence

Dennis Rödder, Herpetological Section, Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Adenauerallee 160, D-53113, Bonn, Germany. Email: d.roedder@leibniz-zfmk.de

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Abstract

One principle threat prompting the worldwide decline of amphibians is the introduction of nonindigenous amphibians. The African Clawed Frog, Xenopus laevis, is now one of the widest distributed amphibians occurring on four continents with ongoing range expansion including large parts of Europe. Species distribution models (SDMs) are essential tools to predict the invasive risk of these species. Previous efforts have focused on correlative approaches but these can be vulnerable to extrapolation errors when projecting species' distributions in nonnative ranges. Recent developments emphasise more robust process-based models, which use physiological data like critical thermal limits and performance, or hybrid models using both approaches. Previous correlative SDMs predict different patterns in the potential future distribution of X. laevis in Europe, but it is likely that these models do not assess its full invasive potential. Based on physiological performance trials, we calculate size and temperaturedependent response surfaces, which are scaled to geographic performance layers matching the critical thermal limits. We then use these ecophysiological performance layers in a standard correlative SDM framework to predict the potential distribution in southern Africa and Europe. Physiological performance traits (standard metabolic rate and endurance time of adult frogs) are the main drivers for the predicted distribution, while the locomotor performance (maximum velocity and distance moved in 200 ms) of adults and tadpoles have low contributions.

KEYWORDS

amphibian, distributional modelling, ecological niche theory, fundamental niche, invasive species management, mechanistic model, nonnative range, physiological adaptation, species distribution models

1 | INTRODUCTION

Amphibians are the most threatened vertebrate class suffering worldwide dramatic population declines in the last decades (Gonzalez-del-Pliego et al., 2019; Wake & Vredenburg, 2008). Nearly 50% of amphibians are estimated to be threatened by extinction (Gonzalez-del-Pliego et al., 2019). One main threat is the introduction of other invasive amphibians (Blaustein et al., 2011; Measey et al., 2016; Nunes et al., 2019) like the African Clawed Frog, *Xenopus laevis* (Daudin, 1802), which has both a direct negative impact on the indigenous invertebrate and amphibian fauna (Courant et al., 2017; Courant et al., 2018; 2018; Lillo et al., 2011; Vogt et al., 2017), and indirect impact as a potential reservoir for chytridiomycosis (Solis et al., 2010).

The African Clawed Frog, X. *laevis*, is a principally aquatic species native to southern Africa (Measey et al., 2012). In the past, X. *laevis* has

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been extensively used for human pregnancy testing and was distributed pan-globally for laboratory research (Gurdon & Hopwood, 2003; van Sittert & Measey, 2016), and pet trade (Herrel & van der Meijden, 2014; Measey, 2017). Escapees and voluntarily released individuals have resulted in numerous invasive populations outside its native range, and today X. laevis is recognized as one of the world's most widely distributed amphibians occurring on four continents (Ihlow et al., 2016; Measey et al., 2012; Wang et al., 2019). For instance, in Europe it was successfully introduced to France (Fouquet, 2001), Portugal (Rebelo et al., 2010), and Italy/Sicily (Lillo et al., 2005) and further expansions up to more than 1 Million km² in Europe are predicted (Measey et al., 2012).

The identification of conditions limiting a species' distribution is particularly important for the assessment of invasion risk (e.g., Jimenez-Valverde et al., 2011; Kearney et al., 2008). For this task, species distribution models (SDMs) can be a useful tool. Important for SDMs is the concept of the ecological niche. The ecological niche is a combination of abiotic (fundamental) and biotic factors (interactions among taxa such as competition, parasitism, mutualism, predator-prey-relationship, etc.). The fundamental niche contains all abiotic factors that are necessary for species persistence and reproduction (Grinnell, 1917; Hutchinson, 1978; Soberón & Peterson, 2005; Soberón, 2007). Climate is one of the main factors driving the ecological niche and potential distribution of a species (Soberón, 2007: Thuiller et al., 2004). This also seems to be the case for invasive anurans that establish and spread in areas matching their native climatic conditions (Rago et al., 2012; Tingley et al., 2010).

Previous efforts to predict the potential distributions of invasive amphibians across space and time (Ficetola et al., 2007, 2010; Kolbe et al., 2010; Nori et al., 2011) have mainly focused on correlative SDMs that statistically link geographic occurrences to environmental conditions (Dudik et al., 2004; Kearney & Porter, 2009; Peterson et al., 2015). It has been shown that projections of correlative SDMs from the native to a nonnative area are sometimes unable to predict the entire range which could be occupied by a species. This make predictions of future distributions for species questionable (Broennimann et al., 2007).

More recently, process-based approaches like mechanistic or ecophysiological SDMs that determine mechanistic interactions between aspects of the fitness of organisms and their environment have been developed to predict species distributions (Ceia-Hasse et al., 2014; Kearney & Porter, 2009). They have since been applied to lizards (e.g., Buckley, 2008; Kearney & Porter, 2004; Sinervo et al., 2010), freshwater invertebrates (e.g., Gilman et al., 2006), plants (e.g., Case & Lawler, 2017) and invasive amphibians (e.g., Kearney et al., 2008; Kolbe et al., 2010). In contrast to correlative SDMs, mechanistic SDMs are trained by data assessed under laboratory conditions (e.g., critical thermal limits), and do not correlate spatially implicit physiological layers with knowledge of occurrence records (Kearney et al., 2008). Hybrid models combine process-based and correlative approaches by using the output of the first as input for the latter (Buckley et al., 2011). Hybrid and process-based models are more data intensive and require more knowledge of the ecology and physiology of a species (Thuiller, 2007). They are constrained by availability of data and the identification of adequate key processes limiting species distributions (Elith et al., 2010). Process-based and hybrid SDMs emphasize those processes involved in determining range constraints (Morin & Thuiller, 2009), and as such they are more robust in terms of space and time (Elith et al., 2010) because they try to assess the fundamental (climatic) niche.

