Invasion biology of amphibians and reptiles: From observations to predictive spatial models

Dissertation
zur
Erlangung des Doktorgrades (Dr. rer. nat.)
der
Mathematisch-Naturwissenschaftlichen Fakultät
der
Rheinischen Friedrich-Wilhelms-Universität Bonn

vorgelegt von
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aus
Fürth

Bonn 2023

Angefertigt mit Genehmigung
der Mathematisch-Naturwissenschaftlichen Fakultät
der Rheinischen Friedrich-Wilhelms-Universität Bonn

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2. Gutachter: Prof. Dr. Wolfgang Wägele

Tag der Promotion: 02.02.2024
Erscheinungsjahr: 2024

„Transportation of species to areas outside their native ranges has been a feature of human culture for millennia. During this time such activities have largely been viewed as beneficial or inconsequential. However, it has become increasingly clear that human-caused introductions of alien biota are an ecological disruption whose consequences rival those of better-known insults like chemical pollution, habitat loss, and climate change. Indeed, the irreversible nature of most alien-species introductions makes them less prone to correction than many other ecological problems. Current reshuffling of species ranges is so great that the present era has been referred to by some as the Homogocene in an effort to reflect the unique magnitude of the changes being made.“

Fred Kraus (2009)

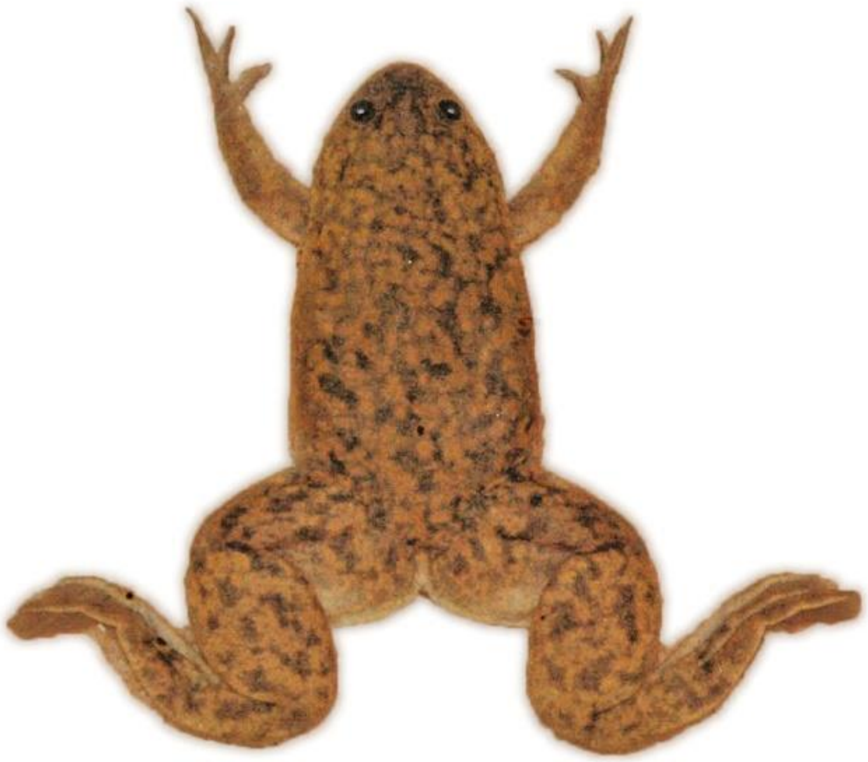

Figure *i*: The African Clawed Frog is among the invasive amphibian species with the largest distribution and the strongest negative impacts (photographed by John Measey and modified by Morris Flecks).

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Acknowledgements

Since 2018, I started my PhD and had the chance to meet and collaborate with great colleagues from LIB and other institutions, and to contribute to amazing projects. I am grateful for all the experiences I could gather, even for the hard times. Concerning my publications, the acknowledgements are already included in the respective sections. In particular, I want to thank my supervisor and doctor father Dennis Rödder, who taught me scientific working and large-scale thinking. Furthermore, I want to thank John Measey, Anthony Herrel, Jean Secondi, Natasha Kruger, Carla Wagener, Mohlamatsane Mokhatla, Laurie Araspin, Rui Rebelo, Francisco D. Moreira, Raquel Marques, Felix Deiß, Carl-Henning Loske and Nick Wei Cheng Tan for collaboration and co-authorships. I also thank Morris Flecks for all his technical support, particularly with formatting or creating nice figures, Ulla Bott for proof-reading many manuscripts and correcting typos, and all colleagues of the herpetology section. Special thanks go to Claudia Koch, John Measey, and Natasha Kruger, as they supported me with nice photographs to illustrate my thesis.

Overall, I want to thank all my friends, from and outside work, and my family, which supported and motivated me, discussed private, political or philosophical issues, during hard times or were just there to relax and enjoy times. Due to my disability it was important for me to master the challenge of PhD and without all these people that have been giving me support and believed in me, it would not be possible.

Thank you!

Summary

My thesis entitled "*Invasion biology of amphibians and reptiles: From observations to predictive spatial models*" comprises of six publications (see bibliographic information below for details). Overall, my thesis is broadly-folded, comprises several target species across different taxonomic groups (i.e., anurans, urodeles, squamates), scales (i.e., local, regional, macro-ecological landscapes) and methodological approaches (i.e., population size estimation, connectivity modelling, correlative and mechanistic species distribution modelling, mechanistic quantification of activity time budgets). The focus of my thesis relies on the methodological approaches and therefore, the red line in here starts with relatively simple models and ends with a novel, complex mechanistic approach.

Furthermore, three publications consider the African Clawed Frog, *Xenopus laevis* (Daudin, 1802), which is among the most invasive amphibian species of the world. Two further publications focus on the Oriental Garden Lizard, *Calotes versicolor* (Daudin, 1802) complex, a wide-spread but neglected invader with potential negative impacts, and the Italian Cave Salamander, *Speleomantes italicus* (Dunn, 1923), which is non-native but locally very restricted with no known negative impacts yet. Another publication considers the invasive fungal disease *Batrachochytrium salamandrivorans* Martel et al. 2013 (Bsal), which has substantial negative impacts on macro-ecological scales, and one of its host species, the European Fire Salamander, *Salamandra salamandra* (Linnaeus, 1758).

Bibliographic information

The following publications, ordered by the year of publication, are included in this thesis:

Publication	**Chapter in thesis**
Deiß, F., Ginal, P., & Rödder D. (submitted). Microclimatic growth rates of *Batrachochytrium salamandrivorans* under current and future climates: A very high spatial resolution SDM for Bsal and *Salamandra salamandra* (Linnaeus, 1758) within forest habitats of the European hotspot area. *Salamandra*.	Chapter 4
Ginal, P., Kruger, N., Wagener, C., Araspin, L., Mokhatla, M., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2023). More time for aliens? Performance shifts lead to increased activity time budgets propelling invasion success. *Biological Invasions*, *25*(1), 267-283. https://doi.org/10.1007/s10530-022-02903-6	Chapter 6
Ginal, P., Tan, W. C., & Rödder, D. (2022). Invasive risk assessment and expansion of the realized niche of the Oriental Garden Lizard *Calotes versicolor* species complex (Daudin, 1802). *Frontiers of Biogeography*, *14*(3), e54299. https://doi.org/10.21425/F5FBG54299	Chapter 3

Publication	Chapter in thesis
Ginal, P., Loske, C. H., Hörren, T., & Rödder, D. (2021a). Cave Salamanders (*Speleomantes* spp.) in Germany: Tentative species identification, estimation of population size and first insights into an introduced salamander. *Herpetology Notes*, *14*, 815-822.	Chapter 1
Ginal, P., Mokhatla, M., Kruger, N., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2021b). Ecophysiological models for global invaders: Is Europe a big playground for the African Clawed Frog. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *335*(1), 158-172. https://doi.org/10.1002/jez.2432	Chapter 5
Ginal, P., Moreira, F. D., Marques, R., Rebelo, R., & Rödder, D. (2021). Predicting terrestrial dispersal corridors of the invasive African Clawed Frog *Xenopus laevis* in Portugal. *NeoBiota*, *64*, 103-118. https://doi.org/10.3897/neobiota.64.60004	Chapter 2

1. General introduction

The cited words of Kraus (2009) in the prologue of my dissertation already demonstrate that the introduction of non-native species is amongst the main threats responsible for the current 6th mass extinction of species. However, the problem of invasive species is not a novel issue, those species and their ecological and economic impacts were long neglected. Despite Charles Elton (1958) provided first thorough insights on the negative impacts of invasive species, it took another two decades till the scientific community focused more on this topic. Since the 1980's several books concerning the biology of invasive species were published (Drake et al., 1989; Groves & Burdon, 1986; Mooney & Drake, 1986) and began to initiate broader scientific (Mooney, 2005; Mooney & Hobbs, 2000; Nentwig, 2007; Williamson, 1996) and public (Baskin, 2002; Bright, 1998; Low, 1999; Van Driesche & Van Driesche, 2000) interest on this „new“ problem. Nowadays, invasion biology is ranked among the other well established disciplines in the field of biology and the introduction of non-native species is recognized as a main threat to global biodiversity.

The terminology concerning non-native species and their invasion process changed over the years and among authors. Several terms occur, which are used more or less in synonymy, i.e., „alien“, „naturalized“, „non-native“, „non-indigenous“, „exotic“, „feral“, and lead to confusion. For the purpose of this dissertation, I will use the terms „non-native“ and „non-indigenous“ synonymously referring to those taxa that were released or transported outside their native ranges caused by human activities. The respective event is referred to as „introduction“. However, not all introduction events of non-native species to novel ranges lead to established populations of those species and not all non-native taxa show an invasive character. The term „invasive“ is used for the subset of non-indigenous species that have a demonstrated negative impact on the native ecosystem or on human goods (Kraus, 2009). Another, broader definition declares a non-native species as invasive, if it disperses, survives and reproduces at multiple localities across several habitats and extent of occurrence (sensu Blackburn et al., 2011).

As mentioned above, the introduction of non-native species has been a part of human history for millennia. Also the process of human-mediated dispersal is not *per se* different from dispersal by other faunistic vectors, such as the attachment to the fur of a big mammal or the foot of a duck. However, the spatio-temporal resolution of those dispersal processes strongly differs from each other. From a spatial point-of-view, taxa are now being mixed among continents that have been separated for 250 million years and geographical barriers like oceans, mountain ranges, rivers, etc. have been overridden. Also the physical dispersal ability of a species seems irrelevant anymore and even poor dispersers – i.e. those taxa that do not travel to very close localities – have been spread worldwide. Also temporally, novel introductions of species occur nowadays in a far greater rate than previously observed in Earth's history. Particularly, on oceanic islands, in freshwater and marine ecosystems non-native species establishments occur on dramatically high rates (Ricciardi, 2007). The extreme case of the Hawaiian Islands demonstrates this increase very well: While the establishment of new species is estimated to occur naturally on a scale of one species per 35,000 years, it is now estimated to occur between 20 to 30 new establishments per year (Beardsley, 1962, 1979; Loope, 1998; Miller & Holt, 1992).

The percentage of invasive to non-native species is not so easy to quantify as biological systems are highly complex and the classification of invasiveness is restricted to two caveats (Kraus, 2009). First, the assessment of invasiveness often underlies an anthropocentric perspective that depends on the investigated question(s) of interest and the implemented study design. For example, if we could not find any negative impact of an introduced salamander on other native amphibians (i.e., because it does not prey on amphibians or does not obviously carry diseases like chytrid fungi), the results might change if we would have a closer look to the impact on other taxa, i.e., insects or mollusca. Hence, the numbers of invasive species will most likely increase over time and with increasing scientific effort.

Second, extrapolations from one locality to other regions are problematic as a species that is invasive in one or a few localities might have no demonstrated negative impact in other regions. This phenomenon is known from several taxa i.e., the Traveller's Palm (*Ravenala madagascariensis* Sonn.), which is widely planted across the tropics without any known negative impact but is invasive on the Mascarene Islands (Cronk & Fuller, 1995). For this reason, a species that might have no known negative impact in one region cannot be classified as non-invasive for another locality due to the high complexity and dynamics of ecological systems.

1.1. Two misconceptions

Kraus (2009) already mentions two typical misconceptions that are often used as justification to introduce non-native species or to neglect the potential negative impacts they have. According to the first misconception, non-native species are enrichment to local diversity as they might increase the total number of species in an area and thus have positive effects to local biodiversity. However, this misconception equates the pure species number and biodiversity, and excludes the relative abundance of the community assembly. According to the Convention on Biological Diversity (CBD), biodiversity is defined as:

“The variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems.”

Therefore, the species number is just a small part of the diverse facets of biodiversity. When one invasive species dominates the community assembly and native species are present but become rare, which is how invasive species typically behave (Kraus, 2009), biological diversity decreases even if the pure species number is higher than prior to the invasion. Furthermore, invasive species are a main driver for biotic homogenization, the process where formerly distinct ecosystems and their species assemblies assimilate, when unique biotic elements are replaced through widespread invasive taxa (Olden et al., 2011).

The second misconception claims that the movement of species is a natural process also including the human-mediated spread of non-native species. As already mentioned in the chapter „What is an invasive species?“, the temporal and spatial scale of human-mediated species dispersal quantitatively differs from all natural dispersal processes. For example, the African Clawed Frog, *Xenopus laevis*, which is used as target species in three publications included in my dissertation, is a predominantly aquatic frog, native to sub-Saharan Africa and due to human-mediated transport, this invasive frog can now be found on five continents (Africa, Asia, Europe, South and North America). With an ongoing expansion in most localities and due to its strong negative impacts, it is ranked among the world's most invasive amphibians (Kraus, 2015; Measey et al., 2012), however naturally this expansion would not have been possible.

1.2. Invasion process

The invasion process comprises four stages: (1) introduction due to transport or release, (2) establishment, (3) expansion and (4) impact (Kraus, 2009).

Introduction of invasive species: Transport or release

The first stage of the invasion process is introduction due to transport or release of a non-native species to its novel environment (Kraus, 2009; Rouget et al., 2016). Often the transport of these aliens is done unintentionally, mostly resulting from species that are stowaways in cargo or the vehicles used in transport (Kraus, 2009). Famous herpetological examples include the Brown Treesnake [*Boiga irregularis* (Bechstein, 1802)] on Guam, which reached the island in salvaged war material (Rodda et al., 1992), or several geckos [i.e., *Hemidactylus frenatus* (Dumeril & Bibron, 1836), *Lepidodactylus lugubris (*Dumeril & Bibron, 1836)] as stowaways of cargo in the tropics and subtropics (a comprehensive list is found in Kraus, 2009). Also included in this category, is the unintentional spread of disease-causing agents, like the two fungal diseases *Batrachochytrium dendrobatidis* (Longcore et al., 1999) and *Batrachochytrium* *salamandrivorans*, which are main drivers for the global amphibian decline and are vectorised by the trade of amphibians (Nguyen et al., 2017; Schloegel et al., 2010; Schloegel et al., 2009).

But the transport or release can also happen intentionally, primarily then when those species provide a value to people, which might include the use as pets, furs, human or livestock food, horticulture and biocontrol agents (Kraus, 2009). Herpetological examples include the Cane Toad [*Rhinella marina* (Linnaeus, 1758)] in Australia, which was deliberately introduced in 1935 as an attempt to control the Cane Beetle (Shanmuganathan et al., 2010), or Italian Cave Salamanders (*Speleomantes italicus*) in Germany, which were most likely released from an animal trader in this region (Schulz et al., 2021). A summary across the taxonomic groups reveals that as a rule of thumb, marine invertebrates, insects or land snails are predominantly introduced unintentionally, while plants, fish, birds and mammals are introduced intentionally (Kraus, 2009). For amphibians and reptiles, the pathways of transport or release are diverse and include both, unintentional as well as intentional human-mediated dispersal (Kraus, 2009).

Establishment: The conceptual understanding of the ecological niche

The second stage of invasion is the establishment of a reproducing population in the novel environment (Kraus, 2009; Rouget et al., 2016). How and whether a species establishes itself in a new area is complex and depends on a number of factors (Kraus, 2009). Important for this process is the conceptual understanding of the ecological niche. Historically, the ecological niche was defined by several authors and among the most commonly used definitions are the following:

(1) The **Grinnellian niche** focuses on the macro-niche of a species defined by sceno-poetic variables that cannot be consumed. Therefore, the niche concept of Grinnell (1917) is determined by the habitat in which a species lives and its accompanying behavioural adaptations that are necessary for survival and reproduction (Grinnell, 1917). This perspective therefore focuses on abiotic

relationships such as environmental variables, i.e. temperature, precipitation, solar radiation, etc., and leaves out biotic factors (Grinnell, 1917). For example, the behaviour of the California Thrasher [*Toxostoma redivivum* (Gambel, 1845)], a member of the New World passerine bird family Mimidae, is strongly influenced by the chaparral habitat in which it lives, breeds and flees from predators. Its Grinnellian niche is characterised by its behaviour, physical characteristics (camouflage colour, short wings, strong legs) and the sum of all habitat requirements (Grinnell, 1917). Further, the climate niche of a species, which is composed of all the climatic requirements that are essential to survive and reproduce, also represents a fraction of the Grinnellian niche of a species.

(2) The **Eltonian niche** focuses on the functional role within the food web, such as predator-prey relationships and consumer-resource dynamics, and on the impact upon the environment (Chase & Leibold, 2009; Elton, 1927). This perspective emphasizes biotic interactions such as foraging behaviour for food or escape from predators. For example, the Eltonian niche of birds of prey that feed on small mammals, such as shrews and mice, is filled by kestrels in the open grasslands, whereas it is occupied by tawny owls in the oak forest (Elton, 2001). Even if the community composition of shrews and mice differs between the different habitat types, the functional role of birds of prey is similar between the two habitats and the persistence of the carnivore niche of the birds of prey depends on the presence and abundance of their food items, represented by small mammals.

(3) The **Hutchinsonian niche** is an n-dimensional hypervolume, illustrated by a multi-dimensional coordinate system, where the dimensions, or axes, are environmental conditions or resources that are relevant for a species' persistence and reproduction (Hutchinson, 1957). The Hutchinsonian niche is subtly different from the Grinnellian perspective. While Grinnell focuses more on the ecological role of a species that may or may not be actually filled in its environment, Hutchinson defines the niche as the occupied ecological space of a species.

These three commonly used conceptual understandings of an ecological niche are neither contradictory nor does one of them comprehend the whole picture of reality. However, all three perspectives can help us to understand and respond to essential questions in ecology, such as “how do species coexist?”, “how are species distributed?” or “why do some species or populations decline or even disappear?”. For illustration purposes, an ecological niche can be seen in two perspectives, in **environmental space** (E-space), but also in **geographical space** (G-space) (Soberón, 2007; Soberón & Nakamura, 2009). While the E-space can be displayed as an n-dimensional coordinate system, which axes represent the environmental conditions, such as precipitation, temperature, radiation etc., that exist in the distributional range of a species (see also Hutchinsonian niche definition above), G-space is the realised distribution in the geographical realm, i.e., the distributional range. However, the distribution of a species and also the environmental conditions that occur in this range, do not emphasize the whole ecological niche of a species as well (Owens et al., 2013; Soberón, 2007).

Furthermore, the ecological niche and its associated distributional range is composed of and driven by several fractions (ecological niche sensu Soberón, 2007; Soberón & Nakamura, 2009). First, the **fundamental niche (A)** is the sum of all the abiotic factors that are necessary for a species to survive and build populations. However, the fundamental niche is not only the environmental conditions that exist in a species’ distributional range, but represents the real physiological constraints (i.e., critical thermal limits; Soberón, 2007; Soberón & Nakamura, 2009). Second, **biotic interactions (B)** such as predator-prey relationships, competition, parasitism, etc., are parts of an ecosystem as well and they also shape the distributions of species (Soberón, 2007; Soberón & Nakamura, 2009). Third, if a species occurs or does not occur in a specific geographic range is also influenced by the species’ dispersal ability and the associated **geographical accessibility (M)** of an area. Thus, mountain ranges, seas, large canyons, etc. can build geographic barriers and hamper or block the dispersal of a species, even if this area might be climatically suitable (Soberón, 2007; Soberón & Nakamura, 2009). The interplay of these three fractions is then the distributional range where a species occurs in reality, the so-called **realised niche** or **actual geographical distribution (G_0)** (Grinnell, 1917; Hutchinson, 1957; Soberón, 2007; Soberón & Nakamura, 2009). If geographical accessibility is not a limiting factor, for example if geographical barriers are overcome with anthropogenic support, the overlap of fundamental niche (A) and biotic interactions (B) reveals the **potential distribution (G_1)** of a species (Soberón, 2007; Soberón & Nakamura, 2009).

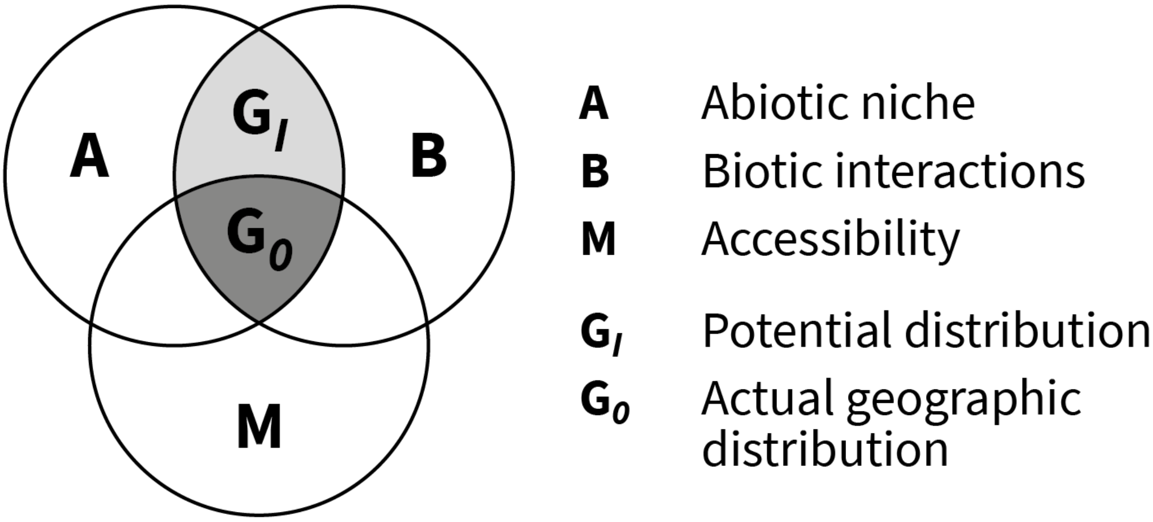

Figure 1.1: BAM diagram introduced by Soberón (2007) modified by Morris Flecks.

As quantified by phylogeographic studies (i.e., Barros et al., 2020; Cordellier & Pfenninger, 2009), species tend to retain their ancestral ecological characteristics and seem to conserve their ecological niches, or at least their climate niches, over space and time (**niche conservatism**), instead of persisting and adapting to novel climatic conditions (**niche shift**). However, as indicated by geographical mismatches, based on the environmental conditions, between the native and invasive distributional ranges of an invasive species, numerous studies suggest that shifts in the climate niche might occur

(Broennimann et al., 2007; Christina et al., 2020; Orsted & Orsted, 2019). However, it is often impossible to state if these mismatches represent real shifts in the fundamental niche of a species and in the species' physiological constraints or in the realised niche only. For a better understanding of the complexity of ecological niches, several quantification metrics were introduced, such as **niche breadth** (the variety of resources or habitats used by a given species), **niche partitioning** (resource differentiation by coexisting species), and **niche overlap** (overlap of resource requirements by different species) (Chase & Leibold, 2009).

Expansion: Hypotheses for invasion success

The next stage of the invasion process is the expansion of the species into further regions (Kraus, 2009; Rouget et al., 2016). If and how fast a non-native species expands is often difficult to predict. Some species establish populations with a small number of individuals but do not spread across larger areas and others show an “explosive” expansion and conquer whole ecosystems, countries or even continents. While the latter one is the best example for an invasive species, the first case does not fulfil the criteria of invasiveness (Kraus, 2009). However, the range of case studies stretches between both examples and cover the whole spectrum in between. For most cases, it is strongly debated if a species is invasive or just non-native, and a concise decision often requires long and intense data collection.

Several ecological and evolutionary hypotheses have been stated, why some invasive species might be so successful (reviewed in Hufbauer & Torchin, 2007). Below, I briefly introduce three ecological and three evolutionary hypotheses:

(1) Ecological hypotheses

(1a) Empty niche (Arnan et al., 2021; Elton, 1958):

This hypothesis relies on the ecological niche concept and posits that non-native species are able to use resources that are not used by native species or use them more efficiently, and thereby fill an empty niche of the species community in the novel range. Furthermore, strong invasions might be explained by a broader niche breadth in the novel environment. This hypothesis is also linked to the biotic-resistance hypothesis.

(1b) Enemy release (Darwin, 1859; Hartshorn et al., 2022; Torchin & Mitchell, 2004):

The enemy release hypothesis postulates that due to several mechanisms of invasion process parasites, pathogens, specific predators or herbivores, or other natural enemies that dominate the invasive species in its original range, might be filtered out (Keane & Crawley, 2002; Torchin et al., 2003). Thereby the non-native species has now resources available that were formerly used to escape from the natural enemies. Furthermore, it is hypothesised that the novel range harbours fewer enemies than the original range and the invaders are less likely affected by the enemies of the novel range than the native competitors are. These key assumptions are neither mutually exclusive nor do they necessarily occur simultaneously.

(1c) Biotic resistance (Beaury et al., 2020; Elton, 1958; Levine et al., 2004):

According to this hypothesis, species-rich communities provide more biotic resistance against invaders as species-poor communities do. For example, non-native species face resistance directly from those species that are able to prey on the new invaders or use them as hosts. However, the relative resistance of a species depends on its interactions to higher trophic levels. It is also assumed that species communities with close relative species of the invader resist heavier as it is more likely that they harbour natural enemies and provide stronger competitions through the close relatives, than those, where no relative species occur. The idea of biotic resistance is linked with the enemy release and empty niche hypotheses.

(2) Evolutionary hypotheses

(2a) Founder event (Mayr, 1954; Sherpa et al., 2020):

Biological invasions can be seen as founder events which suggests, that a subset of genotypes from a population enters a novel environment. It is proposed that founder events are a mechanism for rapid evolution and speciation (Barton & Charlesworth, 1984; Gavrilets & Hastings, 1996; Regan et al., 2003) as this event breaks up co-adapted gene complexes and boosts additive genetic variation in phenotypic traits (Bryant & Meffert, 1995; Goodnight, 1987), which allows the population to respond rapidly to the novel selective regime.

(2b) Evolution of increased competitive ability (Blossey & Notzold, 1995; Li et al., 2022):

The evolution of increased competitive ability (EICA) hypothesis can be seen as the evolutionary perspective to the enemy release hypothesis. This hypothesis assumes that escaping from enemies leads to an allocation of resources that were previously used to defend against the enemy and now the resources are available for growth, reproduction or other fitness-related performance traits (Li et al., 2022). This hypothesis leads to the two assumptions that 1) introduced populations should exhibit a loss of defensive mechanisms against enemies from the original range and 2) grown or raised individuals of the introduced population should be locally adapted to the novel environment and thereby, should be fitter compared to conspecifics of the original range. In contrast, it is assumed that a small number of founder individuals lead to a genetic bottleneck (founder event) and to inbreeding depressions, which decreases the chances of adaptive evolution to the novel environment, particularly when the population size remains small for multiple generations (Lande, 1980). However, it is also known that founder effects may convert the epistatic variance into additive genetic variance and thereby boost the potential of response to selection (Bryant & Meffert, 1995; Goodnight, 1987).

(2c) Hybridisation (Ellstrand & Schierenbeck, 2000; Shivaramu et al., 2019): Hybridisation of different genetic lineages or even species is known to be a booster for the invasion process as it generates genetic variation, evolutionary novelty and hybrid vigour (Vila & D'Antonio, 1998). Initially, hybridisation may lead to decreased fitness, however, due to selection combined with backcrossing subsequent generations may be fitter than the parent individuals (Arnold & Hodges, 1995; Arnold et al., 2001; Shivaramu et al., 2019). However, many invasive taxa are of hybrid origin, it is difficult to directly link hybridisation with changes that boost invasion success. The two assumptions behind are that 1) due to the invasion process, it is more likely that different genetic lineages or species that would not meet naturally come together, and 2) due to hybridisation and subsequently an increase of fitness, the hybrids are able to invade novel ranges that are unsuitable for the parent individuals.

These hypotheses are just a subset of the proposed assumptions that may lead to strong invasion events. However, there is often a strong indication for the truth of these hypotheses, due to the complexity of biological systems, most of them are difficult to test. Further in reality there might be synergetic effects among different hypotheses.

Impact: Consequences of invasive species

The final stage of invasion process is the impact that an invasive species has ecologically and socio-economically (Kraus, 2009; Rouget et al., 2016). Overall, it is known that invasive species can have remarkable and variable impacts including species extinctions, biotic homogenization, alteration of food-webs, changes to primary productivity of ecosystems, alteration of soil formation, changes of community structures, conversion or replacement of ecosystems, alteration in nutrient cycles, collapse of fisheries, degradation of watersheds, promotion of increased fire events, increases in soil erosion and flooding, losses in agriculture, damage to human structures, disease epidemics, aesthetic losses of ecosystems, and degradation of human life quality (Allen et al., 2011; Clavero & Garcia-Berthou, 2005; Jordan et al., 2008; Kauppi et al., 2017; Kraus, 2009 and references therein; Marbuah et al., 2014; McLeod et al., 2016; Sanders et al., 2003). Considering amphibians and reptiles these taxa have long been underestimated and neglected as potential invaders and their potential impacts have been poorly understood yet (reviewed in Kraus, 2009). Over the last years it has been shown that herpetofaunal invaders can have similar strong negative impacts as other taxa (i.e., case of Burmese Pythons, *Python bivittatus* Kuhl, 1820, in Florida; Guzy et al., 2023; Reed et al., 2012; Sovie et al., 2016) but for the most species the number of studies focusing on ecological and socio-economical impacts is limited as amphibians and reptiles are no common economical pests and in most cases are not directly harmful for humans (reviewed Kraus, 2009).

Several of these studies concern the negative ecological impacts of herpetofaunal invaders linking them to extinction events of native species. The case of the Brown Treesnake, *Boiga irregularis*, on Guam, for example, is well-studied and represents one of the worst-case scenarios of biological invasions (McCoid, 1991; Rodda & Fritts, 1992; Rodda et al., 1997; Rodda et al., 1999; Savidge, 1987). The introduction of this apex predator to Guam led to the extinction of several native bird, bat and reptile species. Subsequently, the disappearance of these species might have further negative impacts on plant pollination and seed dispersal of Guam’s native flora (McCoid, 1991; Rodda & Fritts, 1992; Rodda et al., 1997; Rodda et al., 1999; Savidge, 1987).

Furthermore, herpetological invaders can outcompete native species and thereby causing their extinction. The Asian House Gecko, *Hemidactylus frenatus* Duméril & Bibron, 1836 is an invasive species that is wide-spread across the tropics and subtropics (see comprehensive list in Kraus, 2009). The invaders expel the endemic Night Geckos of the genus *Nactus* Kluge, 1983 on the Mascarene Islands from their shelter refugia and thereby the Night Geckos are exposed to stochastically higher risks such as for predation. Hence, the Asian House Geckos are associated with the decline and local extinction of the Night Geckos on the Mascarene Islands (Cole et al., 2005).

Invasive species are potential vectors of diseases or parasites, which can threaten native herpetological communities. The American Bullfrog [*Lithobates catesbeianus* (Shaw, 1802)] and the African Clawed Frog [*Xenopus laevis*, for example, both invasive species of global concern, serve as vectors for the amphibian pathogen Bd without facing strong negative courses from it (Ghirardi et al., 2011; Rödder et al., 2013; Tinsley et al., 2015; Urbina et al., 2018). Most likely, the African Clawed Frog might even be the origin of global Bd spread (Weldon et al., 2004), which has been caused amphibian declines and extinctions worldwide (Lips, 2016). Furthermore, both species are large-sized generalist predators that prey on all types of food items that fit in their mouths (Liu et al., 2015).

For other herpetological invaders, it was already found that they can have impacts on ecosystem processes. For the Greenhouse Frog (*Eleutherodactylus coqui* Thomas, 1966) it was demonstrated that the species can impact ecosystem primary productivity and litter decomposition. This is possible as the frogs prey on a variety of small arthropods, which are herbivorous and detritivorous, thereby the frogs top-down regulate the arthropods, which indirectly affects the ecosystem processes (Beard et al., 2003). Its congeneric *E. johnstonei* Barbour, 1914 even has negative socio-economic impacts as due to its loud choruses the little frogs cause noise pollution, which led to real estate depreciation (Kraus & Campbell, 2002; Kraus et al., 1999; Lever, 2003; Melo et al., 2014; Pimentel et al., 2000).

Often the negative impacts of invasive species are much more complex, i.e. if we consider indirect impacts, and it takes a lot of time and effort till these impacts are recognised and supported by evidence. For example, the introduction of Burmese Python, *Python bivittatus*, in Florida, USA led to the decline of medium- and large-sized mammals, which can be seen as direct impact of the invader to the local fauna. However, recently it was also found that this decline of mammals shifts the host use of vector mosquitos towards reservoir hosts of the Everglades virus leading to a potential increase for human infections by the virus (Burkett-Cadena et al., 2021; Hoyer et al., 2017). This indirect impact could have never been predicted, but it states evidence that due to indirect impacts the Burmese Python potentially threatens human health. Overall, these are just some examples on the negative impacts of herpetological invaders. For more examples as well as a comprehensive overview see Kraus (2009).

Delayed invasion: The phenomenon of invasion debt

The whole invasion process, or just some stages of it, can be delayed. This phenomenon of time-lag is called invasion debt (Essl et al., 2011; Rouget et al., 2016; Seabloom et al., 2006). The four stages of invasion debt include:

(1) Introduction debt: Additional number of species that could become introduced;

(2) Establishment debt: Additional number of species that could become established (species-specific);

(3) Spread debt: Additional area that could be invaded (area-specific);

(4) Impact debt: Additional number of ecological or socio-economic impacts that could be caused from an invader (impact-specific).

The time-span covering the whole invasion process strongly varies among taxa and for vertebrates, it was shown that long time-periods can pass till a species can become invasive (Nehring et al., 2015; Toledo & Measey, 2018). For example, the invasion debt (introduction debt + establishment debt + spread debt) of the Guttural Toad (*Sclerophrys gutturalis* [Power, 1927]) took five years, whereas for the African Clawed Frog (*Xenopus laevis*) it took even 35 years (for details see Van Sittert & Measey, 2016; Vimercati et al., 2017). However, the quantification or prediction of invasion debt requires comprehensive data and is therefore pretty complex (Rouget et al., 2016).

2. Aims, methodological overview and author contributions

Invasive species are among the main issues threatening global biodiversity. However, the research on invasive species has strongly been increased over the last years, the increasing globalisation and worldwide connectivity leads to an increasing number of non-native species and while some of them seem to have little or no known negative impact on local biodiversity and human needs, others are responsible for local catastrophes (i.e., alteration of ecosystems, extinction events of species, economical losses; Kraus, 2009). Concerning amphibians and reptiles, the current research has often been focussed on some “global players”, such as the American Bullfrog (*Lithobates catesbeianus*) (Gobel et al., 2019; Laufer et al., 2021; Laufer et al., 2018), the Cane Toad (*Rhinella marina*)(Kosmala et al., 2017; Kosmala et al., 2020a, b) or the African Clawed Frog (*Xenopus laevis*) (Herrel et al., 2020; Ihlow et al., 2016; Vogt et al., 2017), while many other local non-natives have been neglected. For the neglected taxa, every gathered information might help to assess the potential invasiveness of these species, and in case, to introduce measures to prevent further spread, to restrict the species’ distribution on a local scale and, if possible, to eradicate the species from its invasive range. For the “global players”, in theory the aims are the same, however, in practice it is often difficult or impossible to control or manage invasive species, if they already occur on large scales. In these cases, it is necessary to understand the species’ invasion process and to develop and evaluate novel tools and strategies, which allow species management or even control.

As already suggested by the title, the aims of this work are broadly folded and cover “global players” such as the African Clawed Frog (*Xenopus laevis*), which is distributed across five continents with an ongoing expansion and strong negative impacts on biodiversity and human welfare (Ihlow et al., 2016; Measey et al., 2020c; Rödder et al., 2017), but also neglected taxa, such as the Oriental Garden Lizard (*Calotes versicolor*), which is widely distributed but still neglected considering its invasion process and potential impacts, and the Italian Cave Salamander (*Speleomantes italicus*), which only acts on a very local scale with no known negative impact yet. The used approaches include “simple” population size estimation (Chapter 1), connectivity modelling (Chapter 2) and correlative species distribution modelling (SDM; Chapters 3 and 4), up to “complex” mechanistic SDM on microclimatic scale (Chapter 4) and macroclimatic scale (Chapter 5), as well as a novel mechanistic approach to quantify activity time budgets (Chapter 6). Furthermore, the scales and objectives of the chapters also differ from each other and cover local (Chapters 1 and 2), regional (Chapter 4) to macro-ecological scales (Chapters 3, 5, and 6).

2.1. Chapter 1 – Introduced Cave Salamanders in Germany

Ginal, P., Loske, C. H., Hörren, T., & Rödder, D. (2021). Cave Salamanders (*Speleomantes* spp.) in Germany: Tentative species identification, estimation of population size and first insights into an introduced salamander. *Herpetology Notes*, *14*, 815-822.

Figure 2.1: Italian Cave Salamander (*Speleomantes italicus*) from the German population in Holzminden, Lower Saxony (photographed by Morris Flecks).

Aims

Non-native amphibians can be introduced in a variety of ways. Historically, amphibians were introduced to control pests, to provide food or for research. The pet trade is now the most important source for the introduction of amphibians into new areas (Kraus, 2009). However, these introductions of amphibians are mainly related to anurans, while cases of urodeles are more unusual (Kraus, 2009; Lunghi et al., 2018; Riley et al., 2003). Since 2013, it has been known that a population of European Cave Salamander, *Speleomantes* spp. Dubois, 1984, is established in Germany. However, the size of this population was not known and it was not known to which of the very similar looking *Speleomantes* species it belongs.

(I) Therefore, we used a recently published photographic database containing more than 1,000 images of all eight *Speleomantes* species to determine the species identity of the German population.
(II) Furthermore, we used log-linear models to estimate population size.

Methods

For the purpose of population size estimation, we used the Rcapture package, an R package for capture-recapture experiments (Baillargeon & Rivest, 2019). The input data resemble the capture history of each individual, displayed as vectors of zeros (no capture) and ones (capture), over the t capture occasions of the experiment. The package can be used to fit three types of models:
(1) Closed population: This approach is to estimate the population size N under the assumption that the population size remains constant throughout the experiment. Thus, migration, births and deaths are excluded. Rcapture provides several estimators for this model, which estimate a different population size N, depending on the variation of the animals’ capture probabilities;
(2) Open population: This model assumes that migration, deaths and births occur in populations and thus, it allows the estimation of survival rates. Rcapture can fit the basic Cormack-Jolly-Seber and Jolly-Seber model for open populations;

(3) Robust design: This model combines the other two approaches as it applies a closed population estimator for the primary sampling period and uses models for open populations between the periods.
Most of the implemented models of the Rcapture package rely on a Poisson regression and resemble log-linear form. The package implements the novelty of applying several different ways to model capture probabilities heterogeneity between individuals in both closed population models and the primary periods of a robust design. Furthermore, it allows several approaches developed by R. M. Cormack for open population estimation (Baillargeon & Rivest, 2019). For the estimation of the population size of the German *Speleomantes* population, we decided to perform an open population model, including the model settings of equal and unconstrained capture probabilities. Due to the low number of recaptures, we also performed a sensitivity analysis by simulating additional recaptures.

Results and discussion

Our results suggest that the population consists of 170 to 485 individuals (± 134 to 320). However, the sensitivity analysis reveals that our results are sensitive to additionally captured salamanders with a dropdown to 17–35 % of the originally estimated population size. Based on the colour pattern, the population is most likely *S. italicus*, which is native in the northern and central Apennines from the provinces Reggio Emilia to Lucca, southwards to Pescara at 80 to 1600 m elevation (Frost, 2020). The German population is c. 800 km away from the species' known native range and thus, this population can be seen as non-native and also as the northernmost European Cave Salamander population. In addition, we provide the first evidence of reproduction and further insights into this non-native salamander population.

Author contributions

PG was the leading author and had the idea for this study. Furthermore, PG did the main part of model construction and the statistical analyses. PG and CHL conducted the field work to collect and photograph the salamanders. CHL identified the individual salamanders and compared them to the photographic database. TH and DR gave advice for the study design and statistical analyses. All authors contributed thoroughly to the manuscript.

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2.2. Chapter 2 – Dispersal of invasive *Xenopus* in Portugal

Ginal, P., Moreira, F. D., Marques, R., Rebelo, R., & Rödder, D. (2021). Predicting terrestrial dispersal corridors of the invasive African Clawed Frog *Xenopus laevis* in Portugal. *NeoBiota*, *64*, 103-118. https://doi.org/10.3897/neobiota.64.60004

Figure 2.2: The ponds of a golf-course in Portugal serve as stepping stones for the African Clawed Frog to disperse between the Barcarena and Laje rivers (photographed by Rui Rebelo).

Aims

Invasive species, such as the mainly aquatic African Clawed Frog, *Xenopus laevis*, are a major threat to global biodiversity (Ihlow et al., 2016; Rödder et al., 2017). In Portugal, *Xenopus laevis* has been recorded from two nearby rivers in Oeiras County ca. 20 km west of Lisbon. From Laje River the first record dates back till 2006. However, it is suggested that the date of introduction was much earlier and most likely it is related to a strong winter flood event in 1979/80, when the frogs escaped from a nearby research laboratory (Rebelo et al., 2010; Sousa et al., 2018). In Barcarena, a second parallel-flowing river, the species was recorded in 2008 (Rebelo et al., 2010) and it is suggested that *Xenopus* invaded Barcarena by using a terrestrial dispersal corridor. The identification of dispersal corridors is necessary to limit the further spread of invasive species, and helps to develop management plans for their control and eradication. For this reason, we (I) reconstructed past dispersal routes between Laje and Barcarena rivers in Portugal, and (II) highlighted areas at high risk for future expansion.

Methods

Connectivity modelling is a common and useful tool to calculate the connectivity or, alternatively, the resistance of landscapes based on several landscape features, such as vegetation cover, elevation or slope (Landguth et al., 2012). As multiple paths can occur between two points, either multiple low-cost paths or kernel density estimation (KDE) can be used to calculate the landscape connectivity (Cushman et al., 2009; Pinto & Keitt, 2009). KDE relies on smoothed output paths using a probability-density function and this approach allows a variety of smoothing functions (Gaussian, Epanechnikov, uniform, triangle, biweight, triweight and cosine function; Li & Racine, 2007). Here we used remote sensing derived resistance surfaces, based on the normalised difference vegetation index (NDVI) and the normalised difference water index (NDWI) accounting for behavioural and physiological dispersal limitations of *X. laevis* to calculate resistance kernels. The resistance kernels were combined with elevation layers to determine fine scale, terrestrial dispersal patterns of invasive populations of *X. laevis* in Portugal, where the frog had established populations in two rivers.

Results and discussion

Our results suggest terrestrial dispersal corridors connecting Laje and Barcarena, and identify artificial waterbodies as stepping stones for overland movement of *X. laevis*. Most likely, *X. laevis* used golf-course ponds located between the two rivers to invade the Barcarena River. These golf-course ponds are the only possible corridor between Laje and Barcarena, and frogs have also been found in the golf-course ponds. We also found several potential stepping stones to new areas, providing concrete information for invasive species management. The Jamor River basin, to the east of the study area, is protected by a high level of landscape resistance and natural dispersal of African Clawed Frogs seems impossible. The Carregueira Mountains, a small forested area with farms and golf-courses (including lakes) in the northeast of the study area, shows low landscape resistance, but the area is not currently covered by the connectivity kernel. However, considering the further spread of *Xenopus*, a potential invasion might start from the western edge. In addition, the northern region in the vicinity of the Barcarena River has several small waterbodies that could be potential stepping stones to new areas. We recommend blocking these corridors, e.g. with toad fences or by enclosing artificial waterbodies with walls to prevent further expansion of the African Clawed Frog.

Author contributions

PG was the leading author of this study. He did the main part of writing and contributed to the model performance. FDM, RM and RR did the field work in Portugal and provided their data for the models. DR performed the UNICOR models and was the main supervisor. All authors contributed to the manuscript, shared comments and knowledge.

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2.3. Chapter 3 – Invasive risk assessment of *Calotes versicolor*

Ginal, P., Tan, W. C., & Rödder, D. (2022). Invasive risk assessment and expansion of the realized niche of the Oriental Garden Lizard *Calotes versicolor* species complex (Daudin, 1802). *Frontiers of Biogeography*, *14*(3). https://doi.org/10.21425/F5FBG54299

Figure 2.3: Oriental Garden Lizard (*Calotes versicolor* sensu lato) (photographed by Claudia Koch).

Aims

Correlative species distribution modelling (SDM) can be a useful tool to quantify a species' realized niche and to predict its potential distribution for non-native ranges (Chapman et al., 2019; Srivastava et al., 2019). The agamid lizard *Calotes versicolor* sensu lato (s.l.) belongs to the most widely distributed reptile taxa worldwide (Uetz et al., 2021b). In the past, *C. versicolor* s.l. has been introduced to several countries, including regions in the Oriental, the Neotropical and the Afrotropical realm, where strong negative impact on the local fauna is assumed (Diong et al., 1994; Mauremootoo et al., 2003; Uetz et al., 2021b). Due to the complicated taxonomy and the existence of several cryptic species, which are covered by this taxon (Gowande et al., 2021), we used *C. versicolor* s.l. and its four subtaxa [*C. versicolor* sensu stricto (s.s.), *C. irawadi*, *C. vultuosus*, *C. farooqi*] as target species.

(I) We computed correlative SDMs for *C. versicolor* s.l. and its subtaxa and projected them across the globe to highlight climatically suitable areas of risk for future invasion, and

(II) based on the ecological niche concept, we investigated if the species complex expanded its realized climatic niche during the invasion process.

Methods

Species distribution modelling (SDM), also referred to as ecological niche modelling, is a tool in biology that tries to emphasize the ecological niche, or a fraction of it (reviewed in Srivastava et al., 2019). SDM was already applied for several biological and ecological purposes, including projecting the potential impact of climate change on species distributions (Medley, 2010; Padalia et al., 2015), predicting species invasions (Di Febbraro et al., 2016; Williamson, 2006), characterizing and exploring the ecological niche requirements (Leibold, 1995; Meentemeyer et al., 2008), for conservation and policy making (Breiner et al., 2015; Meller et al., 2014), assessing the impacts of land cover change and human footprint on species distributions (Fuller et al., 2012; Thuiller et al., 2004), testing ecological theories (Elith & Leathwick, 2009; Guisan & Thuiller, 2005), for species risk assessment (Kariyawasam et al., 2019; Venette et al., 2010) and to assess the risk of diseases (Alkishe et al., 2018; Vaclavik et al., 2010). Correlative SDM links geographic occurrences with environmental data such as temperature, precipitation or radiation. However, correlative SDM is relatively simple, compared to mechanistic approaches, these models have the caveat that they are only able to reflect the realized niche of a species and not its physiological limits. Considering this caveat, correlative SDM can still provide useful information (reviewed in Srivastava et al., 2019).

In Chapter 3, we used two different correlative SDM approaches, namely n-dimensional hypervolumes (Blonder et al., 2017) and Maxent (Phillips & Dudik, 2008). N-dimensional hypervolumes are a non-hierarchically ranked approach, which is a useful tool to investigate the expansion in the realized niche, while Maxent, a hierarchically ranked model, is used to focus on potentially suitable areas for future invasion. We calculated two final models for *C. versicolor* s.l., one based on records from the native range and one based on records from the native and invaded range, as well as one model for each subtaxon.

Results and discussion

Our results show a geographic expansion into novel climatic conditions as well as an expansion in the realized niche of *C. versicolor* s.l.. Our results reveal that *C. versicolor* s.l. is currently inhabiting 13 % of its potential range but could find suitable climatic conditions on a global surface area between 14,025,100 km^2 and 53,142,600 km^2. Our predictions reveal large areas of highly suitable climatic conditions for the Oriental, Australian, Afrotropical and Neotropical realms, whereas only small regions of the Palearctic and Nearctic realms provide moderately suitable conditions. Further, some localities, especially those with a high amount of human traffic like ports or airports, might act as multiplicators and might therefore be a stepping stone into further areas. Considering this, as well as the species' dispersal history and evidence for negative impacts on the native biodiversity, this lizard should be further monitored.

Regions with a high degree of endemism (i.e. islands like Mascarenes, Madagascar) might be particularly sensitive to an invasion by this lizard and the subsequent negative impacts [i.e. *Duttaphrynus melanostictus* on Madagascar (Moore et al., 2015)]. Furthermore, the introduction of *C. versicolor* s.l. to regions of other genetic lineages of this species complex might most likely lead to hybridizations and might threaten close relatives that are endemic to small areas, which is the case for many *Calotes* species. Therefore, strategies to hamper and prevent further spread of *C. versicolor* s.l. are urgently needed. Strategies to prevent stowaways, especially in regions with a high amount of human traffic as ports or airports, are also required. Lastly, a further systematic revision of this species complex will result in different predictions for each species and will be subsets of our current prediction.

Author contributions

PG was the leading author and had the idea for this study. He did the main part of writing as well as the data preparation, model performance and statistical analyses. WCT supported PG in writing and with his advice. DR supervised the study and shared his knowledge. All authors contributed thoroughly to the manuscript.

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2.4. Chapter 4 – Microclimatic growth rates of Bsal

Deiß, F., Ginal, P., & Rödder, D. (in preparation). Microclimatic growth rates of *Batrachochytrium salamandrivorans* under current and future climates: A very high spatial resolution SDM for Bsal and *Salamandra salamandra* (Linnaeus, 1758) within forest habitats of the European hotspot area.

Figure 2.4: European Fire Salamander (*Salamandra salamandra*) from Asberg, Westerwald, Rhineland-Palatinate (photographed by Morris Flecks).

Aims

Nowadays, chytridiomycosis is one of the greatest threats to the diversity of amphibians worldwide (Fu & Waldman, 2022). Caused by both, the well-known chytrid fungus *Batrachochytrium dendrobatidis* (Bd) and the chytrid fungus *Batrachochytrium salamandrivorans* (Bsal), they play a decisive role in species declines. Bsal, which most likely originates in Southeast Asia (Laking et al., 2017; Martel et al., 2014), is particularly harmful to the European Fire Salamander *Salamandra salamandra*, as it causes epidermal ulcerations, anorexia and ataxia, which ultimately lead to death (Farrer et al., 2017; Lötters, Veith, et al., 2020; Van Rooij et al., 2015). While most studies have focused on the expansion of the pathogen in Europe (Beukema et al., 2021; Lötters, Wagner, et al., 2020), there is little high-resolution information available hitherto, which would be necessary for effectively implementing conservation measures on local scales.

In this study, therefore, a three-step approach was chosen:

(I) We used a mechanistic SDM to project the microclimatic growth rate of Bsal within forest habitats of its current invasive range on a very high spatial resolution (25 m).

(II) Furthermore, we performed a correlative SDM to predict the potential distribution of *S. salamandra*, and

(III) applied n-dimensional hypervolumes to quantify the realized microclimatic niches of both species and examine their overlaps.

Future trends were estimated based on comparisons among three climate scenarios, the current (current2010-2015) microclimatic conditions, and two climate change scenarios assuming an increase in the global annual mean temperature of +2°C and +4°C (future2 and future4).

Methods

Mechanistic or process-based SDM try to emphasize key ecological processes, such as locomotion, water loss, metabolic rates, etc., and critical thermal limits and thereby, they rely on the fundamental niche of a species. Unfortunately, mechanistic approaches are more data-intense as correlative SDM. For example, they require thermal performance data that must be accessed under time-consuming laboratory performance trials, which are strongly regulated by law and often need specific permits (reviewed in Srivastava et al., 2019).

For this chapter, we performed the first high-resolution (25 m) microclimatic model on the Central European hotspot area for Bsal. To simulate the microclimatic conditions of forest habitats, we used microclimatic temperature offset layers for the whole of European forests (Haesen et al., 2021). These layers show the average monthly offset between the microclimatic temperature in the forest and the macroclimatic temperatures in the open landscape and are provided in a resolution of 25 m for the monthly average over the years 2000 to 2019. The layers were used to correct the current2010-2015, future2 and future4 macroclimate scenarios for the forest microclimate at 5 cm above the ground. Furthermore, we extracted the thermal performance curve published by Beukema et al. (2021). The thermal response of Bsal was used as input for our microclimatic models. The microclimatic layers and the growth rate curve of Bsal were used as input for the PerfGAMM function of the Mapinguari package (B. Sinervo, pers. comm.) to simulate the microclimatic growth rate of Bsal across the study area by applying generalized additive mixed models (GAMMs).

In a second step, we predicted the potential distribution of European Fire Salamanders within our study area. The correlative SDM framework Maxent was used (Phillips et al., 2006). As environmental variables, we used the microclimatic temperature layers and elevational heterogeneity in terms of aspect, slope and topographic wetness index.

In a third step, we quantified and compared the microclimatic niches of Bsal positive and negative records as well as for the Fire Salamander to investigate potential overlaps of the fungus and its host. For this purpose, we used the hypervolume_svm function of the hypervolume package for R (Blonder et al., 2022; R Core Team, 2021).

Results and discussion

We found that Bsal is not restricted by microclimatic temperatures and therefore, the fungus has suitable growth conditions everywhere within our study area. The microclimatic suitable areas within the Bsal hotspot area strongly overlap with the predicted distribution of the Fire Salamander, which is also reflected in the statistics of the niche quantification. Under current climatic conditions, the highest growth rates occur during autumn (September) and spring (May), whereas the lowest growth rates are found during winter (December to February). Considering global warming scenarios of +2°C and +4°C, respectively, the highest growth rates for Bsal shift towards November and December, whereas the lowest growth rates will occur in summer (June to August). Surprisingly, the correlative SDMs predict that the potential distribution of *Salamandra salamandra* extends towards higher altitudes and will increase with rising temperatures. Hence, both global warming scenarios seem beneficial for the Fire Salamander but as the future scenarios require extrapolation beyond the training range of the models, upper thermal limits might be reached at some point. Furthermore, it must be mentioned that our models focus on microclimatic temperatures, while other important factors, such as precipitation are not considered.

Author contributions

FD did the main part of writing and model performance together with DR and used the data to submit his master thesis. PG co-supervised FD, supported him during model performance and statistical analyses and contributed strongly to re-write the manuscript in its current form. DR was the chief supervisor, designed the model performance and statistical analyses, and computed the final models. All authors contributed thoroughly to the manuscript and shared their knowledge.

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This article is not published yet.

2.5. Chapter 5 – Ecophysiological models for global invaders

Ginal, P., Mokhatla, M., Kruger, N., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2021). Ecophysiological models for global invaders: Is Europe a big playground for the African Clawed Frog? *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *335*(1), 158-172. https://doi.org/10.1002/jez.2432

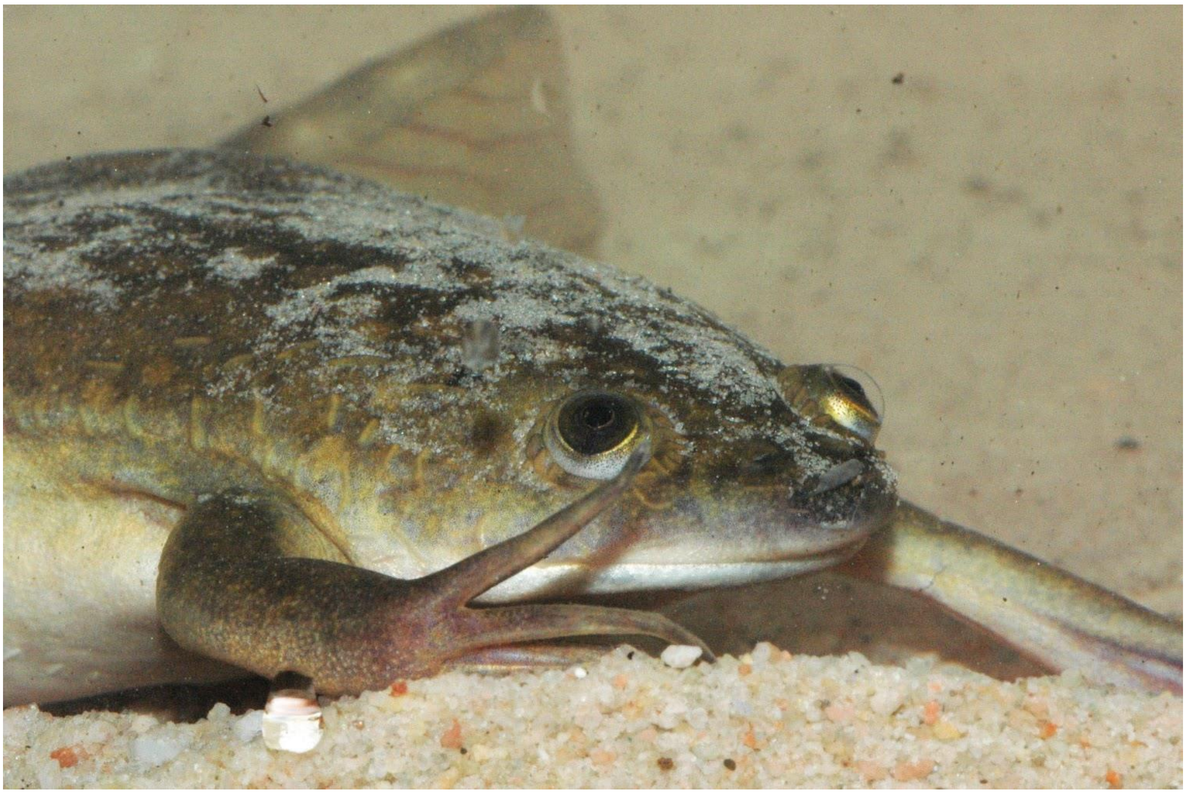

Figure 2.5: Portrait of an African Clawed Frog *Xenopus laevis* (photographed by John Measey).

Aims

One principle threat prompting the worldwide decline of amphibians is the introduction of non-native amphibians. The African Clawed Frog, *Xenopus laevis*, is now one of the widest distributed amphibians occurring on five continents with ongoing range expansion including large parts of Europe (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017; Wang et al., 2019). 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 non-native ranges (Broennimann et al., 2007). Recent developments emphasise more robust mechanistic or process-based models, which use physiological data like critical thermal limits and performance, or hybrid models combining correlative and mechanistic approaches (Ceia-Hasse et al., 2014; McEntire & Maerz, 2019). Previous correlative SDMs predict different patterns in the potential future distribution of *X. laevis* in Europe (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017), but it is likely that these models do not assess its full invasive potential.

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.

Methods

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. Furthermore, the critical thermal limits (CT_{min} and CT_{max}) of adult and tadpole *X. laevis* were also assessed. Based on the results of these performance trials, we used the Mapinguari package and its relevant functions in R (B. Sinervo, pers. comm.)(R Core Team, 2020) to compute 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, Maxent (Phillips et al., 2006), to predict the potential distribution of *X. laevis* in southern Africa and Europe.

Results and discussion

For adult frogs and tadpoles, the ecophysiological rasters reveal significant differences in locomotor performance, but similar patterns for hours of activity and hours of restriction. 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 has 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.

According to our ecophysiological SDMs, *X. laevis* has a much higher invasive potential than previous correlative approaches had suggested (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017). An area of 1,949,900 km^2 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 (Vimercati et al., 2020). River networks may assist the expansion even in areas with moderately suitable conditions. Moreover, the establishment of new populations through release or escape is quite 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.

Author contributions

PG was the leading author and did the main part of writing, model performance and statistical analyses. MM and NK did the main parts for the laboratory performance experiments. JS, AH and JM supervised the laboratory experiments. DR supervised the model performance and statistical analyses. All authors contributed thoroughly to the manuscript, shared comments and knowledge.

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2.6. Chapter 6 – More time for aliens?

Ginal, P., Kruger, N., Wagener, C., Araspin, L., Mokhatla, M., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2023). More time for aliens? Performance shifts lead to increased activity time budgets propelling invasion success. *Biological Invasions*, *25*(1), 267-283. https://doi.org/10.1007/s10530-022-02903-6

Figure 2.6: The African Clawed Frog prefers muddy waters (photographed by John Measey).

Aims

In the Grinnellian niche concept, the realized niche and potential distribution is characterized as an interplay among the fundamental niche, biotic interactions and geographic accessibility (Grinnell, 1917; Hutchinson, 1978). Climate is one of the main drivers for this concept and is essential to predict a taxon’s distribution (Soberón, 2007; Thuiller et al., 2004). Mechanistic approaches can be useful tools, which use fitness-related aspects like locomotor performance and critical thermal limits to predict the potential distribution of an organism (Enriquez-Urzelai et al., 2019; Kearney & Porter, 2009). These mechanistic approaches allow the inclusion of key ecological processes like local adaptation and can account for thermal performance traits of different life-history stages. The African Clawed Frog, *Xenopus laevis*, is a highly invasive species occurring on five continents. The French population is of special interest due to an ongoing expansion for 40 years and a broad base of knowledge (Louppe et al., 2018; Padilla et al., 2019; Padilla et al., 2020; Vimercati et al., 2020). Recent laboratory performance trials, of adult frogs from two native South African (Western Cape and KwaZulu-Natal) populations and one European (France) population, revealed a shift in the locomotor performance, represented by the proxies endurance time and distance, of the French population, suggesting local adaptation to the cooler European climate (Araspin et al., 2020). This shift may represent a change in the species´ fundamental climate niche. However, these data are restricted to adult specimens and similar data is lacking for other life-history stages like tadpoles. Moreover, it is currently unknown how the local adaptation of *X. laevis* relates to its potential geographic distribution.

Consequently, we tested the following hypotheses:

(I) Considering the shift in temperature dependent performance of adult frogs from France, we hypothesize that the French population exhibit increased in activity time in the invasive European range that could be devoted to fitness-relevant activity, and

(II) tadpoles may have less activity time available than adult frogs from the same range because larval stages may be more sensitive to environmental conditions like temperature variation.

Methods

We investigated how thermal performance traits translate into activity time budgets and how local adaptation and differences in the thermal responses of life-history stages may boost the European *Xenopus* invasion. We used a mechanistic approach based on generalized additive mixed models (GAMMs), where thermal performance curves were used to predict the hours of activity and to compare the potential activity time budgets for two life-history stages of native and invasive populations. We used performance datasets from previous studies. For adult frogs, Araspin et al. (2020) measured endurance distance (EndDist), which is relevant in the context of mate-searching or dispersal and they found rapid shifts in the temperature dependence of locomotor performance. For tadpoles, maximum velocity (MaxVel) was recorded by Kruger (2020) and Wagener et al. (2021), which is relevant in the context of predator escape. Based on the laboratory performance trials, we computed temperature dependent performance functions for adults and tadpoles using the PerfGAMM() function of the Mapinguari package (Caetano et al., 2019); B. Sinervo, pers. comm.) for R. The function uses generalized additive mixed models (GAMMs), selected by Akaike information criterion (AIC), with temperature as a smooth predictor. In subsequent steps, we computed the minimum and maximum temperatures at the 80% maximum performance breadth interval (T_{pb80}) for each population and life-history stage. Daily hours of activity were estimated applying the sin_h() function (Caetano et al., 2019). The function estimates the activity time budget of a species while simulating daily variation in temperature for each grid cell by applying a sine function between daily thermal limits and counting the time above a specific threshold (T_{pb80} limits herein). We used the biovars() function of the dismo package (Hijmans et al., 2017) to create activity layers for annual activity, activity during the warmest quarter and activity during the coldest quarter.

Results and discussion

For adult frogs and tadpoles, we found that the differences in daily activity time in Europe are highest between the French and the KwaZulu-Natal individuals regardless of life-history stage, followed by the difference between the French and the Western Cape population, and then between the two native South African populations. Our results suggest that for the European range, annual activity time budgets, as well as activity time budgets during the warmest and coldest quarter are highest for the French population, followed by activity time of the Western Cape and then KwaZulu-Natal animals. Furthermore, in adults T_{pb80} was distinctly lower among the two native and invasive populations with a left-shift in temperature- dependence of performance for the French population, while for tadpoles no significant differences were found.

The results of our novel approach suggest that invasive populations are able to adapt to novel environments by going through a shift in their fundamental Grinnellian niche, which results in more time available for activity. This gain in the activity time budget might allow individuals to survive and reproduce better, as a result of enhanced foraging or predator evasion, and might allow populations to expand in novel environments. Furthermore, the investigation of temperature-dependent responses of different life-history stages gives deeper insights into the physiology and invasion biology of a species and allows us to identify the life-history stage limiting the geographical expansion of a population. Both types of information, local adaptation and stage limited expansion, are crucial for the risk assessment of alien invasive species. Our study suggests that accounting for local adaptation in the different life-history stages of invasive populations might greatly improve the robustness or reliability of SDM predictions, even those using mechanistic approaches.

Author contributions

PG was the leading author. He did the main part of writing and performed the models and statistical analyses. NK, CW, LA, MM did the main parts for the laboratory experiments. JS, AH and JM supervised and designed the laboratory experiments. DR designed the methodological analyses. All authors contributed to the manuscript, shared comments and knowledge.

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3. Discussion and conclusion

Invasive species, including the spread of diseases such as the two chytrid fungi Bd and Bsal, contribute to biodiversity crisis and however, some “global players” get increased attention from science, public and policy, others remain neglected and potentially underestimated. If an invasive species is already established, it takes a lot of time, effort and money to manage or control the invaders and often it is just too late for this. For this reason, prevention of invasive species remains the most effective strategy (Kraus, 2009).

3.1. From correlative to mechanistic SDM
The European *Xenopus* invasion (Chapters 4, 5, and 6)

Novel methodological approaches and increased computational power allow us to better predict the risks of invasions and to understand the invasion processes. Particularly, SDM approaches remain useful tools to predict the invasion risks. SDM developed strongly during the last decades, starting with correlative SDM that only links geographical occurrences with environmental data but only reflecting the realized niche of a species, now increasingly mechanistic SDM is applied, which focuses on the key ecological processes of a species (Kearney & Porter, 2009; Soberón, 2007; Srivastava et al., 2019).

In the case of the African Clawed Frog, *Xenopus laevis*, for example, multiple previous approaches tried to estimate the potential invasive risk of the species for Europe (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017). Due to the different algorithms used and different predictors, the predicted distributions strongly differ among each other. However, all of these approaches provide useful first information to predict potential risks of invasion it is hard to decide, which of these models predicts reality best. In addition, correlative SDMs do not allow to investigate the impact of local adaptation or life history stages appropriately, thereby these predictions have strong limitations. All these caveats can be addressed with mechanistic SDM, although these types of models require intense data but provide a more realistic prediction (Kearney & Porter, 2009; Soberón, 2007; Srivastava et al., 2019). Due to the increase of computational power the models' resolution currently shifts from a previous macroclimatic scale to more microclimatic scales, further the temporal resolution of models also increases, which allows concise predictions on a local or regional scale and supports management or control actions in site.

Currently, one restriction of SDMs, particularly mechanistic models, is the availability of adequate predictors, such as high-resolution environmental data as well as performance data. However, already published thermal performance data can provide suitable and worthy input data for models. By doing so, the step of intense data collection can be skipped (as demonstrated in Chapter 4). Public databases such as AmphiBIO (Oliveira et al., 2017), which collects amphibian ecological traits, or the Reptile Development Database (Noble et al., 2018), which provides information on thermal developmental plasticity of reptiles, might be useful sources. Hence, it can be guessed that future SDM approaches will include several different performance variables, i.e., performance data on locomotion, water loss, metabolic rates, growth, reproduction, survival rates, etc.

Furthermore, future mechanistic SDM might also allow the inclusion of different perspectives, i.e. a high-resolution microclimatic model that emphasizes the biophysics (external processes on heat and water exchange) and metabolism (internal processes) of an organism. Current frameworks like the NicheMapR (Kearney et al., 2021; Kearney & Porter, 2017, 2020) or the microclima (Maclean et al., 2019) packages in the R environment already exist but due to the high computational power needed and the potential infinite complexity of mechanistic models, current applications are often restricted and only use a subset of these perspectives. Additionally, it is likely that future SDMs will also emphasize other factors such as biotic interactions (Fern et al., 2019; Godsoe et al., 2017) or dispersal of species (Monsimet et al., 2020; Shipley et al., 2022). Hence, it can be expected that future SDM approaches will provide more information on a finer scale, spatially and temporally, and will predict invasion processes and risks more realistically.

Unfortunately, SDM approaches cannot predict the dynamic processes of selection and evolution yet. In the case of the African Clawed Frog in France (Chapters 5 and 6), it was found that the species evolved in only 40 years and adapted to the much cooler climatic conditions there, resulting in a shift in the fundamental niche of the species. However, it seems that at least the critical thermal limits of the species remain similar among frogs from different localities (Araspin et al., 2020). Hence, it might be that these limits are physiologically fixed, which makes the number of potential predictive invasion scenarios limited and not infinite. Furthermore, we found that different life history stages of *Xenopus laevis*, in this case adult frogs and tadpoles, show different thermal-dependant responses (Chapters 5 and 6). Whereas adult frogs adapted to the cooler climate in France and have more activity time compared to conspecifics from South Africa, tadpoles did not show this adaptation. This indicates that adult frogs face different selective pressures than tadpoles, probably caused by the fact that tadpoles occur only for a short time period and also under suitable and no extreme climatic conditions. This makes tadpoles particularly more vulnerable to extreme climatic conditions or weather events than adult frogs (Chapter 6). This might give first tentative indications for management or control actions. It can be speculated that increased eradication efforts after extreme climatic conditions or weather events might have stronger impacts assuming that the *Xenopus* populations might be particularly more vulnerable during this time periods. However, concise investigations and more knowledge is needed to test this hypothesis. More details on thermal performance traits of other life history stages, i.e. eggs, different tadpole stages, metamorphs, and the thermal responses of other performance traits might help here.

3.2. Correlative SDM

The neglected invasion of the Oriental Garden Lizard (Chapter 3)

Considering the global but still neglected spread and potential invasive risk of the Oriental Garden Lizard *Calotes versicolor* s.l., we provided first correlative SDMs that predict large parts of the tropics and subtropics as climatically suitable for this species complex (see Chapter 3). Taking the species wide native range and its invasion history into account, these results are not surprising. Furthermore, correlative SDM have strong caveats, particularly compared to mechanistic SDM (Kearney & Porter, 2009; Soberón, 2007; Srivastava et al., 2019), but our results provide first tentative predictions for the species complex and give more attention to its neglected invasion process.

Our SDMs included multiple feature class combinations, regularization multipliers as well as a ranking of the best fitted models according to corrected Aikake information criterion (AICc) and we also emphasized the recent taxonomic situation of the species complex (Gowande et al., 2021). However, the recent but overdue split of *Calotes versicolor* s.l. into four distinct species/subtaxa caused a low number of available occurrence records for *Calotes farooqi* Auffenberg & Rehmann, 1995 (15 records) and *Calotes versicolor* sensu stricto (27 records), which led to suboptimal predictions. Higher sampling effort, certain identification of already existing species records as well as a species-specific tuning for the model’s settings may enhance this issue. Future mechanistic models, which may reveal more realistic predictions, should also emphasize the different subtaxa. However, it seems that the taxonomic situation of this species complex is far from solved yet (see *Calotes irawadi* s.l. Zug, Brown, Schulte & Vindum, 2006 and *Calotes farooqi* in Gowande et al., 2021). Overall, we recommend giving more attention to the species’ invasion process before it is too late for species management or controlling measures. Currently, the species is already found in at least twelve non-native countries/islands (see Table 1 in Ginal et al. 2022). Furthermore, the most frequent introduction pathways for the species include unintentional transport by ornamental plants or other nature products and in many cases the species first report is assigned to shipment hubs, airports or railway lines (see introduction of publication of Chapter 3 for details). Hence, it can be expected that the species will further be spread into novel areas. However, there are suggestions that the species may have negative impacts on local faunas (Diong et al., 1994; Matyot, 2004; Mauremootoo et al., 2003; Vinson, 1968), concise studies are lacking and the species impact remains not investigated yet.

3.3. Connectivity models

The *Xenopus* invasion in Portugal (Chapter 2)

The African Clawed Frog already invaded two nearby rivers in Portugal. However, the species was undetected for 25 years in this densely populated area (Sousa et al., 2018), the *Xenopus* invasion is, despite suitable climatic conditions (Ihlow et al., 2016; Measey et al., 2012) but due to the low habitat quality (i.e., polluted urban rivers, predatory fish), relatively slow. It is known, for example, that in lotic waterbodies, the number of metamorphs is lower, the metamorph size is smaller and it takes longer for the animals to reach the reproductive size compared to lentic environments (Moreira et al., 2017). *Xenopus laevis* is a mainly aquatic species, despite, some triggers, such as high population density or specific weather conditions, can lead to terrestrial movement (De Villiers & Measey, 2017), even with a maximum dispersal distance of up to 2.36 km (De Villiers, 2015).

We found that the topographic features and the urban area of the two rivers explain the current distribution patterns pretty well. We could further reconstruct the most likely dispersal scenario from Laje into Barcarena River and according to our connectivity model two small tributaries were used to reach the golf-course ponds, which are in the centre between the two rivers. These were then used as stepping stones to finally reach Barcarena River. We also identified multiple stepping stones into novel areas, which can be used to block these corridors using toad barriers or draining artificial ponds in a radius of 5 km around the colonised waterbodies (twice of the maximum known terrestrial dispersal distance). Hence, our results provide useful information to manage and control the *Xenopus* invasion in Portugal.

However, the applied approach of connectivity modelling provides realistic scenarios, the approach is particularly limited by the number of starting points and the resolution of raster layers, as both increase the computational time tremendously. Similar to the above mentioned perspectives for mechanistic SDM, the increase of future computational power will also be beneficial for this approach. Furthermore, a higher resolution of raster layers may also address the current issue that some fine-scale barriers remain undetected.

3.4. Population size estimation Recommendations for Cave Salamanders in Germany (Chapter 1)

In the case of the Italian Cave Salamanders (*Speleomantes italicus*) in Germany (Chapter 1), the species can be seen as an established non-native species. Our models revealed that our estimations for population size were insufficient for reliable estimations because the number of re-captures was too low (only three out of 70 caught salamanders were re-caught) and it is indicated that the population consists of several hundreds, maybe even much more, individuals. However, for the estimation of large population sizes a (semi-)automated individual identification software such as Wild-ID is required (Renet et al., 2019). Unfortunately, in most cases automated identification software requires standardized photographic images, i.e., from above in the same angle on a white background, which we couldnot realize in the field. Simultaneously to our study and our tentative species identification based on morphological characteristics, Schulz et al. (2021) confirmed genetically that the species is indeed *Speleomantes italicus*. As the closest certain native record of the species is around 800 km away and Cave Salamanders are poor dispersers with high site fidelity (Lunghi & Bruni, 2018; Salvidio, 2013), it can be assumed that the species was introduced. Schulz et al. (2021) provided an introduction scenario, where the species was released by a pet trader and quarry owner, which dates back until between 1914 and 1977. According to our observations, the species was only found in close proximity to the study area (transect of 40 m) and we could not confirm an expansion into other areas. Hence, the species can be classified as non-native but not as invasive yet (Ricciardi & Cohen, 2006). Interestingly, we found Cave Salamanders in very close proximity to other native amphibian species such as Fire Salamanders [*Salamandra salamandra* (Linnaeus, 1758)] or Alpine Newts [*Ichthyosaura alpestris* (Laurenti, 1768)], partially even in the same rock crevices. However, concise studies on the species ecological impact are lacking yet. Hence, we recommend further monitoring and investigations before the species' potential invasive risk can be evaluated.

3.5. Conclusion

The ongoing improvement of existing methodological and technical approaches as well as the development of novel approaches allows a better understanding and prediction of the processes driving invasion biology. However, by comparing my four non-native/invasive target species [*Speleomantes italicus* (Chapter 1), *Xenopus laevis* (Chapters 2, 5 and 6), *Calotes versicolor* s.l. (Chapter 3) and *Batrachochytrium salamandrivorans* (Chapter 4)] it remains unclear why for example the African Clawed Frog or Bsal are so successful in contrast to the Oriental Garden Lizard or the Italian Cave Salamander.

Considering some of the mentioned hypotheses thriving invasion success (see "Invasion process" in introduction) it can be suggested that the success of the African Clawed Frog in Europe (Ginal et al., 2021b, 2023; Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017) might be related to the empty niche hypothesis (Arnan et al., 2021; Elton, 1958). Particularly, the tadpoles with their filter-feeding lifestyle (Gradwell, 1975) might have an advantage when competing with other European tadpoles that require larger food items. Furthermore, especially the French population and its ongoing invasion might also be boosted by the positive effects of hybridization (Ellstrand &

Schierenbeck, 2000; Shivaramu et al., 2019) as this population consists of two different genetic lineages (De Busschere et al., 2016).

The success of Bsal is likely due to the missing co-evolution of European urodeles and a lacking immune response from the salamanders (Laking et al., 2017; Martel et al., 2014; Nguyen et al., 2016). This could be explained by the EICA-hypothesis and it might be suggested that due to the missing immune response of European salamanders, the fungus can allocate more resources into growth and spread (Blossey & Notzold, 1995; Li et al., 2022).

The empty niche hypothesis (Arnan et al., 2021; Elton, 1958) might also be an explanation for the establishment but not invasiveness of the Italian Cave Salamander in Germany (Ginal et al. 2021a). The niche of cave-dwelling amphibians is not occupied in Germany, even if some amphibians use rock crevices as hiding or hibernation places for short-term periods. The narrow niche breadth of the species might explain that it is still very restricted to a small geographical area. However, this might also be due to the phenomenon of delayed invasion/invasion debt (see “Invasion process” in introduction; Essl et al., 2011; Rouget et al., 2016; Seabloom et al., 2006).

In the case of the Oriental Garden Lizard it is difficult to explain its potential success as the invasion of the species seems pretty neglected, also from the herpetological community. During the review process of Ginal et al. (2022) it was hard to convince the reviewers that the species should be seen as potentially invasive, even if it is found in at least twelve non-native countries/islands with potential strong negative impacts (Diong et al., 1994; Mauremootoo et al., 2003; Uetz et al., 2021b).

Overall, the neglect of non-native species by society and authorities is a general issue and in many cases non-native species are tolerated till they become established and their populations are too large to eradicate or control (Kraus, 2009). For example, the Italian Cave Salamander population in Germany is currently seen as not invasive as it only occurs in a very restricted geographical area without expansion or observed negative impacts yet (Ginal et al. 2021a; Schulz et al., 2021). Schulz et al. (2021) even state:

"For the Speleomantes population in the Solling we emphasise that there is no need to take particular management or even eradication actions, and recommend conserving these salamanders."

Despite, I also enjoyed observing and working with these urodeles in their allochthonous habitat in Germany, non-native species should not be seen as biological enrichment (see "Two misconceptions" in introduction) and the phenomenon of invasion debt must be considered (see "Invasion process" in introduction). Economically, the prevention of expansion, establishment or introduction of non-native species is more efficient than their control (Kim et al., 2006; Leung et al. 2002). Unfortunately, the effectiveness of prevention measures is difficult to quantify as the pathways of introduction and concise distribution data are scarce for most species (Couch et al., 2023). Overall, the mind set of people, especially authorities but also colleagues, must change and non-native/invasive species should be seen as a serious issue and threat to biodiversity and economics.

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Appendix 1 – List of publications

Peer reviewed journals

Gabeleia, M., Tarkhnishvili, D., Adriaens, D., Ginal, P., Misof, B., & Wipfler, B. (in preparation). Climate-correlated phenotypes in Caucasian Rock Lizards.

Deiß, F., Ginal, P., & Rödder D. (submitted). Microclimatic growth rates of *Batrachochytrium salamandrivorans* under current and future climates: A very high spatial resolution SDM for Bsal and *Salamandra salamandra* (Linnaeus, 1758) within forest habitats of the European hotspot area. *Salamandra*.

Harrer, S., Ginal, P., Tan, W. C., Binaday, J., Diesmos, A., Manalo, R., Ziegler, T., & Rödder, D. (submitted). Disappearing archosaurs – An assessment of established protected areas in the Philippines to save the critically endangered and endemic Philippine Crocodile *Crocodylus mindorensis*. *Salamandra*.

Ginal, P., Stahlberg, J., Rauhaus, A., Wagner, P., Rödder, D., & Ziegler, T. (2023). Threatened turtles and tortoises (Testudines) in zoos: A ZIMS database analysis for improved One Plan Approach to Conservation actions. *Salamandra*, *59*(3), 262-274.

Rech, I., Ginal, P., Ziegler, T., & Rödder, D. (2023). Geckos in zoos: A global approach on distribution patterns of threatened geckos (Gekkota) in zoological institutions. *Journal of Nature Conservation*, 126467. https://doi.org/10.1016/j.jnc.2023.126467

Ginal, P., Flecks, M., & Hartmann, T. (2023). First genetic confirmation of Theloderma stellatum (Anura: Rhacophoridae) from Cambodia and notes on its distribution. *Salamandra*, *59*(1), 87-91.

Ginal, P., Kruger, N., Wagener, C., Araspin, L., Mokhatla, M., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2022). More time for aliens? Performance shifts lead to increased activity time budgets propelling invasion success. *Biological Invasions*, *25*(1), 267-283. https://doi.org/10.1007/s10530-022-02903-6

Ginal, P., Schmitz, L., & Rödder, D. (2022). Larval description of *Theloderma albopunctatum* (Liu & Hu, 1962) (Anura: Rhacophoridae) from northern Vietnam, with comparison between the North-Vietnamese and North-eastern Thai clades. *Zootaxa*, *5214*(4), 595-599. https://doi.org/10.11646/zootaxa.5214.4.7

Schmitz, L., Clement, V. F., Ginal, P., & Rödder, D. (2022). Spatiotemporal patterns of habitat use by the Sand Lizard (*Lacerta agilis* Linnaeus, 1758): Effects of climatic seasonality? *Salamandra*, *58*(4), 302-316.

Ginal, P., Tan, W. C., & Rödder, D. (2022). Invasive risk assessment and expansion of the realized niche of the Oriental Garden Lizard *Calotes versicolor* species complex (Daudin, 1802). *Frontiers of Biogeography*, *14*(3), e54299. https://doi.org/10.21425/F5FBG54299

Ginal, P., Loske, C. H., Hörren, T., & Rödder, D. (2021). Cave Salamanders (*Speleomantes* spp.) in Germany: Tentative species identification, estimation of population size and first insights into an introduced salamander. *Herpetology Notes*, *14*, 815-822.

Tan, W. C., Ginal, P., Rhodin, A. G. J., Iverson, J. B., & Rödder, D. (2021). A present and future assessment of the effectiveness of existing reserves in preserving three critically endangered freshwater turtles in Southeast Asia and South Asia. *Frontiers of Biogeography*, *14*(1). https://doi.org/10.21425/F5FBG50928

Ginal, P., Muehlenbein, L. E., & Rödder, D. (2021). The advertisement calls of *Theloderma corticale* (Boulenger, 1903), *Theloderma albopunctatum* (Liu & Hu, 1962) and *Theloderma licin* McLeod & Ahmad, 2007 (Anura: Rhacophoridae). *North-Western Journal of Zoology*, *17*(1), e201513.

Ginal, P., Moreira, F. D., Marques, R., Rebelo, R., & Rödder, D. (2021). Predicting terrestrial dispersal corridors of the invasive African Clawed Frog *Xenopus laevis* in Portugal. *NeoBiota*, *64*, 103-118. https://doi.org/10.3897/neobiota.64.60004

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Zoology Part A: Ecological and Integrative Physiology, *335*(1), 158-172. https://doi.org/10.1002/jez.2432

Non-peer reviewed journals

Ginal, P., Measey, J., Herrel, A., Secondi, J., Rebelo, R., Courant, J., & Rödder, D. (2023). Unbekannte Eindringlinge: Der Glatte Krallenfrosch in Europa – Sechs Jahre später. *Elaphe, 2023*(3): 74-85.

Ginal, P. (2023). Neue Vertreter der Moosfrosch-Gattung *Theloderma*: Taxonomie, Schutzstatus und Erhaltungszucht. *Elaphe, 2023*(2): 12-27.

Ginal, P., & Loske, C.-H. (2021). Italienische Höhlensalamander in Deutschland? *Elaphe, 2021*(6): 84-89.

Ginal, P., & Rech, I. (2021). Süßigkeiten aus Mexiko. *Reptilia, 26*(1): 62-65.

Ginal, P. (2021). Lebende Fossilien – Haltung und Nachzucht der bedrohten Mallorca-Geburtshelferkröte (*Alytes muletensis*). *Reptilia, 25*(5): 54-62.

Ginal, P. & Kasten, M. (2020). Eiffelturm, Louvre und Terrarien - Der Zoo de Vincennes (Paris) als Beispiel für einen modernen Zoo. *Elaphe, 2020*(4): 70-75.

Ginal, P. (2015). Herpetologischer Rundgang – Reptilien und Amphibien im Tiergarten Nürnberg. *Terraristik, 3*(1): 58-61.

Ginal, P. (2013). Haltung tropischer Tausendfüßer. *Reptilia,18*(4): 39-43.

Appendix 2 – List of conference contributions

Talks

Ginal, P., Kruger, N., Wagener, C., Araspin, L., Mokhatla, M., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2022). More time for aliens? Performance shifts lead to increased activity time budgets propelling invasion success. European Congress of Herpetology, Belgrade, Serbia.

Ginal, P., Kruger, N., Wagener, C., Araspin, L., Mokhatla, M., Secondi, J., Herrel, A., Measey, J., Moreira, F. D., Marques, R., Rebelo, R., & Rödder, D. (2022). Mechanistic SDMs and connectivity models: The highly invasive African Clawed Frog (*Xenopus laevis*) in Europe. IBS (International Biogeography Society), Vancouver, Canada.

Ginal, P., Mokhatla, M., Kruger, N., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2021). Ecophysiology meets conservation biogeography: High invasion risk of the African Clawed Frog *Xenopus laevis* in Europe. Early Career IBS (International Biogeography Society), online.

Ginal, P., Mokhatla, M., Kruger, N., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2021). High invasion risk of the African Clawed Frog, *Xenopus laevis*. DGHT (German Society of Herpetology and Terraristics), Bad Wildungen, Germany.

Ginal, P., Mokhatla, M., Kruger, N., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2020). Ecophysiology predicts the fundamental niche of native and invasive populations of the African Clawed Frog *Xenopus laevis*. WCH9, World Congress of Herpetology, New Zealand.

Ginal, P., Mokhatla, M., Kruger, N., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2019). Ecophysiology predicts the fundamental niche of native and invasive populations of the African Clawed Frog *Xenopus laevis*. European Congress of Herpetology, Milano, Italy.

Posters

Harrer, S., Ginal, P., Tan, W. C., Binaday, J., Diesmos, A., Manalo, R., Ziegler, T., & Rödder, D. (2022). Disappearing archosaurs: An assessment to save the critically endangered Philippine Crocodile. European Congress of Herpetology, Belgrade, Serbia.

Ginal, P., Mokhatla, M., Kruger, N., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2020). Fundamental niche change in an invasive population of the African Clawed Frog. WCH9, World Congress of Herpetology, New Zealand.

Ginal, P., Mokhatla, M., Kruger, N., Secondi, J., Herrel, A., Measey, J., & Rödder, D. (2020). Ecophysiology meets conservation biogeography: High invasion risk of the African Clawed Frog *Xenopus laevis* in Europe. Leibniz-Evaluation for Excellence, ZFMK, Bonn, Germany.

Appendix 3 – Introduced Cave Salamanders in Germany

Herpetology Notes, volume 14: 815-822 (2021) (published online on 31 May 2021)

Cave salamanders (*Speleomantes* spp.) in Germany: tentative species identification, estimation of population size and first insights into an introduced salamander

Philipp Ginal[1,*], Carl-Henning Loske[2], Thomas Hörren[3], and Dennis Rödder[1]

Abstract. The pathways of introduction of non-native amphibians are diverse, as historically amphibians were used as pest control agents, food stock, or were introduced to perform research. Today, the pet trade is the main source for amphibian introductions into novel ranges. However, these introductions mainly concern anurans, whereas cases involving urodeles are less common. Since 2013, a population of European cave salamanders, *Speleomantes* spp. Dubois, 1984, is known to be present in Germany. However, knowledge on the size of this population is missing, and it is unknown to which of the similar-looking species of *Speleomantes* it belongs. Here, we applied loglinear capture-recapture models to estimate population size, and used a recently published photographic database, including more than 1000 images of all eight *Speleomantes* species, to determine the species identity of the German population. According to our estimates, the population consists of 170 to 485 individuals (± 134 to 320). Based on colour pattern the population most likely belongs to *S. italicus* (Dunn, 1923). We additionally provide the first evidence for reproduction and give further insights into this non-native salamander population.

Keywords. Plethodontidae, lungless salamanders, amphibians, non-native species, loglinear models

Introduction

The introduction of non-native amphibians outside their natural range often has strong negative impact on the local native fauna (Kraus, 2015; Measey et al., 2016). The pathways of introduction of non-native amphibians are diverse, as historically amphibians were used as pest control agents, food stock, or were introduced to perform research. Today, the pet trade is the main source for amphibian introductions into novel ranges (Kraus, 2009). Most cases of amphibian introduction into non-native areas relate to anurans, while cases involving urodeles are less common (Kraus, 2009; Fitzpatrick et al., 2010; Lunghi et al., 2018b).