In ectothermic organisms such as amphibians, physiological performance is strongly influenced by environmental parameters, impacting physiological processes such as muscle contraction (James et al., 2012) and ultimately affecting performance traits such as locomotion (Feder & Burggren, 1992; Herrel & Bonneaud, 2012a; Wilson et al., 2000). The close dependence of ectotherms on environmental conditions (Miller et al., 2004; Parmesan & Yohe, 2003; Sinervo et al., 2010) makes amphibians ideal subjects for species distribution modelling.

Previous maximum entropy (Maxent) models based on native and invasive species records were used to predict suitable areas for X. laevis on a global scale (Ihlow et al., 2016; Measey et al., 2012). The Maxent and ensemble SDMs of Ihlow et al. (2016), however, projected a broader suitable distribution than the Maxent models of Measey et al. (2012). A recent hypervolume model, trained with the complete set of species records across the globe and based on PCA relying on 19 bioclimatic variables, predicted a fragmented distribution of X. laevis across the invaded range (Rödder et al., 2017). Additionally, the hypervolume models' projected distribution in southern Africa resembles the species' current natural distribution well.

Although all of these correlative SDMs predict guite different patterns in the potential distribution across Europe, it is likely that these models do not predict the full invasive potential of this species. Increased funding (for instance by INVAXEN [Invasive biology of X. laevis in Europe: ecology, impact, and predictive models]) and resultant laboratory research have resulted in a copious amount of literature and provided input data for models (van Wilgen et al., 2018). For example, field and laboratory research has provided information on environmental constraints affecting the species' diurnal and annual activity patterns, reproduction, and thermal tolerances (De Villiers & Measey, 2017; Eggert & Fouquet, 2006; McCoid & Fritts, 1989; Measey, 2016; Wilson et al., 2000). These studies indicate that X. laevis is a species with a strongly underestimated invasive potential.

Temperature affects physiological traits, such as digestive and locomotive performance, and is one of the most important extrinsic factors affecting the biology of ectotherms (Angilletta et al., 2002; Bennet, 1990; Huey & Kingsolver, 1989). In pipid frogs, such as X. laevis, temperature affects fitness-relevant traits like reproduction, larval development (Balinsky, 1969), endurance capacity (Herrel & Bonneaud, 2012a), sprint performance (Miller, 1982), and swimming velocity (Herrel & Bonneaud, 2012a; Wilson et al., 2000), of adults and tadpoles (Wilson et al., 2000). Additionally, these physiological traits give an indicator for energy use and balance, and are critical traits in amphibian biology (Wygoda, 1984). Here we use ecophysiological models to assess the potential distribution of the African Clawed Frog, X. laevis, across Europe, and compare relevant performance traits of tadpoles and adult frogs from the native population.



Full variable name	Abbreviation	Description
Maximum velocity	MaxVel	Maximum swimming velocity
Distance moved in 200 ms	D200	Distance moved in 200 ms
Endurance distance	EndurDist	Distance moved until animal is exhausted
Endurance time	EndurTime	Time until animal is exhausted
Standard metabolic rate	SMR	Standard metabolic rate of an animal
Evaporative water loss	EWL	Water loss of an animal due to evaporation
Hours of activity	h_a	Daily hours when performance is possible
Hours of restriction	h_r	Daily hours when performance is not possible
Critical thermal minimum	CT _{min}	Minimum temperature at which performance of an animal is 0
Critical thermal maximum	CT _{max}	Maximal temperature at which performance of an animal is 0
Optimum temperature	T _{opt}	Temperature at which performance is at its maximum
Predicted performance	Pred_perf	Predicted performance at T_{opt}

2 | METHODS

2.1 | General methodological approach

Based on the results of physiological performance trials (for performance variables and their abbreviations see Table 1), we computed temperature (for tadpoles and adults) and body-size dependent (adults only) response surfaces characterizing the performance of tadpole and adult *X. laevis* in geographic space. These surfaces were scaled to a range matching the physiological limits (critical thermal minimum and maximum, CT_{min} , CT_{max}). Environmental layers were then used to assess the predicted performance of the species in geographic space. These ecophysiological performance layers were subsequently used in a popular correlative SDM framework to predict the potential distribution of *X. laevis* in southern Africa and Europe.

2.2 | Selection of specimens and traits

Phylogeographic studies assume the most likely origin for most invasive populations in Europe is the south-western Cape of South Africa's winter rainfall region (De Busschere et al., 2016), which is supported by climate matching analyses (Rödder et al., 2017) and export records (Measey et al., 2020; van Sittert & Measey, 2016). However, the French invasive population consists of a mixture of clades from both of South Africa's winter and summer rainfall regions (De Busschere et al., 2016). Thermal performance trials were made on adult frogs collected in Port Elizabeth Eastern Cape province, which could be characterized as an all year round rainfall region, indicative of the southern Cape region. It is located between both regions, and has genetic clades representing both areas (Measey et al., 2017). For thermal performance trials of tadpoles, we used tadpoles bred from adult frogs sampled from Stellenbosch and

Potchefstroom, South Africa. Stellenbosch, Western Cape province, is an area in the winter rainfall region, while Potchefstroom, north-west province, was chosen to represent the summer rainfall region.

Under laboratory conditions, the following physiological performance data were determined for adult frogs: burst swimming performance measured as maximum velocity (MaxVel), evaporative water loss (EWL), standard metabolic rate (SMR), endurance time (EndurTime) and endurance distance (EndurDist). For tadpoles, the following physiological performance data was assessed: maximum velocity (MaxVel) and distance moved in the first 200 ms (d200) after a startle response.