The genus *Speleomantes* Dubois, 1984, commonly known as European cave salamanders, comprises eight species, which are endemic to Italy and a small part of south-eastern France. Three species are distributed along the northern and central Apennine chain on the European mainland (*S. ambrosii* [Lanza, 1955], *S. italicus* [Dunn, 1923], *S. strinatii* [Aellen, 1958]), whereas the other five species (*S. flavus* [Stefani, 1969], *S. genei* [Temminck and Schlegel, 1838], *S. imperialis* [Stefani, 1969], *S. sarrabusensis* Lanza et al., 2001, and *S. supramontis* [Lanza et al., 1986]) endemic to Sardinia, Italy (Kwet, 2010, Glandt, 2015). Only two mainland species, *S. ambrosii* and *S. italicus*, come naturally into contact and give birth to hybrids in a small area (Ficetola et al., 2019). In past decades, *Speleomantes* were introduced to several non-native areas as well, which led to establishment of several reproducing populations (Lunghi et al., 2018b). *Speleomantes* are lungless, and require cold and moist environmental conditions for efficient cutaneous respiration (Lanza, 2006; Ficetola et al., 2018). The common name, cave salamanders, is misleading because they are not real troglobionts (obligate cave dwellers). *Speleomantes* often colonise subterranean habitats such as caves, but also other habitats like mines or crevices, where a cold and moist environment is provided throughout the year (Culver and Pipan, 2009). *Speleomantes* maintain stable populations and reproduce in those habitats (Lunghi et al., 2015; Lunghi et al., 2018a), mostly leaving them

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only to reach areas with high prey availability (Manenti et al., 2015; Lunghi et al., 2018c). Although, in several cases surface populations are known, such as those on the forest floor or on dry stone walls (Manenti, 2014; Costa and Salvidio, 2016).

Since 2013, the German herpetological community has been aware of an introduced *Speleomantes* population in the Weserbergland/Solling, Niedersachsen, Germany. However, identification of *Speleomantes* based on morphology alone is difficult (Kwet, 2010; Glandt, 2015) and thus the species identity of the German population is currently unknown, while studies on this non-native population are lacking. Further, it is unclear whether the species is established (i.e. a self-sustaining, reproductive population) at the non-native locality, or if it is just composed of a few individuals that persist there for some years. For this reason, we provide a tentative identification of the German *Speleomantes* population to species-level and estimate its population size. We used a recently published photographic database containing more than 1000 images of all eight European cave salamander species. For population size estimation, we used loglinear capture-recapture models for open populations.

Material and Methods

Study area. The study area is located in Holzminden, Lower Saxony, Germany (Fig. 1A). This area is located in between the natural area categories of *367.0 Weseraue und Weserterrassen* and *370.0 Nördlicher Solling* (Hövermann 1963). The biogeographical region is continental, but located close to the border of the Atlantic region in nearby North Rhine-Westphalia (Europäische Umwelt-Agentur, 2010). The present vegetation could be classified as *Asperulo-Fagetum*, following Pott (1992). It should be mentioned that our vegetation recording is not complete due to the late date of assessment, and presence of crucial species for determination, which were out of season like *Allium ursinum* L., could not be assessed. The salamander microhabitat (Figure 1B) is characterised by a scarp with some mosses and ferns (*Asplenium trichomanes* L.). Several blackberry (*Rubus fruticosus* L.) twigs hang over the scarp. The surrounding area is characterised by older trees (some up to hundreds of years). These trees are mainly Common beeches (*Fagus sylvatica* L.), some Common oaks (*Quercus robur* L.), few younger larches (*Larix decidua* Mill.) and some maple trees (*Acer*

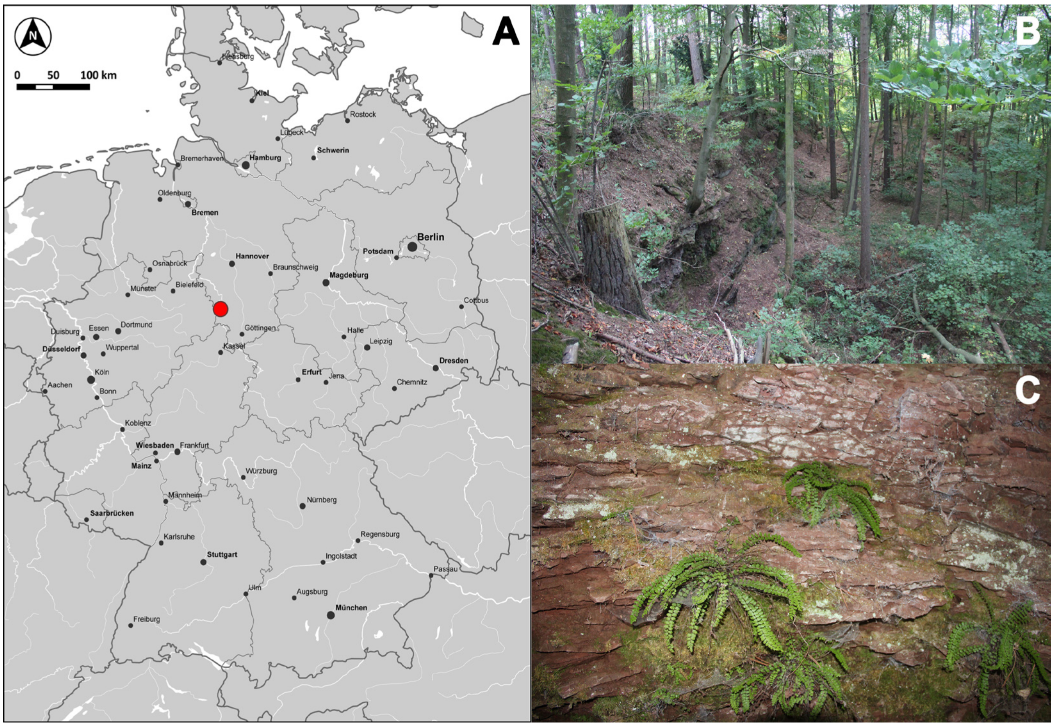

Figure 1. Study area: (A) location in Germany and (B and C) habitat.

pseudoplatanus L.). The herb layer mainly consists of blackberry and stinging nettle (*Urtica dioica* L.) with fewer woodruff (*Galium odoratum* [L.] Scop.) and honeysuckle (*Lonicera xylosteum* L.), which indicates a very eutrophic habitat. The ground is covered by a thick layer of mainly beech-foliage and some deadwood. The area is highly impacted by humans, which is indicated by a high amount of garbage, graffiti on parts of the scarp, self-made mountain bike trails, and a well-trodden path above and to the scarp. The closest buildings are just around 50 m away. The scarp has a maximum height of c. 6 meters and a length of c. 40 meters. Parts of the scarp are largely eroded and covered by leaf-litter. At some points, water is leaking out of the scarp, keeping it moist. Salamanders were only found in close vicinity to the scarp.

Study design. For species identification and estimation of population size, we selected a transect of 40 m length and 5 m width along the scarp. We visited the study area six times between 29 August 2020 and 31 October 2020 during cold (< 15 °C) nights with high probability of rain. Starting at sunset, we searched for salamanders until no more could be found along the transect. To avoid temporal autocorrelation and stress effects on the cave salamanders, surveys were separated by at least seven days. We searched for salamanders on the forest floor and in crevices along the scarp. Directly after collection, salamanders were photographed using a camera (Canon EOS 60D with EF-S 18-135 mm objective and a resolution of 5184x3456). We took several dorsal and dorsolateral pictures of each individual salamander, so that all individually specific markings in colour pattern were recorded. For this, each salamander was placed on a rock in their natural environment. We took the photos when the salamander was fully stretched moving forward. Further, the total length of each salamander was measured using a ruler, when the salamander was fully stretched. The ratio between adults and juveniles was determined according to Lunghi et al. (2020), which used the threshold of 68 mm of total length for European mainland cave salamanders when maturity is reached. To avoid direct recapture of the same individual, the salamanders were kept in a box prepared with moist leaf litter and moss from their natural habitat until the sampling was finished that day. After each transect run, all salamanders were released at their collection locality.

Species identification. Most *Speleomantes* species are similar in appearance and variable in colour pattern, which makes species identification based on small numbers of individuals difficult (Kwet, 2010; Glandt, 2015). However, when looking at population level, tendencies in morphology and colour pattern characterise species (Lunghi et al., 2020). Accordingly, we used a recently-published photographic database (Lunghi et al., 2020) to compare photographic images of 70 different individuals from the German population with other *Speleomantes* populations throughout their native range. The database contains a total number of 1052 standardised images of dorsally photographed salamanders of all eight *Speleomantes* species (> 55 photographed specimens per species) from at least two different locations per species.

Estimation of population size. *Speleomantes* spp. show a complex dorsal pattern which is unique for each individual and stays stable when maturity is reached (Lunghi et al., 2019). This makes cave salamanders ideal subjects for capture-recapture studies. For individual identification, we chose up to 10 individually specific body markings (depending on the complexity of the individual colour pattern) to visually compare each salamander to salamanders of other sampling visits. When a salamander was assumed to be recaptured, all images of the specimen were compared in detail to ensure the identity. We used the *closure.test()*-function in the *secr*-package to test whether a population sampled by capture-recapture is closed to losses and gains over the period of sampling (Efford, 2020). Subsequently, we assumed an open population for further analyses. To estimate capture probabilities and the population size, we used the *openp()*-function of *Rcapture*-package (Baillargeon and Rivest, 2019) for R v. 3.6.2 (R Core Team, 2019). Following the guidelines of the *Rcapture*-package, we ran models setting unconstrained and equal capture probabilities (*openp()*-function set *m*-argument to “up” = uncontrained probabilities and “ep” = equal probabilities; Baillargeon and Rivest, 2019). The best model was selected according to the lowest Akaike Information Criterion (AIC). Furthermore, we performed a chi-square goodness of fit test based on the deviance. Considering the low number of recaptures, we performed a sensitivity analysis for the best model and simulated the effect of additional recaptures on the estimation of population size. For this task, we added a simulated capture occasion, where we ‘recaptured’ one to five additional salamanders (called sim 1 - 5).

Results

A total of 70 cave salamanders were caught at six sampling dates. The majority of salamanders could be caught only one time (n = 67), whereas three salamanders were caught twice/recaptured once (Table 1). On each occasion, a mean of 12 ± 9 (range: 4 – 31) salamanders were caught. On average, the recaptured salamanders were caught 19 ± 8 (range: 14 – 28) days after their first capture. The measured salamanders' total length ranged from 40 mm to 119 mm (mean: 92.6 ± 19.0 mm, n = 58). Fifty salamanders were above 68 mm and determined as mature individuals, while eight juveniles were found (n = 58).

Species identification. Sixty-nine out of 70 captured *Speleomantes* showed dark ventral colouration, with small lighter spots, and dark brown dorsal colouration interrupted by brown to red patterns of different brightness and density (Fig. 2A, B). Some specimens showed a grey stripe above the front legs. Within the red pattern, some individuals, especially smaller and probably juvenile to sub-adult salamanders, tended to show a colour gradient from spine to distal lateral body from red to yellow (Fig. 2C). A single individual showed distinctly paler colouration (Fig. 2D). According to Lanza (2006), all five Sardinian *Speleomantes* show light ventral colouration, whereas the three mainland species show a dark venter. Therefore, we assume that the German population derives from the European mainland. A comparison with the photo-database (Lunghi et al., 2020) supports this. Further, the only two species in the photo-database that appeared similar to almost identical in colour patterns and morphology to the German individuals were *S. ambrosii* and *S. italicus*. Two out of four *S. ambrosii* populations (see *S. ambrosii* populations 1 + 2 in Lunghi et al., [2020]) show a similar colour pattern, but the extent and intensity of their pattern is less while only few markings are dorsally centred or located between their hind limbs, which characterise most German salamanders. Compared to the German population, an almost identical colour pattern and morphology was only found for three out of four *S. italicus* populations (see *S. italicus* populations 1 – 3 in Lunghi et al., [2020]). The fourth *S. italicus* population holds around a half of individuals with a similar pattern. For this reason, we conclude that the German *Speleomantes* population can most likely be assigned to *S. italicus*.

Estimation of population size. The closure test revealed that population closure over the period of sampling cannot be assumed ($z = -1.39$, $p = 0.08$). The two models, one set with unconstrained capture probabilities ("up"-model) and the other one set with equal capture probabilities ("ep"-model), showed significant goodness of fit ($p<0.05$). According to the lowest AIC and an unrealistically high standard error in the "up"-model, we selected the "ep"-model to estimate the population size and the capture probabilities (Table 2). For all six sampling occasions, the averaged capture probabilities for the "ep"-model were 0.11 ± 0.07. The estimated population size for the original dataset was 485 ± 320 individuals. However, the sensitivity analysis (sim1 - 5) revealed strong sensitivity of our dataset for additionally captured salamanders with a dropdown to 17–35 % of the originally estimated population size (Table 3).

Discussion

The German *Speleomantes* population is morphologically most similar to some populations of *S. italicus*. This species is native in the northern and central Apennines from the provinces Reggio Emilia to Lucca,

Table 1. Descriptive frequency statistics of capture-recapture trials on the German *Speleomantes* population: Number of salamanders captured i times (i = 1, 2, 3, 4, 5, 6), number of salamanders captured for the first and the last time on occasion i and number of salamanders captured on occasion i.

	Number of salamanders captured i times	Number of salamanders captured for the first time on occasion i	Number of salamanders captured for the last time on occasion i	Number of salamanders captured on occasion i
i = 1	67	10	9	10
i = 2	3	6	6	7
i = 3	0	4	4	4
i = 4	0	11	12	12
i = 5	0	9	8	9
i = 6	0	30	31	31

Figure 2. *Speleomantes* cf. *italicus* from the German population: (A) adult specimen with brown dorsal colouration, (B) adult specimen with red dorsal colouration, (C) juvenile and (D) adult specimen with pale colouration. Photographs by Carl-Henning Loske.

southwards to Pescara at 80 to 1600 m elevation (Frost, 2020). The German population is c. 800 km away from the species' known native range. Therefore, the German population can be seen as non-native and also as the northernmost European cave salamander population. Further, Lucente et al. (2016) mention that in past decades some translocation/introduction experiments, often scientifically unpublished, were made throughout the mainland part of European cave salamanders' range. Lunghi et al. (2018b) also mention that six of these introduction experiments are known, which all seem to be established populations, partially composed by two or also three *Speleomantes* species from the European mainland. The latter authors also note the existence of the German *Speleomantes* population as an example of a translocation experiment, but without any other details.

Speleomantes species from the European mainland are extremely variable in their pattern and colouration and the photographic database does not include all known populations (i.e. populations of *S. ambrosii bianchii*). Furthermore, there might be a chance that the German population is composed of hybrids by two or even more

Table 2. Model output for the *open population* models: Deviance, degrees of freedom (df), AIC, p-value of chi-square goodness of fit test and estimated abundance ± standard error (SE) for the two models, one set with unconstrained probabilities, the other one set with equal probabilities.

	Deviance	df	AIC	p-value	Estimated abundance ± SE
Unconstrained probabilities	1.70	50	57.93	<0.001	236 ± 675521
Equal probabilities	4.07	53	54.30	<0.001	485 ± 320

Speleomantes species. Particularly, hybrids of *S. italicus* and the very similar looking *S. ambrosii* might be nearly impossible to detect using morphological characteristics alone. Thus, future studies that include genetic analysis will help to clarify this issue definitely.

Of the 70 individuals caught, one showed a distinctly paler colouration than the other conspecifics (Fig. 2D). Cases of anomalies in colouration are known from several amphibians including also the cave salamanders *S. sarrabusensis, S. flavus* and *S. supramontis,* from which cases of albinism, leucism and melanism have been reported (Lunghi et al., 2017a, b).

Considering the modest number (n = 70) of salamanders caught, with only three recaptures, population size estimates showed strong variation (485 ± 320) and sensitivity analysis revealed that the estimation is highly sensitive to additional recaptures (Table 3). Also, the capture probabilities of 0.11 ± 0.07 seem high, considering that only three out of 70 salamanders were recaptured. The model revealed that our dataset was insufficient to clearly estimate the population size of the German population. However, sensitivity analysis also showed that the dropdown in the estimated population size strongly decreases when two or more additional recaptures would be made (sim2: 24 %, sim3: 20 %, sim 4: 18 %, sim 5: 17 %; Table 3). Nevertheless, it seems unrealistic that two to five additional recaptures might be achieved during a single sampling occasion, especially without any new captures. Therefore, we assume that the realistic population size might be set between 170 and 485 (sim1 and sim0) individuals.

The German population was first recognized in 2013. However, it can be assumed that the population occurred there for many more years, or even decades. During our field work, we could find a pregnant female and several juvenile specimens of c. 40 mm total length, which is the first evidence for reproduction in this area. Therefore, the German *Speleomantes* can be characterised as an established, reproducing population. The broad variation in colour pattern could be an indication for a broad base of founder animals. Unfortunately, we could not clarify the pathway of introduction. We assume that a private amphibian enthusiast released some founder animals. Non-native amphibians can have strong impacts on the native fauna including other amphibians (Ryan et al., 2009; Measey et al., 2015, 2016; Courant et al., 2018). At the time of the investigation the species was non-invasive according to the definitions of Ricciardi and Cohen (2006) because the German population has been confined to a small area since it was first detected. However, several authors have shown that long time-periods can pass before non-native vertebrates first appear in the wild or even become invasive (e.g., Nehring et al., 2015; Toledo and Measey, 2018). For amphibians, it is known that this phenomenon also known as invasion debt, the time span between the introduction and establishment phase of an invasion, can be highly variable (35 years for *Xenopus laevis* [Daudin, 1802], while five years for *Sclerophrys gutturalis* [Power, 1927], introduction debt + establishment debt + spread debt; for details see Van Sittert and Measey, 2016; Vimercati et al., 2017). Therefore, this requires monitoring of non-native species in order to be able to evaluate the potential impact of each taxon over time. So far, there is no official open access platform to report 'new' alien species but approaches to assess the invasiveness of wild non-native species in Germany (Nehring et al., 2015; Rabitsch and Nehring, 2017). Interestingly, we found several native amphibian species (*Bufo bufo* [Linnaeus, 1758], *Ichthyosaura alpestris* [Laurenti, 1768], *Lissotriton helveticus* [Razoumowsky, 1789], *Lissotriton vulgaris* [Linnaeus, 1758], *Salamandra salamandra* [Linnaeus, 1758]), some in high numbers, syntopic with *Speleomantes*. Particularly, several *I. alpestris* and *S. salamandra* were found in the same crevices as the cave salamanders. Furthermore, the cave salamanders seem to be restricted to the collection transect and its close vicinity. After intense survey at two other scarps (distance of 150–200 m), which we assumed to be also suitable habitats, no *Speleomantes* could be found. For cave salamanders, it has been shown that their dispersal ability is very limited and they seem to show a high site fidelity even if other suitable habitat is available in close proximity (Salvidio, 2013; Lunghi and Bruni, 2018). However, we conclude that further investigation on the potential impact on native fauna and the potential dispersal ability is needed.

Table 3. Estimated population size (mean ± SE) of the original dataset (sim0) and the sensitivity analysis (sim1 - 5) for the "ep"-model.

	Population size	Percentage [%]
Sim 0	485 ± 320	100
Sim 1	170 ± 134	35
Sim 2	112 ± 52	24
Sim 3	96 ± 30	20
Sim 4	88 ± 21	18
Sim 5	84 ± 16	17

Acknowledgements. We want to thank the Lower Nature Conservation Authority (Untere Naturschutzbehörde) of Holzminden for providing the necessary licenses. Further, we want to thank the following persons who supported our field work: Shalin Barzel, Jens Hoberg, Paul Bachhausen, Stephan Bürger and all helpers in the salamander-hiking-group, Amadeus Plewnia, Christian Stepf, Niklas Banowski and Sebastian Dörnemann. Finally, we acknowledge the support of Enrico Lunghi, Sebastiano Salvidio, Wouter Beukema and John Measey for thoroughly reviewing our manuscript and providing constructive comments. While the proof stage of this manuscript, Schulz et al. (2021) could genetically identify the German population as *Speleomantes italicus*. Further, they provided a suggestion for the most likely introduction scenario.

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Accepted by Wouter Beukema

Appendix 4 – Dispersal of invasive *Xenopus* in Portugal

NeoBiota 64: 103–118 (2021)
doi: 10.3897/neobiota.64.60004
https://neobiota.pensoft.net

RESEARCH ARTICLE

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Predicting terrestrial dispersal corridors of the invasive African clawed frog *Xenopus laevis* in Portugal

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Academic editor: W. Rabitsch | Received 25 October 2020 | Accepted 17 December 2020 | Published 28 January 2021

Citation: Ginal P, Moreira FD, Marques R, Rebelo R, Rödder D (2021) Predicting terrestrial dispersal corridors of the invasive African clawed frog *Xenopus laevis* in Portugal. NeoBiota 64: 103–118. https://doi.org/10.3897/neobiota.64.60004

Abstract

Invasive species, such as the mainly aquatic African clawed frog *Xenopus laevis*, are a main threat to global biodiversity. The identification of dispersal corridors is necessary to restrict further expansion of these species and help to elaborate management plans for their control and eradication. Here we use remote sensing derived resistance surfaces, based on the normalised difference vegetation index (NDVI) and the normalised difference water index (NDWI) accounting for behavioural and physiological dispersal limitations of the species, in combination with elevation layers, to determine fine scale dispersal patterns of invasive populations of *X. laevis* in Portugal, where the frog had established populations in two rivers. We reconstruct past dispersal routes between these two invaded rivers and highlight high risk areas for future expansion. Our models suggest terrestrial dispersal corridors that connect both invaded rivers and identify artificial water bodies as stepping stones for overland movement of *X. laevis*. Additionally, we found several potential stepping stones into novel areas and provide concrete information for invasive species management.

Keywords

Amphibian, distribution, invasive species management, NDVI, resistance kernel

Introduction

Worldwide, invasive species are a main threat to biodiversity (e.g. Fritts and Rodda 1998; Rosenzweig 2001; Chornesky and Randall 2003; Davis 2003; Doherty et al. 2016), having also played a role in global amphibian decline (e.g. Gibbons et al. 2000; Chornesky and Randall 2003; Falaschi et al. 2020). Some invasive amphibians are known to have disastrous impacts on native ecological communities and to alter sensitive ecological relationships through competition for resources, predation or spread of infectious diseases (Kraus 2009; Kraus 2015 and references therein; Measey et al. 2016 and references therein; Kumschick et al. 2017).

The African clawed frog (*Xenopus laevis*) is native to southern Africa and has been moved worldwide as a model organism for laboratory research (Measey et al. 2012; van Sittert and Measey 2016). This species has unique physiological and demographical traits, including a tolerance to saltwater and eutrophic conditions and behavioural adaptations, such as terrestrial migration or the ability to burrow into substrate to persist in drought and extreme temperature events. This trait combination confers it with an enormous invasive potential (for a thorough review, see Measey et al. 2012; Sousa et al. 2018; Scalera et al. 2019). Recently, it was ranked second amongst all invasive amphibian species considering its environmental and socio-economic impacts (Measey et al. 2016).

To date, *X. laevis* has established invasive populations in numerous countries across four continents due to both deliberate and accidental release of laboratory animals and the pet trade (Measey et al. 2012). In Europe, it successfully invaded lotic and lentic freshwater habitats (Moreira et al. 2017) and established populations are known in the U.K., France, Sicily (Italy) and Portugal (see Measey et al. 2012 and references therein). Comparisons of mitochondrial DNA suggest that all the Portuguese frogs resulted from presumably a single introduction event and descend from animals exported from the South-western Cape clade, in Mediterranean from South Africa (De Busschere et al. 2016). Correlative SDM approaches revealed the Mediterranean region of Portugal as climatically highly suitable for *X. laevis* (Measey et al. 2012; Ihlow et al. 2016). However, while the populations in Sicily and France are spreading fast (Faraone et al. 2008; Louppe et al. 2017), the expansion of the Portuguese populations was comparatively slow – approximately 30 years after the introduction event, the species was still confined to a 30 km^2 region (Sousa et al. 2018).

Dispersal is essential for successful spread of an invasive species (cf. Blackburn et al. 2011). Animal dispersal occurs at different life stages and is triggered to evade competition, to acquire resources, to reduce mortality or for reproduction (Bowler and Benton 2005 and references therein; Van Dyck and Baguette 2005). Amphibians are often referred to as poor dispersers, but some species disperse over considerable distances of more than 10 km, for example, from the terrestrial habitats to spatially disjunct breeding sites for migration (e.g. Avise 2000; Smith and Green 2005 and references therein). Traditionally, *X. laevis* was thought to be strictly aquatic with all life stages inhabiting the same aquatic environment, constraining the invasive potential of the species to connected aquatic habitats. However, there is now sufficient evidence that the species migrates overland amongst various types of lentic and lotic water bodies, which significantly expanded our view of the species' dispersal and, therefore, invasive potential (see Measey et al. 2016 for recent review). Terrestrial movement seems to be constrained to a fraction of the population (21–36% [Measey and Tinsley 1998]), involves adults of both sexes (De Villiers and Measey 2017), occurs mostly nocturnally, involves Euclidean distances up to 2.36 km (De Villiers 2015) and a maximum velocity of 0.2 km/h (Measey and Tinsley 1998). It is known that a drying habitat or the reduction of resources due to high numbers of conspecifics can lead to mass migration events, although other potential factors that trigger terrestrial dispersal remain unknown (Measey et al. 2016).

To predict dispersal pathways and, therefore, be able to block or hamper further expansion of an invasive species, it is possible to build resistance surfaces that reflect different costs for a species to move through the landscape using vegetation cover, elevation, slope or other landscape features (Landguth et al. 2012). As a multitude of paths may exist between two points, either multiple low-cost paths or smoothed output paths using a probability-density function can be considered (Cushman et al. 2009; Pinto and Keitt 2009). The latter approach allows a variety of smoothing functions (Gaussian, Epanechnikov, uniform, triangle, biweight, triweight and cosine function) referred to as kernel density estimations (Li and Racine 2007).

In the present study, we used occurrence records of *X. laevis* in Portugal and fine scale remote sensing data to build landscape resistance kernels that predict the influence of landscape structure on the dispersal dynamics of this invasive frog. Landscape resistance is subsequently used to identify past dispersal routes and to highlight areas at risk of future invasion by *X. laevis*. This study provides insights into the role of landscape configuration on dispersal patterns and provides a tool for future management of this species, as well as of others with similar dispersal patterns.

Materials and methods

Study area

West Portugal is characterised by a Mediterranean-type climate (Rubel and Kottek 2010). The first record of *X. laevis* in western Portugal occurred in Laje River, which runs through a densely-urbanised part of Oeiras County ca. 20 km west of Lisbon, in 2006 (Sousa et al. 2018) (Fig. 1A). However, this introduction likely occurred much earlier and is probably the result of accidental escape from nearby research laboratories after the strong winter floods of 1979/80 (Rebelo et al. 2010; Sousa et al. 2018). Due to its cryptic lifestyle combined with a lack of interest in the wildlife of urban rivers, the species established and spread along the river, undetected for more than 25 years (Sousa et al. 2018). The frog then spread from Laje River into a close parallel-flowing second river (Barcarena), where it was found in 2008 (Rebelo et al. 2010). The maximum invaded area by the frog on the river sections occurred along 5.86 km in the main

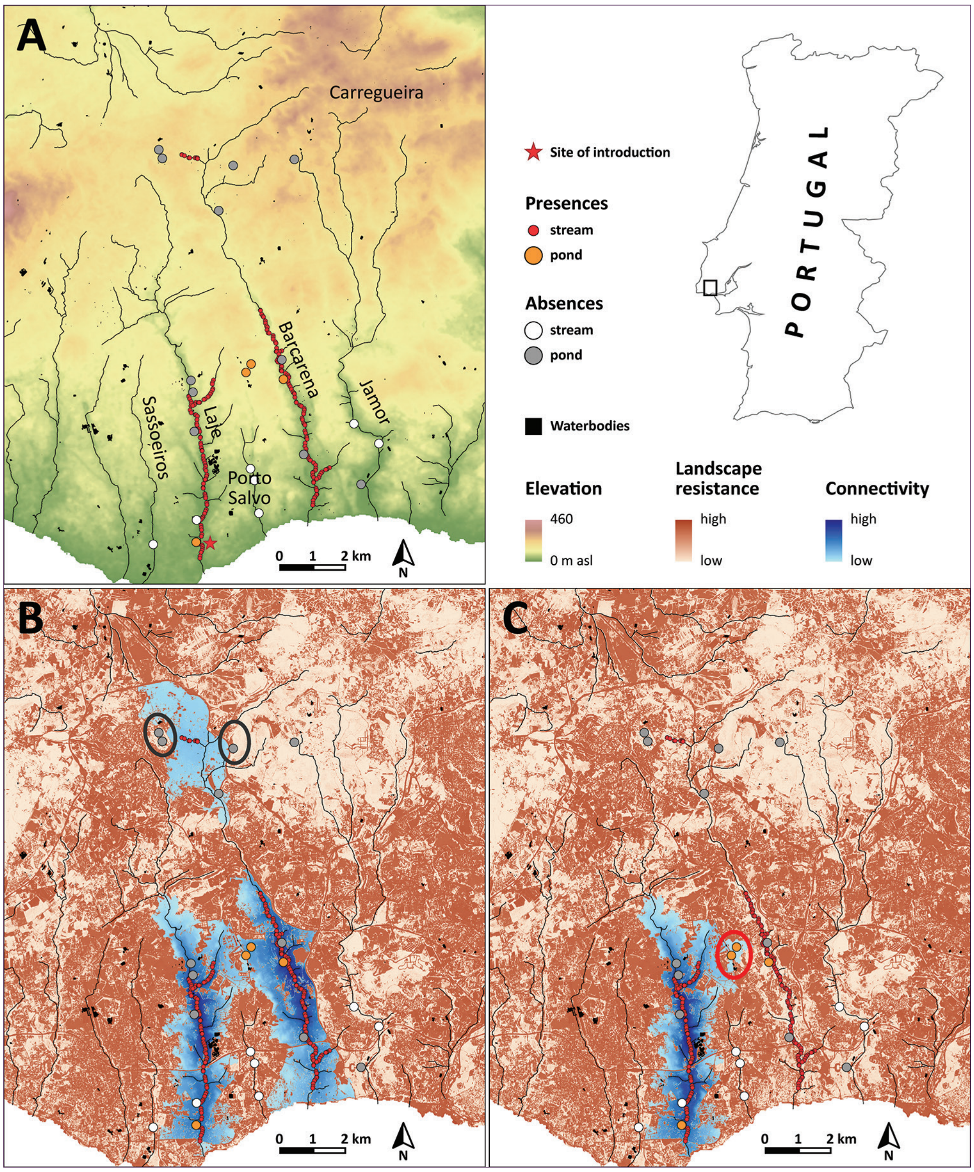

Figure 1. Study area **A** overview of study area: Elevation and important locations (i.e. the two invaded rivers and other localities that could be threatened by invasion). Features as presence and absence points (streams and ponds), water bodies and the site of introduction are highlighted **B** areas of low and high risk of invasion: Landscape resistance and the connectivity (including all presences as starting points) of the study area. Features as presence and absence points (streams and ponds) and water bodies are highlighted. Two areas of low but possible risk of invasion are surrounded by black circles **C** reconstruction of past dispersal from Laje into Barcarena River: Landscape resistance and the connectivity (including only presences from Laje River as starting points) of the study area. Features as presence and absence points (streams and ponds), and water bodies are highlighted. The golf-course ponds, which were used as stepping stones into Barcarena River, are surrounded by a red circle.

stream of Laje plus one of its tributaries and 6.39 km in the main stream of Barcarena plus three tributaries (Moreira et al. 2017). The invaded river basins are roughly 3 km apart, but the headwaters of two small tributaries of Laje River are nearby (ca.1 km) to the headwaters of a tributary of Barcarena River (Fig. 1A). Both rivers are permanent, approximately 10 m wide in most stretches and 2 m deep in summer in the deepest stream pools (Moreira et al. 2017). The tributaries inhabited by *X. laevis* are also permanent, ca. 1 m wide and up to 1.5 m deep (Moreira et al. 2017). Both rivers flow into the Tagus estuary and, although *X. laevis* can tolerate a moderate salinity, it seems unlikely that it has used this path to cross between both river basins (Sousa et al. 2018). The area has just a few still and artificial water bodies, most of them 20–110 m apart from the streams (Moreira et al. 2017). Three large golf-course ponds are located between the headwaters of two tributaries flowing in opposite directions, one to each river. The invasive populations seem constrained to the two rivers, some of their tributaries, the three golf-course ponds and some man-made ponds, covering a total area of approximately 30 km^2.

Landscape resistance

We calculated fine scale resistance kernels to determine connectivity and predict potential overland dispersal for the invasive Portuguese population. We used literature-based GPS data of confirmed presences (Rebelo et al. 2010), updated them to a total of 201 locations and added 19 confirmed absences along the streams, as well as in isolated ponds, according to our own field research. To define the study area, we chose a circular buffer of 5 km around the GPS-points, which is about twice the maximum documented terrestrial dispersal distance during a dispersal event of the frog (Measey 2016).

Remote sensing derived resistance surfaces

We obtained high resolution multispectral satellite imagery containing the invaded Portuguese distribution range (625 km^2 × 4 title IDs = 2500 km^2) as A3 products of the RapidEye satellite (Blackbridge 2014). We used the satellite images with title-IDs 2956913, 2956914, 2957013 and 2957014 and card IDs 26196070, 26196539, 26196860, 26195477, 26196831, 26196078, 26196867, 26196894 and 26196746. The dataset contains four orthorectified raster images, each with five remote sensing channels (blue: 440–510 nm, green: 520–590 nm, red: 630–685 nm, red edge: 690–730 nm, NIR: 760–850 nm wavelengths). Each raster image covers an area of 625 km^2. The spatial resolution is 5 m grid cell size and spatial accuracy is 10 m (Blackbridge 2014). The subsequent corrections were applied to the five raw remote sensing channels*:* 'top of atmosphere correction' (TOA), 'cloud cover correction' and 'histogram correction' using the packages LANDSAT (Goslee 2011), RASTER (Hijmans 2015) and LMODEL2 (Legendre 2014) for R according to the product specifications. Using RS TOOLBOX (Leutner and Horning 2016) and the above-mentioned packages for R, the raster images for each study area were mosaicked before the 'Normalised

Difference Vegetation Index' (NDVI) as a measure for vegetation cover and the 'Normalised Difference Water Index' (NDWI), showing differences in the water content of vegetation, were computed.

Based on remote sensing variables using a threshold-based water detection method, the larger still and flowing freshwater bodies within the study area were detected (Klemenjak et al. 2012; Tetteh and Schönert 2015). To improve the algorithms' capacity to detect water, the precise locations of all verified water bodies were identified manually in Google Earth and used to train a bioclim model using the DISMO package for R (Hijmans, Phillips et al. 2013; R Core Team 2017). The output of the bioclim model was again verified by hand. Small water bodies that had not been detected by this measure were georeferenced by hand using Google Earth. We used only one randomly selected occurrence record per 50 × 50 m grid cell because computation time increases exponentially with the number of species occurrences and the size of the study area. We collected seven presences comprising two invaded river sections (Laje 5.6 km and Barcarena 6.3 km) and identified 612,536 locations potentially adequate for invasion.

We calculated resistance surfaces by combining NDVI and NDWI scores giving higher priority to vegetation cover, but acknowledging that humid areas may be preferred by the frogs (i.e. NDVI + NDWI / 10). We applied an inverse monomolecular transformation using relevant functions of the RESISTANCEGA package for R (Peterman 2014, Peterman et al. 2014) to account for the higher expected permeability of areas covered by humid vegetation. The equation of the inverse monomolecular transformation is $y = -r(1 - exp^{-bx})$, with r = resistance surface, which is controlled by shape (x) and magnitude (b) parameters that are varied during optimisation (see Peterman 2018 for more details). This transformation appreciates that the permeability of vegetated areas may not shift too much with declining vegetation cover. However, resistance increases exponentially in more open landscapes, especially in the Mediterranean climate, characterised by hot and dry summers. As our resistance surface is based on vegetation and humidity indices, we can differentiate various states of vegetation, but less so for bare soil. Bare soil usually falls within an NDVI range between 0.1–0.2 and plants will always have positive values between 0.2 and 1. Therefore, an exponential function counterbalances the differences in the discrimination ability of our indices. The resistance surfaces were scaled to range from 0–1. Subsequently, a threshold was determined to detect man-made surfaces, such as roads and buildings by comparing all scores between 0.70–0.85 in steps of 0.01 to areal pictures of the same area and reclassifying all scores above the best-matching threshold to a resistance of 50. This threshold does not differentiate between roads, which are semi-permeable and buildings which represent absolute barriers. A score of 50 allows the frogs to cross a maximum of up to 6 grid cells of 5 m (ca. 30 m) man-made surfaces, making roads semi-permeable, but areas with a high density of man-made structures become impermeable.

Elevation data

Laboratory trials, using *X. laevis* individuals from Portugal, were used to quantify the effect of slope on dispersal. These trials showed an increasing difficulty to overcome slopes, with 60 degrees as the upper limit. An elevation layer with a spatial resolution of 30 m derived from the 'Advanced Spaceborne Thermal Emission and Reflection Radiometer' 'Global Digital Elevation Model' (ASTER GDEM) was obtained from the online database of the NASA Land Processes Distributed Active Archive Centre (LP DAAC) of the USGS/Earth resources observation and science (EROS) centre (https://lpdaac.usgs.gov). We re-sampled it to a resolution of 5 m using bidirectional interpolation, available in the RASTER package (Hijmans 2015) for R.

Resistance kernels

The remote sensing derived resistance surfaces, in combination with the elevation data, were used to calculate resistance kernels that quantify permeability of the landscape after Compton et al. (2007), using the UNICOR package for python (Landguth et al. 2012; Fig. 2). The resistance kernel approach combines a kernel density estimator with a directional least-cost matrix to produce a multidirectional probability distribution representing variability in habitat quality (Compton et al. 2007). This measure considers land use and elevation derived from remote sensing data and equals higher permeability with higher connectivity as it suggests a higher probability of a dispersing frog to arrive at the water bodies (Compton et al. 2007).

Based on the laboratory trials, the slope function was defined so that an upward slope of 60 degrees is the maximum, while downward slopes were considered as generally permeable (upward slope function as determined, based on trials: $y = 3.1051\ e^{0.038x}$, scaled to 0–1; downward resistance = 0; settings UNICOR: Type_Direction = Hiking; 6;-3).

Based on capture-mark-recapture data from South Africa (De Villiers 2015), we determined the maximum cumulative resistance, which is observed in the field using least cost paths, calculated with the same set of remote sensing derived resistance plus elevation data. For this, we used the satellite images with the title-IDs 3423406, 3423407, 3423307 and 3423207 and Card-IDs 26195795, 26195801, 26195803 and 26196899. The highest cumulative resistance detected was used to parameterise the dispersal models for the study area (maximum cumulative resistance = 308). Model accuracy was evaluated by extracting the values of the resistance kernel for the used presence records. Further, true absence records were used in the same way to check if they were in- or outside of the predicted kernel area.

Results

UNICOR outputs show the cumulative density of optimal paths buffered by the kernel density estimation (Fig. 1C). As for model accuracy, the 201 presence records had a mean cumulative density of 51.21 ± 20.02 (range: 2.19–80.32), while, for the 19 absence records, this was 19.21 ± 28.13 (range: 0–70.52). Eleven of the 19 absences (57.9%) were outside of the kernels' range. The resistance kernels also located functionally well-connected water bodies and complexes in close vicinity to the existing populations (Fig. 1B – invaded ponds).

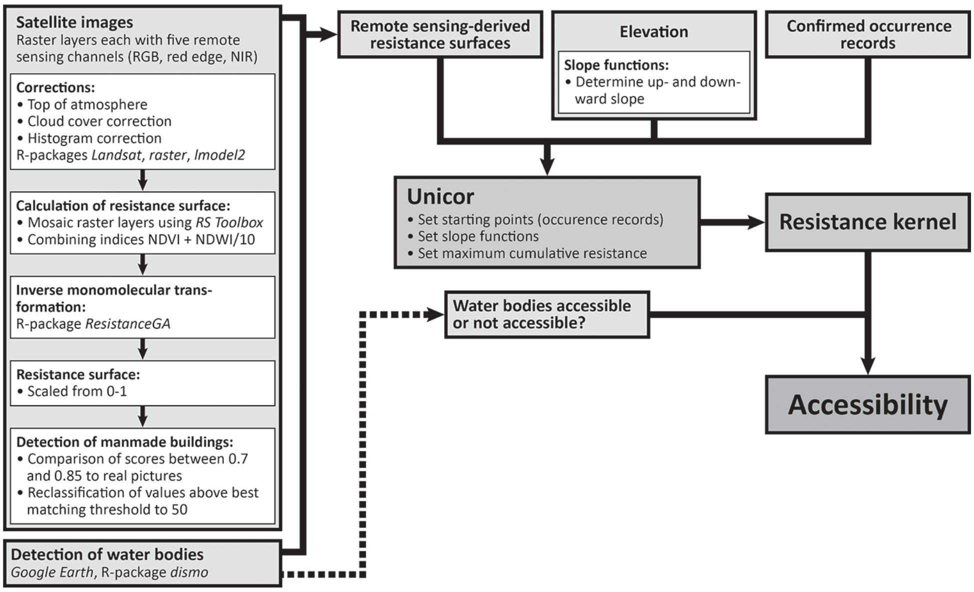

Figure 2. Schematic figure of methodological approach for the calculation of resistance kernels

The known *X. laevis* populations, occupying the two rivers, are evidently constrained by landscape resistance and high permeability was attributed only to the valley bottoms around the river beds of Laje and Barcarena. Importantly, our results explain the current distribution of the species, including its absence from nearby streams and locate the probable contact route between the two invaded basins, supporting the hypothesis of a natural colonisation of Barcarena by overland dispersal. In fact, areas of low (but still possible) permeability connect the two valleys at two locations, but the isolated animals found upstream of Barcarena seem to have no connectivity with the main downstream population (Fig. 1B).

Discussion

With this work, it was possible to reconstruct the most probable past dispersal routes, terrestrial corridors for overland dispersal and water bodies that function as stepping stones, fostering the *X. laevis* invasion. Additionally, we found potential stepping stones into novel areas, now considered of high invasion risk.

Pace of invasion

Despite its dispersal abilities, which include terrestrial movements up to 2.36 km (De Villiers 2015), an ascertained maximum velocity of 0.2 km/h (Measey and Tinsley 1998) and the apparently ideal climatic conditions (Measey et al. 2012; Ihlow et al.

2016), the *X. laevis* invasion in Portugal was quite slow. This is probably the result of a mostly aquatic (lotic) dispersal route, rather than the terrestrial overland dispersal documented on the species' original range (De Villiers and Measey 2017). Dispersal along flowing waters – and, in this case, opposed to the water flow in the first river to be colonised (Fig. 1A) – is affected by a combination of the species' dispersal ability, the location of the introduction site, the hydrological regime and landscape resistance.

The landscape of the Laje and Barcarena basins is hostile to a semi-terrestrial frog (see below). In fact, only a few isolated ponds were colonised (Fig. 1C); several ponds at 50 to 80 m from the streams were not reached by *X. laevis*. A few triggers of *X. laevis* terrestrial movement have been identified (De Villiers and Measey 2017). One of the most important triggers seems to be population density, which is here relatively low (Moreira et al. 2017), probably due to the low habitat quality – heavily polluted urban rivers. This low abundance also explains why the species went undetected for more than 25 years (Sousa et al. 2018). Although *X. laevis* can live, disperse through and successfully reproduce in flowing waters (Lobos and Jaksic 2005; Courant et al. 2017; Moreira et al. 2017), these seem not to be ideal for the species. Lotic habitats have been mostly identified as pathways for dispersal, while breeding is commonly referred to take place in lentic water bodies, like pools or ponds (Fouquet and Measey 2006; Faraone et al. 2008; Measey 2016). In Portugal and probably due to the poor habitat quality of the two streams and/or presence of predatory fish, the number of metamorphs is much lower in lotic than in lentic environments; metamorph size is also smaller, whereby reaching the reproductive size takes longer (Moreira et al. 2017).

Some features of the Mediterranean climate may have also contributed to the slow dispersal. The annual period where terrestrial dispersal could take place is not certain, as the mostly dry and hot summers seem too risky for terrestrial movement. The mild winters could be very suitable for dispersal overland, because these Mediterranean streams are typically subject to high water level variability; the rainy winters regularly cause river floods (Boix et al. 2010), spreading the species along the river valley. However, the site of initial introduction was located downstream, close to the mouth of the River Laje (Fig. 1A), meaning that, until the colonisation of Barcarena, only upstream dispersal was possible. Events like the 1979/80 flood, when the species escaped in Laje River, could boost its dispersal, but hardly upstream.

Distribution

We found that the modelled landscape connectivity correlates well with the distribution of this frog. In the areas of high connectivity along the river-beds of Laje and Barcarena rivers, the species' dispersal is hampered by > 22° slopes and > 60° slopes seem to be nearly unconquerable. Landscape connectivity along large parts of the river sections is further constrained by cement walls instead of natural riverbank. Further, the rivers have several physical barriers like waterfalls, hampering the connectivity amongst populations and reducing landscape permeability (Sousa et al. 2018). In fact, the lack of continuity upstream of the Barcarena basin (Fig. 1C) results from a ~250 m long tunnel through which the stream flows beneath two highways (detected as roads by remote sensing). Frogs were recently (June 2020) found just upstream and downstream of the tunnel and are very probably able to pass through the tunnel.

Away from the riverbeds, connectivity decreases very quickly along the steep, non-urbanised slopes to the very low connectivity of the highly-urbanised plateaus. If the frogs manage to leave the stream, they become hampered or blocked by traffic and buildings. This complex topology constrains connectivity amongst the invaded locations and the few other water bodies within the study area. According to our model, topography and urban areas are therefore sufficient to explain the non-colonisation of the three nearest streams – Sassoeiros to the west, Jamor to the east and Porto Salvo in between the two colonised rivers (Fig. 1C).

Past dispersal routes

Due to road and building constructions after the year 2000, the maps that we used for this work may not depict all the dispersal corridors that were available in the 1980s and 1990s. However, our models show that Barcarena was very probably invaded from Laje by frogs that dispersed overland and used the golf-course ponds as stepping stones. According to the model, dispersing frogs may have used two small tributaries to reach the golf-course ponds. The northernmost tributary is the strongest candidate as a past dispersal route, given the large population that was found there. The golf ponds were dug and filled in 2002 and are located exactly in the single suitable corridor identified. As noted by other authors on less hilly landscapes (cf. Faraone et al. 2008), small water bodies can be used as stepping stones during the rainy season to reach suitable habitat. However, we cannot fully exclude other non-accounted factors, such as the intentional release by amphibian keepers.

Areas of high risk

All factors, low habitat quality, restricted availability of water bodies and hampered dispersal ability, probably explain the comparatively slow invasion of *X. laevis* in Portugal. Still, the species has managed to colonise two rivers and this work suggests that it used artificial water bodies as stepping stones on a terrestrial pathway in a densely-urbanised area, highlighting the risks of further invasions.

Possible stepping stones for dispersal into other streams should be identified, monitored and, if possible, altered (e.g. by encircling them with walls, since there are no natural ponds in the area) to hamper further overland spread. The Jamor River basin and Carregueira Mountain are two semi-natural regions not yet invaded, located east and northeast of the currently-invaded area (Figure 1A). Jamor River is apparently protected by a high landscape resistance (Fig. 1C) and is, therefore, not naturally reachable by terrestrially dispersing *X. laevis*. However, landscape resistance is low at Carregueira, a small forested mountain range with farms and golf-courses (including lakes), which also contains the headwaters of Jamor River. Currently, this area is not in the range of the connectivity kernel, but a *X. laevis* invasion is possible starting at its western edge. In the northern limit of the Barcarena population, there are also several small water bodies that could be used as possible stepping stones into novel areas.

The current eradication plan for this species in Portugal (Sousa et al. 2018) can be informed by this study. Regular monitoring of the water bodies that are within reach of the species, according to our model, is strongly advised. If possible, toad barriers could be built on the main pathways for overland dispersal, particularly at the edges of Carregueira and around the northern isolated population, which should effectively block further spread. As the number of colonised sites is reduced by the eradication programme, we recommend to verify (and if possible, to block) all paths within a radius of 5 km around the colonised water bodies (double the species currently known maximum terrestrial dispersal ability during a dispersal event) to minimise expansion risk. Our results are also relevant for other countries where *X. laevis* occurs, highlighting the importance of blocking strategic overland routes of dispersal, either by using toad fences or by draining ponds that may be used as stepping stones.

Advantages and limitations

The fine-scale remote sensing derived resistance surfaces, based on NDVI and NDWI, in combination with elevation layers, allowed us to reconstruct potential past dispersal routes between the two invaded rivers and highlighted areas at high risk of invasion. This provides a detailed map highlighting areas which are threatened by invasion and knowledge of potential corridors for the invasive species. However, the computational power and time needed for this method increases with the number of starting points and with the resolution of raster layers. Furthermore, this approach is based on species-specific knowledge about biology and physiology and model accuracy strongly depends on evaluation by experts. Some very fine scale dispersal barriers may remain undetected by remote sensing, such as waterfalls with seasonally varying intensities or smooth walls. These landscape features may further restrict the dispersal potential on a local scale.

Acknowledgements

This study was funded by ERANET BiodivERsA (project title: “Invasive biology of *Xenopus laevis* in Europe: ecology, impact and predictive models”) and the Deutsche Forschungsgemeinschaft (DFG RO 4520/3-1) for which we are very grateful. All distribution data were collected under the scope of the “Plano de erradicação de *Xenopus laevis* nas ribeiras do Concelho de Oeiras”, coordinated by Instituto da Conservação da Natureza e das Florestas (Portugal). In addition, we thank BlackBridge for providing the high resolution RapidEye satellite images used for this study free of charge. Further, we want to thank Erin Landguth, Morris Flecks and Ursula Bott for technical assistance.

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Appendix 5 – Invasive risk assessment of *Calotes versicolor*

Frontiers of Biogeography 2022, 14.3, e54299

RESEARCH ARTICLE

Frontiers of Biogeography
the scientific journal of
the International Biogeography Society

Invasive risk assessment and expansion of the realized niche of the Oriental Garden Lizard *Calotes versicolor* species complex (Daudin, 1802)

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Abstract

Correlative species distribution modelling (SDM) can be a useful tool to quantify a species' realized niche and to predict its potential distribution for non-native ranges. The agamid lizard *Calotes versicolor* s.l. belongs to the most widely distributed reptile taxa worldwide. In the past, *C. versicolor* s.l. has been introduced to several countries, including regions in the Oriental, the Neotropical and the Afrotropical realms, where strong negative impact on the local fauna is assumed. Due to the complicated taxonomy and the existence of several cryptic species, which are covered by this taxon, we used *C. versicolor* sensu lato and its four subtaxa (*C. versicolor* sensu stricto, *C. irawadi*, *C. vultuosus*, *C. farooqi*) as target species to (1) compute correlative SDMs for *C. versicolor* s.l. and its subtaxa and project them across the globe to highlight climatically suitable areas of risk for future invasion and (2) based on the ecological niche concept, we investigate if the species complex expanded its realized climatic niche during the invasion process. We use two different SDM approaches, namely n-dimensional hypervolumes and Maxent. N-dimensional hypervolumes are a non-hierarchically ranked approach, which is a useful tool to investigate the expansion in the realized niche, while Maxent, a hierarchically ranked model, is used to focus on potentially suitable areas for future invasion. We calculated two final models for *C. versicolor* s.l., one based on records from the native range and one based on records from the native and invaded range, as well as one model for each subtaxon. Our results show a geographic expansion into novel climatic conditions as well as an expansion in the realized niche. Our results reveal that *C. versicolor* s.l. is currently inhabiting 13% of its potential range but could find suitable climatic conditions on a global surface area between 14,025,100 km^2 and 53,142,600 km^2. Our predictions reveal large areas of highly suitable climatic conditions for the Oriental, Australian, Afrotropical and Neotropical realms, whereas only small regions of the Palearctic and Nearctic realms provide moderately suitable conditions. Further, some localities, especially those with a high amount of human traffic like ports or airports, might act as multiplicators and might therefore be a stepping stone into further areas.

Highlights

- The potentially invasive Oriental Garden Lizard *Calotes versicolor* species complex has been introduced to several areas across the globe and its invasion has long been neglected.
- We used two different correlative SDM approaches: The n-dimensional hypervolumes were used to quantify the expansion in the realized niche due to the invasion process, while Maxent was used to highlight areas of potential future invasion.
- *C. versicolor* s.l. shows an expansion in the realized niche due to its ongoing invasion process.
- The SDMs predict large areas of highly suitable climatic conditions for the Oriental, Australian, Afrotropical and Neotropical realms.
- According to our basal risk assessment *C. versicolor* s.l. is currently inhabiting 13% of its potential range but could find suitable climatic conditions on a global surface area between 14,025,100 km^2 and 53,142,600 km^2.

Keywords: agamid lizard, AIC, global invader, hypervolumes, Maxent, SDM

e-ISSN: 1948-6596 https://escholarship.org/uc/fb doi:10.21425/F5FBG54299

Introduction

Anthropogenic habitat alterations, climate change, and increased human-mediated transport, alter the distribution of organisms, which leads to novel invasions and the expansion of established populations of non-indigenous species (Fordham et al. 2012, Kearney et al. 2008, Todd et al. 2008, Shabani et al. 2020). As a result, non-native taxa spread worldwide (Sala et al. 2000, Shabani et al. 2020). Thus, identifying the limits of an organisms' distribution is particularly important for invasive risk assessments (Kearney et al. 2008, Jimenez-Valverde et al. 2011).

Species distribution modelling (SDM) can be a first step in invasive risk assessments. For this task, the concept of the ecological niche of a species is essential. The ecological niche comprises abiotic (fundamental) and biotic factors (interactions among organisms like competition, parasitism, mutualism, predator-prey-relationship, etc.). The fundamental niche comprises all abiotic factors that are necessary for species' survival and reproduction (Grinnell 1917, Hutchinson 1978, Soberón & Peterson 2005, Soberón 2007). The intersection among biotic and abiotic factors and geographic accessibility determines the species' realized niche (Grinnell 1917, Hutchinson 1978, Soberón & Peterson 2005, Soberón 2007). Climate is one of the main parameters determining the ecological niche and the potential distribution of taxa (Soberón 2007, Thuiller et al. 2004). Therefore, ectothermic organisms such as reptiles are ideal subjects for SDM assessments as they have a strong dependency on climatic conditions. To predict the potential invasive risk of species, correlative SDM approaches linking geographic occurrence data with environmental predictors, can be used (Merow et al. 2013, Guisan & Thuiller 2005).

In the past, the realized niche of a species was assumed to be conservative among space and time (Peterson 2011). However, subsequent studies provide a more complex pattern with some degree of flexibility. Shifts in the realized niche were found for plants (Broennimann et al. 2007) and animals (i.e. Medley 2010, Rödder et al. 2017), including reptiles (Nania et al. 2020).

The Oriental Garden Lizard, *Calotes versicolor* (Daudin, 1802) complex is among the rather widespread agamid lizards. However, the taxon comprises several cryptic species (Zug et al. 2006). The type locality of *C. versicolor* is unknown and the holotype was lost (Auffenberg & Rehman 1993). A neotype was designated from Pondicherry University Campus, Kalapet, Pondicherry, India (Gowande et al. 2016), which was invalidated one year later related to the complicated taxonomic status of this species complex (Chaitanya et al. 2017). Despite the taxons' wide-ranging distribution across large parts of Asia, in historical times most taxonomists did not recognize other populations to be a different species. This phenomenon may be explained by the seemingly uniform appearance of this taxon and the ease of labelling an already existing scientific name to collected or observed specimens (Zug et al. 2006). However, some researchers also noticed subtle differences among populations (i.e. Kästle et al. 2013, Radder 2006). As a result, Auffenberg and Rehman (1995) described a Pakistani population as the only currently recognized subspecies, *C. v. farooqi*, next to the nominal form (Uetz et al. 2021). Since the last two decades, some authors started to particularly shed light into the species' complex phylogenetic relationships (Huang et al. 2013), distributional patterns (Liu et al. 2021) and elevated some populations to distinct species level (Zug et al. 2006). However, the majority of populations is still assigned to *C. versicolor* sensu lato (below abbreviated s.l.). Recently, Gowande et al. (2021) published a phylogeny based on the mitochondrial 16S and CO1 genes and supported this by morphological data to disentangle the Indian taxa of the *C. versicolor* complex. According to the latter authors, the species complex contains at least four distinct lineages: (1) *C. versicolor* s.str. from South India and parts of the Southeast coast, (2) *C. irawadi* s.l. Zug et al., 2006 from Northeast India across Southeast Asia, (3) *C. vultuosus* (Harlan, 1825) (resurrected synonym of *C. versicolor*) from the eastern Indo-Gangetic plains, and (4) *C. farooqi* Auffenberg & Rehman, 1993 (former subspecies of *C. versicolor*) from Pakistan and adjacent regions. However, it must be mentioned that at least *C. irawadi* is still known to be a species complex and also *C. farooqi* includes another distinct phylogenetic lineage and further surveys are required to clarify these issues. Furthermore, Gowande et al. (2021) found that *C. calotes* (Linnaeus, 1758) is a phylogenetic sister taxon to *C. farooqi* and is therefore also included in the *C. versicolor* complex.

C. versicolor s.l. naturally occurs across large parts of the Oriental realm from eastern Iran (Anderson 1999, Mobaraki et al. 2013), and Afghanistan (Clark et al. 1969), eastwards to China and southwards to the Malay Peninsula (Smith 1935, Auffenberg & Rehman 1993, Zug et al. 2006). In the past, this agamid lizard has been introduced to several countries worldwide where it could establish reproducing populations. These areas include regions in the Oriental (i.e. Das et al. 2008, Pili 2019), the Neotropical (Enge & Krysko 2004) and the Afrotropical realms (i.e. Sandera 2009, Spawls et al. 2018, see Table 1 for an overview). It has a semi-arboreal, heliophile (= "sun loving") lifestyle and prefers open, often anthropogenic or disturbed landscapes like open forest, grassy savanna, scrubland, wasteland, gardens, cemeteries, parks and areas along roadsides (Diong et al. 1994, Erdelen 1984, Stuart 1999, Khan & Mahmoud 2003, Blanchard 2000, Permalnaick et al. 1993). The taxon avoids dense forest with closed canopy (Permalnaick et al. 1993, Diong et al. 1994, Pawar 1999). *C. versicolor* s.l. occurs in the lowlands (Stuart 1999) but also in much higher altitudes (Kästle et al. 2013, Nanhoe &Ouboter 1987, Srinivasulu et al. 2014, Vassilieva et al. 2016), even up to 3,200 m (Gautam et al. 2020).

Studies investigating the lizard's impact on the native biodiversity are limited to very few localities and mostly rely on observations that have not been tested. In Singapore, it was found that *C. versicolor*

Table 1. Introduction of *Calotes versicolor*: An overview across the biogeographic regions.

Geographic region	Reference
Neotropical realm	
Florida (USA)	Enge & Krysko 2004, Krysko et al. 2011
Afrotropical realm	
Réunion and Mauritius including Rodrigues (Mascarene Archipelago)	Permalnaick et al. 1993, Staub 1993, Henkel & Schmidt 2000, Vinson & Vinson 1969
Seychelles	Matyot 2004
Kenya	Sandera 2009, Spawls et al. 2018
Oman	Seufer et al. 1999, van der Kooij 2001, Grossmann & Kowalski 2019
Oriental realm	
Borneo (Brunai)	Das et al. 2008
Celebes (= Sulawesi, Indonesia)	Erdelen 1978
Philippines	Pili 2019, Emerson 2013
Maldives	Hasen Didi 1993
Singapore	Lim & Chou 1990, Lim & Lim 1992, Chou 1994, Diong et al. 1994
Andaman Islands (India)	Biswas & Sanyal 1980, Das 1999, for review see Lever 2003
Diego Garcia (Chagos Archipelago of the British Indian Ocean Territory)	Kraus 2003

s.l. to some extent displaced the native agamid lizard *Bronchocela cristatella* (Kuhl, 1820) (Diong et. al. 1994). Further, Mauremootoo et al. (2003) stated that, on Mauritius, *C. versicolor* s.l. competes with endemic geckos by preying on native invertebrates. Vinson (1968) speculated that the absence and decrease in population size of endemic stick insects (Insecta: Phasmatodea) on Mauritius and Réunion is related to the presence of this non-native lizard. It was shown that this lizard is an opportunistic generalist that preys on several kinds of invertebrates as well as small vertebrates and plant material (Matyot 2004). Furthermore, *C. versicolor* s.l. may act as vector to spread several parasites on native species (Matyot 2004). Concluding these observations and facts provide strong evidence that *C. versicolor* s.l. may have strong negative impact on the native biodiversity.

The existing literature provides evidence that *C. versicolor* s.l. could spread by a combination of multiple, natural and manmade, factors and the pathways of introduction seem various. Most likely, *C. versicolor* s.l. started a natural invasion of the Malay Peninsula in the late 19th or early 20th century, as the taxon was not listed in the comprehensive first herpetological literature for this region (Cantor 1847). Later, Boulenger (1912) documented the lizard from the northern portion of the Malay Peninsula, where it was very abundant, while it could not be observed in the southern parts. In the 1980s, *C. versicolor* s.l. reached Singapore, where it has been established (Lim & Chou 1990, Lim & Lim 1992, Chou 1994, Diong et al. 1994). It was suspected that the species might have benefited from the direct railroad from Thailand and northern Malaysia to Singapore (Tan et al. 2007). In the early 20th century, a single specimen of *C. versicolor* s.l. was observed in the very North of Sumatra (De Rooij 1915), from where the lizard started to spread across the region (Brongersma 1931). Das et al. (2008) suggested an introduction from the western coast of the Malay Peninsula, which is located c. 65 km northeast of Sumatra at the closest point of the Strait of Malacca. Recently, new records of the lizard were also documented for Iran (Damadi et al. 2018). For the Philippines, the introduction of *C. versicolor* s.l. on Luzon as stowaway is assumed as the international airport is in proximity (Emerson 2013). In Oman, the lizard was first recorded in 1982. Its introduction most likely occurred unintentionally as stowaway of shipments of ornamental plants or other nature products (Grossmann & Kowalski 2019).

For the Seychelles, two distinct introduction events were suggested. The first one on Mahé in 1985-86, which has been unsuccessful, and the second one on Ste Anne in 2003, which succeeded in a reproducing and dispersing population (Matyot 2004). Most likely *C. versicolor* s.l. arrived at the Seychelles by unintentional transport by humans, which is also the case for the Mascarenes (Réunion), where the lizard is guessed to be a stowaway in a shipment of sugarcane cuttings in year 1865 from Java, Indonesia (Permalnaick et al. 1993, Staub 1993). However, the presence of the taxon is not mentioned for Java yet (Uetz et al. 2021).

In Florida (USA) it is known that several *C. versicolor* s.l. escaped in 1978 from a local reptile dealer. These animals may most likely derive of a shipment from Pakistan (Enge & Krysko 2004, Krysko et al. 2011), where *C. versicolor* s.l. is the only member of the genus (Auffenberg & Rehman 1993). In Florida, until 2004 the taxon already invaded an area of a maximum extend of 11.7 km east-west and 9.3 km north-south direction (Enge & Krysko 2004, Krysko et al. 2011).

Considering this geographic range expansion into non-native regions in combination with negative impact on local biodiversity, a first step for global invasive risk assessment is strongly required for this species complex. Thus, the aims of this study are two-folded: (1) we calculated correlative SDMs for *C. versicolor* s.l. and projected them across the globe to highlight climatically suitable areas of risk for future invasion and (2) based on the ecological niche concept, we investigated if the species complex expanded its realized climatic niche during the invasion process. To assess the invasive risk of *C. versicolor* s.l., we computed 8625 Maxent models for each taxon (*C. versicolor* s.l., *C. versicolor* s.str., *C. irawadi* s.l., *C. vultuosus*, *C. farooqi*) including 23 regularization multipliers, and 15 feature class combinations, each combination 25 times to find the best fitting model to highlight areas of high climatic suitability. To investigate an expansion in the realized niche, we used an n-dimensional hypervolume approach, which uses support vector machines to assess if geographic occurrences and their linked climatic conditions are in or out of the species' realized niche volume.

Materials and Methods

Data preparation

Considering the high degree of cryptic diversity and the lack of knowledge on the origin of the introduced specimens, we calculated SDMs for *C. versicolor* s.l. and added SDMs for the four subtaxa as sensitivity analysis. To predict the invasive risk of *C. versicolor* s.l., we obtained 1705 occurrence records from GBIF (https://doi.org/10.15468/dl.axawsq) covering the native and invasive range of the taxon based on preserved specimens only. Further, we georeferenced six occurrence records from the literature (see Table 1) using GEOLocate (https://www.geo-locate.org/) to increase the number of records for the invasive range. Furthermore, we used 93 genetically confirmed records from Gowande et al. (2021) to increase the number of records. After checking the dataset for outliers in ArcMap (ESRI 2020)(see distribution in introduction), we corrected the dataset for potential sampling bias (see systematic sampling in Fourcade et al. 2014) and spatial autocorrelation using the raster package (Hijmans 2016) and the ecospat.mantel.correlogram() function in the ecospat package (Di Cola et al. 2017) for R (R Core Team 2021). For systematic sampling, occurrence records in a defined radius are subsampled to reveal a regular distribution of records in geographic space. Subsampling reduces spatial aggregation of records but does not correct low sampling efforts in some areas. This approach underestimates highly suitable areas, where the number of sampled occurrence records reflects the real abundance of a species (Fourcade et al. 2014). Considering the ecospat.mantel.correlogram(), we subsampled the dataset and deleted neighbouring occurrence points in a radius of 50 km to reduce the mantel r value to zero. Finally, we used 195 occurrence records from the native range and 209 records from the native and invaded range for modelling (see Supplemental Material S1).

As Gowande et al. (2021) recently split *C. versicolor* s.l. into four distinct subtaxa, we conducted a sensitivity analysis and also calculated SDMs for each of those subtaxa. For this purpose, we split the mentioned occurrence records and assigned them to one of the four species based on geographic proximity. We only used occurrence records that could clearly be assigned to one of the four species and removed uncertain ones that were found in transition zones. Finally, we used 27 occurrences for *C. versicolor* s.str., 97 for *C. irawadi* s.l., 56 for *C. vultuosus* and 15 records for *C. farooqi*. Despite, Gowande et al. (2021) found *C. calotes* to be a phylogenetic sister species to *C. farooqi*, we did not include the taxon into our sensitivity analysis as it is morphologically easily distinguishable from *C. versicolor* s.l., it has never been synonymised with the latter taxon and it seems not to play a role as non-native species yet (Uetz et al. 2022).

We obtained 19 bioclimatic variables from Worldclim 2.0, containing climatic conditions from 1970-2000, at a resolution of 2.5 arc minutes (Fick & Hijmans 2017). We restricted the environmental variables to those reflecting thermal energy and water availability for an ectothermic organism (i.e. minimal, maximal and mean values at the species' records and rejected derived variables [mean diurnal range (bio2), isothermality (bio3), temperature seasonality (bio4), precipitation seasonality (bio15)]. As correlative SDMs are sensitive to multi-co-linearity of predicting variables, we computed variance inflation factor (VIF) between all possible pairs of predictors across the species' background area (see below for explanation) using the vifstep() function of the usdm package for R (Naimi et al. 2014). We restricted the predictor pairs to only one variable, whenever VIF exceeds 10.

For the Maxent models of *C. versicolor* s.l., the final variables comprised temperature annual range (bio7), mean temperature of wettest quarter (bio8), mean temperature of driest quarter (bio9), precipitation of wettest month (bio13), precipitation of driest month (bio14), precipitation of warmest quarter (bio18) and precipitation of coldest quarter (bio19). For the four subtaxa, which were used as sensitivity analysis, a subset of the 19 worldclim variables was used (see results for details).

Species distribution modelling

For SDM calculation and model fitting, we combined two SDM approaches, namely the hypervolume package (Blonder & Harris 2019) for R ver. 4.0.5 (R Core Team 2021) and Maxent ver. 3.4.4 (Phillips et al. 2006). While the hypervolume approach gives a broad visualization of the realized niche based on non-hierarchically ranked variables, Maxent is an approach providing predictions based on hierarchically ranked environmental variables. Using the hypervolume package and Maxent, we computed each two final models for *C. versicolor* s.l., one based on records from the native range and one based on records from the native and invaded range. Furthermore, we ran a sensitivity analysis to consider the recent split of *C. versicolor* s.l. into four distinct subtaxa (Gowande et al. 2021). For each subtaxon, we computed Maxent as well as hypervolume models based on records from the native range only. Unfortunately, most records from the invaded range could not be assigned to one of the four species and therefore we could not include the invaded range as well. Additionally, the R-packages raster (Hijmans 2016), dismo (Hijmans et al. 2017) and

ENMeval (Muscarella et al. 2014) were used for data processing and SDM calculation.

Realized niche expansion - Hypervolumes

To analyse the expansion in the realized niche of *C. versicolor* s.l., n-dimensional hypervolumes were calculated based on the same two datasets used for the Maxent models, one based on records from the native range (SDM_{Hyper_nat}) and the other one from the native and invaded range ($SDM_{Hyper\_nat\_inv}$). As mentioned in the introduction, *C. versicolor* s.l. could spread across several non-native areas and we hypothesise that an expansion in the geographic space also expands the species' realized niche in the environmental space. As we only have a small record number (14 records) from the invaded range and the time of introduction in some cases is uncertain, we could not split the datasets into smaller subsets. For hypervolume construction, we used the hypervolume_svm-algorithm available in the hypervolume package for R building a one-class support vector machine (Blonder & Harris 2019). This one-class support vector machine (SVM) transforms the input data into n-dimensional non-linear space in which the data points can be optimally separated from background by a single hyperplane. The hyperplane is then transformed backwards into the original space, which delineates an adaptive grid of random points next to the original data points. Finally, the SVM predicts if each of these points is in or out of the hypervolume (Blonder & Harris 2019). The SVM is implemented with a radial basis function (RBF), from which only two parameters, svm.nu and svm.gamma, can be defined by the user. The svm.nu-parameter defines the lower bound of support vectors and an upper bound on the fraction of training errors. Lower values reveal in a tighter wrapping of the shape to the data. The gamma-parameter tunes how far the influence of a single training point reaches and it can be seen as the inverse radius of influence of points chosen by the model as support vectors (Blonder & Harris 2019). For model construction, we used the default parameters of svm.nu = 0.01 and svm.gamma = 0.5.

Before hypervolumes were constructed, the predicting environmental variables were masked using an overall climatic envelope model (bioclim)-model (Hijmans et al. 2017) to reduce calculation time as climatically unsuitable areas were excluded. The maximum possible hypervolume-model is thus nested in the bioclim-model (Nania et al. 2020). For hypervolume construction, we conducted a principal component analysis (PCA) to correctly delineate the shape of the hypervolumes to principal components (PCs) with an eigenvalue >= 1. This is necessary, as the hypervolume_svm-algorithm requires an orthogonal space for the correct delineation of the hypervolume shape. For both final hypervolumes and the sensitivity analysis, the same bioclim-model and PCA was conducted from the full record set based on occurrences from the native and invaded range together as this allows a better comparison of the models. Furthermore, it was necessary to use the full set of bioclimatic variables (excluding the derived ones as described above) as the variable selection revealed different final variables for each taxon, which would not allow comparison based on hypervolumes in environmental space. For hypervolume construction, the full record set was subset to perform one hypervolume for the native record set (SDM_{Hyper_nat}) and one for the native and invasive record set ($SDM_{Hyper\_nat\_inv}$). For the sensitivity analysis, we used the respective records of the four subtaxa. Hypervolumes were evaluated by TSS (Allouche et al. 2006).

The hypervolume_variable_importance() function was applied over each 100 replicates for all hypervolumes to compute the PCs contribution to the hypervolumes volume, respectively. Pairwise overlap statistics applying Jaccard and Sorensen index to the plotted hypervolumes for *C. versicolor* s.l. and the four subtaxa were calculated with the respective function of hypervolume package (Blonder & Harris 2019) to quantify the realized niche expansion in environmental space. Further, all hypervolumes were detected to contain holes. For this, a convex shape of the respective hypervolume was assumed and this idealistic shape was compared with the original hypervolume [functions: expectation_convex() and hypervolume_holes()], As the detection of holes for higher dimensions is very time-consuming, we set the number of maximum points to 10,000. We averaged the results of the hypervolume_holes() function across 100 replicates as the function uses a certain number of random points to detect holes. Afterwards, we used the hypervolume_segment() function to cluster the closest occurrence records and hypervolume_prune() function to prune small holes in the hypervolume, which may occur from too low sampling effort (Blonder 2016). Unfortunately, this function may also prune holes that occur naturally in ecological niche space. Finally, the hypervolumes were projected into geographic space using the hypervolume_project() function (Blonder & Harris 2019).

For better visualization and comparison between the native and invasive climate space, we plotted the density distributions of the environmental predictors, which were used for PCA, and the revealed PCs using the sm.density.compare() function of the sm package for R (Bowman & Azzalini 2018). Furthermore, we used the area() function of the raster package (Hijmans 2016) to calculate the predicted areas for all hypervolumes. Due to the inaccuracy of the function the results were rounded to the nearest 100 km^2.

Invasive risk assessment - Maxent models

Maxent is one of the most frequently used correlative SDM software (Srivastava et al. 2019). The algorithm uses the principle of maximum entropy to predict a species' potential distribution from presence-pseudoabsence data and environmental variables. Presence data are confirmed occurrence records of the target species, while the pseudoabsence data are sampled in the species' background area, where the environmental conditions might allow the target species' presence (Phillips et al. 2006). As environmental background, we selected a 500 km radius around each occurrence record to provide a seamless cover across the species' distributional range. The selected background area resembles quite well the IUCN map for this taxon (Wogan et al. 2021).

For model fitting, we tested several regularization multipliers (from 0.5 to 2.5 in 0.1 steps, 5 and 10) and feature classes (L, LP, LQ, LH, LT, LQP, LQH, LQT, LPH, LPT, LHT, LQPT, LQHT, LPHT, LQPHT; L = Linear, P = Product, Q = Quadratic, H = Hinge, T = Threshold). We calculated two final Maxent models for *C. versicolor* s.l. employing the most suitable settings, one based on the native records only (SDM_{Maxent_nat}) and one based on the native and invasive records together ($SDM_{Maxent\_nat\_inv}$).

Using Maxent's raw output, we calculated corrected Akaike Information Criterion [AICc; (Warren & Seifert 2011)] for each 25 replicates of each combination of model settings (Figure 1). The best combination of settings was selected according to the lowest average AICc over 25 replicates and an AUC_{Test} above 0.7 [AUC = Area under the ROC curve (Lobo et al. 2008, Phillips & Dudík 2008, Elith & Graham 2009)]. AUC was calculated by using a bootstrap approach with an 80% data split for model training and 20% used for model testing. The best fitting model was replicated 100 times using again a bootstrap approach with an 80:20 split for model training and testing to calculate the AUC values. Further, True Skills Statistic (TSS) was calculated as second evaluation metric (Somodi et al. 2017, Allouche et al. 2006). The final model was averaged across its 100 replicates. MESS (Multivariate Environmental Similarity Surfaces) maps were provided to highlight areas where the model must be extrapolated and therefore the prediction should be interpreted with caution. We visualised the SDM using Maxents cloglog output format, which provides an estimate between 0 (very unsuitable habitat) and 1 (very suitable habitat). We calculated lowest 5% thresholds for all models based on their respective average output, from which we extracted the Maxent cloglog scores for each occurrence record used for modelling. This threshold was set as threshold for presence-absence and areas below these 5% thresholds were removed [compare to Phillips et al. (2006)]. Finally, we used the area() function of the raster package (Hijmans 2016) to calculate the surface areas used as background and the predicted areas of all models. For the predictions, we calculated the surface areas after the lowest 5% thresholds were applied. Due to the inaccuracy of the function the results were rounded to the nearest 100 km^2.

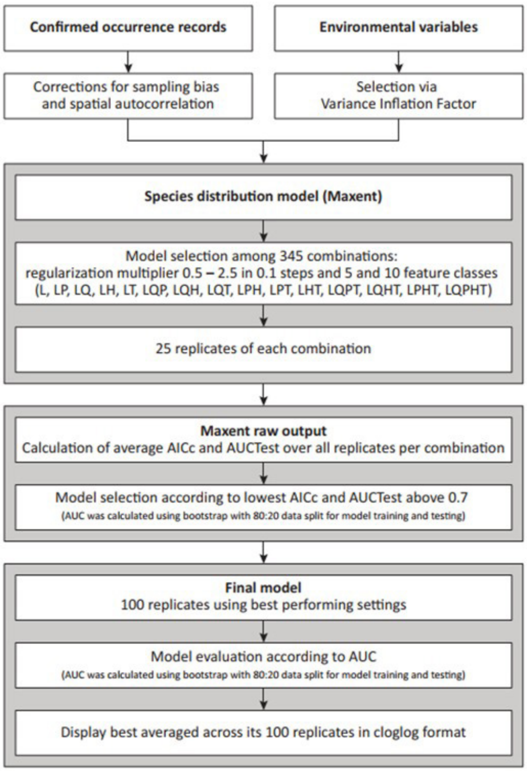

Figure 1. Schematic workflow of Maxent model optimization and fitting for the invasive risk assessment of *Calotes versicolor* s.l. and its four subtaxa.

As sensitivity analysis, we calculated each a final model for *C. versicolor* s.str., *C. irawadi* s.l., *C. vultuosus* and *C. farooqi* following the same procedure described above. Subsequently, we combined the four prediction maps to a single map. For this, we calculated the median of each grid cell across the raster stack, which comprised the four prediction maps. As combined MESS area we used the areas where all four subtaxa showed MESS areas.

Results

Realized niche expansion - Hypervolumes

The performed bioclim-model predicts and excludes larger unsuitable areas in northern North America, the Andes, the Pole regions, northern and south-eastern Africa, northern, central and western Asia and north-western and southern Australia. The conducted PCA reveals four PCs with an eigenvalue >=1 (Table 2). PC1 is mainly correlated (factor loadings >0.70 or <-0.70) with annual mean temperature (bio1), minimum temperature of coldest month (bio6), mean temperature of driest (bio9), wettest (bio8), coldest (bio11) and warmest quarter (bio10). PC2 is mainly correlated with annual precipitation (bio12), maximum temperature of warmest month (bio5), precipitation of wettest month (bio13) and quarter (bio16). PC3 is mainly correlated with precipitation of driest month (bio14) and quarter (bio17). PC4 only shows low correlations but is strongest correlated with precipitation of warmest quarter (bio18). For all models, the PCs' variable importance over 100 replicates to the models' volume reveals the greatest importance for PC1 and PC2 (Table 2). Most models show a moderate performance (>0), however, the hypervolumes of *C. versicolor* s.str. (27 records) and *C. farooqi* (15 records) perform poor due to the

Table 2. Results of the PCA for the predicting environmental variables (factor loadings, eigenvalue, explained variance) and variable importance [mean ± SD] to the hypervolumes for *Calotes versicolor* s.l. and its four subtaxa.

Environmental parameter	**Abbreviation**	**PC1**	**PC2**	**PC3**	**PC4**
Annual mean temperature	bio1	0.96	0.25	0.08	0.04
Max temperature of warmest month	bio5	0.48	0.73	0.18	0.35
Min temperature of coldest month	bio6	0.94	-0.16	-0.06	-0.22
Temperature annual range	bio7	-0.62	0.56	0.15	0.41
Mean temperature of wettest quarter	bio8	-0.72	0.32	0.11	0.42
Mean temperature of driest quarter	bio9	0.92	0.12	-0.02	-0.24
Mean temperature of warmest quarter	bio10	0.72	0.58	0.16	0.27
Mean temperature of coldest quarter	bio11	0.97	-0.03	0.01	-0.19
Annual precipitation	bio12	0.33	-0.87	0.25	0.20
Precipitation of wettest month	bio13	0.25	-0.72	0.54	0.06
Precipitation of driest month	bio14	0.23	-0.30	-0.83	0.33
Precipitation of wettest quarter	bio16	0.25	-0.76	0.53	0.14
Precipitation of driest quarter	bio17	0.24	-0.32	-0.84	0.31
Precipitation of warmest quarter	bio18	-0.11	-0.54	0.11	0.62
Precipitation of coldest quarter	bio19	0.25	-0.35	-0.55	-0.15
Eigenvalues		5.66	3.85	2.44	1.35
Explained variance		37.75	25.67	16.26	9.00
Variable importance					
$\mathrm{SDM}_{\mathrm{Hyper\_nat}}$		3.46 ± 0.03	3.62 ± 0.03	1.81 ± 0.01	1.90 ± 0.02
$\mathrm{SDM}_{\mathrm{Hyper\_nat\_inv}}$		3.85 ± 0.03	3.84 ± 0.03	2.24 ± 0.02	2.08 ± 0.02
C. versicolor s.str.		1.32 ± 0.01	2.68 ± 0.01	1.06 ± 0.00	0.56 ± 0.00
C. irawadi		2.34 ± 0.01	2.18 ± 0.01	1.39 ± 0.01	1.97 ± 0.01
C. vultuosus		1.73 ± 0.01	2.04 ± 0.01	0.81 ± 0.00	1.14 ± 0.01
C. farooqi		1.69 ± 0.01	1.21 ± 0.00	0.33 ± 0.00	1.00 ± 0.00

low sample sizes (Table 3). Further, in all hypervolumes several holes are detected. The volumes, point densities and numbers of random points of the holes strongly differ among the models (Table 3).

The density distribution plots can give a more detailed explanation of a potential realized niche expansion. We consider the realized niche expansion when novel environmental conditions are met in the invaded range, which were not found in the native range. For the four PCs, the density plots reveal major expansions in the realized niche of *C. versicolor* s.l. for all PCs (Figure 2). Major expansions in the realized niche can also be found for temperature annual range (bio7), precipitation of driest month (bio14), warmest (bio18) and coldest quarter (bio19), while only minor expansions are found for the remaining variables (Figure 3). Considering the four subtaxa, the density distribution plots reveal strong differences among the taxa and among *C. versicolor* s.l. due to the different geographic distributions and different climatic conditions (Supplementary Material S2). The pairwise overlap statistics for $\mathrm{SDM}_{\mathrm{Hyper\_nat}}$ and $\mathrm{SDM}_{\mathrm{Hyper\_nat\_inv}}$ reveal

Table 3. Hypervolumes: Detection of holes, including volume, point density and number of random points [mean ± SD], and the model performance (TSS).

Hypervolume model	Holes Volume	Holes Point density	Holes Random points	TSS
SDM$_{Hyper\_nat}$	444.05 ± 1.83	13.01 ± 0.11	5776 ± 51	0.29
SDM$_{Hyper\_nat\_inv}$	1034.52 ±3.16	6.73 ± 0.04	6966 ± 49	0.30
C. versicolor s.str.	14.02 ± 0.09	428.85 ± 3.25	6014 ± 46	-0.03
C. irawadi	21.90 ± 0.40	122.96 ± 0.00	2692 ± 50	0.09
C. vultuosus	92.81 ± 0.68	70.03 ± 0.00	6499 ± 47	0.04
C. farooqi	0.21 ± 0.01	3608.25 ± 0.00	753 ± 30	-0.04

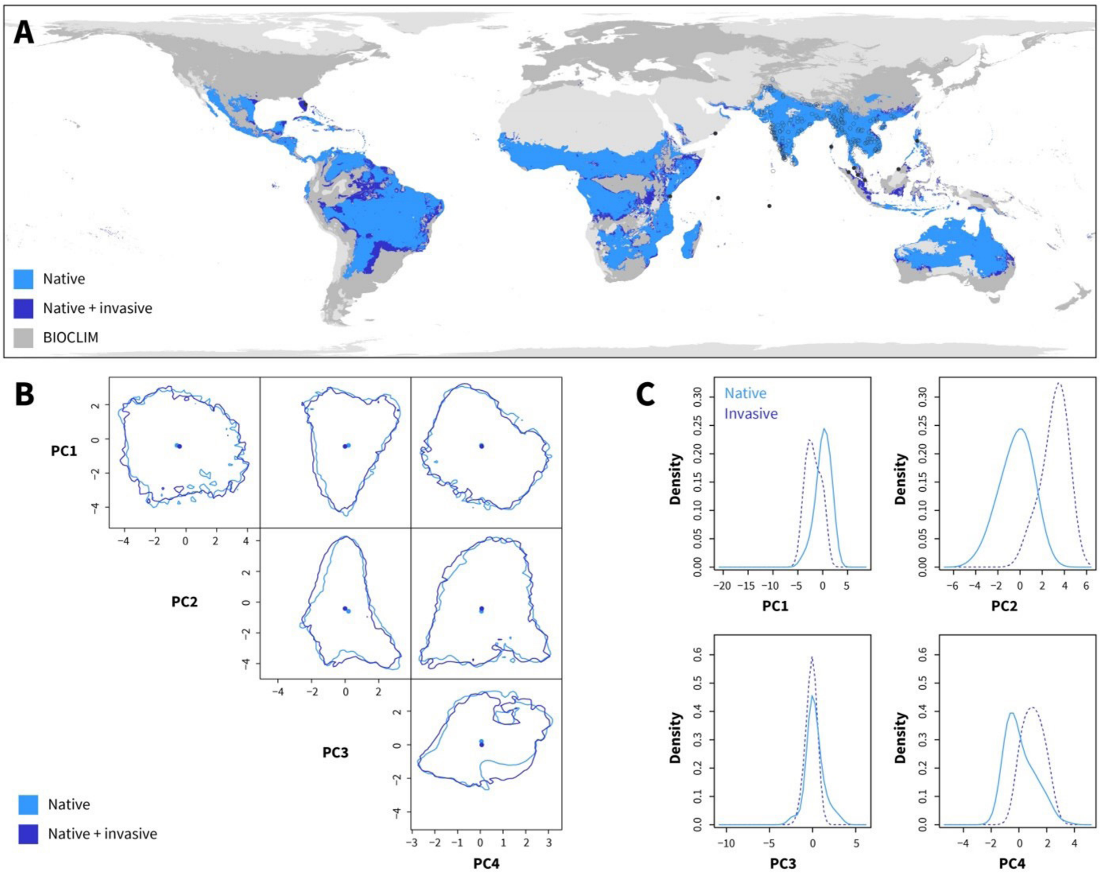

Figure 2. Realized niche expansion of *C. versicolor* s.l. in (A) geographic space and (B) in environmental space. Potential predicted distribution of *C. versicolor* s.l. across the globe according to hypervolume models based on records from the native distribution and records from the native and invaded distribution. The hypervolume models are nested in a bioclim model. (C) Density distributions of the four principal component axes used for hypervolume construction.

a large unique fraction for the latter model, which also indicates an expansion in the realized climate niche due to the invaded ranges. Further, the low Jaccard and Sorensen Indices as well as the unique fractions of the hypervolumes for the four subtaxa show that the respective subtaxa only represent small subsets of the whole climatic niche of *C. versicolor* s.l. (Table 4). The predictions of SDM$_{Hyper\_nat}$ and SDM$_{Hyper\_nat\_inv}$ reveal surface areas of 30,166,500 km^2 and 35,361,100 km^2, respectively, which correspond to a gain of 17%. The hypervolume models for the four subtaxa reveal much smaller surface areas (Table 5).

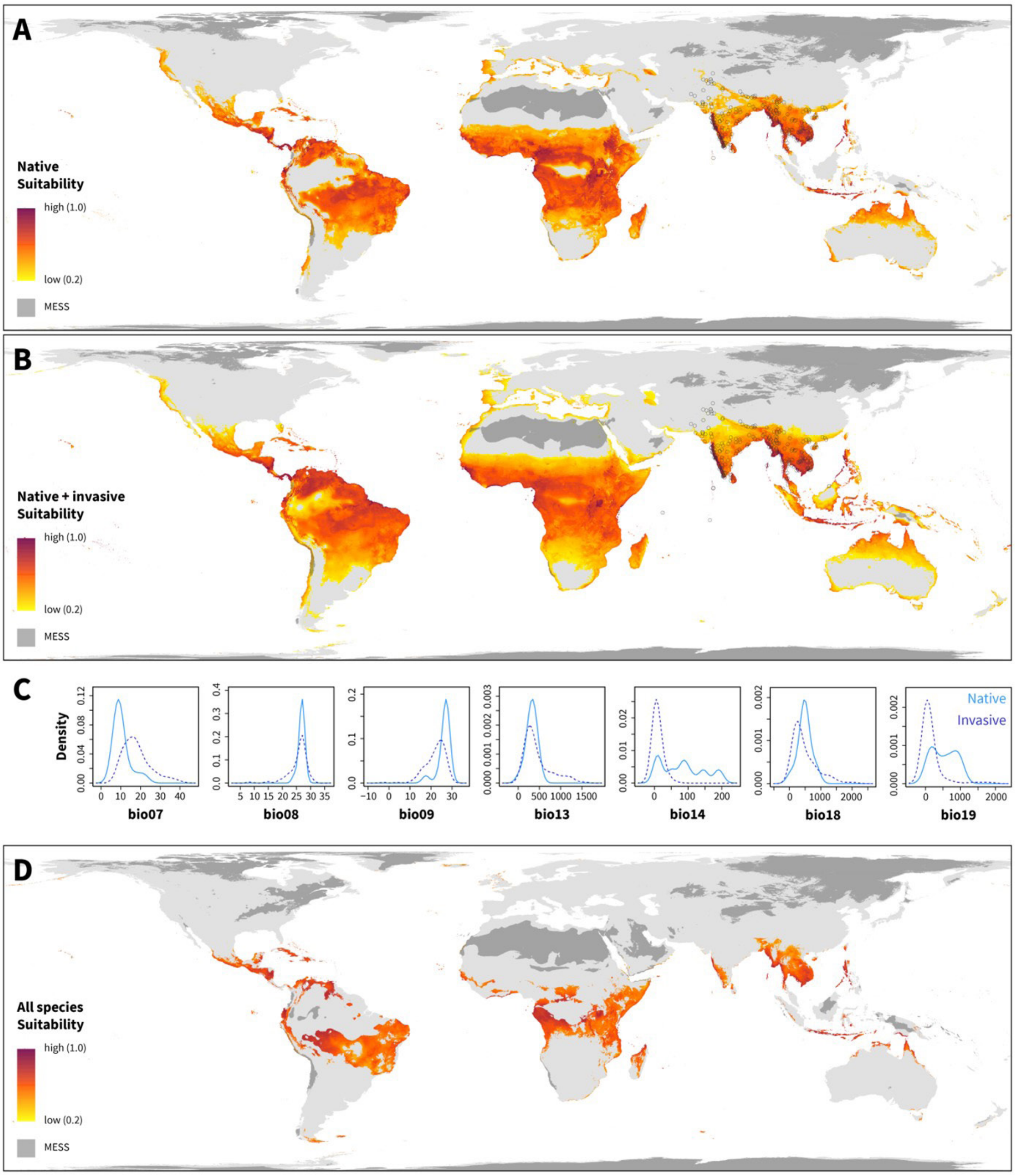

Figure 3. Invasive risk assessment: Potential predicted distribution of *C. versicolor* s.l. across the globe according to Maxent models based (A) on records from the native distribution and (B) records from the native and invaded distribution. Multivariate Environmental Similarity Surfaces (MESS) are provided, where the prediction should be treated carefully. (C) Density distributions of the environmental predictors used for model construction and (D) sensitivity analysis (combined map) based on the four subtaxa *C. versicolor* s.str., *C. irawadi*, *C. vultuosus* and *C. farooqi*.