2.3 | Locomotor performance of adult frogs

The performance trait maximum velocity (MaxVel) was chosen because it provides an indicator for burst performance, important in contexts of prey capture and predation avoidance. Adult X. laevis were kept at 20°C. Swimming speed performance traits were recorded by randomly choosing 10 individuals (5 males and 5 females) for each temperature trial from a pool of 30 individuals. Performance trials were conducted in a climate chamber, ranging from ambient temperatures of 10°C, 15°C, 20°C, 25°C, and 30°C (Herrel & Bonneaud, 2012a, 2012b; Wilson et al., 2000). Before conducting the trials, the climate chamber was set overnight to reach the target temperature and the trials were started only when the temperature was within a 1°C range, measured with a thermocouple thermometer in the climate chamber (Fluke 54IIB, Fluke Corporation, Washington). To minimize any effect of a directional shift in temperature on performance, the sequence of target temperatures was randomly determined. One hour before the trials started frogs were placed in separate boxes with water in an incubator set at the test temperature (Navas, 1996). All performance trials were iterated twice for each individual animal with an intertrial period of one hour, during which

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specimens were removed to the incubator to be retained at the target temperature allowing recovery. Experiments were conducted in a transparent Perspex tank (2.0 m × 0.4 m × 0.4 m), which was marked at 25 cm steps. A mirror with size 1.4 m × 0.4 m was assembled at a 45° angle above the tank to make sure that during experiments, frogs were visible from dorsal and lateral aspects. Only the best aspect was used for processing.

A high-speed digital video camera (Canon PowerShot G15, Canon Inc.) set at 240 frames s⁻¹ (fps) was used to assess burst swimming performance. A light tap on the urostyle was used to initiate swimming. The video clips were cut to contain at least two movement cycles and then analyzed manually. The image tracking software Blender (version 2.74; Blender Foundation) was used to digitize the snout tip and track it across all frames that successfully captured the two movement cycles. The coordinates of the frog were imported in Excel (Microsoft) and the displacement of the individual along its trajectory was computed. An adapted version of Winter (2005) zero phase shift low-pass Butterworth filter version 2 with the cut-off frequency set at 30 Hz was used to smooth the raw displacement profile. Peak instantaneous velocity was computed by numerical differentiation of the smoothed displacement profiles. The maximum velocity across all swimming sequences assessed were extracted for each specimen at each temperature. Thus, maximum velocity may come from different swimming performance trials (Herrel & Bonneaud, 2012a, 2012b; Herrel et al., 2012, 2014).

2.4 Physiological performance of adult frogs

The physiological variables evaporative water loss (EWL), standard metabolic rate (SMR), endurance time (EndurTime), and endurance distance (EndurDist) were used. These variables give an indication of how a species uses energy and balance water loss, which is a critical aspect in amphibian biology (e.g., Wygoda, 1984). An open-flow respirometry system after Lighton (2008) and Stevermark et al. (2005) was used to measure EWL and SMR using a push-through mechanism on non-gravid, post-absorptive frogs during rest (Sinclair et al., 2013). Trials were undertaken at seven temperatures spanning from 5°C to 35°C at 5°C steps (Dunlap, 1971). Eight frogs (four males: four females) were randomly chosen from a pool of 30 individuals for experiments at each temperature and a single trial was conducted on each specimen per temperature step. Individuals were placed separately in appropriately sized air-tight glass metabolic chambers. Metabolic experiments were conducted using Mass Flow respirometry operated on a push-through mechanism. Atmospheric air was scrubbed of water vapor before being passed through the metabolic chambers. Air from the metabolic chambers was sequentially sub-sampled, to record gas concentrations at 20 min intervals, recording an air sample every second. To estimate EWL, we measured water vapor pressure until stability was reached. To ensure that the recorded gas and water vapor readings excluded any sudden movement by the frogs, we used a live video feed to monitor the behavior of the frogs during the experiment. Subsequently, all experimental trials within which animals made sudden movements were excluded from the analysis. An experiment was ended when the temperature trace and water vapor pressure was stable for 20 min or when a frog seemed too distressed to continue with assessment. Experiments lasted no more than 2 h (cf., Mokhatla et al., 2019 for detailed methods and data analysis).

For maximum exertion (endurance) experiments, six adult specimens (three males and three females) were randomly chosen from a pool of 30 for each sprint at five temperatures spanning 10-30°C at 5°C intervals (10, 15, 20, 25 and 30). We chased an individual animal along a 4.7 m circular track until exhaustion. This was expressed as the point at which the individual was not able to right itself when flipped on its back (Herrel & Bonneaud, 2012a, 2012b). Experiments were undertaken on dry surface only. We recorded mass to the nearest 0.01g before and after the experimental run. Similar to the burst speed performance trials, we made sure that body temperature was within 1°C of the target temperature before trial by recording the cloacal temperature using a thermocouple probe (Fluke 54IIB, Fluke Corporation). The floor of the track was covered with a high friction matting (GECKO® Non-slip matting, Cape Town) to improve traction. For each individual, we recorded both the total distance (EndurDist) and the time (EndurTime) spent moving until exhaustion (Herrel & Bonneaud, 2012b).

2.5 Locomotor performance of tadpoles

We followed an adapted version of the protocol to measure activity of tadpoles in response to acute temperature designed by Wilson et al. (2000). X. laevis tadpoles were lab-reared at 22°C until NF stage 45-47 (Nieuwkoop & Faber, 1994). Developing eggs and tadpoles were kept in 12:12 day:night cycle, fed Frog Brittle® for tadpoles (NASCO), and kept at a high density of 15 specimens L^{-1} to decelerate development (Tejedo & Reques, 1994). For performance trials, ten specimens from each site were chosen for burst swimming speed performance at five temperature levels: 5°C, 10°C, 20°C, 30°C, and 35°C.

Tadpoles were acclimated for the trials by changing the tank water temperature at a rate of 0.2°C min⁻¹ until the target temperature was reached. Trials were randomized by assigning random numbers to each trial. We filmed at least five burst swimming responses for each specimen at each specific temperature level to assess burst swimming performance. Each tadpole was only tested once at one test temperature and then euthanized by an overdose of tricaine methanesulfonate (ms-222). The initial burst swimming sequence was filmed with a camera (Olympus, TG-4) at 120 frames s^{-1} . Tadpoles were touched with a fine wire at the tip of their tail to initiate movement. We used a 0.42 m × 0.08 m × 0.17 m clear plastic tank filled with 1 L aged tap water for performance trials. For better visualization of movement by tadpoles in the lateral plane we used a mirror attached to the side of the tank at an angle of 45°. The bottom of the tank was covered with a false bottom where water could circulate through custom-built copper pipes. A water bath (Julabo F12, 4.5 L, max flow 15 Lmin^{-1} , pressure = 0.35 bar) maintained the desired water temperature.