Invasive risk assessment - Maxent models

For *C. versicolor* s.l ($\text{SDM}_{\text{Maxent\_nat}}$ and $\text{SDM}_{\text{Maxent\_nat\_inv}}$) and the four subtaxa, we computed each a total of 8625 Maxent models (23 regularization multipliers x 15 feature class combinations x 25 replicates). The ranking of the five best performing model settings

Table 4. Hypervolumes: Overlap statistics among SDM$_{\text{Hyper\_nat}}$ and the other models.

SDM$_{\text{Hyper\_nat}}$	Jaccard	Sorensen	Unique fraction 1	Unique fraction 2
SDM$_{\text{Hyper\_nat\_inv}}$	0.71	0.83	0.02	0.29
C. versicolor s.str.	0.04	0.08	0.96	0.02
C. irawadi	0.23	0.38	0.76	0.07
C. vultuosus	0.01	0.02	0.99	0.02
C. farooqi	0.01	0.02	0.99	0.02

Table 5. Predicted surface areas of hypervolume and Maxent models. For Maxent models, the surface areas of the background and the predictions (5% thresholds applied) are provided. The percentage surface area in respect to the model for *C. versicolor* s.l. is given in brackets.

Model	Surface area [km^2]		Maxent Prediction
	Hypervolume	Maxent Background	
C. versicolor s.l. [native]	30,166,500 [100%] [SDM$_{\text{Hyper\_nat}}$]	6,932,200 [100%] [SDM$_{\text{Maxent\_nat}}$]	40,250,800 [100%] [SDM$_{\text{Maxent\_nat}}$]
C. versicolor s.l. [native+ invasive]	35,361,100 [117%] [SDM$_{\text{Hyper\_nat\_inv}}$]	6,941,200 [0.1%] [SDM$_{\text{Maxent\_nat\_inv}}$]	53,142,600 [132%] [SDM$_{\text{Maxent\_nat\_inv}}$]
Sensitivity analysis			
Combined map	-	-	14,025,100 [35%]
C. versicolor s.str.	4,718,200 [16%]	869,700 [13%]	80,663,400 [200%]
C. irawadi	11,491,300 [38%]	3, 094,700 [45%]	22,416,200 [56%]
C. vultuosus	10,289,100 [34%]	2,926,700 [42%]	48,648,700 [21%]
C. farooqi	2,168,700 [7%]	1,330,600 [19%]	124,106,100 [308%]

according to AICc reveals moderate to high AUC values for all SDMs. We selected the model with the lowest AICc for further processing (Table 6).

All final models also perform moderate to high AUC and TSS values across their 100 replicates (Table 6). For SDM$_{\text{Maxent\_nat}}$, temperature annual range (bio7) contributes highest to the models performance, followed by precipitation of wettest (bio13) and driest month (bio14). For SDM$_{\text{Maxent\_nat\_inv}}$, the variables contribute similar to the model with temperature annual range (bio7) followed by precipitation of wettest month (bio13) and mean temperature of driest quarter (bio9), whereas the contribution for the models of the four subtaxa differs from the latter two models (Table 7).

The used background areas reveal surface areas of 6,932,200 km^2 (SDM$_{\text{Maxent\_nat}}$) and 6,941,200 km^2 (SDM$_{\text{Maxent\_nat\_inv}}$), respectively, while the predictions (5% thresholds applied) result in an area of 40,250,800 km^2 and 53,142,600 km^2. This corresponds to gains of 481% and 666%. The sensitivity analysis (combined map of the four subtaxa; Fig 3) reveals a surface area of 14,025,100 km^2, which is 35% of the predicted area of SDM$_{\text{Maxent\_nat}}$. For the four subtaxa, the predicted surface areas strongly differ among each other (Table 6).

Species complex vs. subtaxa

In contrast to the Maxent models, the hypervolumes reveal similar but rougher predictions as they provide presence-absence maps without probabilities (Figure 2, Supplementary Material S2). For the invasive risk assessment, we therefore focus on the Maxent models. The two Maxent models for *C. versicolor* s.l., SDM$_{\text{Maxent\_nat}}$ and SDM$_{\text{Maxent\_nat\_inv}}$, reveal similar global predictions and show highly suitable environmental conditions across large parts of the Oriental realm (Figure 3). The native distribution of *C. versicolor* s.l. largely covers this region, where both models predict highly suitable environmental conditions. Habitat suitability decreases towards the Himalaya and towards drier regions (i.e. northeast India, Afghanistan, Pakistan) where the number of occurrence records is also lower or no records are confirmed (Figure 3). According to our models, the Pacific and Indian Ocean islands of the Oriental realm towards the Wallace line are climatically moderately to highly suitable including the already invaded regions [Borneo, Celebes (= Sulawesi), Philippines, Maldives, Singapore, Andaman

Table 6. Results of the five best Maxent ensembles according to AICc. Models for *C. versicolor* s.l., based on records from the native range (SDM_{Maxent_nat}) and the native and invaded range ($SDM_{Maxent\_nat\_inv}$), and a sensitivity analysis based on the four subtaxa (*C. versicolor* s.str., *C. irawadi* s.l., *C. vultuosus*, *C. farooqi*): Regularization multiplier, feature classes, number of parameters, AICc, $AUC_{Training}$ and AUC_{Test}. The model used for further processing is highlighted in bold font.

Regularization	Features	nParameters	AICc	$AUC_{Training}$	AUC_{Test}	TSS_{Train}	TSS_{Test}
SDM_{Maxent_nat}							
1.3	**LQT**	**41**	**2698.51**	**0.81**	**0.75**		
1.3	LT	43	2711.28	0.81	0.73		
0.6	LT	29	2712.54	0.77	0.73		
1.6	LQPT	34	2715.67	0.78	0.74		
1.4	LT	36	2716.37	0.80	0.74		
Final model							
1.3	**LQT**			**0.81**	**0.75**	**0.60**	**0.54**
$SDM_{Maxent\_nat\_inv}$							
1.7	**LPT**	**27**	**2903.58**	**0.78**	**0.73**		
1.3	LQT	37	2908.17	0.79	0.73		
1.6	LPT	29	2908.56	0.78	0.70		
1.3	LPQT	45	2909.03	0.81	0.72		
1.5	LT	34	2912.18	0.79	0.73		
Final model							
1.3	**LQT**			**0.76**	**0.72**	**0.73**	**0.70**
Sensitivity analysis							
C. versicolor s.str.							
1.7	**LPQ**	**6**	**340.41**	**0.89**	**0.85**		
1.7	LT	3	340.69	0.86	0.82		
1.2	LT	4	341.18	0.87	0.85		
1.6	LP	3	341.36	0.86	0.84		
1.6	L	3	341.44	0.86	0.83		
Final model							
1.3	**LQT**			**0.88**	**0.86**	**0.30**	**0.26**
C. irawadi							
0.7	**LPQT**	**8**	**1405.48**	**0.71**	**0.68**		
1.1	LQT	8	1406.27	0.70	0.67		
0.5	LQT	10	1406.68	0.71	0.67		
1.6	LQT	7	1407.46	0.70	0.65		
1.1	LQ	7	1407.71	0.70	0.64		
Final model							
1.3	**LQT**			**0.70**	**0.66**	**0.67**	**0.63**
C. vultuosus							
1.2	**LPQT**	**10**	**760.34**	**0.82**	**0.76**		
0.5	LPQ	13	763.63	0.83	0.80		
1.1	LPQT	10	765.65	0.82	0.80		
1.0	LPQ	11	768.85	0.81	0.78		
1.5	LPQT	9	768.97	0.82	0.79		
Final model							
1.2	**LPQT**			**0.82**	**0.76**	**0.52**	**0.48**
C. farooqi							
1.4	LH	2	222.44	0.66	0.55		

Table 6. Continued...

Regularization	Features	nParameters	AICc	$\text{AUC}_{\text{Training}}$	AUC_{Test}	$\text{TSS}_{\text{Train}}$	TSS_{Test}
1.5	**LT**	**2**	**223.01**	**0.72**	**0.61**		
1.3	LPT	3	223.11	0.70	0.56		
1.7	LPT	2	223.13	0.71	0.59		
1.3	LP	3	223.14	0.71	0.67		
Final model							
1.3	**LQT**			**0.81**	**0.77**	**0.73**	**0.65**

Table 7. Maxent variable contribution of the best fitting SDM for *Calotes versicolor* s.l., based on records from the native range ($\text{SDM}_{\text{Maxent\_nat}}$) and records from the native and invaded range ($\text{SDM}_{\text{Maxent\_nat\_inv}}$) together, and for the sensitivity analysis, based on the four subtaxa that are comprised in *C. versicolor* s.l.

Environmental parameter	Abbreviation			Variable contribution [%]	
				$\text{SDM}_{\text{Maxent\_nat}}$	$\text{SDM}_{\text{Maxent\_nat\_inv}}$
Temperature annual range	bio7			32.8	46.5
Precipitation of wettest month	bio13			26.7	25.6
Precipitation of driest month	bio14			14.5	6.6
Mean temperature of driest quarter	bio9			11.7	10.0
Mean temperature of wettest quarter	bio8			6.1	5.7
Precipitation of coldest quarter	bio19			4.2	1.8
Precipitation of warmest quarter	bio18			4.0	3.8
	Sensitivity analysis				
		***C.versicolor* s.str.**	***C.irawadi***	***C. vultuosus***	***C. farooqi***
Max temperature of warmest month	bio5	53.5			
Temperature annual range	bio7		50.1	54.9	4.9
Mean temperature of wettest quarter	bio8	0.0	10.6	5.2	43.8
Mean temperature of driest quarter	bio9	32.6		1.7	5.4
Precipitation of wettest month	bio13	1.7	8.0	23.6	3.8
Precipitation of driest month	bio14	7.4	18.4	0.8	11.6
Precipitation of driest quarter	bio17			7.7	
Precipitation of warmest quarter	bio18	2.3	2.8	2.2	23.2
Precipitation of coldest quarter	bio19	2.5	10.2	3.9	1.4

Islands and Diego Garcia]. According to the Maxent models, particularly northern and eastern mainland Australia as well as the coastal regions and several islands of the Australian realm seem climatically lowly to moderately suitable for *C. versicolor* s.l. (Figure 3). Compared to $\text{SDM}_{\text{Maxent\_nat}}$, $\text{SDM}_{\text{Maxent\_nat\_inv}}$ reveals less suitable climatic space for some areas i.e. north-central India, northern Indochina, Borneo, New Guinea, mainland Australia etc., where the latter model predicts lowly suitable climatic conditions. For both models, some areas of New Guinea comprise Multivariate environmental Similarity Surface (MESS) areas, where the prediction should be interpreted with caution.

Both Maxent models reveal that very large parts of the Afrotropics (Figure 3) are climatically suitable for *C. versicolor* s.l.. Especially, the regions along the equator and the coastal regions as well as the Indian Ocean islands, including all already invaded regions (Mascarene archipelago, Seychelles, Kenya, Oman), provide moderately to highly suitable conditions. Habitat suitability decreases towards the Sahel zone and the deserts of the Arabian Peninsula where only the very coastal regions show lowly to moderately suitable environmental conditions. Furthermore, large MESS areas are found across the Sahara, the Arabian Peninsula and the coastal regions of southern Africa. $\text{SDM}_{\text{Maxent\_nat\_inv}}$ also predicts less climatically suitable area than $\text{SDM}_{\text{Maxent\_nat}}$.

For the Neotropics, our Maxent SDMs predict high climatic suitability across most parts of this biogeographic region including the Caribbean, Central America, northern and central South America (Figure 3). Southern Florida, where *C. versicolor* s.l. was already confirmed, also shows lowly to moderately suitable environmental conditions for both SDMs. MESS areas are found in parts of the Andes and some southern parts of mainland South America. The MESS areas are decreasing for $\mathrm{SDM}_{\mathrm{Maxent\_nat\_inv}}$.

Considering the Maxent models as well as the sensitivity analysis, the Palearctic and Nearctic realms are found to be almost entirely climatically unsuitable or low habitat suitability is predicted for both Maxent models (Figure 3). For the Palearctic realm, the only moderately suitable areas are found along some coastal regions and islands of the Mediterranean Sea and the Atlantic coast of the Iberian Peninsula. Furthermore, in Asia the transition zone to the Paleotropics is also partially predicted as lowly to moderately suitable. Large MESS areas are shown in North Africa, the Middle East and North to East Asia. For the Nearctic realm, only the transition zone to the Neotropics shows some regions with lowly to moderately suitable environmental conditions. Large MESS areas are found in the North towards the North Pole.

Compared to the models for *C. versicolor* s.l., the averaged map of the sensitivity analysis (Figure 3) reveals less suitable area in the Oriental realm (i.e. southern India, Sri Lanka, large parts of mainland Southeast Asia and Indonesia) and the Australian realm (i.e. coastal region of northern, eastern and southern Australia), Large MESS areas are found on Borneo, New Guinea and several adjacent islands. Large parts of mainland Africa across the equator as well as Madagascar are climatically suitable for most of the four subtaxa. Further, several coastal areas i.e. of southern Africa and the Arabian Peninsula are suitable as well. Large MESS areas are found across the Sahara and the deserts of the Arabian Peninsula. Large parts of Central America, the Caribbean, northern and central South America are climatically suitable for most of the four subtaxa. Furthermore, small parts of southern South America are suitable as well. Large fragmented MESS areas are found across the Pacific coast of South America. The predictions for each subtaxon used for the sensitivity analysis differ strongly among each other (Supplementary Material S2). Particularly, the models for the species with low sample sizes reveal large MESS areas and it must be mentioned that more accurate predictions require a more species-specific tuning and a higher sample size.

Discussion

The geographic expansion into novel climatic conditions reveals an expansion of the realized climatic niche for *C. versicolor* s.l. which is supported by the hypervolumes and density plots. The results of the invasive risk assessment predict large areas of suitable climatic conditions for most parts of the tropics and subtropics for the species complex and the four subtaxa. Furthermore, the models for the species complex reveal larger surface area predictions and also partially more realistic predictions as the sensitivity analysis.

Introduction pathways

The unintentional introduction as stowaway from ornamental plants, timber or other nature products, seems to be the most frequent introduction pathway into non-native oversea regions for this lizard (see introduction for details). While a combination of deforestation and manmade transport might also boost the species' expansion in its native range. A comparison with maritime bottlenecks of container traffic revealed that several core and secondary trading routes are intersecting with the species' range (https://porteconomicsmanagement.org/pemp/contents/part1/interoceanic-passages/connectivity-pattern-worlds-major-maritime-bottlenecks/) and might be likely introduction pathways into the Afrotropical, Australian and further regions of the Oriental realms, where our models predict suitable climatic conditions for large areas. Our invasive risk assessment reveals that coastal regions often provide more climatically suitable conditions, also if main parts of the country are predicted as unsuitable (i.e. Oman). Considering that *C. versicolor* s.l. prefers open and often anthropogenic landscapes, coastal ports with high amount of traffic could serve as stepping stones and might allow to disperse easily into novel and even far distant regions. The Strait of Malacca is one of the most important trading routes worldwide and the main passage between the Indian and Pacific Oceans. Specifically, the port of Singapore, which is among the most important trans-shipment hubs, might be an important stepping stone for *C. versicolor* s.l. to reach novel regions. For Kenya it is suggested that the species derives from the introduced populations of Réunion and Mauritius (Sandera 2009). Also for other reptiles such as *Lepidodactylus lugubris* it was discussed that its invasion success is linked to maritime bottlenecks (Nania et al. 2020).

Our results reveal that the already invaded regions provide suitable climate for all four subtaxa and based on this, we cannot assign a certain species to an invaded locality. However, due to geographic proximity, it can be assumed that the non-native populations on Borneo, Sulawesi, the Philippines and the Andaman Islands most likely belong to *C. irawadi* s.l., which should also be the case for the populations in Malaysia and Singapore, if they truly derive from natural invasions. According to Enge & Krysko (2004) and Krysko et al. (2011), the population in Florida (USA) derives from animals from Pakistan and if so, they would belong to *C. farooqi* s.l. Unfortunately, genetic data on the non-native populations are scarce and only the populations on the Maldives were assigned to *C. versicolor* s.str. (Gowande et al. 2021).

Next to stowaway, the pet trade is one of the main pathways of introduction for non-native reptiles and amphibians (Kraus 2009). However, only the population in Florida (USA) seems to derive from escaped animals from the pet trade (Enge & Krysko 2004, Krysko et al. 2011). According to own observations (PG), *C. versicolor* s.l. is rarely kept long-terms in captivity as the species is very sensitive and often subject to poor husbandry conditions. This might be the reason that no other population derives from this source and the risk of invasion due to the pet trade seems low.

Despite *C. versicolor* s.l. has a huge native range, surprisingly only few occurrences are known from outside this area. Reasons for this might be that the taxon is just neglected by biologists and labelled as "unspectacular lizard". Urban environments, where the species is found, might often be understudied as they seem uninteresting for most herpetologists. The case of the African Clawed Frog (*Xenopus laevis*) in Portugal shows that exotic species can be undetected for several decades, even in densely urbanised landscapes (Sousa et al. 2018). Alternatively, the species might arrive in novel and climatically suitable environments much more often than it is observed but it cannot establish populations, how it was observed on Mahé in 1985-86 (Matyot 2004). Reasons for this might be complex and often include biotic interactions (i.e. competition with other species) but also stochastic effects (i.e. low number of founder individuals; Kraus 2009).

Realized niche expansion

Our hypervolumes, the pairwise overlap statistics and the density distributions reveal an expansion of the realized niche in geographic as well as in environmental space during the invasion process. For the novel invaded regions, *C. versicolor* s.l. meets a lower temperature annual range and less precipitation in the driest month, warmest and coldest quarter compared to the native range (Figure 3). For all four PCs, the density distribution plots reveal a major expansion of the realized niche as well.

A closer view on the Maxent sample predictions (Supplementary Material S1 and S2) shows that the records from the invaded range in average reveal higher suitability (mean ± SD [range]: 0.55 ± 0.22 [0.19 – 1.00]) compared to the native records (0.71 ± 0.18 [0.33 – 0.96]), which also indicates that the invaded localities are not on the edge of the species' realized climatic niche but in contrast provide highly suitable climatic conditions. However, particularly for the Maxent models, some predictions of climatically low suitability regions might be an artefact derived from the 500 km buffer around each record used for modelling. This buffer was necessary to obtain seamless cover across the native range of *C. versicolor* s.l. and to provide Maxent contrasting environmental data (absence-pseudoabsence points used for modelling). Further, it allows a better comparison among the different subtaxa. However, some occurrence points close to high mountain ranges (i.e. Himalaya) led to the inclusion of environmental gradients that are outside of the species' ecological niche space and might led to erroneous predictions (i.e. temperate rainforests in Canada).

In both realized niches (SDM_{Hyper_nat} and $SDM_{Hyper\_nat\_inv}$), several holes are detected. Holes in hypervolumes, or modelled ecological niches, respectively, might be explained by the hypothesis that niche evolution does not always proceed through simple shifts. Genetic or developmental constraints or natural selection might prevent the presence of certain phenotypes, leading to the presence of holes in trait or potential niche space (Blonder 2016). Furthermore, holes might be the result of a genetically diverse fitness landscape. Populations of very different phenotypes can be connected by a small number of intermediate genotypes (Blonder 2016). This hypothesis is supported by the fact that *C. versicolor* s.l. and even its subtaxa are a complex of several cryptic species (see introduction for details). Further, the most holes might most likely be an artefact from undersampled niche space as *C. versicolor* s.l. is a very abundant and widespread taxon. Unfortunately, data on real absences of the species were not available. Furthermore, the holes might also derive from too restrictive settings used for hypervolume construction.

Conclusion

In summary, much of the tropical and subtropical regions seem climatically suitable for the *C. versicolor* species complex. Considering this, as well as the species' dispersal history and evidence for negative impacts on the native biodiversity, this lizard should be further monitored. According to our basal risk assessment ($SDM_{Maxent\_nat\_inv}$), the species is currently inhabiting 13% of its potential range but could find suitable climatic conditions on a global surface area between 14,025,100 km^2 (sensitivity analysis) and 53,142,600 km^2.

Regions with a high degree of endemism (i.e. islands like Mascarenes, Madagascar) might be particularly sensitive to an invasion by this lizard and the subsequent negative impacts (i.e. *Duttaphrynus melanostictus* on Madagascar; Moore et al. 2015). Furthermore, the introduction of *C. versicolor* s.l. to regions of other genetic lineages of this species complex might most likely lead to hybridizations and might threaten close relatives that are endemic to small areas, which is the case for many *Calotes* species. Therefore, strategies to hamper and prevent further spread of *C. versicolor* s.l. are urgently needed. Strategies to prevent stowaways, especially in regions with a high amount of human traffic as ports or airports, are also required. Lastly, a further systematic revision of this species complex will result in different predictions for each species and will be subsets of our current prediction.

Acknowledgements

We want to thank Morris Flecks and Ursula Bott for technical and graphical support. Further, we are grateful for the thorough reviews of Janet Franklin and Shai Meiri.

Author Contributions

PG did the main work of model construction and the main part of writing. NWCT and DR contributed in model construction and gave advice. All authors read the MS several times and contributed to the final version.

Data Accessibility

The data that support the findings of this article are available on request from the corresponding author (PG).

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb

Table S1. Maxent sample predictions and coordinates for $\mathrm{SDM}_{\mathrm{Maxent\_nat}}$, $\mathrm{SDM}_{\mathrm{Maxent\_nat\_inv}}$ and the models for C. versicolor s.str., C. irawadi, C. vultuosus and C. farooqi as well as the mean values ± SD [min - max] across the sample predictions for each model

Appendix S2. Hypervolume and Maxent models as well as the relevant density distribution plots for the four subtaxa C. versicolor s.str., C. irawadi, C. vultuosus and C. farooqi and plot of the sample predictions for $\mathrm{SDM}_{\mathrm{Maxent\_nat\_inv}}$

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Submitted: 29 July 2021
First decision: 14 October 2021
Accepted: 13 June 2022

Edited by Janet Franklin

Table S1. Maxent sample predictions and coordinates for SDM$_{\text{Maxent\_nat}}$, SDM$_{\text{Maxent\_nat\_inv}}$ and the models for *C. versicolor* s.str., *C. irawadi*, *C. vultuosus* and *C. farooqi* as well as the mean values ± SD [min - max] across the sample predictions for each model.

Species	mean	sd	min	max
versicolor_sl_nat	0.6809628	0.2010117	0.1873044	0.9982902
versicolor_sl_nat_inv	0.6547973	0.2163278	0.1860059	0.998496
versicolor	0.7286812	0.198734	0.2489369	0.9562798
irawadi	0.6355434	0.1589856	0.3633665	0.9568925
vultuosus	0.6261986	0.2919668	0.09117575	0.99814844
farooqi	0.662497	0.08204769	0.5672498	0.8126167

Species	Lat	Long	Raw.prediction	Cloglog.prediction	Native_invasive
versicolor_sl_nat	65.643553	28.478488	8.31E-05	0.34153561	nat
versicolor_sl_nat	66.924167	27.7035	5.34E-05	0.2847129	nat
versicolor_sl_nat	67.203172	24.892908	9.08E-05	0.4004058	nat
versicolor_sl_nat	69.4662	23.403723	0.00024439	0.62377699	nat
versicolor_sl_nat	69.722333	25.249667	8.27E-05	0.3891042	nat
versicolor_sl_nat	69.787833	24.704167	0.00010696	0.45537935	nat
versicolor_sl_nat	69.7878333	24.7041667	NA	NA	nat
versicolor_sl_nat	69.970111	34.516319	0.00021499	0.5155017	nat
versicolor_sl_nat	70	30	8.42E-05	0.39766583	nat
versicolor_sl_nat	70.754333	24.349167	0.00016172	0.56148419	nat
versicolor_sl_nat	71.083258	34.129764	0.00025003	0.58912289	nat
versicolor_sl_nat	71.69962	32.88789	6.31E-05	0.31202817	nat
versicolor_sl_nat	72.64083	34.5825	7.04E-05	0.33810537	nat
versicolor_sl_nat	72.6502	34.625	8.76E-05	0.36625244	nat
versicolor_sl_nat	72.715556	24.5925	0.0004901	0.87995771	nat
versicolor_sl_nat	72.809003	33.752158	7.52E-05	0.36332191	nat
versicolor_sl_nat	72.833302	19.054763	0.00032611	0.8395221	nat
versicolor_sl_nat	72.858944	19.122083	0.00031448	0.83208548	nat
versicolor_sl_nat	72.876517	19.220752	0.0006124	0.96156235	nat
versicolor_sl_nat	72.9488	20.592877	0.0004075	0.85016292	nat
versicolor_sl_nat	73.016907	23.301978	5.79E-05	0.3101562	nat
versicolor_sl_nat	73.07362	32.76047	0.00011023	0.46661111	nat
versicolor_sl_nat	73.184751	17.494956	0.00133876	0.99360001	nat
versicolor_sl_nat	73.242976	17.487176	0.00085097	0.98440505	nat
versicolor_sl_nat	73.283318	17.487815	0.00073451	0.92749245	nat
versicolor_sl_nat	73.553701	19.094677	0.00113362	0.97793328	nat
versicolor_sl_nat	73.571024	17.116997	0.00048636	0.86210442	nat
versicolor_sl_nat	73.671666	19.969659	0.00018167	0.67341717	nat
versicolor_sl_nat	73.802882	17.353979	0.00049818	0.9283584	nat
versicolor_sl_nat	73.819425	32.850492	8.48E-05	0.41005394	nat
versicolor_sl_nat	73.838054	17.588824	0.00082694	0.96717945	nat
versicolor_sl_nat	73.843056	15.470833	0.00074967	0.96658698	nat
versicolor_sl_nat	74.124075	18.399982	0.00012785	0.54367378	nat
versicolor_sl_nat	74.175043	16.114078	0.00081925	0.98247212	nat
versicolor_sl_nat	74.227216	15.375353	0.0007024	0.97511217	nat
versicolor_sl_nat	74.343808	14.906596	0.0007373	0.96955042	nat
versicolor_sl_nat	74.381949	15.387411	0.00102421	0.96377689	nat
versicolor_sl_nat	74.50872	15.194521	0.00091711	0.98575294	nat
versicolor_sl_nat	74.666875	16.240033	0.00021267	0.73424666	nat

versicolor_sl_nat	75.220469	19.954399	9.29E-05	0.45190575	nat
versicolor_sl_nat	75.425253	13.055808	0.00059058	0.92747165	nat
versicolor_sl_nat	75.705144	13.261725	0.0010708	0.98542827	nat
versicolor_sl_nat	75.780403	11.248017	0.00066451	0.93468599	nat
versicolor_sl_nat	75.956851	11.94163	0.00213142	0.99644116	nat
versicolor_sl_nat	76.018432	11.787336	0.0011159	0.99316941	nat
versicolor_sl_nat	76.099921	11.590192	0.00166232	0.99829017	nat
versicolor_sl_nat	76.516911	10.915256	0.00035476	0.83919277	nat
versicolor_sl_nat	76.57886	14.432159	0.00015987	0.61555523	nat
versicolor_sl_nat	76.592757	10.303516	0.00086411	0.97237689	nat
versicolor_sl_nat	76.593296	18.48759	0.00010098	0.46897791	nat
versicolor_sl_nat	76.6310301	20.7131441	7.90E-05	0.39569036	nat
versicolor_sl_nat	76.646118	11.558786	0.00041745	0.91039956	nat
versicolor_sl_nat	76.681371	12.498362	0.000206	0.72356721	nat
versicolor_sl_nat	76.699433	12.499482	NA	NA	nat
versicolor_sl_nat	76.701717	10.114067	0.00024243	0.7601416	nat
versicolor_sl_nat	76.797819	30.360993	0.00012106	0.4980589	nat
versicolor_sl_nat	76.949239	8.485497	0.00051007	0.9229671	nat
versicolor_sl_nat	76.965868	30.898562	0.00014317	0.57578542	nat
versicolor_sl_nat	77	20	9.82E-05	0.46409654	nat
versicolor_sl_nat	77.067806	9.406926	0.00053472	0.92651937	nat
versicolor_sl_nat	77.136464	8.624487	0.00043896	0.8937361	nat
versicolor_sl_nat	77.1484822	8.6756595	0.00068166	0.95207523	nat
versicolor_sl_nat	77.232834	9.971362	0.00051578	0.91456522	nat
versicolor_sl_nat	77.268805	8.921367	0.00023701	0.73895892	nat
versicolor_sl_nat	77.370315	8.71068	0.00022467	0.71994652	nat
versicolor_sl_nat	77.5547	8.151478	0.00058814	0.94201774	nat
versicolor_sl_nat	77.558796	8.151024	NA	NA	nat
versicolor_sl_nat	77.781	12.8981	0.00017386	0.66445742	nat
versicolor_sl_nat	77.833333	9.833333	0.00012609	0.52848962	nat
versicolor_sl_nat	78.8166321	14.4431902	0.0001555	0.54523013	nat
versicolor_sl_nat	78.8367	9.354447	0.00017922	0.64453118	nat
versicolor_sl_nat	78.962889	20.593694	9.54E-05	0.45186406	nat
versicolor_sl_nat	79.435296	21.694081	7.62E-05	0.38587055	nat
versicolor_sl_nat	79.7028	9.0778	0.00040655	0.85448437	nat
versicolor_sl_nat	79.847778	6.931944	0.00017882	0.58735471	nat
versicolor_sl_nat	79.8503	12.029	0.00016132	0.60202409	nat
versicolor_sl_nat	79.93	8.08	0.00041482	0.89170487	nat
versicolor_sl_nat	80.255222	13.042483	0.00014703	0.56702626	nat
versicolor_sl_nat	81.0025	7.933056	0.00020444	0.69831603	nat
versicolor_sl_nat	81.613351	21.167388	0.00012983	0.55862097	nat
versicolor_sl_nat	81.616641	22.555019	0.00012403	0.53247415	nat
versicolor_sl_nat	81.663083	16.865011	0.00014442	0.60256044	nat
versicolor_sl_nat	82	17.77	0.00014658	0.60927259	nat
versicolor_sl_nat	82.893071	18.338233	0.00019133	0.68589025	nat
versicolor_sl_nat	82.965264	22.197267	0.00012092	0.52036583	nat
versicolor_sl_nat	83.16667	21.33333	0.00010636	0.49356413	nat
versicolor_sl_nat	83.2	29.5	3.27E-05	0.18730436	nat
versicolor_sl_nat	83.218472	17.686806	0.00017866	0.66642931	nat
versicolor_sl_nat	83.945115	28.216925	9.82E-05	0.45780814	nat
versicolor_sl_nat	85.290353	27.579942	9.71E-05	0.43758883	nat
versicolor_sl_nat	85.931189	27.230181	7.31E-05	0.37687567	nat

versicolor_sl_nat	87.247939	27.10795	7.64E-05	0.38894357	nat
versicolor_sl_nat	87.802356	27.532442	0.00016703	0.57594008	nat
versicolor_sl_nat	87.849536	23.256032	0.00011399	0.50336516	nat
versicolor_sl_nat	88.363044	22.562627	0.00014129	0.57187737	nat
versicolor_sl_nat	88.36611	27.038378	0.00022995	0.72282576	nat
versicolor_sl_nat	88.5	27.75	4.10E-05	0.22819859	nat
versicolor_sl_nat	89.489687	22.05415	0.00020213	0.68750178	nat
versicolor_sl_nat	91.2764	23.8479	8.92E-05	0.43936928	nat
versicolor_sl_nat	91.796903	24.34115	0.00010162	0.47961641	nat
versicolor_sl_nat	92.25	23	0.00012297	0.54608896	nat
versicolor_sl_nat	93.164722	20.65875	0.00055586	0.95336671	nat
versicolor_sl_nat	93.524556	19.282333	0.00041489	0.91822835	nat
versicolor_sl_nat	93.565028	22.786694	0.00024735	0.68290712	nat
versicolor_sl_nat	93.646556	23.349083	0.00020464	0.68286229	nat
versicolor_sl_nat	93.826361	21.363639	0.00030629	0.80850879	nat
versicolor_sl_nat	94.152167	19.314361	0.00043134	0.92676623	nat
versicolor_sl_nat	94.166778	22.208278	0.0001131	0.51479191	nat
versicolor_sl_nat	94.552972	20.075167	0.00013924	0.58282289	nat
versicolor_sl_nat	94.616739	17.484533	0.00046241	0.92788789	nat
versicolor_sl_nat	94.750361	16.295639	0.00033893	0.86730233	nat
versicolor_sl_nat	94.864389	18.67525	0.00026841	0.80768058	nat
versicolor_sl_nat	94.978944	21.561972	0.00017932	0.64434005	nat
versicolor_sl_nat	95.216667	19.366667	0.00015403	0.60546771	nat
versicolor_sl_nat	95.249472	20.890278	0.00018467	0.67724034	nat
versicolor_sl_nat	95.287861	25.33475	0.00010301	0.47033484	nat
versicolor_sl_nat	95.875972	23.499028	0.00010508	0.49958128	nat
versicolor_sl_nat	95.954972	21.906903	0.00018558	0.66406233	nat
versicolor_sl_nat	96.083333	22	0.00017357	0.6481948	nat
versicolor_sl_nat	96.08504	18.8167	0.00014085	0.59581076	nat
versicolor_sl_nat	96.283944	18.140833	0.00025479	0.7956154	nat
versicolor_sl_nat	96.328194	25.278806	0.00014788	0.56514092	nat
versicolor_sl_nat	96.342139	23.071056	9.90E-05	0.47756703	nat
versicolor_sl_nat	96.350306	24.755722	7.11E-05	0.37060154	nat
versicolor_sl_nat	96.355944	21.097861	0.00017349	0.66160043	nat
versicolor_sl_nat	96.481351	17.335214	0.0003678	0.89160034	nat
versicolor_sl_nat	96.565861	20.6355	0.00017381	0.6603263	nat
versicolor_sl_nat	96.704278	26.4435	0.00017598	0.63957379	nat
versicolor_sl_nat	97.044889	20.781556	0.00022423	0.73375112	nat
versicolor_sl_nat	97.099306	17.444111	0.00030836	0.85490492	nat
versicolor_sl_nat	97.181806	25.313833	0.00012088	0.53597441	nat
versicolor_sl_nat	97.687361	16.34325	0.00057561	0.94953359	nat
versicolor_sl_nat	97.8	25.833333	0.00020014	0.5798591	nat
versicolor_sl_nat	98.200194	14.555083	0.00043238	0.92450567	nat
versicolor_sl_nat	98.282611	13.865444	0.00068418	0.97953348	nat
versicolor_sl_nat	98.844833	25.115611	0.00010819	0.48941996	nat
versicolor_sl_nat	98.984683	18.790375	0.00014642	0.60792624	nat
versicolor_sl_nat	99	14	0.00020547	0.72865554	nat
versicolor_sl_nat	99.390361	10.740889	0.00036003	0.78667129	nat
versicolor_sl_nat	99.6	7.55	0.00027971	0.7827389	nat
versicolor_sl_nat	99.9	13.05	0.00016277	0.6372926	nat
versicolor_sl_nat	99.9583	12.2458	0.00023861	0.76794269	nat
versicolor_sl_nat	100	15	0.00017562	0.67029651	nat

versicolor_sl_nat	100.021	9.75	0.000339	0.81278896	nat
versicolor_sl_nat	100.1095	20.447139	0.00015513	0.62441657	nat
versicolor_sl_nat	100.117	7.7833	0.00018576	0.64773836	nat
versicolor_sl_nat	100.542	13.77	0.00013325	0.56595013	nat
versicolor_sl_nat	100.57	14.52	0.00016773	0.65279697	nat
versicolor_sl_nat	100.812	13.15	0.00039902	0.87805788	nat
versicolor_sl_nat	100.906677	22.77998	0.00013288	0.564287	nat
versicolor_sl_nat	101.422	14.7125	0.00017047	0.66622047	nat
versicolor_sl_nat	101.454	12.5625	0.00042044	0.89861926	nat
versicolor_sl_nat	101.5	18	0.00011199	0.51537492	nat
versicolor_sl_nat	101.747902	18.5502	0.00012058	0.53822969	nat
versicolor_sl_nat	101.92	14.5	0.0001773	0.68000525	nat
versicolor_sl_nat	102.38333	12	0.00094919	0.98921413	nat
versicolor_sl_nat	102.62	17.97	0.00012648	0.54893634	nat
versicolor_sl_nat	103.043098	18.2369	0.00017537	0.6732524	nat
versicolor_sl_nat	103.2911	10.6845	0.00057351	0.95054847	nat
versicolor_sl_nat	104.02	13.67	0.00026335	0.80087719	nat
versicolor_sl_nat	104.04868	13.644277	0.00024493	0.78507915	nat
versicolor_sl_nat	104.051201	10.6586	0.00065294	0.95352245	nat
versicolor_sl_nat	104.433691	14.060463	0.0002438	0.78710573	nat
versicolor_sl_nat	104.82	13.87	0.00026475	0.80376912	nat
versicolor_sl_nat	104.87	15.225	0.00016429	0.64968843	nat
versicolor_sl_nat	105.175797	17.433599	0.00024785	0.77624493	nat
versicolor_sl_nat	105.5	15.3083	0.00020692	0.72963796	nat
versicolor_sl_nat	105.641389	21.454167	0.00012215	0.53086459	nat
versicolor_sl_nat	105.858	14.1083	0.00024925	0.78138927	nat
versicolor_sl_nat	106.166603	16.9718	0.00015352	0.61468738	nat
versicolor_sl_nat	106.2174	15.0664	0.00029463	0.76791228	nat
versicolor_sl_nat	106.65	22.15	9.91E-05	0.44674874	nat
versicolor_sl_nat	107	11	0.00029495	0.81845948	nat
versicolor_sl_nat	107.00455	14.20795	0.00035018	0.83710824	nat
versicolor_sl_nat	107.371674	11.643566	0.00051279	0.9248945	nat
versicolor_sl_nat	107.375	11.459167	0.00049731	0.92285765	nat
versicolor_sl_nat	107.649	22.261	7.08E-05	0.36627005	nat
versicolor_sl_nat	107.79922	21.30342	0.00015886	0.59269736	nat
versicolor_sl_nat	107.891129	10.812461	0.00049794	0.92549993	nat
versicolor_sl_nat	107.928333	15.085556	0.00026507	0.79845523	nat
versicolor_sl_nat	107.94329	21.83097	0.00010084	0.46300475	nat
versicolor_sl_nat	108.049999	12.666667	0.00016279	0.64611473	nat
versicolor_sl_nat	108.157919	16.027419	0.00030686	0.8221498	nat
versicolor_sl_nat	108.28	10.93	0.00050592	0.93087571	nat
versicolor_sl_nat	108.3508	11.4733	0.00062973	0.9491143	nat
versicolor_sl_nat	108.35468	14.40564	0.00021975	0.72939283	nat
versicolor_sl_nat	108.7	13.06666	0.00021806	0.74316506	nat
versicolor_sl_nat	108.83	19.12	0.00010494	0.49160711	nat
versicolor_sl_nat	109.56	19.4	0.00011614	0.52321258	nat
versicolor_sl_nat	109.92	19.87	9.99E-05	0.47058146	nat
versicolor_sl_nat	110.21	20.28	0.00012385	0.54285102	nat
versicolor_sl_nat	110.41667	19.25	0.00014795	0.60408882	nat
versicolor_sl_nat	112.533	23.1667	7.64E-05	0.38207369	nat
versicolor_sl_nat	113.38333	22.91667	7.46E-05	0.37582867	nat
versicolor_sl_nat	113.883642	22.222938	0.00012492	0.54136921	nat

versicolor_sl_nat_inv	-7.2716	72.3715	0.00029331	0.75073376	inv
versicolor_sl_nat_inv	-4.6121	55.4979	0.00048288	0.89956055	inv
versicolor_sl_nat_inv	-4.0575	39.660278	0.00022296	0.77807919	inv
versicolor_sl_nat_inv	1.36667	103.8	0.00024441	0.7347107	inv
versicolor_sl_nat_inv	3.083333	101.5	0.00011639	0.53946068	inv
versicolor_sl_nat_inv	3.98333	98.48333	0.00025292	0.75813953	inv
versicolor_sl_nat_inv	4.174065	73.508794	0.0005389	0.93026858	inv
versicolor_sl_nat_inv	4.95	114.95	0.00018303	0.6126026	inv
versicolor_sl_nat_inv	4.97	114.9	0.0001769	0.6218091	inv
versicolor_sl_nat_inv	5.374622	100.249139	0.00026168	0.78337911	inv
versicolor_sl_nat_inv	6.931944	79.847778	0.00040542	0.88053477	nat
versicolor_sl_nat_inv	7.55	99.6	0.00020865	0.74664455	nat
versicolor_sl_nat_inv	7.7833	100.117	0.00024069	0.78727148	nat
versicolor_sl_nat_inv	7.933056	81.0025	0.00022017	0.76609562	nat
versicolor_sl_nat_inv	8.08	79.93	0.00031125	0.85696054	nat
versicolor_sl_nat_inv	8.151024	77.558796	NA	NA	nat
versicolor_sl_nat_inv	8.151478	77.5547	0.00039779	0.91289758	nat
versicolor_sl_nat_inv	8.485497	76.949239	0.00037843	0.90494463	nat
versicolor_sl_nat_inv	8.624487	77.136464	0.00031753	0.86598666	nat
versicolor_sl_nat_inv	8.6756595	77.1484822	0.00035436	0.88874571	nat
versicolor_sl_nat_inv	8.71068	77.370315	0.0001747	0.69326207	nat
versicolor_sl_nat_inv	8.921367	77.268805	0.00016378	0.67532436	nat
versicolor_sl_nat_inv	9.0778	79.7028	0.00038558	0.90090016	nat
versicolor_sl_nat_inv	9.354447	78.8367	0.000162	0.66975471	nat
versicolor_sl_nat_inv	9.406926	77.067806	0.00025736	0.81808966	nat
versicolor_sl_nat_inv	9.75	100.021	0.00043306	0.91644546	nat
versicolor_sl_nat_inv	9.833333	77.833333	0.00011572	0.54210081	nat
versicolor_sl_nat_inv	9.971362	77.232834	0.00029265	0.83595402	nat
versicolor_sl_nat_inv	10.114067	76.701717	0.00031603	0.85185368	nat
versicolor_sl_nat_inv	10.303516	76.592757	0.00052345	0.94160778	nat
versicolor_sl_nat_inv	10.6586	104.051201	0.00039666	0.90702871	nat
versicolor_sl_nat_inv	10.6845	103.2911	0.00054357	0.96906775	nat
versicolor_sl_nat_inv	10.740889	99.390361	0.00022184	0.76343193	nat
versicolor_sl_nat_inv	10.812461	107.891129	0.00029033	0.85574099	nat
versicolor_sl_nat_inv	10.915256	76.516911	0.000365	0.88548601	nat
versicolor_sl_nat_inv	10.93	108.28	0.00032079	0.87122131	nat
versicolor_sl_nat_inv	11	107	0.00021474	0.77122873	nat
versicolor_sl_nat_inv	11.248017	75.780403	0.00053673	0.94330409	nat
versicolor_sl_nat_inv	11.459167	107.375	0.00027508	0.82850931	nat
versicolor_sl_nat_inv	11.4733	108.3508	0.00028526	0.83680361	nat
versicolor_sl_nat_inv	11.558786	76.646118	0.00024319	0.79745326	nat
versicolor_sl_nat_inv	11.590192	76.099921	0.00136074	0.99849602	nat
versicolor_sl_nat_inv	11.643566	107.371674	0.00030158	0.85798577	nat
versicolor_sl_nat_inv	11.787336	76.018432	0.00086213	0.99016519	nat
versicolor_sl_nat_inv	11.94163	75.956851	0.00122619	0.98981021	nat
versicolor_sl_nat_inv	12	102.38333	0.00058691	0.97585046	nat
versicolor_sl_nat_inv	12.029	79.8503	0.00017677	0.69128601	nat
versicolor_sl_nat_inv	12.2458	99.9583	0.00021111	0.76870907	nat
versicolor_sl_nat_inv	12.498362	76.681371	0.00016298	0.67358037	nat
versicolor_sl_nat_inv	12.499482	76.699433	NA	NA	nat
versicolor_sl_nat_inv	12.5	92.75	0.00052245	0.95918	inv
versicolor_sl_nat_inv	12.5625	101.454	0.00030027	0.8494247	nat

versicolor_sl_nat_inv	12.666667	108.049999	0.00015684	0.66033527	nat
versicolor_sl_nat_inv	12.8981	77.781	0.00013226	0.59898033	nat
versicolor_sl_nat_inv	13.042483	80.255222	0.00017541	0.68621808	nat
versicolor_sl_nat_inv	13.05	99.9	0.00017348	0.69905294	nat
versicolor_sl_nat_inv	13.055808	75.425253	0.00068086	0.96492592	nat
versicolor_sl_nat_inv	13.06666	108.7	0.00016571	0.68262029	nat
versicolor_sl_nat_inv	13.15	100.812	0.00025724	0.82016803	nat
versicolor_sl_nat_inv	13.261725	75.705144	0.00066968	0.95891419	nat
versicolor_sl_nat_inv	13.644277	104.04868	0.00020094	0.75260688	nat
versicolor_sl_nat_inv	13.67	104.02	0.00021048	0.767498	nat
versicolor_sl_nat_inv	13.77	100.542	0.00015482	0.65459458	nat
versicolor_sl_nat_inv	13.865444	98.282611	0.00068576	0.98272728	nat
versicolor_sl_nat_inv	13.87	104.82	0.0002211	0.78139137	nat
versicolor_sl_nat_inv	14	99	0.00016254	0.67594392	nat
versicolor_sl_nat_inv	14.060463	104.433691	0.00022017	0.78460746	nat
versicolor_sl_nat_inv	14.1083	105.858	0.00025329	0.82599893	nat
versicolor_sl_nat_inv	14.20795	107.00455	0.00020257	0.74151682	nat
versicolor_sl_nat_inv	14.40564	108.35468	0.00014912	0.62787492	nat
versicolor_sl_nat_inv	14.432159	76.57886	0.0001222	0.56601862	nat
versicolor_sl_nat_inv	14.4431902	78.8166321	9.91E-05	0.49285952	nat
versicolor_sl_nat_inv	14.485833	121.016389	0.00021016	0.76072449	inv
versicolor_sl_nat_inv	14.5	101.92	0.000148	0.64439638	nat
versicolor_sl_nat_inv	14.52	100.57	0.00015509	0.6589313	nat
versicolor_sl_nat_inv	14.555083	98.200194	0.00045657	0.94590665	nat
versicolor_sl_nat_inv	14.7125	101.422	0.00014167	0.62528636	nat
versicolor_sl_nat_inv	14.906596	74.343808	0.00085835	0.98873604	nat
versicolor_sl_nat_inv	15	100	0.00015767	0.6624056	nat
versicolor_sl_nat_inv	15.0664	106.2174	0.0001914	0.71500206	nat
versicolor_sl_nat_inv	15.085556	107.928333	0.00014838	0.6325203	nat
versicolor_sl_nat_inv	15.194521	74.50872	0.00094874	0.99221021	nat
versicolor_sl_nat_inv	15.225	104.87	0.00016056	0.67284856	nat
versicolor_sl_nat_inv	15.3083	105.5	0.00021418	0.77409873	nat
versicolor_sl_nat_inv	15.375353	74.227216	0.00075903	0.98394063	nat
versicolor_sl_nat_inv	15.387411	74.381949	0.001055	0.97326168	nat
versicolor_sl_nat_inv	15.470833	73.843056	0.00084068	0.98617011	nat
versicolor_sl_nat_inv	16.027419	108.157919	0.00018183	0.70670722	nat
versicolor_sl_nat_inv	16.114078	74.175043	0.00078069	0.98363875	nat
versicolor_sl_nat_inv	16.240033	74.666875	0.00016155	0.66955347	nat
versicolor_sl_nat_inv	16.295639	94.750361	0.00036819	0.91213061	nat
versicolor_sl_nat_inv	16.34325	97.687361	0.00075105	0.98142155	nat
versicolor_sl_nat_inv	16.865011	81.663083	0.00012213	0.5739555	nat
versicolor_sl_nat_inv	16.9718	106.166603	0.0001179	0.56208455	nat
versicolor_sl_nat_inv	17.108833	54.5515	0.00010177	0.4908943	inv
versicolor_sl_nat_inv	17.116997	73.571024	0.00034118	0.844678	nat
versicolor_sl_nat_inv	17.335214	96.481351	0.00038513	0.91746047	nat
versicolor_sl_nat_inv	17.353979	73.802882	0.00043692	0.93242097	nat
versicolor_sl_nat_inv	17.433599	105.175797	0.00019066	0.72384891	nat
versicolor_sl_nat_inv	17.444111	97.099306	0.00033358	0.89163362	nat
versicolor_sl_nat_inv	17.484533	94.616739	0.00034218	0.89687587	nat
versicolor_sl_nat_inv	17.487176	73.242976	0.00078381	0.98133467	nat
versicolor_sl_nat_inv	17.487815	73.283318	0.00073559	0.92693189	nat
versicolor_sl_nat_inv	17.494956	73.184751	0.00076817	0.9836958	nat

versicolor_sl_nat_inv	17.588824	73.838054	0.00049606	0.94199688	nat
versicolor_sl_nat_inv	17.686806	83.218472	0.00015354	0.65438068	nat
versicolor_sl_nat_inv	17.77	82	0.00012947	0.59545715	nat
versicolor_sl_nat_inv	17.97	102.62	0.00012319	0.57555912	nat
versicolor_sl_nat_inv	18	101.5	0.00010153	0.50455682	nat
versicolor_sl_nat_inv	18.140833	96.283944	0.00023565	0.80102839	nat
versicolor_sl_nat_inv	18.2369	103.043098	0.00014388	0.62418013	nat
versicolor_sl_nat_inv	18.338233	82.893071	0.00013514	0.60308462	nat
versicolor_sl_nat_inv	18.399982	74.124075	9.41E-05	0.47821734	nat
versicolor_sl_nat_inv	18.48759	76.593296	7.64E-05	0.4147279	nat
versicolor_sl_nat_inv	18.5502	101.747902	0.00011789	0.56070698	nat
versicolor_sl_nat_inv	18.67525	94.864389	0.00023352	0.80081089	nat
versicolor_sl_nat_inv	18.790375	98.984683	0.00011928	0.56559474	nat
versicolor_sl_nat_inv	18.8167	96.08504	0.000113	0.54661077	nat
versicolor_sl_nat_inv	19.054763	72.833302	0.00034608	0.88574016	nat
versicolor_sl_nat_inv	19.094677	73.553701	0.00094475	0.98320015	nat
versicolor_sl_nat_inv	19.12	108.83	0.00010201	0.50950459	nat
versicolor_sl_nat_inv	19.122083	72.858944	0.00033269	0.87423102	nat
versicolor_sl_nat_inv	19.220752	72.876517	0.00061289	0.97274996	nat
versicolor_sl_nat_inv	19.25	110.41667	0.00010365	0.51336333	nat
versicolor_sl_nat_inv	19.282333	93.524556	0.00031377	0.88117034	nat
versicolor_sl_nat_inv	19.314361	94.152167	0.00031041	0.87311256	nat
versicolor_sl_nat_inv	19.366667	95.216667	0.00011915	0.55381477	nat
versicolor_sl_nat_inv	19.4	109.56	0.00010627	0.52869271	nat
versicolor_sl_nat_inv	19.87	109.92	8.87E-05	0.46476058	nat
versicolor_sl_nat_inv	19.954399	75.220469	7.31E-05	0.40309735	nat
versicolor_sl_nat_inv	19.969659	73.671666	0.0001524	0.65596451	nat
versicolor_sl_nat_inv	20	77	6.68E-05	0.37694437	nat
versicolor_sl_nat_inv	20.075167	94.552972	0.00011094	0.53814815	nat
versicolor_sl_nat_inv	20.28	110.21	9.66E-05	0.48837969	nat
versicolor_sl_nat_inv	20.447139	100.1095	0.00012508	0.58605268	nat
versicolor_sl_nat_inv	20.592877	72.9488	0.00023778	0.79690431	nat
versicolor_sl_nat_inv	20.593694	78.962889	7.18E-05	0.39678038	nat
versicolor_sl_nat_inv	20.6355	96.565861	0.00013802	0.61143793	nat
versicolor_sl_nat_inv	20.65875	93.164722	0.00042553	0.9265997	nat
versicolor_sl_nat_inv	20.7131441	76.6310301	6.66E-05	0.37096896	nat
versicolor_sl_nat_inv	20.781556	97.044889	0.00015854	0.65483455	nat
versicolor_sl_nat_inv	20.890278	95.249472	0.00013303	0.59943922	nat
versicolor_sl_nat_inv	21.097861	96.355944	0.00013849	0.61987397	nat
versicolor_sl_nat_inv	21.167388	81.613351	0.00010665	0.52242442	nat
versicolor_sl_nat_inv	21.30342	107.79922	9.78E-05	0.48763297	nat
versicolor_sl_nat_inv	21.33333	83.16667	8.46E-05	0.44818147	nat
versicolor_sl_nat_inv	21.363639	93.826361	0.0002256	0.76196476	nat
versicolor_sl_nat_inv	21.454167	105.641389	9.62E-05	0.48916177	nat
versicolor_sl_nat_inv	21.561972	94.978944	0.00011679	0.54716655	nat
versicolor_sl_nat_inv	21.694081	79.435296	6.40E-05	0.35922691	nat
versicolor_sl_nat_inv	21.83097	107.94329	8.15E-05	0.41789515	nat
versicolor_sl_nat_inv	21.906903	95.954972	0.00014152	0.61941473	nat
versicolor_sl_nat_inv	22	96.083333	0.00012508	0.57281387	nat
versicolor_sl_nat_inv	22.05415	89.489687	0.0001581	0.65941865	nat
versicolor_sl_nat_inv	22.15	106.65	7.29E-05	0.4012322	nat
versicolor_sl_nat_inv	22.197267	82.965264	9.52E-05	0.48471498	nat

versicolor_sl_nat_inv	22.208278	94.166778	0.0001045	0.51709544	nat
versicolor_sl_nat_inv	22.222938	113.883642	9.53E-05	0.48488307	nat
versicolor_sl_nat_inv	22.261	107.649	5.26E-05	0.30845804	nat
versicolor_sl_nat_inv	22.555019	81.616641	0.00010705	0.52692161	nat
versicolor_sl_nat_inv	22.562627	88.363044	0.0001226	0.56814228	nat
versicolor_sl_nat_inv	22.77998	100.906677	0.00010085	0.50090406	nat
versicolor_sl_nat_inv	22.786694	93.565028	0.00014652	0.60490006	nat
versicolor_sl_nat_inv	22.91667	113.38333	6.22E-05	0.35180464	nat
versicolor_sl_nat_inv	23	92.25	0.00012296	0.57121056	nat
versicolor_sl_nat_inv	23.071056	96.342139	9.34E-05	0.4828084	nat
versicolor_sl_nat_inv	23.1667	112.533	5.69E-05	0.32529471	nat
versicolor_sl_nat_inv	23.256032	87.849536	0.00010203	0.50925734	nat
versicolor_sl_nat_inv	23.301978	73.016907	6.76E-05	0.37803905	nat
versicolor_sl_nat_inv	23.349083	93.646556	0.00016065	0.65013056	nat
versicolor_sl_nat_inv	23.403723	69.4662	7.65E-05	0.40438135	nat
versicolor_sl_nat_inv	23.499028	95.875972	9.43E-05	0.48433968	nat
versicolor_sl_nat_inv	23.8479	91.2764	9.97E-05	0.49999337	nat
versicolor_sl_nat_inv	24.34115	91.796903	0.00010271	0.50895409	nat
versicolor_sl_nat_inv	24.349167	70.754333	7.03E-05	0.37974278	nat
versicolor_sl_nat_inv	24.5925	72.715556	0.00024324	0.77906074	nat
versicolor_sl_nat_inv	24.7041667	69.7878333	NA	NA	nat
versicolor_sl_nat_inv	24.704167	69.787833	6.10E-05	0.34105804	nat
versicolor_sl_nat_inv	24.755722	96.350306	7.57E-05	0.41640821	nat
versicolor_sl_nat_inv	24.892908	67.203172	8.98E-05	0.39691899	nat
versicolor_sl_nat_inv	25.115611	98.844833	8.28E-05	0.43615187	nat
versicolor_sl_nat_inv	25.249667	69.722333	5.67E-05	0.31494625	nat
versicolor_sl_nat_inv	25.278806	96.328194	0.0001069	0.51473143	nat
versicolor_sl_nat_inv	25.313833	97.181806	0.00010044	0.49817497	nat
versicolor_sl_nat_inv	25.33475	95.287861	0.00010685	0.51060189	nat
versicolor_sl_nat_inv	25.833333	97.8	0.00010491	0.50711464	nat
versicolor_sl_nat_inv	26.4435	96.704278	0.0001369	0.59357348	nat
versicolor_sl_nat_inv	27.038378	88.36611	0.00017256	0.66461399	nat
versicolor_sl_nat_inv	27.10795	87.247939	7.62E-05	0.41124361	nat
versicolor_sl_nat_inv	27.230181	85.931189	6.86E-05	0.38390188	nat
versicolor_sl_nat_inv	27.462383	-80.497217	5.99E-05	0.33237339	inv
versicolor_sl_nat_inv	27.532442	87.802356	0.00011462	0.52038743	nat
versicolor_sl_nat_inv	27.579942	85.290353	9.90E-05	0.46518498	nat
versicolor_sl_nat_inv	27.7035	66.924167	4.61E-05	0.25979745	nat
versicolor_sl_nat_inv	27.75	88.5	4.63E-05	0.26749279	nat
versicolor_sl_nat_inv	28.216925	83.945115	0.00011015	0.51708593	nat
versicolor_sl_nat_inv	28.478488	65.643553	2.97E-05	0.18600588	nat
versicolor_sl_nat_inv	29.5	83.2	3.79E-05	0.22861981	nat
versicolor_sl_nat_inv	30	70	6.44E-05	0.35509779	nat
versicolor_sl_nat_inv	30.360993	76.797819	5.81E-05	0.32720966	nat
versicolor_sl_nat_inv	30.898562	76.965868	8.23E-05	0.43412795	nat
versicolor_sl_nat_inv	32.76047	73.07362	5.30E-05	0.29666015	nat
versicolor_sl_nat_inv	32.850492	73.819425	3.85E-05	0.23340551	nat
versicolor_sl_nat_inv	32.88789	71.69962	3.72E-05	0.22905307	nat
versicolor_sl_nat_inv	33.752158	72.809003	3.14E-05	0.19348848	nat
versicolor_sl_nat_inv	34.129764	71.083258	5.32E-05	0.27483481	nat
versicolor_sl_nat_inv	34.516319	69.970111	7.85E-05	0.29250639	nat
versicolor_sl_nat_inv	34.5825	72.64083	3.07E-05	0.19041243	nat

versicolor_sl_nat_inv	34.625	72.6502	3.10E-05	0.18637209	nat
versicolor	6.931944	79.847778	0.00085873	0.9562798	nat
versicolor	7.933056	81.0025	0.00033992	0.80529	nat
versicolor	8.08	79.93	0.00058474	0.93340955	nat
versicolor	8.151024	77.558796	NA	NA	nat
versicolor	8.151478	77.5547	0.00031622	0.79201323	nat
versicolor	8.485497	76.949239	0.00047891	0.89065048	nat
versicolor	8.624487	77.136464	0.00049221	0.90276195	nat
versicolor	8.6756595	77.1484822	0.0005261	0.90103946	nat
versicolor	8.71068	77.370315	0.0002367	0.64788346	nat
versicolor	8.921367	77.268805	0.00028726	0.7324996	nat
versicolor	9.0778	79.7028	0.00046546	0.88259345	nat
versicolor	9.354447	78.8367	0.00011382	0.44054912	nat
versicolor	9.406926	77.067806	0.00051814	0.89527404	nat
versicolor	9.833333	77.833333	9.20E-05	0.37920179	nat
versicolor	9.971362	77.232834	0.00054691	0.86878179	nat
versicolor	10.114067	76.701717	0.00039262	0.77375346	nat
versicolor	10.303516	76.592757	0.00042195	0.83933432	nat
versicolor	10.915256	76.516911	0.00030931	0.75748284	nat
versicolor	11.248017	75.780403	0.00038668	0.81346952	nat
versicolor	11.558786	76.646118	0.00022876	0.66985675	nat
versicolor	11.590192	76.099921	0.00049043	0.85419916	nat
versicolor	11.787336	76.018432	0.00034985	0.78483921	nat
versicolor	12.029	79.8503	0.0001118	0.44700625	nat
versicolor	12.498362	76.681371	0.00017847	0.59076904	nat
versicolor	12.499482	76.699433	NA	NA	nat
versicolor	13.042483	80.255222	0.00010106	0.40915424	nat
versicolor	14.4431902	78.8166321	5.22E-05	0.24893687	nat
irawadi	7.55	99.6	0.00012001	0.52848659	nat
irawadi	7.7833	100.117	0.00012994	0.56939845	nat
irawadi	9.75	100.021	0.00011691	0.55131684	nat
irawadi	10.6586	104.051201	0.00044405	0.90694954	nat
irawadi	10.6845	103.2911	0.00051404	0.95689252	nat
irawadi	10.740889	99.390361	0.00021254	0.74555327	nat
irawadi	10.812461	107.891129	0.00026037	0.84393849	nat
irawadi	10.93	108.28	0.00024083	0.82823355	nat
irawadi	11	107	0.00028141	0.87799012	nat
irawadi	11.459167	107.375	0.00027927	0.8648509	nat
irawadi	11.4733	108.3508	0.00024823	0.82086611	nat
irawadi	11.643566	107.371674	0.00030188	0.87493107	nat
irawadi	12	102.38333	0.00031369	0.89962694	nat
irawadi	12.2458	99.9583	0.00020032	0.77401598	nat
irawadi	12.5625	101.454	0.00023655	0.83474314	nat
irawadi	12.666667	108.049999	0.00016177	0.71035221	nat
irawadi	13.05	99.9	0.0001555	0.69747713	nat
irawadi	13.06666	108.7	0.00014825	0.68451807	nat
irawadi	13.15	100.812	0.00027235	0.87110196	nat
irawadi	13.644277	104.04868	0.00013561	0.65043302	nat
irawadi	13.67	104.02	0.00013966	0.65852094	nat
irawadi	13.77	100.542	0.00022739	0.82320991	nat
irawadi	13.865444	98.282611	0.00043902	0.93006296	nat
irawadi	13.87	104.82	0.00015077	0.69067874	nat

irawadi	14	99	0.00011659	0.60132289	nat
irawadi	14.060463	104.433691	0.0001464	0.6778504	nat
irawadi	14.1083	105.858	0.00017158	0.73658583	nat
irawadi	14.20795	107.00455	0.00015163	0.68032777	nat
irawadi	14.40564	108.35468	0.00014809	0.65979346	nat
irawadi	14.5	101.92	0.00011052	0.5755126	nat
irawadi	14.52	100.57	0.00015184	0.68891655	nat
irawadi	14.555083	98.200194	0.00034714	0.90349334	nat
irawadi	14.7125	101.422	0.00010262	0.5479082	nat
irawadi	15	100	0.00014388	0.6662556	nat
irawadi	15.0664	106.2174	0.00011273	0.57298415	nat
irawadi	15.085556	107.928333	0.00013729	0.6383117	nat
irawadi	15.225	104.87	0.00013585	0.6514917	nat
irawadi	15.3083	105.5	0.00016315	0.71417893	nat
irawadi	16.027419	108.157919	0.00011216	0.55357807	nat
irawadi	16.295639	94.750361	0.0002659	0.8531427	nat
irawadi	16.34325	97.687361	0.00052204	0.93829918	nat
irawadi	16.9718	106.166603	0.00016065	0.71177066	nat
irawadi	17.335214	96.481351	0.00023772	0.8209267	nat
irawadi	17.433599	105.175797	0.00016751	0.71178366	nat
irawadi	17.444111	97.099306	0.00020259	0.76719606	nat
irawadi	17.484533	94.616739	0.00027979	0.86456986	nat
irawadi	17.97	102.62	0.00013783	0.66063729	nat
irawadi	18	101.5	0.00010118	0.55313781	nat
irawadi	18.140833	96.283944	0.00013944	0.65476055	nat
irawadi	18.2369	103.043098	0.00013771	0.65075301	nat
irawadi	18.5502	101.747902	0.00010104	0.54888436	nat
irawadi	18.67525	94.864389	0.00012639	0.6202974	nat
irawadi	18.790375	98.984683	0.00010147	0.55239905	nat
irawadi	18.8167	96.08504	9.89E-05	0.54134227	nat
irawadi	19.12	108.83	0.00012371	0.61888934	nat
irawadi	19.25	110.41667	0.00018763	0.75444512	nat
irawadi	19.282333	93.524556	0.00024265	0.83115405	nat
irawadi	19.314361	94.152167	0.00021885	0.80082401	nat
irawadi	19.366667	95.216667	8.11E-05	0.4683996	nat
irawadi	19.4	109.56	0.00015891	0.70671033	nat
irawadi	19.87	109.92	0.00015873	0.69587236	nat
irawadi	20.075167	94.552972	7.22E-05	0.43323619	nat
irawadi	20.28	110.21	0.00017914	0.73434792	nat
irawadi	20.447139	100.1095	9.71E-05	0.5317414	nat
irawadi	20.6355	96.565861	7.77E-05	0.45176069	nat
irawadi	20.65875	93.164722	0.00027674	0.83848049	nat
irawadi	20.781556	97.044889	8.68E-05	0.48290927	nat
irawadi	20.890278	95.249472	7.47E-05	0.44246431	nat
irawadi	21.097861	96.355944	0.00010846	0.57191789	nat
irawadi	21.30342	107.79922	0.00019007	0.73952284	nat
irawadi	21.363639	93.826361	9.63E-05	0.50919965	nat
irawadi	21.454167	105.641389	8.11E-05	0.47419551	nat
irawadi	21.561972	94.978944	6.45E-05	0.39335683	nat
irawadi	21.83097	107.94329	8.25E-05	0.46258218	nat
irawadi	21.906903	95.954972	0.00010548	0.55705241	nat
irawadi	22	96.083333	0.00010911	0.56888736	nat

irawadi	22.15	106.65	6.16E-05	0.38043662	nat
irawadi	22.208278	94.166778	7.89E-05	0.46501699	nat
irawadi	22.222938	113.883642	0.00013541	0.63959517	nat
irawadi	22.261	107.649	6.64E-05	0.39433111	nat
irawadi	22.77998	100.906677	8.72E-05	0.49395166	nat
irawadi	22.786694	93.565028	8.34E-05	0.46474789	nat
irawadi	22.91667	113.38333	8.83E-05	0.48317828	nat
irawadi	23	92.25	0.00011231	0.58611108	nat
irawadi	23.071056	96.342139	7.95E-05	0.47069448	nat
irawadi	23.1667	112.533	6.98E-05	0.41605371	nat
irawadi	23.349083	93.646556	8.36E-05	0.4754306	nat
irawadi	23.499028	95.875972	7.38E-05	0.43897918	nat
irawadi	23.8479	91.2764	7.82E-05	0.45877393	nat
irawadi	24.34115	91.796903	7.12E-05	0.42905126	nat
irawadi	24.755722	96.350306	5.75E-05	0.36336654	nat
irawadi	25.115611	98.844833	7.24E-05	0.44103209	nat
irawadi	25.278806	96.328194	8.69E-05	0.49593759	nat
irawadi	25.313833	97.181806	7.11E-05	0.43220402	nat
irawadi	25.33475	95.287861	6.70E-05	0.40656361	nat
irawadi	25.833333	97.8	6.44E-05	0.39475551	nat
irawadi	26.4435	96.704278	0.00010019	0.53698695	nat
vultuosus	11.94163	75.956851	0.00116654	0.92157867	nat
vultuosus	12.8981	77.781	0.0001936	0.60393277	nat
vultuosus	13.055808	75.425253	0.00123078	0.98954305	nat
vultuosus	13.261725	75.705144	0.00128041	0.96346608	nat
vultuosus	14.432159	76.57886	0.00020185	0.61500036	nat
vultuosus	14.906596	74.343808	0.00138118	0.9937198	nat
vultuosus	15.194521	74.50872	0.00154336	0.99814844	nat
vultuosus	15.375353	74.227216	0.0012996	0.99439056	nat
vultuosus	15.387411	74.381949	0.00156026	0.99763452	nat
vultuosus	15.470833	73.843056	0.00132063	0.98782414	nat
vultuosus	16.114078	74.175043	0.00117207	0.99273209	nat
vultuosus	16.240033	74.666875	0.00029034	0.74819879	nat
vultuosus	16.865011	81.663083	0.00010977	0.42307414	nat
vultuosus	17.116997	73.571024	0.00086281	0.96745034	nat
vultuosus	17.353979	73.802882	0.00097858	0.98016663	nat
vultuosus	17.487176	73.242976	0.00118456	0.98233122	nat
vultuosus	17.487815	73.283318	0.00104629	0.98502139	nat
vultuosus	17.494956	73.184751	0.00127606	0.98252133	nat
vultuosus	17.588824	73.838054	0.00134693	0.99144336	nat
vultuosus	17.686806	83.218472	0.0001634	0.52424036	nat
vultuosus	17.77	82	0.00022134	0.65036554	nat
vultuosus	18.338233	82.893071	0.00021694	0.63970137	nat
vultuosus	18.399982	74.124075	0.0001321	0.46862947	nat
vultuosus	18.48759	76.593296	0.00010159	0.39492705	nat
vultuosus	19.054763	72.833302	0.00057817	0.90483557	nat
vultuosus	19.094677	73.553701	0.00124614	0.99050883	nat
vultuosus	19.122083	72.858944	0.00056838	0.90268742	nat
vultuosus	19.220752	72.876517	0.0007846	0.95904431	nat
vultuosus	19.954399	75.220469	9.21E-05	0.36322336	nat
vultuosus	19.969659	73.671666	0.00032552	0.77081294	nat
vultuosus	20	77	8.42E-05	0.34868756	nat

vultuosus	20.592877	72.9488	0.0004036	0.81564944	nat
vultuosus	20.593694	78.962889	6.67E-05	0.28375248	nat
vultuosus	20.7131441	76.6310301	5.63E-05	0.2525773	nat
vultuosus	21.167388	81.613351	0.0001084	0.4047589	nat
vultuosus	21.33333	83.16667	8.00E-05	0.33630836	nat
vultuosus	21.694081	79.435296	6.25E-05	0.26947749	nat
vultuosus	22.05415	89.489687	0.00012215	0.44061936	nat
vultuosus	22.197267	82.965264	0.00010016	0.39349279	nat
vultuosus	22.555019	81.616641	0.00013663	0.47390483	nat
vultuosus	22.562627	88.363044	9.08E-05	0.35203058	nat
vultuosus	23.256032	87.849536	6.83E-05	0.29598254	nat
vultuosus	23.301978	73.016907	7.33E-05	0.31073729	nat
vultuosus	23.403723	69.4662	6.22E-05	0.25924504	nat
vultuosus	24.349167	70.754333	4.28E-05	0.19745089	nat
vultuosus	24.5925	72.715556	0.00058586	0.90983387	nat
vultuosus	27.038378	88.36611	0.00027778	0.6787506	nat
vultuosus	27.10795	87.247939	8.30E-05	0.33694836	nat
vultuosus	27.230181	85.931189	7.39E-05	0.31081867	nat
vultuosus	27.532442	87.802356	0.00014701	0.50569124	nat
vultuosus	27.579942	85.290353	0.0001681	0.53778201	nat
vultuosus	27.75	88.5	0.00013611	0.45896028	nat
vultuosus	28.216925	83.945115	0.00013424	0.43920656	nat
vultuosus	29.5	83.2	0.0001026	0.38151008	nat
vultuosus	30.360993	76.797819	1.76E-05	0.09117576	nat
vultuosus	30.898562	76.965868	6.85E-05	0.29461569	nat
farooqi	24.7041667	69.7878333	NA	NA	nat
farooqi	24.704167	69.787833	0.00010532	0.63700294	nat
farooqi	24.892908	67.203172	0.00010487	0.61370474	nat
farooqi	25.249667	69.722333	0.00010445	0.62395916	nat
farooqi	27.7035	66.924167	0.00010998	0.63892022	nat
farooqi	28.478488	65.643553	9.01E-05	0.57372287	nat
farooqi	30	70	0.00010711	0.6223562	nat
farooqi	32.76047	73.07362	0.00011278	0.64748807	nat
farooqi	32.850492	73.819425	0.00014981	0.72510287	nat
farooqi	32.88789	71.69962	0.00012247	0.6703349	nat
farooqi	33.752158	72.809003	0.00017799	0.76501028	nat
farooqi	34.129764	71.083258	9.08E-05	0.56724979	nat
farooqi	34.516319	69.970111	9.08E-05	0.57638639	nat
farooqi	34.5825	72.64083	0.00025381	0.80110346	nat
farooqi	34.625	72.6502	0.00025925	0.81261672	nat

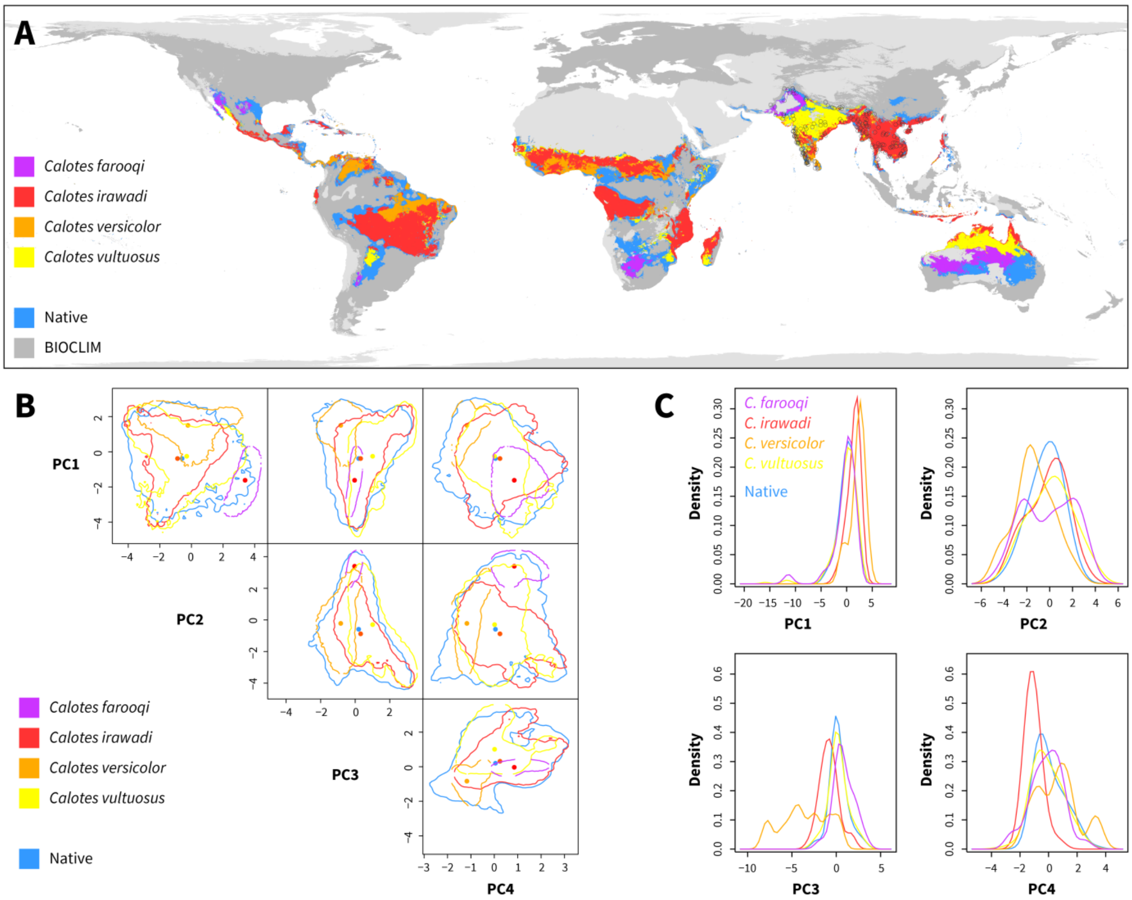

Figure S2.1. Realized niche of *Calotes versicolor* s.str., *Calotes irawadi*, *Calotes vultuosus* and *Calotes farooqi* in (A) geographic space and (B) in environmental space. Potential predicted distribution of the four subtaxa in respect to *C. versicolor* s.l. across the globe according to hypervolume models. The hypervolume models are nested in a bioclim model. (C) Density distributions of the four principal component axes used for hypervolume construction.

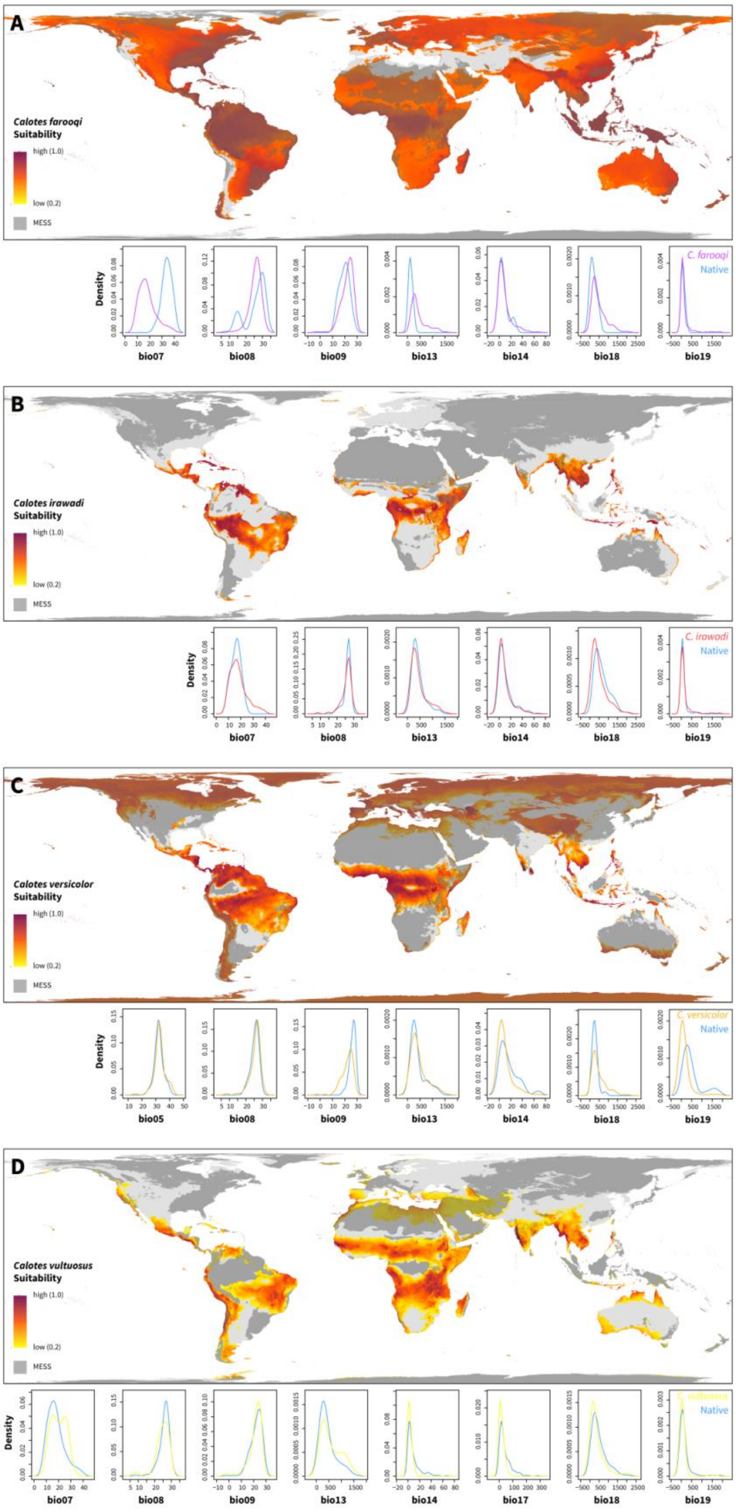

Figure S2.2. Invasive risk assessment: Potential predicted distribution of (A) *C. farooqi*, (B) *C. irawadi*, (C) *C. versicolor* s.str. and (D) C. *vultuosus* across the globe according to Maxent models. Multivariate Environmental Similarity Surfaces (MESS) are provided, where the prediction should be treated carefully. Density distributions of the environmental predictors used for model construction.

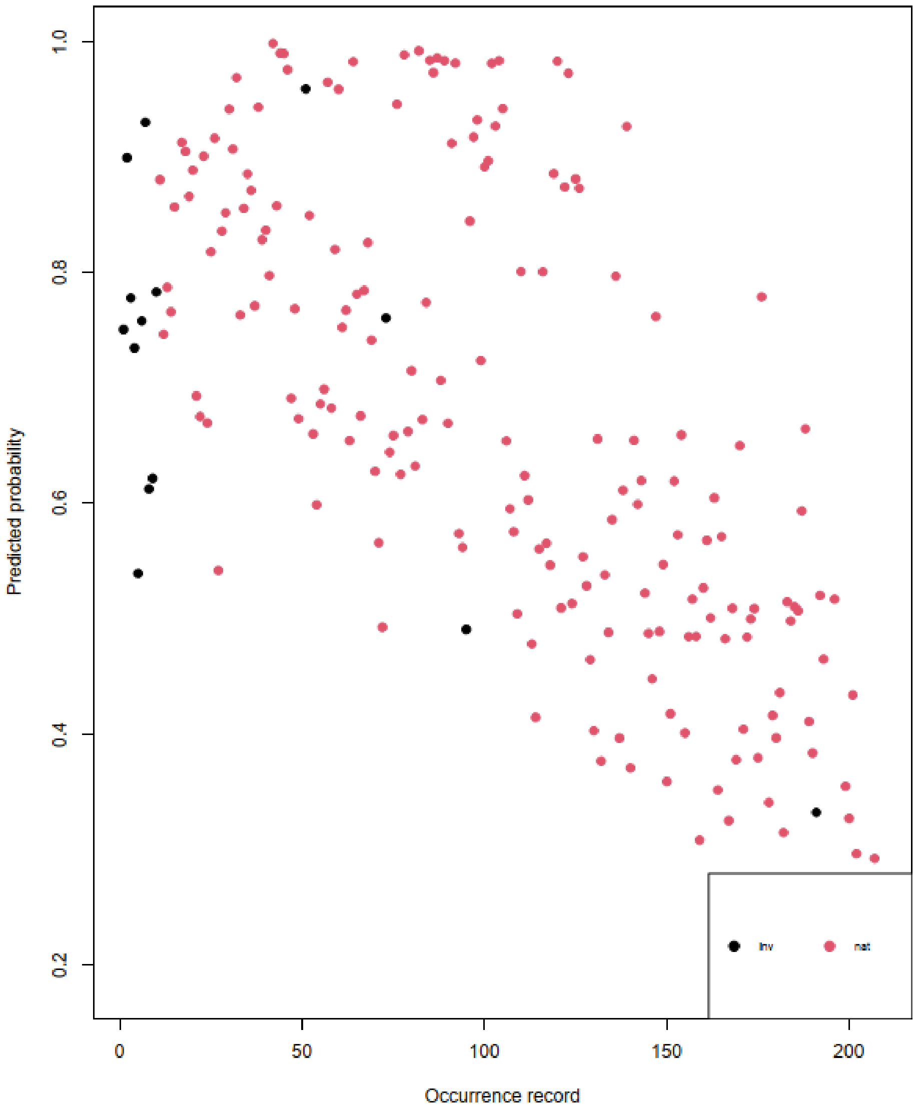

Figure S2.3. Maxent sample predictions: Cloglog suitability scores for $\mathrm{SDM}_{\mathrm{Maxent\_nat\_inv}}$.

Appendix 6 – Microclimatic growth rates of Bsal

Microclimatic growth rates of *Batrachochytrium salamandrivorans* under current and future climates: A very high spatial resolution SDM for Bsal and *Salamandra salamandra* (LINNAEUS, 1758) within forest habitats of the European hotspot area

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Abstract. Nowadays, chytridiomycosis is one of the greatest threats to the diversity of amphibians worldwide. Caused by both chytrid fungus, *Batrachochytrium dendrobatidis* (Bd) and *Batrachochytrium salamandrivorans* (Bsal), it plays a decisive role in species declines. Bsal is particularly harmful to the European fire salamander (*Salamandra salamandra),* causing ulcerations, anorexia and ataxia, which ultimately lead to death. While most studies have focused on the geographic expansion of the pathogen in Europe, there is little high-resolution information available. In this study a three-step approach was chosen: We (I) used a mechanistic distribution model to project the microclimatic growth rate of Bsal within forest habitats of its current invasive range on a spatially very high resolution (25 m). We (II) used a correlative distribution model to predict the potential distribution of *S. salamandra* and (III) applied n-dimensional hypervolumes to quantify the realized microclimatic niches of both species and examine their overlaps. Future trends were estimated based on comparisons among three climate scenarios, the current microclimatic conditions, and two climate change scenarios assuming an increase in the global annual mean temperature of +2°C and a +4°C. We demonstrated that Bsal finds suitable growth conditions everywhere within our study area, thus putting *S. salamandra* at high risk. Further, our future projections suggest that the months providing optimal growth conditions for Bsal will likely shift from summer to winter months and that the thermal conditions get on average less suitable for Bsal, whereas the potential distribution of *S. salamandra* may increase under both global warming scenarios.

Key words. Chytridiomycosis, chytrid fungus, fire salamander, high-resolution forest microclimate, climate change, species distribution model, mechanistic model

Introduction

Amphibians represent the global decline of species like no other group of vertebrates, with 41% of all species facing extinction, according to the International Union for Conservation of Nature (IUCN). Besides the loss, degradation and fragmentation of habitats (HAMMER & MCDONNELL 2008), the increased pollution of the environment (POLO-CAVIA et al. 2016), the appearance of invasive species (SNOW & WITMER 2010), and climate change (BLAUSTEIN et al. 2010), one major threat arose from the global spread of pathogens (FU & WALDMAN 2022). One of these pathogens is the chytrid fungus, *Batrachochytrium salamandrivorans* (Bsal; Chytridiomycota: Rhizophydiales), which originates in Southeast Asia and most likely spread to Europe through the pet trade (MARTEL et al. 2014, LAKING et al. 2017, NGUYEN et al. 2017).

The fungus causes chytridiomycosis, particularly in salamanders and newts (Caudata), which leads to multifocal superficial erosions and deep epidermal ulcerations in the skin of infected caudata (FARRER 2019). Furthermore, the animals stop eating (anorexia) and suffer from muscle spasms (ataxia), lack of interest (apathy) and skin shedding (VAN ROOIJ et al. 2015). These symptoms only appear in the final stage of the disease, before the hosts die within an average of 12 to 18 days after infection (MARTEL et al. 2013).

The first, subsequently confirmed case of Bsal in Europe dates back to 2004, when a mass mortality of the European fire salamander (*Salamandra salamandra)* occurred in Vichtbach, North Rhine-Westphalia, Germany (LÖTTERS et al. 2020a). At that time, however, the exact cause for the die-off was not yet known. In 2010, another mass mortality event was reported in the Netherlands (SPITZEN-VAN DER SLUIJS et al. 2013), but it was not until 2013 when it became clear, that these events were linked to Bsal. As a result, the fire salamander populations of the Netherlands had collapsed by 96% and are threatened with extinction ever since (MARTEL et al. 2013). In 2014, the first cases were reported from Belgium, in an area 57 km from the Dutch outbreak site (STEGEN et al. 2017). Bsal then made its way to Germany and with the areas of the southern and northern Eifel, as well as the Ruhr district, represents today's hotspots (SPITZEN-VAN DER SLUIJS et al. 2016, DALBECK et al. 2018, LÖTTERS et al. 2020b, SCHULZ et al. 2020, EUROPEAN COMMISION 2021, BEZIRKSREGIERUNG ARNSBERG 2022). Isolated outbreaks have even been reported in more distant areas, such as Montnegre i el Corredor National Park, Spain (MARTEL et al. 2020) and Ebrach, Bavaria, Germany (BAYRISCHES LANDESAMT FÜR UMWELT 2020, EUROPEAN COMMISION 2022). As of today, the fungus has been detected in natural fire salamander populations in four countries, namely the Netherlands, Belgium, Germany and Spain.

Since the spread of the pathogen can quickly lead to extirpation within a susceptible host population, one of the most effective approaches seems to be the prediction of its dispersal (CANESSA et al. 2018). In this regard, temperature appears to be the most important environmental variable affecting the growth of Bsal (BLOOI et al. 2015, CARTER et al. 2021). Bsal exhibits positive growth rates when the host’s body temperature ranges between 0°C to 25°C, with optimal growing conditions between 10°C and 15°C (MARTEL et al. 2013), making it very well adapted to climatic conditions in the temperate climate of Central Europe (BEUKEMA et al. 2021a). Therefore, it is questionable how the fungus will behave with respect to global warming. The IPCC Assessment Report 6 currently considers five future scenarios, namely SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5, suggesting an increase in the global annual mean temperature of between 1.0°C – 1.8°C (SSP1-1.9) and 3.3°C – 5.7°C (SSP5-8.5). As it is most likely that the 1.5 °C mark is already reached by the early 2030s (DIFFENBAUGH & BARNES 2023), it might be beneficial to take climatic changes into account.