High-speed videos were filmed from the bottom of the tank and the image in the mirror. All burst swimming sequences were visually proofed and only recordings perpendicular to the filming camera were chosen. We used the motion analysis software Tracker (Open Source Physics; Brown, 2009) to obtain X and Y coordinates from the high-speed videos. Coordinates were exported to Excel (Microsoft) and the displacement (cm) of the specimen was computed. We chose a fourth order zero-phase shift low-pass Butterworth filter (Winter, 2005) with 12 Hz filter frequency to filter the displacement data. Cut-off frequency was chosen as a 10th of the recording frame rate. From the filtered data, maximum velocity and distance moved in 200 ms were extracted. Temperatures were recorded with a thermocouple (to the nearest 0.01°C).

Ecophysiological response surfaces and 2.6 ecophysiological rasters

Based on information obtained under laboratory conditions we computed temperature and size dependent response surfaces for adults and tadpoles applying the PerfGAMM2()-function of the Mapinguari package (Sinervo, unpubl.) for R ver. 3.6.2 (R Core Team, 2020). Applying generalized additive models (GAM) with temperature as a smooth predictor and size as linear predictor, the response surfaces were scaled to population-specific critical thermal minimum and maximum by adding these critical thresholds with a performance of zero. By doing so, the data frame used for GAM fitting contained both the performance per temperature step as measured during the experiments and the CT_{min} and CT_{max} values where performance is assumed to be zero. Based on literature CT_{min} was set at 3°C for the native and invasive population and CT_{max} was set at 35°C for the native population and 39°C for invasive population (Courant & Herrel, pers. comm.). Finally, the PerfGAMM2()function estimated the predicted performance (pred perf) at optimum temperature (T_{opt}) and the critical thermal thresholds (CT_{min} and CT_{max}). As these performance surfaces showed for all variables only very marginal effects of body size for the adult frogs, we subsequently used results for a specimen of 70 mm snout-vent length and translated the respective function in geographic space. For environmental layers we obtained monthly temperature minimum, maximum and averages with a spatial resolution of 2.5 arc min from www.worldclim.org

(Hijmans et al., 2005). Furthermore, we computed ecophysiological layers describing the annual hours of activity and hours of restriction by applying the Senoid option in the EcophysRaster()-function of the Mapinguari package for R (Sinervo, unpubl.). This function simulates daily variation in temperature for each grid cell by computing a sine wave between maximum and minimum temperature at each grid cell and can be used to estimate the annual energetic budget of the species.

2.7 Species distribution modelling

For data preparation and correlation analyses we used QGIS ver. 3.10 (QGIS Team, 2020), ArcMap ver. 10.6 (ESRI, 2008), R ver. 3.6.2 (R Core Team, 2020) and R's raster package ver. 3.0.12 (Hijmans, 2016). As correlative species distribution modelling (SDM) is sensitive to multi-colinearity of predictors, which can be assumed when measuring the temperature dependence of performance via multiple physiological responses, we computed pairwise Spearman rank correlations between all possible pairs of predictors for tadpoles and adults (Tables 2 and 3). Among pairs with rho exceeding 0.75 we selected only one ecophysiological variable for further processing.

For SDM development we used Maxent 3.4.1 (Elith et al., 2011; Phillips et al., 2006). A total of 616 native species records were compiled from a combination of own field work, and records with > 1s accuracy from Measey (2004). Modelling range shifts in species such as invasive taxa is especially challenging as in invasive ranges the basic assumption of a range equilibrium with environmental conditions is frequently not met (Elith et al., 2010), which is also the case for invasive populations of X. laevis in Europe (Rödder et al., 2017). Therefore, we restricted our analyses to the native range and projected the results onto the European invasive range.

For the environmental background we selected an area defined by a circular buffer of 200 km around each grid cell containing water in southern Africa. For this, global layers containing surface waterbodies that persist at least 50% of the year were obtained from Pekel et al. (2016) in a 30 m resolution and subsequently clipped to get the

	EndurDist	EndurTime	EWL	MaxVel	h_a	h_r	SMR
EndurDist	1						
EndurTime	0.974	1					
EWL	0.754	0.721	1				
MaxVel	0.095	0.103	0.008	1			
h_a	0.116	0.158	0.254	0.057	1		
h_r	0.113	0.12	0.002	0.116	0	1	
SMR	0.75	0.721	1	0.009	0.265	0.002	1

TABLE 2 Pairwise Spearman rank correlations among ecophysiological rasters developed based on performance of native adult frogs

Abbreviations: EndurDist, endurance distance; EndurTime, endurance time; EWL, evaporative water loss; h_a, hours of activity; h_r, hours of restriction; MaxVel, maximum velocity; SMR, standard metabolic rate.

Values in bold exceed rho of 0.75.

TABLE 3 Pairwise Spearman rank correlations among ecophysiological rasters developed based on the performance of native tadpoles from the SR (summer rainfall) and WR (winter rainfall) region

SR d200 SR MaxVel SR h_a SR h_r WR d200 WR MaxVel WR h_a WR h_r SR d200 NA SR MaxVel NA 1 SR h a NA 0.221 1 SR h_r 0.003 0 1 NA WR d200 NA NA NA NA NA NA WR MaxVel NA 0.781 0.188 0.004 NA 1 WRha NA 0.221 1 0 NA 0.188 1 0 WR h_r NA 0.003 0 NA 0.004 1 1

Abbreviations: d200, distance moved in 200 ms; MaxVel, maximum velocity; h_a, hours of activity; h_r, hours of restriction; SR, summer rainfall; WR, winter rainfall.