Since temperature regimes in micro-habitats play an important role, they can be used to model the possible spread and intensity of the pathogen by applying species distribution models (SDM). Previous studies already predicted the potential distribution of Bsal in Europe. The correlative SDM of LÖTTERS et al. (2020b) focused on its potential distribution derived from a regional climate model in Germany. However, correlative approaches only statistically link geographic occurrences with environmental data and do not necessarily reflect species’ physiological constraints (RÖDDER et al. 2009, FOURCADE et al. 2018). Therefore, correlative SDM can lead to mismatches between the native and predicted invasive distribution (BROENNIMANN et al. 2007, RÖDDER et al. 2009). Furthermore, a mechanistic SDM of BEUKEMA et al. (2021a) was applied on European scale, relying on biophysical processes such as the body temperature of the fire salamander as host for Bsal. However, both approaches are based on broad spatial resolutions (~900 m and ~25 km, respectively) and predictions of the potential distribution of Bsal and its host on micro-climatic scales are currently limited.

Microclimate is defined as the climatic conditions of a specific, small-scale area near the earth's surface (NAIMAN et al. 2005). These local climates have a strong influence on both plants and animals and can even affect growth and mortality rates (SHIRLEY 1929, as cited in NAIMAN et al. 2005). This is especially true for ectothermic species such as fire salamanders, which regulate their body temperature through heat exchange with their environment and are therefore particularly influenced by the surrounding climate (DEUTSCH et al. 2008). At the same time, the body temperature of salamanders influences the growth of Bsal (BEUKEMA et al. 2021a).

In this study, we provide very fine-scale information on the situation in the current Bsal hotspot area (Benelux union, Germany), based on the current climate and each a +2°C and +4°C future global climate scenario. The obtained information might be essential for local conservation and mitigation measurements, taking climate change into account. Therefore, we (I) applied mechanistic SDM to predict the microclimatic growth rates of Bsal on a spatially very high resolution (25 m) within the forest habitats of the European Bsal hotspot area under current and two future climatic scenarios. Furthermore, we (II) used a correlative SDM (Maxent) to predict the potential distribution of the European fire salamander under the same climatic scenarios. Finally, we (III) applied n-dimensional hypervolumes to quantify the currently occupied microclimatic niches of Bsal and the fire salamander to investigate overlaps between the pathogen and its host.

Materials and methods

Study area

To determine the study area, a literature review was performed and all known Bsal outbreaks within Europe were compiled (MARTEL et al. 2013, SPITZEN-VAN DER SLUIJS et al. 2016, DALBECK et al. 2018, Bayrisches Landesamt für Umwelt 2020, LÖTTERS et al. 2020a, LÖTTERS et al. 2020b, MARTEL et al. 2020, SCHULZ et al. 2020, EUROPEAN COMMISION 2021, BEZIRKSREGIERUNG ARNSBERG 2022).

Due to computational limits for high-resolution modelling, we had to spatially restrict our study area. This resulted in a study area including 68 Bsal positive localities of about 37.200

km² located in the border region of Germany and the Benelux. We visualised the map using Quantum GIS 3.22.8 Bialowieza (further referred to as QGIS).

Due to the low number of Bsal positive and negative records and since our microclimatic layers only cover forest habitats (see below), we used the points2nearestcell function of the rSDM package (RODRIGUEZ-SANCHEZ 2022) to assign 16 of the 100 Bsal positive and 64 of the 369 Bsal negative records to the nearest raster cell in forest habitat.

Host species

The *S. salamandra* (Salamandridae) is one of the largest, native caudate amphibians within Europe. Its range extends across western, central, southern and south-eastern Europe, from Portugal to the Carpathians and from northern Germany to southern Greece (KWET 2022). As they depend on both aquatic and terrestrial habitats, they need high-quality and natural habitats. In the first months, still water zones in fish free streams, ponds and shallow water areas of mountain lakes serve as ideal larval habitats (WAGNER et al. 2020).

The adult animals seek damp and cool deciduous broadleaf or mixed forests in the immediate vicinity of water bodies. Coniferous forests are hardly colonised, as they are usually much drier and offer fewer hiding places (BÖRDER et al. 2011). In addition, inland wetlands with permanent rivers, streams or creeks are very suitable habitats, too (IUCN SSC Amphibian Specialist Group 2022). According to the authors, seasonal watercourses, peatlands, permanent or seasonal marshes, bush and herbaceous vegetation areas, as well as semi-natural gardens and urban areas are also marginally colonised. As long as there are enough retreats with a suitable microclimate, such as under piles of leaves or in old tree trunks, the salamanders can even tolerate some habitat modification.

These hiding places serve as brumation quarters, in which the salamanders retreat during the cold months (WILKINSON et al. 2017) and enable the nocturnal animals to hide during the day or unsuitable weather conditions. *S. salamandra* prefers rainy nights with a high humidity and temperatures ranging between 2 and 6°C in winter and a maximum of 20°C during the summer months (BOGAERTS et al. 2021). However, the temperature data vary widely within the literature and seem to be regionally variable (CATENAZZI 2016).

Mechanistic SDMs for *Batrachochytrium salamandrivorans*

Since ambient temperature determines salamander body temperature, which in turn determines Bsal growth rates, we used mapped microclimatic temperatures to (I) simulate the growth rates of Bsal under current and two future climate scenarios to investigate where it finds particularly suitable growing conditions.

We used climate layers for the current climate as well as for two future climate scenarios, assuming +2°C and +4°C of global warming compared to the pre-industrial climate, from the TerraClimate dataset (ABATZOGLOU et al. 2018). To establish the future climate scenarios, ABATZOGLOU et al. (2018) used monthly projections from 23 CMIP5 global climate models and downscaled them by using a pattern scaling approach (QIN et al. 2020). The pseudo-years 1985 to 2015 served as a reference climate system, to which they applied the projected changes in temperature means and variances on a global scale in order to provide projections for the monthly climate of the future scenarios across these years.

We downloaded the monthly maximum and minimum temperatures measured 2 m above the surface in a spatial resolution of 4 km (1/24th degree). The current scenario covering the time period from 2010 to 2019 represents the history of Bsal in Europe (further referred to as current2010-2019). As data on the two future climate scenarios are only available until 2015, we have additionally calculated the current scenario as a reference for the years 2010 to 2015 only (further referred to as current2010-2015, future2 and future4).

We used the averages between the maximum and minimum temperatures to approximate the mean temperatures, as the microclimatic offset for forest habitats provided by HAESEN et al. (2021, see below) is based on monthly means. Hence, these are necessary for the later calculation of bioclimatic variables and as the TerraClimate dataset itself does not contain any information on average temperature. By applying the raster.downscale function of the spatialEco package (EVANS 2021), the temperature layers were downscaled to a 25 m resolution, using a digital elevation model (DEM) as an independent variable to account for altitude as an important determinant of temperature. The DEM was obtained via the get_dem function of the microclima package (MACLEAN et al. 2018). Based on the Bsal distribution, we cropped the layers to the forest habitats within our study area using the projectRaster function of the raster package (HIJMANS 2022). For the coordinate reference system (CRS), an equal area projection in EPSG:3035 (ETRS89-extended/ LAEA Europe) was chosen.

To simulate the microclimatic conditions of forest habitats, we used microclimatic temperature offset layers for the whole of European forests (HAESEN et al. 2021). These layers show the average monthly offset between the microclimatic temperature in the forest and the macroclimatic temperatures in the open landscape and are provided in a resolution of 25 m for the monthly average over the years 2000 to 2019. Finally, we obtained microclimatic layers containing the mean temperatures for each month in forest habitats from 2010 to 2019. The layers were also used to correct the current2010-2015, future2 and future4 climate scenarios for the forest microclimate at 5 cm above the ground.

For the simulation of the growth rate of Bsal, we digitised BEUKEMAS' et al. (2021a) graph of the temperature-dependent growth rate of the fungus using the digitize package (POISOT 2011). This data was used as input for the PerfGAMM function of the Mapinguari package (B. SINERVO, pers. comm.) to simulate the growth rate of Bsal by applying Generalized Additive Mixed Models (GAMMs). Therefore, the PerfGAMM function is applied to each monthly microclimate layer translating temperatures in the growth rate of Bsal. Our simulations resulted in 120 growth rate layers for the current2010-2019 scenario and in 72 growth rate layers for each, the current2010-2015, future2 and future4 scenarios.

We summarised both the climate and growth rate layers into meaningful units in accordance to WorldClim's bioclimatic variables (HIJMANS et al. 2005). Since our growth rate layers are based on monthly mean temperatures only, the bioclimatic variables annual mean temperature (bio1), temperature seasonality ((standard deviation x 100), bio4), mean temperature of warmest month (bio5), mean temperature of coldest month (bio6), temperature annual range (bio5 – bio6), bio7), mean temperature of warmest quarter (bio10) and mean temperature of coldest quarter (bio11) were created. In order to calculate these variables, the biovars function of the dismo package was used (HIJMANS et al. 2022). Further, we used the makeCluster function of the doParallel package (FOLASHADE et al. 2022), to generate these variables simultaneously, thus shortening computation time.

These bioclimatic variables were generated based on the monthly growth rate layers of each year, for the climate scenarios current2010-2019, current2010-2015, future2 and future4. For these, the mean values were calculated for each variable for the respective time period considered, by using the calc function of the raster package (HIJMANS 2022).

Correlative SDMs for *S. salamandra*

In a second step, we (II) predicted the potential distribution of European fire salamanders within our study area. The correlative SDM framework Maxent version 3.4.0 was used to predict the species distribution of the fire salamander (PHILLIPS et al. 2006). Maxent uses occurrence data and links them with environmental layers to predict the potential distribution of a species. We obtained 4956 occurrence records from iNaturalist (cross-linked to GBIF) and 417 records from observation.org (species records in North Rhine-Westphalia between 2010 and 2022). We used spatial filtering to subsample the species records to only one record within a 250 m radius per year to reduce potential spatial autocorrelation resulting in 502 species records for further processing. Additionally, we further reduced a potential sample bias by using a target group background approach, i.e. we used the full set of all amphibian and reptile species records within the study area excluding fire salamanders as SWD-Background file in Maxent, equally filtered by a 250 m radius (BARBER et al. 2022).

As environmental variables, we used the microclimatic temperatures layers and elevational heterogeneity in terms of aspect, slope and the topographic wetness index (TWI) as computed in QGIS as environmental data. Each layer was cropped to the forest habitats. Subsequently we calculated the Spearman rank correlation coefficient to test for multi-co-linearity between the bioclimatic variables and, based on a threshold >0.80, used only the uncorrelated variables TWI, bio1, bio7, bio10 and bio11. Different regularization multipliers (0.5 - 2.5 in 0.1 steps, 5 and 10) and all feature class combinations (L = linear, P = product, Q = quadratic, H = hinge, T = threshold) were tested, in order to fit the model. For each 25 runs we subsetted the species records in 80% used for model training and 20% used for model testing using AUC, which is a measure that indicates the overall accuracy of a model (MANDREKAR 2010).

After obtaining the raw outputs of the models, the average corrected Akaike Information Criterion (AICc; (WARREN & SEIFERT 2011)) and the average AUC test (AUC = Area under the ROC curve; (PHILLIPS 2005)) were calculated for each combination of settings (GINAL et al. 2022). Following GINAL et al. (2022), model selection was based on the lowest AICc and an AUC test score above 0.7. The model that explains the largest amount of variation and uses the smallest number of independent variables has the lowest AIC value and is thus chosen as the best-fitting model (CAVANAUGH & NEATH, 2019). For the final model, 100 replicates were performed using bootstrap. We used a data split with 80% for model training and 20% for model testing. We applied the 10% omission threshold as presence-absence threshold based on the averaged results of the models. The Maxent Cloglog output and QGIS were utilized to create final maps.

In addition, monthly mean temperatures and relative Bsal growth rates extracted from the localities of the salamander records were plotted for the current2010-2015, future2 and future4 scenarios.

Niche quantification

In a third step, we wanted to (III) quantify and compare the microclimatic niches of Bsal positive and negative records as well as for the fire salamander to investigate potential overlaps of the fungus and its host. For this purpose, we used the hypervolume_svm function of the hypervolume package for R version 4.0.5 (BLONDER et al. 2022, R Core Team 2021). This algorithm applies support vector machines to separate data points from background, which reveals an n-dimensional hypervolume of the species microclimatic niche (BLONDER et al. 2014, 2022). We used the above mentioned species records and subset them to obtain occurrences for the fire salamander, for Bsal positive and negative records. The Bsal positive and negative records also include additional samples of other caudate species (data from observation.org). It is possible that the same locality has Bsal positive and negative records in different years; however they are associated with the relative growth rate / microclimates from that respective year. Furthermore, we sampled 10 000 random records across our study area to sample the environmental conditions of our study area.

Computation of hypervolumes require an orthogonal niche space. Hence, a principal component analysis (PCA) was used to reduce the dimensionality of the seven bioclimatic variables (bio1, bio4, bio5, bio6, bio7, bio10, bio11) to principal components (PCs). We used the princomp function of the stats package in R version 4.0.5 (R Core Team, 2021) and selected PCs with an eigenvalue >=1 and calculated their explained variances and factor loadings (Table 1). In addition, we calculated values for the respective volumes of the species niches (Vol1, Vol2), the niche similarity indices of these volume ratios (Jaccard index, Sorensen index) and the proportion of the unique fraction of each hypervolume (Table 2; frac_unique1, frac_unique2).

Results

Microclimatic habitat suitability for *S. salamandra* and *B. salamandrivorans*

The topographic map, based on the DEM, reveals that the distribution of the fire salamander is associated with moderate elevations above 100 m, whereas less populations occur in lower elevations such as the Lower Rhine area. The Bsal positive and negative records are both predominantly located in the hotspot areas for Bsal. Our correlative SDMs reveal that under current climatic conditions, the most suitable areas for the fire salamander are located along the large streams and rivers such as Ruhr, Rhine, Sieg, Ahr, Mosel and Maas, as well as along the Rhenish slate mountains (Fig. 1A). Under future climate scenarios, both +2°C and +4°C scenarios (Fig. 1B + C), we see a tremendously enlarged expansion for the climatically suitable climate space of the fire salamander. For all three scenarios, the variables TWI, slope and annual mean temperature (bio1) contribute most to the models performance. The model performance revealed moderate training AUC values between 0.679 and 0.686. The scenarios marginally differ from each other and predict a high climatic suitability for large parts of the study area, encompassing the low mountain ranges of North Rhine-Westphalia, Rhineland-Palatinate and Belgium. Again, the highest suitability is predicted to be along the largest rivers. Our mechanistic SDM predict that Bsal finds suitable growing conditions all around the year, considering the annual mean temperature (bio1). We predict that Bsal can grow much better under the current climate (Fig. 1D) than under the future climate scenarios of +2°C and +4°C (Fig. 1E+F). Indeed, the fungus finds slightly better growing conditions for the +2°C scenario than for the +4°C scenario, especially for the Eifel region. For all three scenarios the mean temperature of the coldest quarter (bio11) contributed most to the models performance. The model performance revealed moderate training AUC values between 0.604 and 0.629.

To illustrate the drastic differences in salamander distribution and fungal growth rate in relation to the different climate scenarios (current2010-2015, future2 and future4) described above, we plotted the monthly mean temperature for each climate scenario (Fig. 2A). For both the more optimistic +2°C scenario (orange bars) and the more pessimistic +4°C scenario (red bars), the temperatures occurring over the course of the year are increased for each single month and directly affect the growth conditions of Bsal (Fig. 2B). While the relative growth of Bsal increases strongly in the colder months from November to March, it is greatly reduced in the warmer months from April to October, for both the +2°C (orange bars) and +4°C scenarios (red bars). During midsummer, temperatures might get so high that the growth of Bsal will be close to zero. This projection is based on the digitised growth curve of BEUKEMA et al. (2021a), showing the growth rate of Bsal in relation to the body temperature of the fire salamanders (Fig. 2C).

Animations of the monthly fluctuations in growth rates and environmental suitability are available as supplementary material: https://www.dropbox.com/scl/fi/1upldxcc9s7zkcqc1dsfl/Animations-Bdsal.pptx?rlkey=3twqflirpjecitqr26is690l8&dl=0.

Niche quantification

The PCA revealed three principal components with an explaining variance of 87.32 % (Table 1). PC1 correlates strongly with temperature seasonality (bio4), minimum temperature of the coldest month (bio6), temperature annual range (bio7), and mean temperature of coldest quarter (bio11) and explains 52.12 % of the variance. PC2 correlates strongly with annual mean temperature (bio1) and explains 20.03 % of the variance. PC3 correlates strongly with mean temperature of warmest quarter (bio10) and explains 15.17 % of the variance.

The hypervolume statistics (Table 2) reveal that the niches of Bsal positive records and the fire salamander strongly overlap, whereas the Bsal positive records are predominantly nested within the hypervolume of the fire salamander and show a much smaller niche volume. The hypervolumes of Bsal positive and negative records also strongly overlap and reveal a moderate unique fraction for the negative records as well as a larger niche volume for the negative records. The comparison of the hypervolumes of the fire salamander and a hypervolume randomly sampled in the forest habitat also results in the nesting of the fire salamander niche inside the background niche revealing large overlaps between the two hypervolumes, but also a large unique fraction of the background hypervolume (Table 2).

Discussion

Our results suggest that Bsal finds suitable growth conditions throughout the year and everywhere within the forests of our study area. The microclimatic suitable areas within the Bsal hotspot area strongly overlap with the distribution of the fire salamander, which is also reflected in the statistics of the niche quantification. Under current climatic conditions, the highest growth rates occur during autumn (September) and spring (May), whereas the lowest growth rates are found during winter (December to February). Considering global warming scenarios of +2°C and +4°C, respectively, the highest growth rates for Bsal shift towards November and December, whereas the lowest growth rates will occur in summer (June to August). Surprisingly, the correlative SDMs predict that the potential distribution of *S. salamandra* extends towards higher altitudes and will increase with rising temperatures. Hence, both global warming scenarios seem beneficial for the fire salamander but as the future scenarios require extrapolation beyond the training range of the models, upper thermal limits might be reached at some point.

Current situation

Our mechanistic SDM reveals that Bsal finds optimal growth conditions within the European hotspot area during autumn (September) and spring (May), while only low, but still positive, growth rates occur during winter from December to February. Furthermore, the microclimatic conditions in this area seem suitable (no negative growth rates) for the fungus overall of the whole year. These findings are in accordance with the results presented by BEUKEMA et al. (2021a) and can be explained that due to the buffer capacity of the forest microclimate, caused by dense vegetation and canopy cover (DE FRENNE et al. 2021), the fungus rarely faces unsuitable climatic extremes. During summer, the leaf-cover of the trees provides shade, which leads to much cooler climates than the ambient temperatures outside of forests, and during winter, the vegetation ensures reduced heat loss. Consequently, animals in the forest experience a somewhat more moderate climate than their conspecifics in the open landscape (KEARNEY et al. 2009). BEUKEMA et al. (2021a) also found that due to the nocturnal activity of host amphibians, such as the fire salamander, and the avoidance of thermal extremes, it is unlikely that Bsal exhibits temperatures above 25°C or below 0°C under natural conditions. These circumstances prevent effective mitigation strategies, such as behavioural fever, which is a strategy of ectothermic animals where the host deliberately seeks out warmer temperatures outside its thermal comfort zone to control its disease.

Considering the microclimatic niches and their quantification, we found that only a fraction of the forest habitat is microclimatically suitable for the fire salamander (Table 2; *S. salamandra* vs. Background). Our correlative SDMs reveal that the occurrence of fire salamanders and high habitat suitability is associated with the valleys of rivers and streams (Fig. 1). A comparison between the Bsal positive records and the fire salamander’s niches shows that the fire salamander has a large unique fraction that is not shared by Bsal yet. Similarly, the microclimatic niche of Bsal negative records also shows a unique fraction that is not shared by Bsal positive records yet. However, as our SDMs predict suitable microclimatic conditions overall of the year and across the whole study area, we suggest that Bsal just did not spread into these areas yet but unfortunately we could not find any evidence for microclimatic refugia for the fire salamander in this area. Furthermore, almost the whole microclimatic niche space, where Bsal positive records are sampled, is also suitable for the fire salamander (Table 2; Bsal pos. vs. *S. salamandra* and Bsal neg. vs. Bsal pos.). This is also supported by some mass mortality events that already happened in the past, which led to collapses of some populations with mortality rates of up to 96% (MARTEL et al. 2013).

As geographic accessibility seems to be the only limitation for Bsal in the European hotspot area, prevention of further spread into novel areas seems to be the most effective strategy. We support the outlined management of Bsal according to the European Commission's Bsal-Action-Plan (GILBERT et al. 2020) and recommend prioritising the proposed minimisation of the risk of Bsal introduction. The development of an Early Warning System (EWS) based on area-wide monitoring to locate new outbreaks and separate affected populations, seems to be one of the most effective instruments. Since the set up of such a system takes time, it is advisable to start monitoring in regions that are particularly at risk. As suggested by BEUKEMA et al. (2021b), a southward spread of the chytrid fungus across the Ardennes and Rhineland-Palatinate seems very likely and therefore we recommend increased efforts in these areas.

Future investigations should focus on the main dispersal pathways as well as the evaluation of methods that are undertaken. The international pet trade, for example, is an important pathway for Bsal (MARTEL et al. 2014). For this reason, some countries such as the USA restricted the trade with caudate species (YAP et al. 2015). However, these strong restrictions might also affect conservation breeding programmes negatively as the exchange of animals is difficult or impossible. For this reason, we instead recommend the obligate testing of captive salamanders for Bsal. As the possibility of an asymptomatic infection in captive salamanders has recently been demonstrated, all captive animals should be tested, even if they appear healthy at first sight (SABINO-PINTO et al. 2018). Fire salamanders that are tested positively can easily be treated with medication or by thermal treatment to cure the infection (BLOOI et al. 2015). Furthermore, we strongly recommend that every type of field equipment (rubber boots, nets, boxes, etc.) should be thoroughly disinfected (e.g. with hydrogen peroxide) after visiting amphibian habitats as Bsal spreads through contaminated media too (MARTEL et al. 2013).

Future scenarios

Considering global warming, under realistic (+2°C) and extreme (+4°) conditions, we found that Bsal exhibits a shift in its maximum growth rates from September and May (current) towards November, whereas the minimum growth rates, which currently occur during the winter months (December to February) shift towards summer (June to August). Considering the thermal-dependent growth of Bsal and its thermal optimum between 10°C and 15°C (MARTEL et al. 2013, BEUKEMA et al. 2021a), these seasonal shifts seem reasonable. In contrast, our correlative SDMs predict that the fire salamander might benefit from global warming as its predicted climatically suitable area increases with rising temperatures, which may be partly explained by extrapolation. Particularly, higher elevations seem climatically suitable for the fire salamander in the future. However, we note that our predictions for the fire salamander should be treated with caution as our SDMs rely on temperatures only and do not include other important variables such as precipitation. Furthermore, it is predicted that global warming also increases the probabilities of weather extremes such as extremely hot summers, which lead to droughts (VICENTE-SERRANO et al. 2020). Generally, extremely hot and dry weather periods most likely will affect Bsal as well as the fire salamander negatively. During dry periods or brumation in winter the salamanders retreat under deadwood piles or into abandoned underground burrows, sometimes several metres below the surface (BOGAERTS et al. 2021), which might allow surviving these weather extremes. Possible future management actions to support fire salamander populations might therefore include habitat re-structuring i.e., by providing cairns or piles of deadwood.

Acknowledgements

We are grateful for the technical support by MORRIS FLECKS.

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Table 1. Summary of the PCA including factor loadings, eigenvalue and explained variance of the predicting climate variables.

Climate parameter	Bioclimatic variables	PC1	PC2	PC3
Annual mean temperature	bio1	0.43	0.73	0.11
Temperature seasonality	bio4	-0.89	-0.21	-0.03
Mean temperature of the warmest month	bio5	-0.33	0.63	0.59
Mean temperature of the coldest month	bio6	0.95	0.10	-0.07
Temperature annual range	bio7	-0.96	0.02	0.18
Mean temperature of warmest quarter	bio10	-0.07	0.64	-0.73
Mean temperature of coldest quarter	bio11	0.86	0.07	0.36
Eigenvalues		3.65	1.40	1.06
Explained variance		52.12	20.03	15.17

Table 2. Hypervolume statistics and comparisons among Bsal positive records and the fire salamander, Bsal negative and positive records, and fire salamander and random background samples. The hypervolume statistics include the respective volumes, Jaccard and Sorensen indices and the unique fractions of the respective hypervolumes.

Vol1 vs Vol2	Vol1	Vol2	Jaccard	Sorensen	frac_unique_1	frac_unique_2
Bsal.pos vs *S. salamandra*	24.79	75.14	0.30	0.46	0.08	0.70
Bsal.neg vs. Bsal.pos	42.04	24.79	0.54	0.70	0.45	0.06
S.salamandra vs. Background	75.14	152.89	0.47	0.64	0.03	0.53

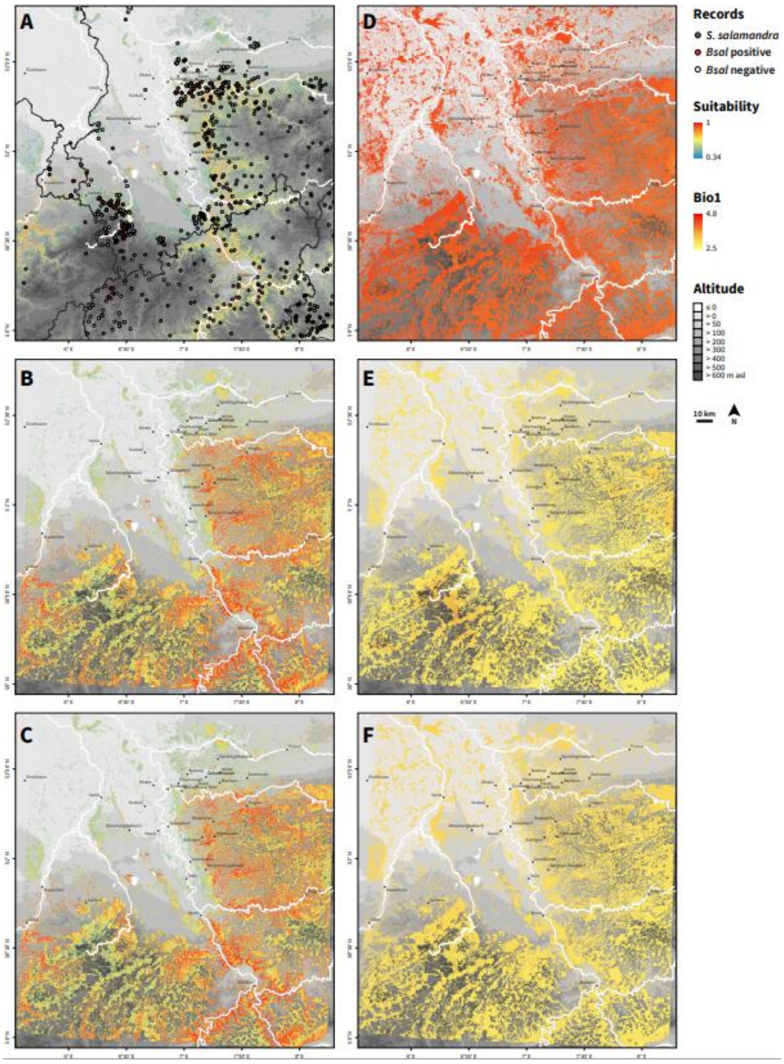

Figure 1. Performance of *Salamandra salamandra* and *Batrachochytrium salamandrivorans* under three climatic scenarios. Distribution of the occurrence records of the *S. salamandra* combined with the Maxent results for the current climate (A), as well as the Maxent results of the future climate scenarios, assuming a global warming of +2°C (B) and +4°C (C). Besides, are the microclimatic growth rates of *Batrachochytrium salamandrivorans* (Bsal) for the annual mean temperature (bio1) under the current climate (D) and the two future climate scenarios, representing a temperature increase of +2°C (E) and +4°C (F). Warmer shades indicate a higher suitability for both, the occurrence of *S. salamandra* and the growth rate of Bsal. The maps projection is EPSG:3035 (ETRS89-extended/ LAEA Europe) and a digital elevation model is added to the background of each map. (**Please print this figure in colour**)

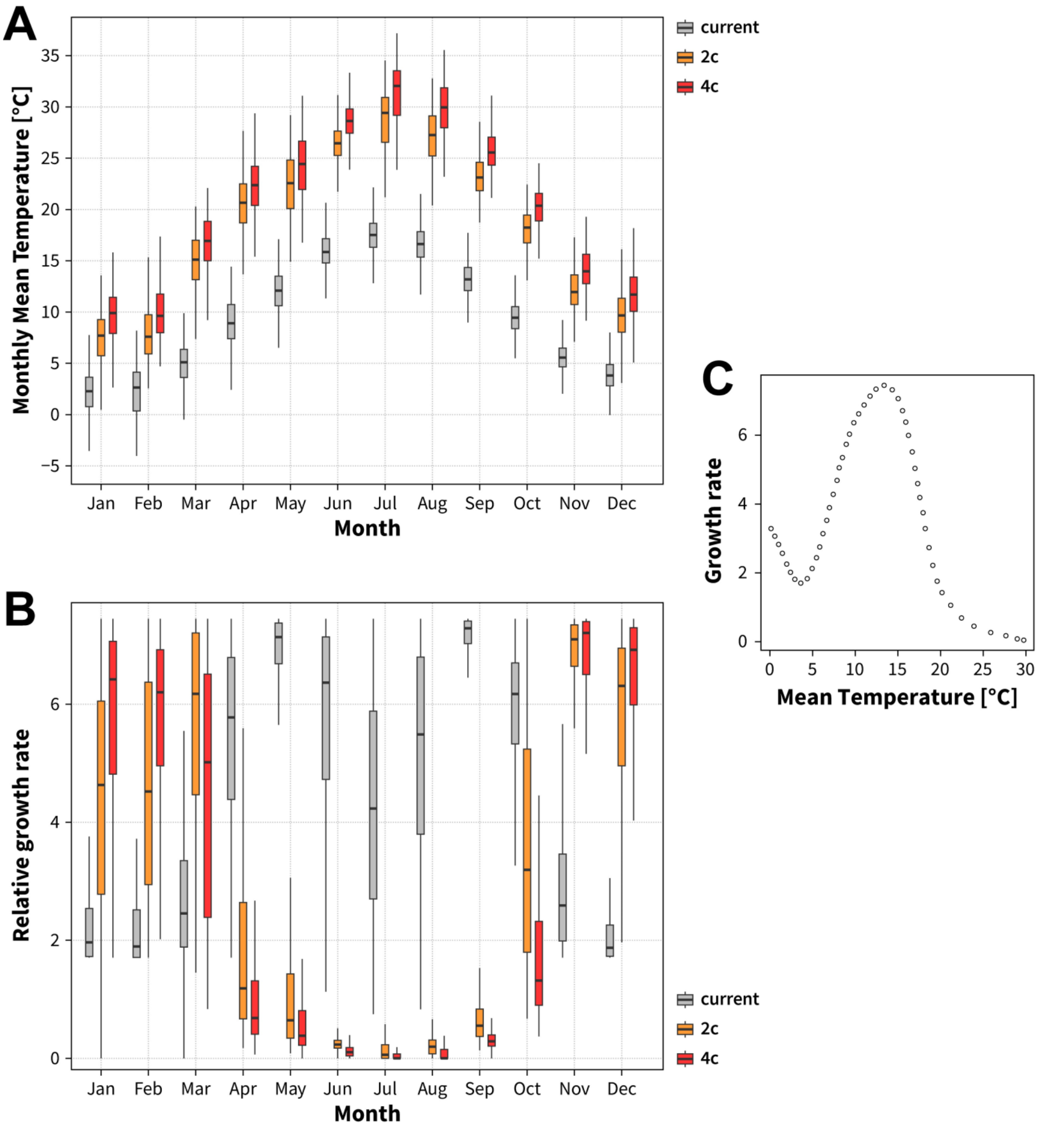

Figure 2. Growth rate of *Batrachochytrium salamandrivorans* in respect to the monthly mean temperature of three climatic scenarios. The figure includes the microclimatic temperature of forest habitats (A), with the current monthly mean temperatures (grey bars) compared to the future mean temperature for the +2°C scenario (orange bars) and the +4°C scenario (red bars). In respect to this microclimatic temperature, the relative growth rates of *Batrachochytrium salamandrivorans* (Bsal) are shown (B), for each month for the current climate scenario (grey bars), as well as for the +2°C (orange bars) and +4°C (red bars) future climate scenarios and are based on the digitised growth curve of Bsal as a function of temperature (C). (**Please print this figure in colour**)

Appendix 7 – Ecophysiological models for global invaders

Received: 24 April 2020 | Revised: 18 October 2020 | Accepted: 15 November 2020
DOI: 10.1002/jez.2432

RESEARCH PAPER

JEZ-A ECOLOGICAL AND INTEGRATIVE PHYSIOLOGY WILEY

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

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Funding information
Eranet Biodiversa / DFG,
Grant/Award Number: RO 4520/3-1

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 temperature-dependent 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 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 km^2 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 quite 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.

TABLE 1 Performance variables and their abbreviations

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 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 Steyermark 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 0.01 g 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 L min^{-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).

2.6 | Ecophysiological response surfaces and 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 > 1 s 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

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

	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**

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	NA	0.003	0	**1**				
WR d200	NA	NA	NA	NA	NA	NA		
WR MaxVel	NA	**0.781**	0.188	0.004	NA	**1**		
WR h_a	NA	0.221	**1**	0	NA	0.188	**1**	
WR h_r	NA	0.003	0	**1**	NA	0.004	0	**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 km^2 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°C, CT_{min} = 2.8°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, CT_{max} = 39.2°C, size = 51.5 mm; SMR: pred_perf = 12.3 ml h^{-1}, 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°C, CT_{min} = 3.2°C, CT_{max} = 38.6°C; native_winterrain: pred_perf = 12.2 cm s^{-1}, T_{opt} = 29.8°C, CT_{min} = 3.4°C, CT_{max} = 38.8°C; d200: native_summerrain: pred_perf = 1.5 cm, T_{opt} = 29.8°C, CT_{min} = 3.4°C, CT_{max} = 38.6°C; native_winterrain: pred_perf = 1.4 cm, T_{opt} = 29.3°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

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

	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	d200	1.4	29.3	3.7	39.3	-

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 ($\text{AUC}_{\text{Training}} = 0.775$, $\text{AUC}_{\text{Test}} = 0.768$, $\text{TSS}_{\text{Training}} = 0.904$, $\text{TSS}_{\text{Test}} = 0.901$). 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 ($\text{AUC}_{\text{Training}} = 0.733$, $\text{AUC}_{\text{Test}} = 0.727$, $\text{TSS}_{\text{Training}} = 0.801$, $\text{TSS}_{\text{Test}} = 0.796$). 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 ($\text{AUC}_{\text{Training}} = 0.777$, $\text{AUC}_{\text{Test}} = 0.766$, $\text{TSS}_{\text{Training}} = 0.900$, $\text{TSS}_{\text{Test}} = 0.896$). 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 km^2 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 km^2), followed by the model for the adults (917,900 km^2), and last tadpoles (904,000 km^2). The correlative approaches predict 35.7%–169.9% of our maximum predicted area.

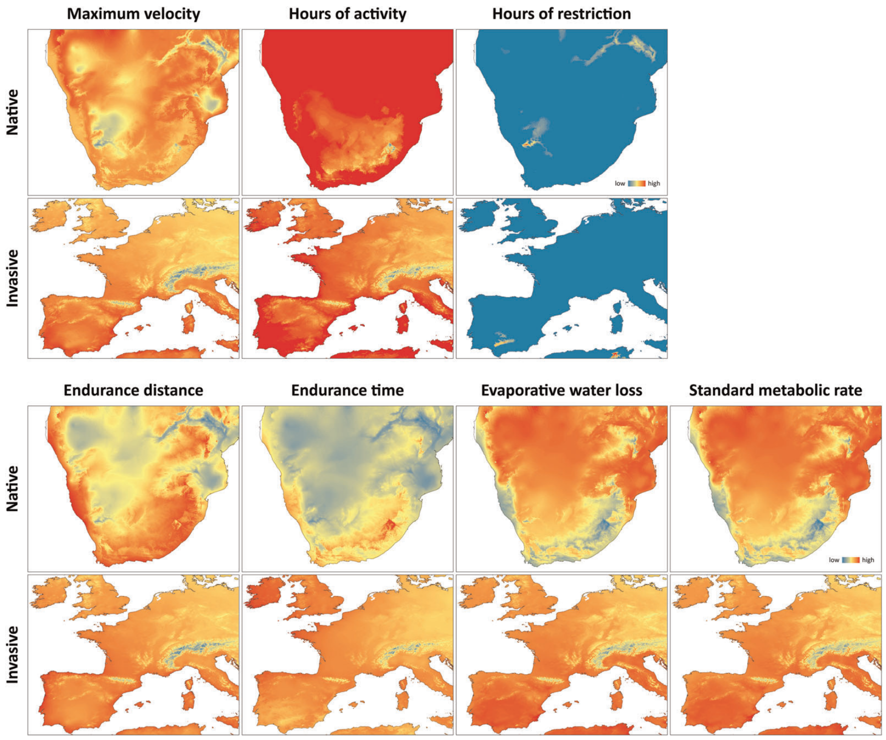

FIGURE 1 Ecophysiological rasters of adult *Xenopus laevis*: Performance assessed by maximum velocity (MaxVel), hours of activity, hours of restriction, endurance distance (EndurDist), endurance time (EndurTime), evaporative water loss (EWL), and standard metabolic rate (SMR) projected to the native 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

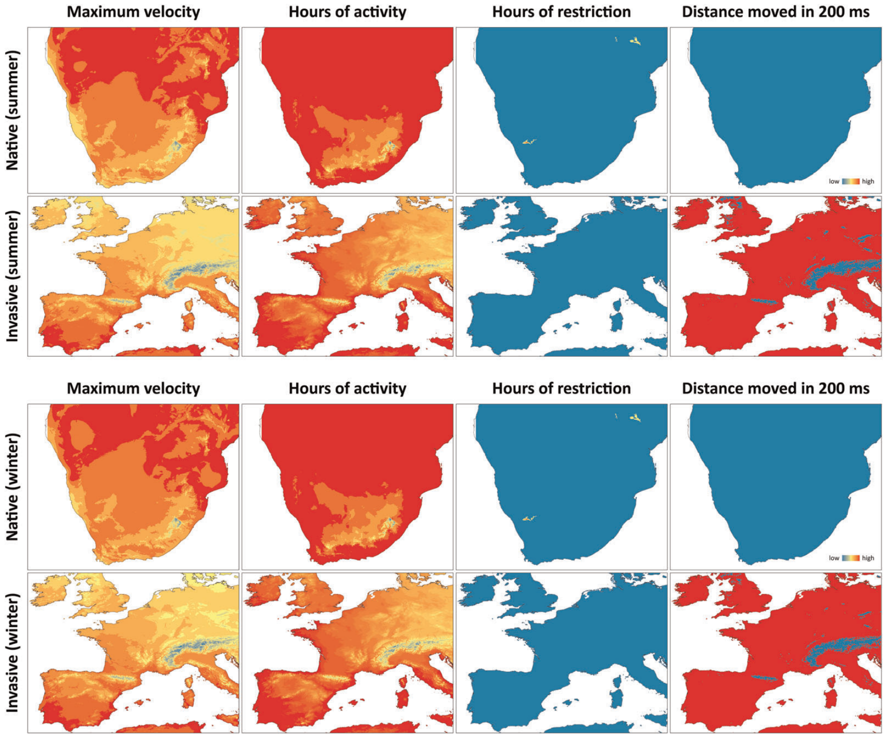

FIGURE 2 Ecophysiological rasters of tadpole *Xenopus laevis* from the summer (upper row) and winter rainfall region (lower row): Performance assessed by maximum velocity (MaxVel), distance moved in 200 ms (d200), hours of activity, and hours of restriction, projected to the native and invasive range. 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 charactierized 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

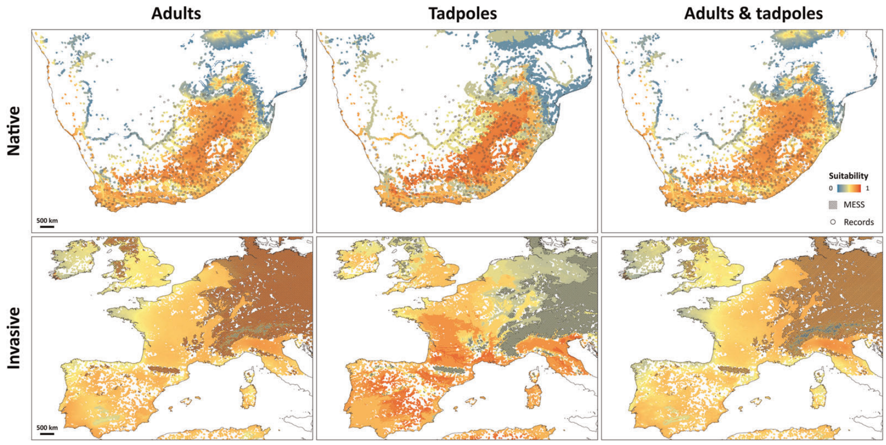

FIGURE 3 Ecophysiological models of adults, tadpoles and adults and tadpoles together based on data assessed from the native population projected to the native range (top) and the invasive European range (bottom). Dark colors represent highly suitable areas while light colors represent unsuitable areas. 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 south-western 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 km^2 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

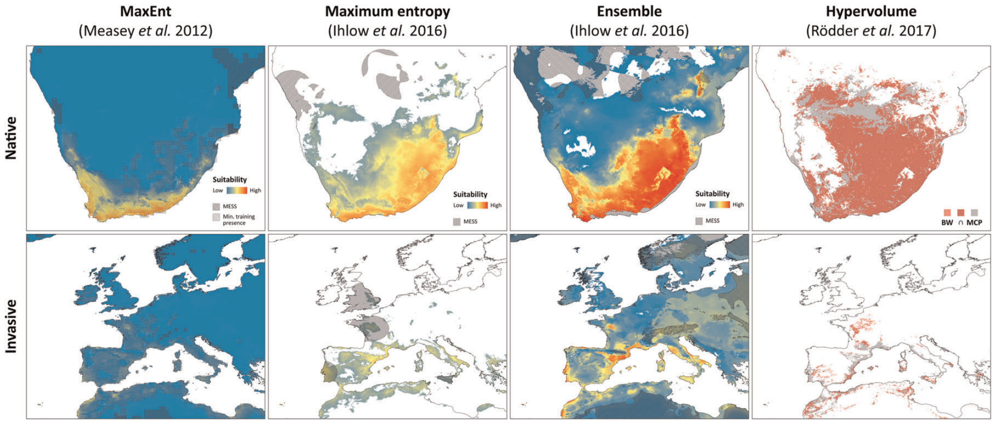

FIGURE 4 Comparison among different correlative SDM approaches from left to right: Maxent (Measey et al., 2012), maximum entropy and ensemble model (Ihlow et al., 2016), hypervolume models: bdw and mcp approach (Rödder et al., 2017). Minimum training presence was calculated as threshold (dark gray). 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.

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 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 km^2 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 quite 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.

ACKNOWLEDGMENTS

This study was funded by an ERA-Net BiodivERsA grant INVAXEN, with the national funders ANR, DFG (RO 4520/3-1), BELSPO and FCT, as part of the 2013 BiodivERsA call for research proposals. Natasha Kruger, Mohlamatsane Mokhatla and John Measey would like to thank the DSI-NRF Centre of Excellence for Invasion Biology (South Africa). Natasha Kruger would like to acknowledge the Ambassade de France en Afrique du Sud (France). Dennis Rödder and Philipp Ginal are grateful to B. Sinervo for sharing his experience and R scripts during a workshop held at the World Congress of Herpetology in Tonglu, China. Ursula Bott helped with her excellent proof reading skills.

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.

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How to cite this article: Ginal P, Mokhatla M, Kruger N, et al. Ecophysiological models for global invaders: Is Europe a big playground for the African clawed frog? *J. Exp. Zool*. 2021; 335:158–172. https://doi.org/10.1002/jez.2432

Appendix 8 – More time for aliens?

Biol Invasions
https://doi.org/10.1007/s10530-022-02903-6

ORIGINAL PAPER

More time for aliens? Performance shifts lead to increased activity time budgets propelling invasion success

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Received: 28 May 2021 / Accepted: 28 August 2022

Abstract In the Grinnellian niche concept, the realized niche and potential distribution is characterized as an interplay among the fundamental niche, biotic interactions and geographic accessibility. Climate is one of the main drivers for this concept and is essential to predict a taxon's distribution. Mechanistic approaches can be useful tools, which use fitness-related aspects like locomotor performance and critical thermal limits to predict the potential distribution of an organism. These mechanistic approaches allow the inclusion key ecological processes like local adaptation and can account for thermal performance traits of different life-history stages. The African Clawed Frog, *Xenopus laevis*, is a highly invasive species occurring on five continents. The French population is of special interest due to an ongoing expansion for 40 years and a broad base of knowledge. We hypothesize that (1) the French population exhibits increased activity time in the invasive European range that could be devoted to fitness-relevant activity and (2) tadpoles may have less activity time available than adult frogs from the same range. We investigate how thermal performance traits translate into activity time budgets and how local adaptation and differences in the thermal responses of life-history stages may boost the European *Xenopus* invasion. We use a mechanistic approach based on generalized additive mixed models, where thermal performance curves were used to predict the hours of activity and to compare the potential activity time budgets for two life-history stages of native and invasive populations. Our results show that adult French frogs have more activity time available in Europe compared to South African frogs, which might be an advantage in searching for prey or escaping from predators. However, French tadpoles do not have more activity time in Europe compared to the native South African populations suggesting that tadpoles do not suffer the same strong selective pressure as adult frogs.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-022-02903-6.