Values in bold exceed rho of 0.75.

waterbody-availability for southern Africa and Europe. We clipped the layers with a high-resolution coastline shapefile to exclude saltwater bodies. Both layers were reclassified to obtain an area of 5 km (twice the maximum recorded terrestrial dispersal distance of *X. laevis*; Measey, 2016) around each grid cell containing water. For southern Africa, the layer was also reclassified to delimit an area of 200 km around each water grid cell, which was used as background-file for modelling. For modelling purposes we resampled each layer to 2.5 arcmin resolution. After modelling, we clipped the resulting SDM maps with the water-availability layers.

The species' records were randomly divided 100 times, with 70% used for model training and 30% used for model evaluation using a bootstrap approach. The Area Under the Receiver Operating Characteristic Curve (Swets, 1988) and True Skill Statistics (Allouche et al., 2006; Somodi et al., 2017) were used to evaluate model performance. We increased the number of maximum iterations from 500 to 5000 to give the model adequate time for convergence, although the model does not over- or under-predict relationships (Young et al., 2011). The average prediction across all 100 replicates was used as our final result. Distribution maps were displayed using Maxent's cloglog output format. "Minimum training presence cloglog threshold" was set as hypothetical thresholds for presence-absence (c.f. Phillips et al., 2006). MESS (Multivariate Environmental Similarity Surfaces) maps were provided to highlight possible extrapolation errors (Elith et al., 2010).

The *area*()-function of the *raster* package (Hijmans, 2016) was applied to predicted areas of the respective ranges, which were corrected by minimum training presence thresholds, to calculate the predicted areas of our SDMs and the correlative SDMs (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017). The results were rounded to 100 km² due to uncertainties in calculation. For calculation, the grid-files of the maps were reclassified with DIVA GIS (Hijmans et al., 2002). We set values above minimum training presence logistic/cloglog threshold as suitable area and reclassified them to get the value "1" while non-suitable area below this threshold was set as "NoData."

3 | RESULTS

3.1 | Ecophysiological performance surfaces

For adult frogs, the performance surfaces revealed significant effects of temperature on performance but very marginal effects of body size for all variables (Table 4). Performance surfaces of MaxVel for adult frogs revealed pred_perf = 2.8 m s^{-1} , $T_{opt} = 29.1^{\circ}\text{C}$, $\text{CT}_{min} = 2.8^{\circ}\text{C}$ and CT_{max} = 35.1°C. The optimum body size to perform the best MaxVel was 72.2 mm. Both endurance variables revealed very low optimum temperatures. Critical thermal limits were similar to the other variables (EndurTime: native: pred_perf = 856.2 s, T_{opt} = 12.3°C, CT_{min} = 2.4°C, CT_{max} = 35.8°C, size = 78.0 mm; EndurDist: native: pred_perf = 35.9 m, T_{opt} = 19.0°C, CT_{min} = 2.9°C, CT_{max} = 36.8°C, size = 74.3 mm). EWL and SMR revealed nearly the same values for temperature and body size dependence (EWL: pred_perf = 0.4 mg h⁻¹, T_{opt} = 31.5°C, CT_{min} = 2.6°C, SMR: pred_perf = 12.3 ml h^{-1} CT_{max} = 39.2°C, size = 51.5 mm; T_{opt} = 31.5°C, CT_{min} = 2.5°C, CT_{max} = 39.5°C, size = 52.1 mm).

For tadpoles, the performance surfaces of MaxVel and d200 revealed a similar pattern shown by the adult frogs (Table 4). Individuals of both rainfall regions show similar values for all categories of both locomotor variables (MaxVel: native_summerrain: pred_perf = 11.5 cm s⁻¹, $T_{opt} = 30.2^{\circ}$ C, CT_{min} = 3.2°C, CT_{max} = 38.6°C; native_winterrain: pred_perf = 12.2 cm s⁻¹, $T_{opt} = 29.8^{\circ}$ C, CT_{min} = 3.4°C, CT_{max} = 38.8°C; d200: native_summerrain: pred_perf = 1.5 cm, $T_{opt} = 29.8^{\circ}$ C, CT_{max} = 38.6°C; native_winterrain: a.4°C, CT_{max} = 38.6°C; native_winterrain: pred_perf = 1.4 cm, $T_{opt} = 29.3^{\circ}$ C, CT_{min} = 3.7°C, CT_{max} = 39.3°C).

3.2 | Ecophysiological rasters

For adult frogs (Figure 1), the projections based on MaxVel showed a fragmented pattern for the native range with tendency of better performance in the north, while for the invasive range a gradient from western-coastal to eastern-continental (high to low values) is visible. Hours of activity for adult frogs are very high in nearly the

	Performance	Pred_perf	Topt (°C)	CTmin (°C)	CTmax (°C)	Body size (mm)
Adult	MaxVel	2.8	29.1	2.8	35.1	72.2
	EndurTime	856.2	12.3	2.4	35.8	78.03
	EndurDist	35.9	19.0	2.9	36.8	74.3
	EWL	0.4	31.5	2.6	39.2	51.5
	SMR	12.3	31.5	2.5	39.5	52.1
Tadpoles	MaxVel	11.5	30.2	3.2	38.6	-
Native SR	d200	1.5	29.8	3.4	38.6	-
Tadpoles	MaxVel	12.2	29.8	3.4	38.8	-
Native WR	4200	14	20.3	37	30.3	

TABLE 4 Results for ecophysiological performance surfaces for adult and tadpole *Xenopus laevis*

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Abbreviations: d200, distance moved in 200 ms; CTmin and CTmax, critical thermal limits; EndurDist, endurance; distance; EndurTime, endurance time; EWL, evaporative water loss; Pred_perf, predicted performance; MaxVel, optimal body size for the performance traits maximum velocity; SMR, standard metabolic rate; Topt, optimum temperature.

entire native range, while for the invasive range a western-coastal to eastern-continental gradient (high to low values) was found. The performance for hours of restriction was very low for both native and invasive range. The projections of EndurDist and EndurTime to the native and invasive range revealed a gradient from coast to inland (high to low values). Compared to EndurDist, EndurTime shows only small areas with high values. The projection of EWL and SMR to the native range revealed a north-south gradient (high to moderate values). The projection to the invasive range resulted in a moderate (western and southern Europe) to low (central-eastern Europe and mountain ranges) EWL performance.

All ecophysiological rasters for tadpoles (Figure 2) revealed similar patterns for summer and winter rainfall populations with no significant differences. For the native range, performance of MaxVel showed a north-south gradient (high to low values), while for the invasive range a gradient from western-coastal to eastern-continental (high to low values) was also found. The performance of d200 showed a uniform pattern in the entire native range, while for the invasive range a discrete pattern with low values in the mountain ranges (Alps, Pyrenees) and high values in the rest of Europe was found. Hours of activity were high in nearly the entire native range and showed a western-coastal to eastern-continental gradient (high to low values) in the invasive range. Hours of restriction were very low in both ranges.

3.3 Species distribution modelling

Acknowledging the pairwise assessment of Spearman rank correlation coefficients between ecophysiological variables (Tables 2 and 3), the final set of predictors comprised MaxVel, hours of activity, hours of restriction, EndurTime and SMR for adult frogs, and MaxVel, hours of activity and hours of restriction all from summer rainfall region for tadpoles. EndurDist and EndurTime, EWL and SMR, as well as MaxVel, hours of activity and hours of restriction from summer rainfall region and their respective counterparts from winter rainfall region were highly correlated (rho > 0.75) and therefore constrained to the predictors EndurTime and SMR for adult frogs, and MaxVel, hours of activity and hours of restriction from summer rainfall region for tadpoles. D200 from both regions did not show specific geographical patterns, and was therefore omitted.

For adult frogs, SMR on average had the highest contribution across the 100 SDMs (72.9%), followed by EndurTime (23.3%), hours of activity (2%), MaxVel (0.9%) and hours of restriction (0.8%). Model performance was good (AUC_{Training} = 0.775, AUC_{Test} = 0.768, TSS_{Training} = 0.904, TSS_{Test} = 0.901). For tadpoles, MaxVel on average had the highest contribution across the 100 SDMs (87.2%), followed by hours of activity (12.7%), and hours of restriction (0.1%). Model performance was good (AUC_{Training} = 0.733, AUC_{Test} = 0.727, $TSS_{Training} = 0.801$, $TSS_{Test} = 0.796$). For adult frogs and tadpoles together, SMR on average had the highest contribution across the 100 SDMs (71.5%), followed by EndurTime (24.6%), hours of activity for adults (0.9%), hours of restriction for adults (0.7%), MaxVel of tadpoles (0.7%), MaxVel of adults (0.7%), hours of activity for tadpoles (0.6%) and hours of restriction for tadpoles (0.2%). Model performance was good (AUC_{Training} = 0.777, AUC_{Test} = 0.766, TSS_{Training} = 0.900, TSS_{Test} = 0.896). All SDMs predict similar patterns with suitable climate space for large parts of southern Africa as well as most of Europe (Figure 3). Large MESS areas are predicted in eastern Europe where predictions should be treated with caution.

Our approaches resulted in the largest area of predicted distribution for X. *laevis* with up to 1,949,900 km² in the European invasive range, while the correlative SDMs predicted much smaller distributions of 6.8%-51% (Table 5). For the native range, the combination model of adults and tadpoles also predicted the largest area among our ecophysiological SDMs (1,022,400 km²), followed by the model for the adults (917,900 km²), and last tadpoles (904,000 km²). The correlative approaches predict 35.7%-169.9% of our maximum predicted area.



FIGURE 1 Ecophysiological rasters of adult *Xenopus laevis*: Performance assessed by maximum velocity (MaxVel), hours of activity, hours of restriction, endurance distance (EndurDist), endurance time (EndurTime), evaporative water loss (EWL), and standard metabolic rate (SMR) projected to the native and invasive range. Warm colors represent high values, while cold colors represent low values [Color figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

For adult frogs and tadpoles, the ecophysiological rasters revealed significant differences in locomotor performance, but similar patterns for hours of activity and hours of restriction (Figure 1+2). Our SDMs show that the physiological performance of adult frogs, especially SMR and EndurTime is the main driver for the predicted distributions. The locomotor performance of tadpoles had low variable contribution to the SDMs. Hours of activity and restrictions for adults and tadpoles and d200 of tadpoles seem to be not a significantly limiting factor for the potential distribution in Europe and southern Africa. The potential distribution suggested by the SDM matches the realized distribution of the species in southern Africa very well. Moreover, major parts of Europe are also characterized as suitable.

4.1 | Locomotor performance

Previous studies suggested that X *laevis* preferred an ambient temperature of 22° C (Miller, 1982) and can withstand temperatures of 14°C to 32°C (Casterlin & Reynolds, 1980). Some authors assumed

X. *laevis* can resist more extreme temperature limits (Nelson et al., 1982). The invasive population in France can withstand critical thermal limits from 2°C to 39°C (Courant & Herrel, personal communication). Laboratory studies indicate a different tolerance of extreme temperatures among the life stages (Balinsky, 1969; Wu & Gerhart, 1991) and ontogenetic shifts during embryonic development appear to affect thermal limits (Nelson et al., 1982). However, thermal tolerance data is limited to adult specimens originating from the Eastern Cape, but the temperature tolerances among the different native populations remains poorly studied (Rödder et al., 2017).

Our results support the observations that adult X. *laevis* can endure a broader temperature spectrum than previously assumed. T_{opt} for locomotor performance traits (MaxVel and d200) were similarly high among adults and tadpoles independent of summer or winter rainfall region (range: 29.1–30.2°C). While CT_{min} was similar among adults and tadpoles (range: 2.8–3.7°C), CT_{max} was much higher for tadpoles (range: 38.6–39.5°C) than for adults (35.1°C). Our results indicate that tadpoles can tolerate a broader temperature spectrum than previously suggested at least for short-term events. Although, it should be mentioned that it is challenging to conclude long-term performance and persistence in habitats from



FIGURE 2 Ecophysiological rasters of tadpole *Xenopus laevis* from the summer (upper row) and winter rainfall region (lower row): Performance assessed by maximum velocity (MaxVel), distance moved in 200 ms (d200), hours of activity, and hours of restriction, projected to the native and invasive range. Warm colors represent high values, while cold colors represent low values [Color figure can be viewed at wileyonlinelibrary.com]

short-term experiments, and it remains unclear how the performance and critical thermal limits change when specimens are exposed to several hours, days or weeks of temperature extremes.

Southern Africa occupies a wide variety of biomes and bioregions from deserts, xeric shrubland, grasslands, Mediterranean forests to (sub-)tropical moist broadleaf forests (Rutherford et al., 2006; van Wilgen et al., 2020). The major parts of the distribution of the south-western Cape clade where most of the European populations were derived (De Busschere et al., 2016) is characterized by a Mediterranean climate (Measey et al., 2012): hot dry summers and cold wet winters. The species occurs in a wide geographic range from the winter rainfall regions in the south-western Cape to summer rainfall regions in the north, and from sea level up to 3000 m in Lesotho (Measey, 2004). According to the hours of activity and restriction the daily temperature variation in nearly all of the native range is suitable for the ecophysiological performance of X. laevis. The ecophysiological rasters show that the daily temperature extremes in southern Africa and Europe have only a marginal effect on the hours of restriction in both ranges.

The climate in western, central, southern and eastern Europe can be classified into three main climate types: Western Europe has

an oceanic climate with mild winters and cool summers, eastern Europe provides a continental climate with cold winters and hot summers, whereas central Europe has a hybrid climate between these climates, and the Mediterranean sea region is characterized by mild, rainy winters and hot, dry summers. Especially the oceanic and Mediterranean regions of Europe seem suitable for new introductions of animals from native populations of *X. laevis*. The more eastern continental regions and mountain ranges (Alps, Pyrenees) seem unsuitable for the species, due to the temperature extremes. However, a recent study revealed that the French *X. laevis* population, which was introduced c. 40 years ago, went through a temperature dependant shift in their locomotor performance indicating a shift in the fundamental niche of the species. French animals are adapted to the colder European climate and endure a broader temperature spectrum than native individuals (Araspin et al., 2020).

4.2 | Physiological performance

Physiological variables such as EWL, SMR, EndurDist, and EndurTime give an indicator for energy use and balance, and are critical traits in



FIGURE 3 Ecophysiological models of adults, tadpoles and adults and tadpoles together based on data assessed from the native population projected to the native range (top) and the invasive European range (bottom). Dark colors represent highly suitable areas while light colors represent unsuitable areas. Dark gray areas represent MESS areas, which should be treated with caution because at least one predicting variable is exceeding the training range of the models and hence require extrapolation. Points represent the records [Color figure can be viewed at wileyonlinelibrary.com]

amphibian biology (Wygoda, 1984). However, for an aquatic species as X. *laevis* EWL is important during terrestrial movement only (Du Plessis, 1966; Measey & Tinsley, 1998; Mokhatla et al., 2019). Specimens from Great Britain are known to move up to 2 km a day (Measey & Tinsley, 1998). Capture-mark-recapture trials in the native region showed that X. *laevis* can move 2.36 km Euclidean distance on land, but mostly move between 200 and 400 m per dispersal event (De Villiers & Measey, 2017). Further, it is assumed that X. *laevis* uses small waterbodies during the rainy season to reach more distant locations (Faraone et al., 2008; Measey, 2016).

Our results show a gradient of SMR in the native range from north (high values) to south (low values) and one of EndurTime with highest values at the southern coast region. Despite this, the *X. laevis* extent of occurrence extends past the northern regions of South Africa (up to Malawi) with high predicted EWL and SMR. It seems more likely that the availability and density of waterbodies restricts the expansion of this species more than SMR, and it has been suggested that man-made impoundments have resulted in an expansion from a much more restricted original native range (Measey et al., 2017; Measey et al., 2020). Major parts of southwestern to north-western regions of southern Africa are characterized by deserts and xeric savanna such as Kalahari, Succulent Karoo, Nama Karoo or Namib (Rutherford et al., 2006), where *X. laevis* is largely absent. Further, *X. laevis* has a broad tolerance spectrum of environmental conditions suffering a high anoxic tolerance (Measey et al., 2012) and can survive up to eight months without water, which is useful to survive droughts and to colonize ephemeral waterbodies (Tinsley & Kobel, 1996). The projection of EWL and SMR

TABLE 5 Comparison among our ecophysiological (Ginal et al., 2020) and previous correlative (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017) Species distribution model (SDM) approaches: Predicted area of distribution in the native and invasive range in km² and percentage relative to the ecophysiological SDM

	Native (km ²)	Native (%)	Invasive (km ²)	Invasive (%)
Ecophysiological SDM—Adults (Ginal et al., 2020)	917,900	89.8	1,949,900	100.0
Ecophysiological SDM—Tadpoles (Ginal et al., 2020)	904,000	88.4	1,949,900	100.0
Ecophysiological SDM—Adults and tadpoles (Ginal et al., 2020)	1,022,400	100.0	1,949,900	100.0
Maxent (Measey et al., 2012)	364,600	35.7	175,600	9.0
Maximum entropy (Ihlow et al., 2016)	908,300	88.8	803,200	41.2
Ensemble (Ihlow et al., 2016)	1,232,000	120.5	993,800	51.0
bdw approach (Rödder et al., 2017)	1,390,100	136.0	132,600	6.8
MCP approach (Rödder et al., 2017)	1,736,800	169.9	132,600	6.8



FIGURE 4 Comparison among different correlative SDM approaches from left to right: Maxent (Measey et al., 2012), maximum entropy and ensemble model (Ihlow et al., 2016), hypervolume models: bdw and mcp approach (Rödder et al., 2017). Minimum training presence was calculated as threshold (dark gray). The middle gray represents the area of extrapolation (MESS/MASK), which should be treated with caution because at least one predicting variable is exceeding the training range of the models and hence require extrapolation. The background is underplayed with a country layer (light gray) [Color figure can be viewed at wileyonlinelibrary.com]

performance onto Europe resulted in a west-east gradient (moderate to low values). Also a moderate to high EWL and SMR seems appropriate for a successful persistence of X. laevis because the currently colonized regions in Europe (Portugal, Rebelo et al., 2010; Sicily, Lillo et al., 2005) resemble the native, Mediterranean conditions most appropriate for the southwestern Cape clade population. Furthermore some of the invasive ranges, that is France (Fouquet, 2001), is characterized by a very high density of waterbodies, and a dense hydrographic network (Vimercati et al., 2020) which suggests that pressures regarding water losses are much milder than in the native range (compare to Figure 3 and see Section 2 for background selection). However, two invasive populations persisted for decades in Great Britain and also reproduced (Measey, 2001), where a moderate EWL and SMR is predicted. It was speculated that their disappearance was linked to extreme weather conditions (cold and drought) of consecutive winters, suggesting climatic conditions surpassed the buffering capacity of the microhabitat (Tinsley et al., 2015). The second key driver of X. laevis distribution is EndurTime which is highest in regions with moderate climate.

The combination of SMR and EndurTime of adult frogs seem to be the best predicting variables for *X. laevis* distribution with highest contribution to the 100 SDMs (SMR: 72.9% for adults and 71.5% for adults and tadpoles combined; EndurTime: 23.3% for adults and 24.6% for adults and tadpoles combined).

4.3 | Comparison among correlative and physiological SDMs

In contrast to previous correlative SDMs (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017), our work reveals a much higher risk of invasion, especially for most parts of Europe (compare to Table 5,

Figures 3 and 4). The ecophysiological SDMs for adult frogs, tadpoles, and both life stages combined revealed similar patterns for the native range and an almost identical pattern for the invasive range, although the SDM taking into account adults and tadpoles together revealed the largest predicted area for the native range. For the native range, particularly southern to eastern southern Africa is predicted as suitable habitat, while the deserts and xeric savanna in the south-western to north-western regions are climatically unsuitable. Cold areas such as mountain ranges like Drakensberg are predicted as mostly unsuitable. despite the known presence of this species there (Measey, 2004). It is possible that the specimens from these regions locally adapted to a much colder high-altitudinal environment. For the invasive European range, especially large parts of western, southern and central Europe as well as large parts of the North African coastline and many Mediterranean islands are predicted as being climatically suitable for X. laevis. This also includes the currently occupied areas Portugal, France, and Wales, while Sicily is predicted as unsuitable, which is probably due to the low density of waterbodies, which is probably as this area could not be assessed by our waterbody availability layer. Further, large MESS areas in central to eastern Europe as well as cold mountain ranges such as Alps and Pyrenees are predicted, where predictions should be treated with caution.

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The assessment of physiological limits indicates that *X. laevis* is a species with high potential to acclimatize to novel environmental conditions that can survive temperature extremes and shows a broad temperature spectrum, allowing it to colonize even temperate regions in Europe. Further, temperature in microhabitats can deviate strongly from those of the wider ecosystems, effectively buffering extremes and therefore reducing mortality rates during extreme weather events (Scheffers et al., 2014). On larger time scales, like monthly averages, the buffering capacity may be reduced as the averages of the microhabitat temperature and ambient temperature may reach equilibrium (Rödder et al., 2017). Water, the principle habitat of *X. laevis*, buffers short-term

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weather extremes of air temperature and provides shelter during these events (Lampert & Sommer, 2007). In lentic habitats, water temperatures in the hypolimnion do not decrease below 4°C (Lampert & Sommer, 2007), effectively protecting submerged frogs from potentially lethal minimum air temperatures. It is known that specimens avoid exposure to critical temperatures by moving into cooler water sections when exposed to high temperatures (47°C) in Arizona (Measey, 1997) or dig pits into the mud (McCoid & Fritts, 1980). Freezing may be a major mortality factor (Eggert & Fouquet, 2006), although specimens were observed moving at 5°C (Wilson et al., 2000) and throughout winter in France (Courant & Herrel, personal communication) and swimming under ice in Wales (Measey, 2001). While adult frogs may be active and foraging under ice-covered water, the development of tadpoles is hampered under these conditions (Measey, 1997).

5 | CONCLUSION

According to our ecophysiological SDMs, X. laevis has a much higher invasive potential than previous correlative approaches had suggested. An area of 1,949,900 km² is predicted as potentially climatically suitable for X. laevis. Especially the oceanic and Mediterranean climate spaces in Europe and North Africa seem to be an ideal habitat. Additionally, an ongoing shift in the fundamental niche of the French population combined with scenarios of climate change could lead to further expansion into new ranges, which are currently predicted to be unsuitable for this species. The French invasive population seems to make use of hydrographic networks and has now reached the Loire River catchment which covers about 20% of the French national territory. River networks may assist the expansion even in areas with moderately suitable conditions. Moreover, the establishment of new populations through release or escape is guite likely. For this reason, further knowledge about expansion pathways and concrete management efforts are necessary to halt the spread or eradicate this high-risk invasive species.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Philipp Ginal ⁽¹⁾ https://orcid.org/0000-0001-6491-554X Mohlamatsane Mokhatla ⁽¹⁾ http://orcid.org/0000-0001-8090-4592 Natasha Kruger ⁽¹⁾ http://orcid.org/0000-0002-6082-3135 Jean Secondi ⁽¹⁾ http://orcid.org/0000-0001-8130-1195 Anthony Herrel ⁽¹⁾ http://orcid.org/0000-0003-0991-4434 John Measey ⁽¹⁾ http://orcid.org/0000-0001-9939-7615 Dennis Rödder ⁽¹⁾ http://orcid.org/0000-0002-6108-1639

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