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Keywords Amphibians · Mechanistic model · Hours of activity · *Xenopus laevis* · Local adaptation · Life-history stages

Introduction

The Anthropocene is characterized by profound environmental changes that have been suggested to be drivers of the sixth mass extinction (Steffen et al. 2011; Ceballos et al. 2017; Maslin and Lewis 2018). Anthropogenic activities, including the introduction of invasive species, are widely recognized to be among the main drivers of biodiversity loss (Early et al. 2016; IPBES 2019). The ecological impacts of invasive species to native taxa can be various and include mechanisms such as predation, herbivory, poisoning, competition, disease transmission, trophic subsidy and hybridization (Blackburn et al. 2014). Particularly for IUCN Critically Endangered species, those invasive aliens constitute a major threat (Duenas et al. 2021). Concurrently, the global emergence of invasive taxa represents unintended experiments providing potentially important insights in range dynamics under changing environmental conditions. The concept of the Grinnellian niche has become a key framework when assessing the impacts of climate change on species. In this concept, the niche and resulting (potential) geographic distribution is described as the interplay of abiotic (fundamental) and biotic factors (interactions among taxa) and geographic climate accessibility (Soberón and Peterson 2005). The fundamental climatic niche is defined as comprising all abiotic environmental conditions that are essential for a species' persistence and reproduction, irrespective of whether these conditions are available in geographic space, while the realized climatic niche considers those conditions that are actually available (Grinnell 1917; Hutchinson 1978; Soberón and Peterson 2005; Soberón 2007).

Climate is one of the main drivers of the ecological niche and is therefore predictive of the potential distribution of species on broad geographic scales (Thuiller et al. 2004; Soberón 2007). Historical range shifts towards and from refugia (e.g. quantified in phylogeographic studies) suggest that species tend to track their Grinnellian niche instead of persisting and adapting to novel environmental conditions (Cordellier and Pfenninger 2009; Barros et al. 2020). Therefore, it is often assumed that a species' climatic niche is conserved across space and time (niche conservatism, Wiens et al. 2010; Strubbe et al. 2013; Dorey et al. 2020).

Biological invasions, however, demonstrate numerous reports of 'niche shifts', as shown by mismatches between the potential distributions of native and non-native ranges (Broennimann et al. 2007; da Mata et al. 2010; Orsted and Orsted 2019; Christina et al. 2020). In most studies, it remains unclear if these 'niche shifts' are associated with shifts in the fundamental niche or in the realized niche only (Petitpierre et al. 2012; Schulte et al. 2012; Strubbe et al. 2013; Poursanidis et al. 2020). Distinguishing between these possibilities is impossible based on correlative models that make use of distribution patterns, since in both native and invaded ranges, species may occupy only a subset of their fundamental niche. Hence, niche shifts may represent a better exploitation of the niche due to a novel accessibility of climate space.

To overcome this limitation, a mechanistic understanding of the climate dependence of physiological processes is necessary. Two different approaches are available for the characterization of the relationship between (potential) distributions and environmental data: (1) the redundant correlative models, which statistically link geographic occurrence data of species with environmental data, and (2) process-based or mechanistic approaches, which determine mechanistic interactions between aspects of the performance as surrogates of the fitness of organisms, like performance and critical thermal limits, and their environment (Kearney and Porter 2009; Ceia-Hasse et al. 2014; Krehenwinkel et al. 2015). Mechanistic SDMs are constrained by availability of data and the identification of essential key processes limiting species' distributions (Elith et al. 2010). While correlative SDMs can capture the realized niche of a species, mechanistic models emphasize the processes involved in determining range constraints (Morin and Thuiller 2009).

Physiological performance traits, like locomotor performance or endurance capacity, are critical to amphibian life-history, and may provide an indicator for potential energy use and balance (Wygoda 1984). Additionally, performance traits that represent those key processes can be translated into hours of activity, the proportion of the day when temperatures allow a specific level of performance (Taylor et al. 2021). For ectotherms, the inclusion of both estimates of performance and activity times in modelling frameworks allows for better predictions of a species' distribution than the sole inclusion of pure environmental variables (Caetano et al. 2020). As such, mechanistic or hybrid SDMs, which combine mechanistic and correlative approaches, are more robust in terms of transferability across space and time (Elith et al. 2010).

Mechanistic models allow the inclusion of key ecological processes like hard thermo-ecological limits [i.e. critical thermal minimum (CT_{min}) and maximum (CT_{max}), which are the thresholds to death or represent the inability to move] or shifts in performance traits among life-history stages, which can have rather soft and different thermal dependent responses affecting fitness (Wilson et al. 2000; Bodensteiner et al. 2021). In amphibians, ontogeny is complex by comprising four distinct life-history stages (i.e. egg, larva/tadpole, metamoph, adult). However, in the past, all studies on amphibians using SDMs have focused on the adult stage, while other life-history stages have been neglected. Despite this, the larval/tadpole stage might be of special interest for an amphibians' distribution as it can last for several weeks, months or even years and it is very sensitive to environmental changes such as pond drying (Sinai et al. 2022). Furthermore, tadpoles represent an important life-history stage because they provide greater opportunity for selection than adults. Due to large clutch sizes in many amphibian species accompanied by often high mortality rates of larvae, they provide ideal model organisms to study selection processes in different life-history stages as genetic and phenotypic variation of tadpoles may be weeded out before selection acts on adults. Furthermore, tadpoles as a life-history stage may have greater capacity for phenotypic plasticity than adults i.e. due to predation pressure (Buskirk and Relyea 1998; Middlemis Maher et al. 2013; Mori et al. 2017), environmental stress (Denver 1997; Bókony et al. 2021), increasing larval density (Gouchie et al. 2008), or different diet (Katayama et al. 2021). In addition, due to different physiological responses of different life-history stages, one life-history stage of a species might be more limited by physiological constraints than other stages and might be a "weak link" for the species in the context of biological invasions.

Previous studies, irrespective of whether they use correlative or mechanistic SDMs, focus on only a few key ecological processes, such as species' dispersal ability and biotic interactions, while mechanisms such as phenotypic plasticity and local adaptation have not been addressed (Garzon et al. 2019). Both mechanisms may occur in natural populations and vary across a species' range. Indeed, performance traits may strongly differ among populations (Savolainen et al. 2013; Valladares et al. 2014; Des Roches et al. 2018). Phenotypic plasticity involves the capacity of a single genotype to express different phenotypes across environmental conditions (Nicotra et al. 2010). In contrast, local adaptation involves selection acting on heritable traits (Savolainen et al. 2013). Recently, a few SDM approaches have addressed local adaptation and phenotypic plasticity (Valladares et al. 2014; Hällfors et al. 2016; Des Roches et al. 2018, as reviewed in Garzon et al. 2019). However, these trait-based SDMs have mainly been applied to plant species (Garzon et al. 2019, reviewed in Peterson et al. 2019). thus, there is still a need to integrate evolutionary processes in predictive modelling of animal invasions.

The African Clawed Frog, *Xenopus laevis* (Daudin, 1802), is one of the world's most widely distributed amphibian species occurring on five continents with an ongoing expansion of its invasive range in many areas (Measey et al. 2012; Ihlow et al. 2016; Wang et al. 2019). The species shows broad tolerance to a variety of environmental conditions (Tinsley and Kobel 1996). Historically, *X. laevis* was exported to be used for human pregnancy testing, laboratory research (Gurdon and Hopwood 2003; van Sittert and Measey 2016 2016) and the pet trade (Herrel and van der Meijden 2014; Measey 2017). In Europe, the species has established populations in Portugal (Rebelo et al. 2010), Italy (Lillo et al. 2005) and France (Fouquet 2001) with a predicted potential expansion of up to 2 million km^2 for Europe (Ginal et al. 2021), such that it is now listed as an invasive species of Union concern (EU Regulation no. 2022/1203). Among the invasive European populations, Western France is of particular concern due to its ongoing expansion for 40 years, now occupying an area of 4000 km^2 (Vimercati et al. 2020). Furthermore, a broad knowledge base of its physiology and morphology (Louppe et al. 2018; Herrel et al. 2019; Padilla et al. 2019, 2020; Kruger et al. 2022), locomotor performance (Louppe et al. 2017; Araspin et al. 2020), reproduction (Courant et al. 2017), behaviour (Kruger et al.

2019), and genetics (De Busschere et al. 2016) has been established. Rödder et al. (2017) showed that the oceanic temperate climate experienced by the French population is different from the native South African climate, which was interpreted as a shift in the realized climatic niche. Recent laboratory performance trials, of adult frogs from two native South African (Western Cape and KwaZulu-Natal) populations and one European (France) population, revealed a shift in the locomotor performance, represented by the proxies endurance time and distance, of the French population, suggesting local adaptation to the cooler European climate (Araspin et al. 2020). This shift may represent a change in the species´ fundamental climate niche. However, these data are restricted to adult specimens and similar data is lacking for other life-history stages like tadpoles. Moreover, it is currently unknown how the local adaptation of *X. laevis* relates to its potential geographic distribution.

Consequently, we tested the following hypotheses: (1) considering the shift in temperature dependent performance of adult frogs from France, we hypothesize that the French population exhibit increased in activity time in the invasive European range that could be devoted to fitness-relevant activity, and (2) tadpoles may have less activity time available than adult frogs from the same range because larval stages may be more sensitive to environmental conditions like temperature variation. We assess how temperature-dependent performance traits translate into activity time budgets and to what degree local adaptation and differences in the thermal responses of life-history stages may foster invasion success. We used performance data in a mechanistic framework to compute performance curves which were selected based on generalized additive mixed models (GAMMs) ranked by information criteria. Best fitting performance curves were used to predict the hours of activity and to compare the potential activity time budgets for two life-history stages (adults and tadpoles) of two native and one invasive population.

Methods

Selection of sampling sites, specimens and traits

Numerous studies have shown that the most likely origin for European *X. laevis* populations is the south-western Cape of South Africa's winter rainfall region (De Busschere et al. 2016; van Sittert and Measey 2016; Rödder et al. 2017; Measey et al. 2020), while the origin of the French population is likely a mixture of two clades from South Africa's winter and summer rainfall region (De Busschere et al. 2016). Under laboratory conditions, we assessed fitness-relevant locomotor performance because it has been shown to have important ecological relevance and is also correlated with individual fitness (Burggren and Warburton 2007; Gvoždík and Van Damme 2008). Herein, we used performance datasets from two previous studies. For adult frogs, Araspin et al. (2020) measured endurance distance (EndDist), which is relevant in the context of mate-searching or dispersal and they found rapid shifts in the temperature dependence of locomotor performance. For tadpoles, maximum velocity (MaxVel) was recorded by Kruger (2020) and Wagener et al. (2021), which is relevant in the context of predator escape. They used common garden experiments to determine whether tadpoles with varying parental origins show adaptive phenotypic variation related to different temperatures experienced in parental environments. For thermal performance trials and breeding of adults, we used specimens collected in the native region from KwaZulu-Natal (summer rainfall region, data from Wagener et al. 2021) and Stellenbosch (Western Cape province, winter rainfall region, Kruger 2020), South Africa and the French invasive area from the Département Deux-Sèvres, France (data from Kruger 2020; Araspin et al. 2020). For climatic information of the three regions see Supplementary Material S1.

Performance of adults

Performance was measured for frogs of both sexes from KwaZulu-Natal (N = 13, 6 males, 7 females), from the Western Cape (N = 13, 4 males, 9 females) and from France (N = 40, 21 males, 19 females; for details see Araspin et al. 2020). EndDist, the distance travelled until exhaustion, was recorded by chasing adult *X. laevis* individually across a 3 m long circular track with a humified cork substrate (Herrel and Bonneaud 2012; Louppe et al. 2017). Frogs were considered exhausted when a specimen was no longer able to right itself. Performance was measured at 19 °C, 23 °C, 27 °C and 31 °C. After each trial, the frogs were returned to their aquarium, fed and left to rest for at least two days. Trials were repeated twice per specimen and the maximal distance was used for further analyses (for details see Araspin et al. 2020). Critical thermal limits were determined by placing the same individuals, which were already used for the performance trials, in containers within an incubator where temperature was increased or decreased slowly (as detailed in Araspin et al. 2020). Animals were inspected regularly for a lack of righting response. Once animals were unable to turn over after being placed on their backs, we considered that temperature to be the animal's critical temperature (Araspin et al. 2020).

Performance of tadpoles

Wild-caught *Xenopus laevis* adults from South Africa (n = 7) and France (n = 4) were bred to produce F1-tadpoles used in all performance experiments. We followed the breeding and husbandry guidelines by Schultz and Dawson (2003) and the OECD (2008) described in Wagener et al. (2021). Tadpoles from each breeding pair were raised at a water temperature of 20.0 °C. The preferred rearing and holding temperatures are between 18 and 24 °C, this aligns with the daily average temperature in their native region during the active period for tadpoles (Schultz and Dawson 2003; OECD 2008; Wagener et al. 2021). 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 individuals L^{-1}. Tadpoles were kept at high densities to slow development rates that would otherwise increase variation of tadpole size tested on subsequent days (Tejedo and Reques 1994).

We followed an adapted version of the protocol to measure velocity of tadpoles in response to acute temperature designed by Wilson et al. (2000) (see Wagener et al. 2021 for details). *Xenopus laevis* tadpoles were lab-reared until NF stage 45–47 (Nieuwkoop and Faber 1994). Tadpoles were tested for burst swimming speed at five temperatures: 5 °C, 10 °C, 20 °C, 30 °C, and 35 °C. Temperatures were verified with a thermocouple (to the nearest 0.01 °C). Each tadpole was only tested once at one test temperature and then euthanized by an overdose of tricaine methanesulfonate (ms-222). Performance was measured for 20 tadpoles from the Western Cape, 30 tadpoles from KwaZulu-Natal and 50 tadpoles from France for each temperature level (see Kruger 2020).

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 (verified with a thermocouple to the nearest 0.01 °C). 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 L min^{-1}, pressure = 0.35 bar) maintained the desired water temperature (for figures see Supplementary Material S2 and S3).

High-speed videos were filmed of the bottom of the tank and the image in the mirror. All burst swimming sequences were visually proofed and only recordings perpendicular to the camera were retained. We used the motion analysis software Tracker (Open Source Physics; Brown 2012) 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 2004) 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.

Critical thermal limits of tadpoles were tested by placing tadpoles individually in a two-compartment cooling/heating chamber (described in Wagener et al. 2021). Tadpoles were placed in the inner chamber which exchanged heat with the outer chamber through which water was pumped at an adjustable rate. Prior to heating (CT_{max}) or cooling (CT_{min}), tadpoles were allowed 10 min to acclimate. Individuals were exposed to a constant heating/cooling rate of 0.3 °C. min^{-1} until an endpoint was attained. The endpoint was determined when a tadpole was unable to right itself after 30 s. CT_{max} and CT_{min} was then recorded as the water temperature beside the tadpole, verified with a thermocouple (to the nearest 0.01 °C). Critical thermal limits were measured for 8 tadpoles from the Western Cape, 48 tadpoles from KwaZulu-Natal and 8 tadpoles from France for each critical thermal limit.

Mechanistic modelling

The two thermal performance datasets (i.e., adults and tadpoles) were tested for significant differences among the three populations using the *pairwise.wilcox.test()* in R ver. 3.6.2 (R Core Team 2019). Based on laboratory performance trials, we computed temperature dependent performance functions for adults and tadpoles using the *PerfGAMM()*-function of the *Mapinguari* package (Caetano et al. 2019; Sinervo, *unpubl.*) for R. The function uses generalized additive mixed models (GAMMs), selected by Akaike Information Criterion (AIC), with temperature as a smooth predictor. The performance functions were scaled to population specific measures of critical thermal minimum (CT_{min}) and maximum (CT_{max}), wherein at both extremes a performance of zero is assumed. Furthermore, the function was projected on an array of temperatures ranging between CT_{min} and CT_{max} with 0.1 °C increments to calculate the optimum temperature (T_{opt}); i.e. the temperature where the highest performance value is reached. Afterwards, we computed the minimum and maximum temperatures at the 80% maximum performance breadth interval (T_{pb80}) for each population and life-history stage. Even if critical thermal limits among different populations or life-history stages may be similar, the T_{pb80} may differ strongly (Taylor et al. 2021).

Monthly temperature minimum, maximum, and averages for South Africa and Europe with a spatial resolution of 2.5 arc min were obtained from www.worldclim.org (Hijmans et al. 2005) as environmental layers. Daily hours of activity were estimated applying the model of Sinervo et al. (2010) in the *Mapinguari* package (*sin_h()*-function, upper and lower limits of T_{pb80} with monthly minimum and maximum temperatures as covariables and a temporal resolution of 15 min; Caetano et al. 2019). The function estimates the activity time budget of a species while simulating daily variation in temperature for each grid cell by applying a sine function between daily thermal limits and counting the time above a specific threshold (T_{pb80} limits herein). Total available activity times were computed by subtracting time above the T_{pb80} upper limit from time above the lower limit. We used the *biovars()*-function of the *dismo* package (Hijmans et al. 2017) to create activity layers for annual activity, activity during the warmest quarter and activity during the coldest quarter. As these bioclimatic variables cover different time spans, we rescaled the activity time budgets to 0–24 h, allowing to compare differences between population or life-history stages as fractions on a daily basis. To obtain the activity time for each population and life-history stage, we extracted the respective values from the activity layers by using occurrence records from the native (616 records) and invasive populations (425 records). The activity time budgets were classified into the categories low (0–6 h/day), moderate (6–12 h/day) and high (more than 12 h/day). Finally, we subtracted the activity budgets based on performance of the European population in Europe to obtain the energetic differences for each population and life-history stage as follows: France—KwaZulu-Natal, France—Western Cape, KwaZulu-Natal—Western Cape. Boxplots are used to visualise the differences between the respective medians, minima and maxima for activity time.

Results

For adult frogs, the pairwise Wilcoxon test reveals that thermal performance breadth intervals (T_{pb80}) are significantly different between the invasive and the two native populations ($p < 0.05$), but not significant for the other groups (Tables 1 and 2, Fig. 1). The lower limit for T_{pb80} is lowest for the French population, followed by the Western Cape population and then KwaZulu-Natal individuals. The upper limit is also lowest for the French population, followed by Western Cape and then KwaZulu-Natal animals. Optimum performance temperature (T_{opt}) is lowest

Table 1 Results of the pairwise Wilcoxon test for adult and tadpole *X. laevis* among the French (FR), KwaZulu-Natal (KZN) and Western Cape (WC) populations (p-values)

Life-history stage		FR	KZN
Adults	KZN	0.010	–
	WC	0.019	0.864
Tadpoles	KZN	0.550	–
	WC	0.210	0.550

Table 2 Thermal performance breadth interval (T_{pb80}) for the two life-history stages (adults and tadpoles) of the two native South African (Western Cape = WC, KwaZulu-Natal = KZN) and the invasive French (FR) population

Life-history stage	Population	T_{pb80} Lower limit	T_{pb80} Upper limit
Adults	FR	12.1	22.4
	WC	14.4	26.4
	KZN	18.4	26.5
Tadpoles	FR	14.3	31.9
	WC	13.1	34.9
	KZN	19.9	36.7

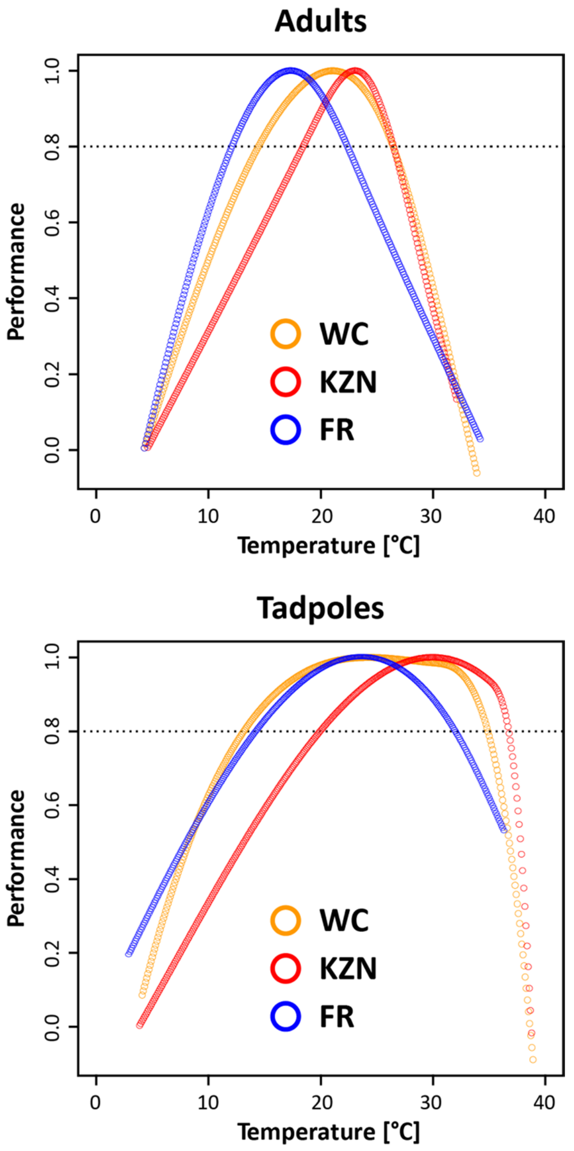


Fig. 1 Thermal performance curves including 80% performance breadth (T_{pb80}) of adults and tadpoles of *Xenopus laevis* from the invasive (France—FR) and native (Western Cape—WC and KwaZulu-Natal—KZN) range

for the French frogs, followed by the Western Cape and then KwaZulu-Natal individuals.

For tadpoles, the lower limit for T_{pb80} is lowest for the Western Cape population, followed by the French population and the KwaZulu-Natal tadpoles. The upper limit is lowest for the French population, followed by Western Cape and then KwaZulu-Natal tadpoles. Tadpoles show a similar pattern for T_{opt} as adult frogs, which is lowest for the French population, followed by Western Cape and then KwaZulu-Natal tadpoles. The average performance values of adults and tadpoles at the respective tested temperatures are provided in the supplementary material (Supplementary Material S4).

Differences among adult frogs

The annual activity of adult frogs from the invasive French population shows a moderate to high potential for activity across most parts of Europe (excluding cold mountain ranges like the Alps and Pyrenees) with highest activity time budgets in the Mediterranean and oceanic regions (Fig. 2). In comparison, adult frogs from the Western Cape population show lower potential for activity with mainly moderate values across Europe. Adult frogs from the KwaZulu-Natal population show the lowest potential for activity across Europe with low to moderate values.

For the activity during the warmest quarter, our results suggest that adult frogs from the invasive French population show a low to moderate potential for activity across most parts of Europe with highest potential for activity in the Mediterranean and oceanic regions (Fig. 2). Compared to the French specimens, adult frogs from the Western Cape population show a lower potential for activity with low values across most parts of Europe and only a moderate potential for activity in some coastal regions. Adult frogs from the KwaZulu-Natal population show the lowest activity across Europe with low values across the whole of Europe.

For the activity during the coldest quarter, adult frogs from the invasive French population show a

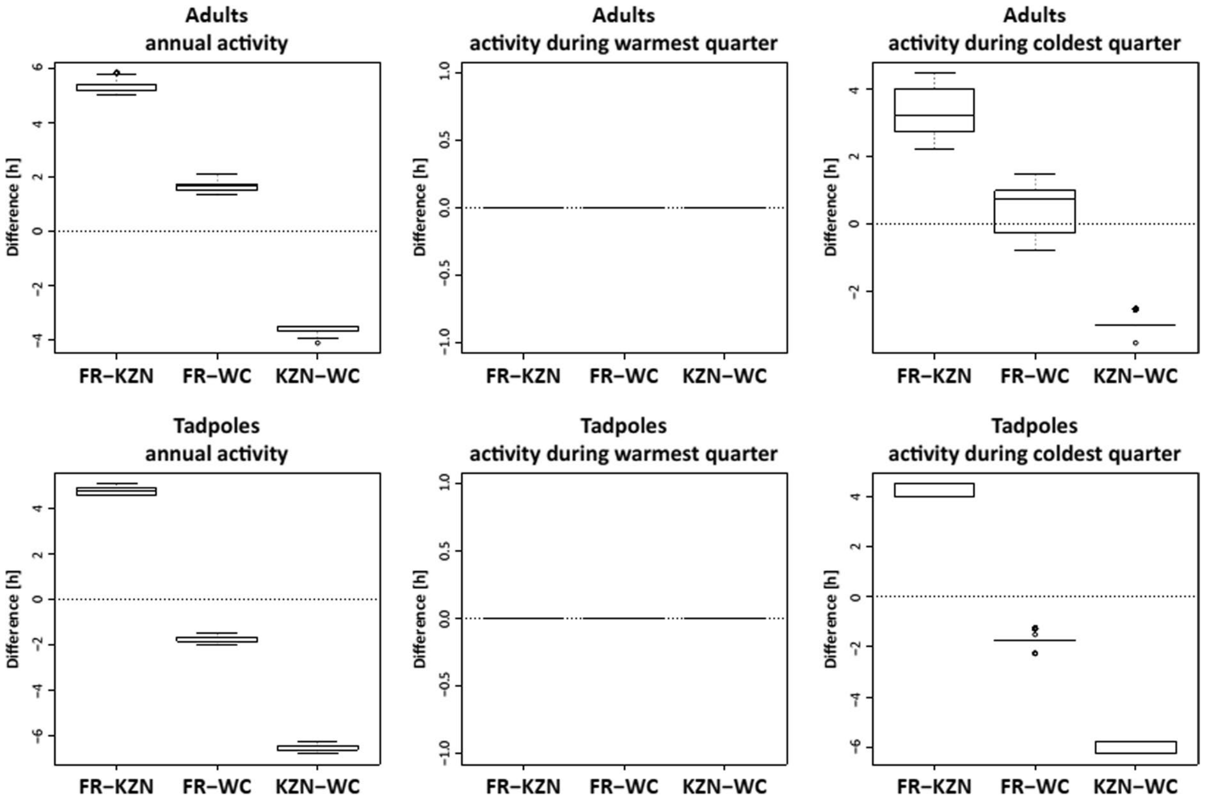


Fig. 2 Activity time budgets for annual activity, activity during the warmest quarter of the year and activity during the coldest quarter of the year of adult and tadpole *Xenopus laevis* for the invasive European range of one invasive (France- FR) and two native (Western Cape—WC and KwaZulu-Natal—KZN) populations. Activity time budgets are scaled to daily activity (0–24 h)

moderate to high potential for activity across most parts of Europe (excluding cold mountain ranges like Alps or Pyrenees) with highest potential for activity in the Mediterranean and oceanic regions (Fig. 2). Compared to the French frogs, adult frogs from the Western Cape population show a lower potential activity with moderate values across Europe. Adult frogs from the KwaZulu-Natal population show the lowest potential activity across Europe with low to moderate values.

Adult French frogs appear to have more time available for activity in Europe (Fig. 3). Annually, an average difference of 5 h more per day (compared to animals from KwaZulu-Natal) or respectively 1.5 h more per day (compared to animals from the Western Cape) is available for activity to the French frogs. While during the coldest quarter, the French frogs have 3 h more per day (compared to animals from KwaZulu-Natal) or respectively 1 h more per day (compared to animals from the Western Cape), no differences in the activity time budget were found during the warmest quarter.

Differences among tadpoles

Our results indicate that for annual activity, tadpoles from the native Western Cape population show moderate potential for activity across most parts of Europe (excluding cold mountain ranges like the Alps or Pyrenees) with highest potential activity in the Mediterranean and oceanic regions (Fig. 2). French tadpoles perform similarly well but show a less contrasting pattern than the Western Cape tadpoles with mainly moderate potential activity in continental Europe. Tadpoles from the KwaZulu-Natal population show the lowest potential for activity across Europe with low to moderate values.

For activity during the warmest quarter, the map indicates that tadpoles from the native Western Cape population may have low to moderate activities across most parts of Europe with highest potential for activity in the South-western Iberian Peninsula (Fig. 2). French tadpoles show similar activity patterns, but with moderate values only at the South-Western coastal regions of the Iberian Peninsula. Tadpoles from the KwaZulu-Natal population show the lowest potential for activity across Europe with low values across all areas.

For activity during the coldest quarter, tadpoles from the native Western Cape population show moderate to high potential activity across most parts of Europe (excluding cold mountain ranges like Alps or Pyrenees) with highest potential for activity in the Mediterranean and oceanic regions (Fig. 2). French tadpoles perform with a similar activity budget, but mainly show a moderate potential activity in continental Europe. Tadpoles from the KwaZulu-Natal population show the lowest activity budgets across Europe with low to moderate values.

Our results suggest that compared to adult frogs, French tadpoles do not necessarily have more time available for activity in Europe (Fig. 3). While annually, an average difference of 4.5 h more per day (compared to KwaZulu-Natal) is available for activity time of the French tadpoles. The activity time of the French tadpoles compared to Western Cape animals is 2 h less per day. As for adult frogs, during the warmest quarter of the year, the activity time among the populations were identical for tadpoles. During the coldest quarter, the French tadpoles have 4 h more available for activity per day (compared to KwaZulu-Natal) or 1.5 h less per day (compared to Western Cape).

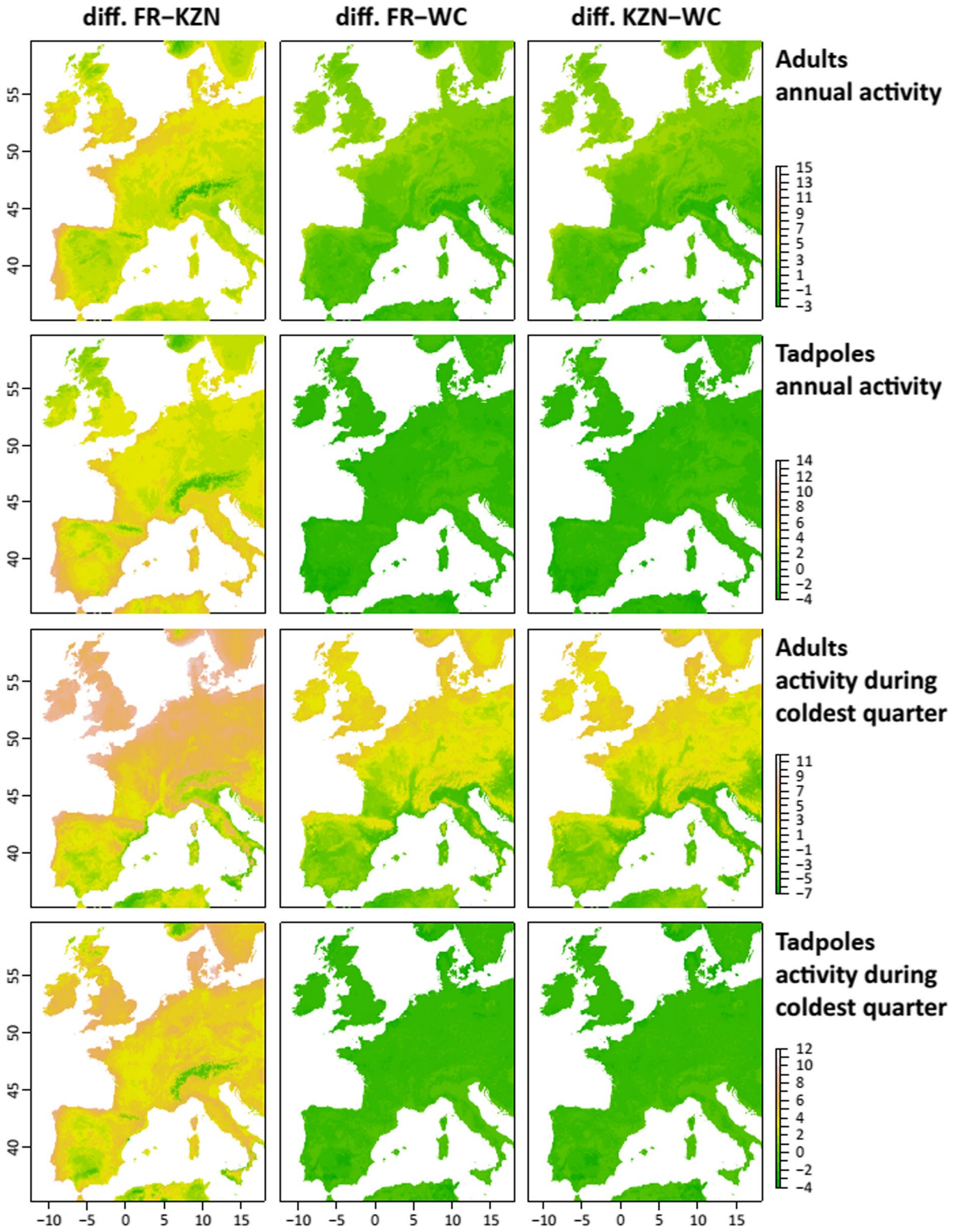
Discussion

For adult frogs and tadpoles, we found that the differences in daily activity time in Europe are highest between the French and the KwaZulu-Natal individuals regardless of life-history stage, followed by the difference between the French and the Western Cape population, and then between the two native South African populations. Our results suggest that for the European range, annual activity time budgets, as well as activity time budgets during the warmest and coldest quarter are highest for the French population, followed by activity time of the Western Cape and then KwaZulu-Natal animals. Furthermore, in adults T_{pb80} was distinctly lower among the two native and invasive populations with a left-shift in temperature-dependence of performance for the French population, while for tadpoles no significant differences were found.

Differences among native and invasive populations

Physiological processes of ectotherms such as muscle contraction are strongly dependent on environmental conditions (i.e. temperature; James et al. 2012; Padilla et al. 2020) and affect performance traits like locomotion (Feder and Burggren 1992; Herrel and Bonneaud 2012; Wilson et al. 2000; Padilla et al. 2020). The higher activity time budget of French adult frogs compared to the South African populations should allow the French animals to spend more time on dispersal, foraging or mating (Measey 2016; Courant et al. 2019a, b). Further, escape from predators may be hampered as well (see Eggert and Fouquet 2006). While during the warmest quarter of the year, no differences in the activity time budgets among the populations were found, during the coldest quarter, the French adult frogs have 3 h (compared to KwaZulu-Natal) or 1 h (compared to Western Cape) more available for activity per day. This may be crucial in a period when activity time is minimal due to suboptimal climatic conditions and allows adult frogs to spend more time on foraging and feeding on prey.

Compared to adult frogs and tadpoles of KwaZulu-Natal, the differences in activity time are lower between the French and Western Cape animals. This is not surprising, considering that most of the European populations originate from Western Cape animals (De Busschere et al. 2016). However, the French population consists of animals of two genetic lineages, from the Western Cape and northern South Africa, including the KwaZulu-Natal area that we tested (De Busschere et al. 2016). The admixture of several genetic lines can boost the expansion of invasive species (Sakai et al. 2001; Frankham 2005; Krehenwinkel et al. 2015), and our results suggest that this has been the case in the invasion in Western France. The increased activity time might be especially beneficial during the tadpole stage. The tadpoles of *X. laevis* are pelagic filter feeders, increased


diff. FR–KZN
diff. FR–WC
diff. KZN–WC
Adults annual activity
15 13 11 9 7 5 3 1 −1 −3
Tadpoles annual activity
14 12 10 8 6 4 2 0 −2 −4
Adults activity during coldest quarter
11 9 7 5 3 1 −1 −3 −5 −7
Tadpoles activity during coldest quarter
12 10 8 6 4 2 0 −2 −4
55 50 45 40
−10 −5 0 5 10 15

◂**Fig. 3** Differences in activity time budgets for annual activity and activity during the coldest quarter of the year of adult and tadpole *Xenopus laevis* for the invasive European range of one invasive (France—FR) and two native (Western Cape—WC and KwaZulu-Natal—KZN) populations. Activity time budgets are scaled to daily activity (0–24 h)

activity time for swimming and feeding may promote growth and fecundity of juvenile frogs (Gouchie et al. 2008), which might be a contributing factor to the success of the French invasion. It is known that within their native range, populations differ in their adaptive and plastic responses with respect to development, morphology and survival (Kruger et al. 2022).

Our study supports the findings of Araspin et al. (2020), finding a left-shift of the thermal optimum in locomotor performance of adult frogs due to the cooler French climate, either caused by local adaptation or phenotypic plasticity. It is known that *X. laevis* shows high phenotypic plasticity among native populations (Du Preez et al. 2009), including plasticity in physiological traits (Wagener et al. 2021; Kruger et al. 2022). However, we suggest that selection caused by novel climatic conditions may have driven local adaptation in the French population rather than plasticity; but this assertion requires further experimentation to determine the potential for different traits to respond in an adaptive and/or plastic nature. This result supports the hypothesis of a shift in the fundamental climatic niche. However, the real differences in activity time budgets among the populations might differ from our calculations as mechanisms such as adaptive behaviour (e.g. by searching climatically suitable microhabitats) might to some degree reduce differences in activity time among populations.

Differences between life-history stages

Different life-history stages of an organism may have different responses in their temperature dependent performance and activity time (Wilson et al. 2000; Bodensteiner et al. 2021). However, in contrast to adult amphibians (Orille et al. 2020), the knowledge about thermal tolerance or temperature-dependent activity of tadpoles is limited (Wilson et al. 2000; Ruthsatz et al. 2018). Although, it was already assumed that thermal limits among different life-history stages of *X. laevis* may differ (Balinsky 1969; Nelson et al. 1982; Wu and Gerhart 1991). Comparing the results obtained for adults and tadpoles, our results suggest that activity time is consistently higher in French compared to Western Cape adult frogs, while lower for tadpoles, which reveals that French tadpoles have less time available for activity in Europe than Western Cape tadpoles. This suggests that tadpoles may be more constrained by physiological limits compared to adult frogs, which could indicate a possible weak link in the European *Xenopus* invasion. In France, breeding was observed between April and June from late spring to early summer (Courant 2017), and metamorphosis duration can be variable depending on food intake and temperature but metamorphosis can be achieved within two months after fertilisation (Nieuwkoop and Faber 1994; Kruger et al. 2022). Therefore, the tadpole stage is mostly active during the summer months where the models suggest no differences among populations. Only adults are likely experiencing thermal selection pressures in the winter, when tadpoles have already metamorphosed. Adults in France have been found to experience selection pressures during spatial sorting which results in the enhancement of their dispersal ability at the periphery (Louppe et al. 2017, 2018; Courant et al. 2017; Courant et al. 2019a, b; Padilla et al. 2019). Tadpoles of *X. laevis* do not experience the same selection pressures as adults with no suggestion that spatial sorting occurs (Kruger et al. 2021). This can be due to decoupling of traits whereby variation of a trait takes place at a particular life-history stage without affecting the expression of traits in other life-history stages (Moran 1994; Sherrat et al. 2017). Therefore, each stage can experience a unique set of constraints and selection pressures (e.g. Bonnet and Blair 2017; Kruger et al. 2021).

We found that the T_{pb80} of tadpoles is much broader than that of adult frogs. It is known that even if critical thermal limits of ectotherms, like amphibians, have little inter- or intra-specific variation, their T_{pb80} might be very different. Moreover, thermal responses among life-history stages may differ (for a recent review see Taylor et al. 2021). However, it should be noted that locomotor performance traits (endurance distance for adult frogs and maximum velocity for tadpoles) respond differently to temperature. While endurance is a proxy for sustained locomotion, maximum velocity represents burst performance. Although more unlikely, it could be possible that the broader performance breadth of tadpoles results from a broader thermal tolerance, which shifts during metamorphosis (Cavieres et al. 2016; Wilson et al. 2000).

We did observe a left-shift in the optimum for locomotor performance of French tadpoles, but the Wilcoxon test indicated no significant differences among the three populations (Table 1, Fig. 1), which may suggest that tadpoles did not go through such a strong thermal dependent selection as adult frogs. Our results revealed that the lower limit of T_{pb80} for the Western Cape tadpoles is closer to that of the French animals. The upper limit for Western Cape tadpoles is closer to those of the tadpoles from KwaZulu-Natal, but both adaptive and plastic differences may still be present (see Kruger et al. 2022). The French tadpoles may thus also show local adaptation to the cooler European climate (compared to climate charts according to Zepner et al. 2020; Supplementary Material S1), indicating a starting shift in the fundamental climatic niche of tadpoles.

This shift seems not to be as strong as for the adult frogs but might increase their chances to survive, successfully escape from predators and/or search for food, which in turn allows faster growth. Further, Western Cape tadpoles adapted to the broadest temperature range, while KwaZulu-Natal tadpoles are more restricted to higher temperatures. This might be due to breeding times. In the summer rainfall region, breeding takes place from September to mid-March from spring to summer (Balinsky 1969). Whereas, in the winter rainfall region breeding takes place from July to September from winter to the onset of spring (Kalk 1960). The performance curves and activity maps of adults and tadpoles suggest that KwaZulu-Natal animals would have much lower chances to establish populations in Europe compared to Western Cape animals. It would be of particular interest to know how the intense selection during this French invasion has acted on genes from the great diversity in the available gene-pool (see de Busschere et al. 2016).

Comparison with previous correlative and mechanistic SDM approaches for Europe

In the past, several correlative approaches tried to predict the invasion risk of *X. laevis* for Europe (i.e. Measey et al. 2012; Ihlow et al. 2016; Rödder et al. 2017). However, correlative approaches all demonstrate the caveat that their predictions can reflect the realized niche of a species only, while the physiology of a species and its critical thermal thresholds as well as local adaptation or different life-history stages are neglected. A recent ecophysiological approach from Ginal et al. (2021), which was also the precursor for this study, provided the first mechanistic SDMs for Europe. According to our knowledge, this was also the first time different life-history stages of an amphibian (tadpoles and adults) were included for modelling purposes. The mechanistic predictions clearly showed a much higher potential invasive risk of *X. laevis* with c. 2 Million km^2 of predicted suitable area in Europe, which is an area up to twice as large as that predicted by the worst-case scenario of the correlative approaches. The authors presented three different models, one including adult frogs only, the other including tadpoles only and the third one including adults and tadpoles together. However, the models' predictions for the native South African range differed from each other, the predictions for Europe revealed the same size of predicted area, which might indicate that tadpoles as a life-history stage might have no impact on the size of potentially colonisable area. In contrast, our findings of this study clearly demonstrate that French tadpoles have less time for activity in Europe compared to their native South African progenitors and are constrained by physiological limits, while adult French frogs already adapted to the much cooler European climate.

Conclusion

The results of our novel approach suggest that invasive populations are able to adapt to novel environments by going through a shift in their fundamental Grinnellian niche, which results in more time available for activity. This gain in the activity time budget might allow individuals to survive and reproduce better, as a result of enhanced foraging or predator evasion, and might allow populations to expand in novel environments. Furthermore, the investigation of temperature-dependent responses of different life-history stages gives deeper insights into the physiology and invasion biology of a species and allows us to identify the life-history stage limiting the geographical expansion of a population. Both types of information, local adaptation and stage limited expansion, are crucial for the risk assessment of alien invasive species. Our study suggests that accounting for local adaptation in the different life-history stages of invasive populations might greatly improve the robustness or reliability of SDM predictions, even those using mechanistic approaches.

Funding Open Access funding enabled and organized by Projekt DEAL. This work was supported by the ERANET BiodivERsA grant INVAXEN, with the national funders Agence Nationale de la Recherche (ANR), Deutsche Forschungsgemeinschaft (DFG), Belgian Federal Science Policy Office (BELSPO), and Fundaçao para a Ciencia e a Tecnologia (FCT), as part of the 2013 BiodivERsA call for research proposals. INVAXEN "Invasive biology of *Xenopus laevis* in Europe: ecology, impact and predictive models". CW, NK, MM and JM thank the DSI-NRF Centre of Excellence for Invasion Biology (South Africa) and the National Research Foundation of South Africa (NRF Grant No. 87759 to JM). NK would like to acknowledge the Ambassade de France en Afrique du Sud (France). This study was part of the project Life Control Strategies of Alien Invasive Amphibians (CROAA)—LIFE15 NAT/FR/000864 funded by the Life program of the European Commission.

Data availability Data are available on request to the corresponding author.

Declarations

Conflict of interest Not applicable.

Ethics approval We thank the Communauté de Communes du Thouarsais and Communauté de Communes du Bressuirais for allowing access to sampling sites and for their technical assistance. Further, we acknowledge that in South Africa collections in KZN occurred under permission from KZN Wildlife (collection permit: OP 3169/2018, import permit: CN28-31–5262), while frogs in WC were collected under permission of CapeNature (CN15-31–5189).

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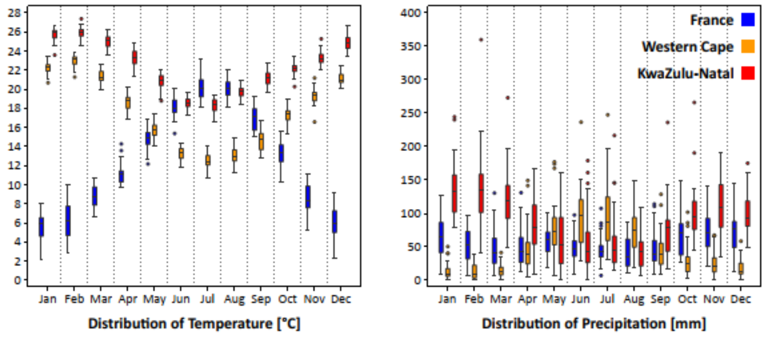
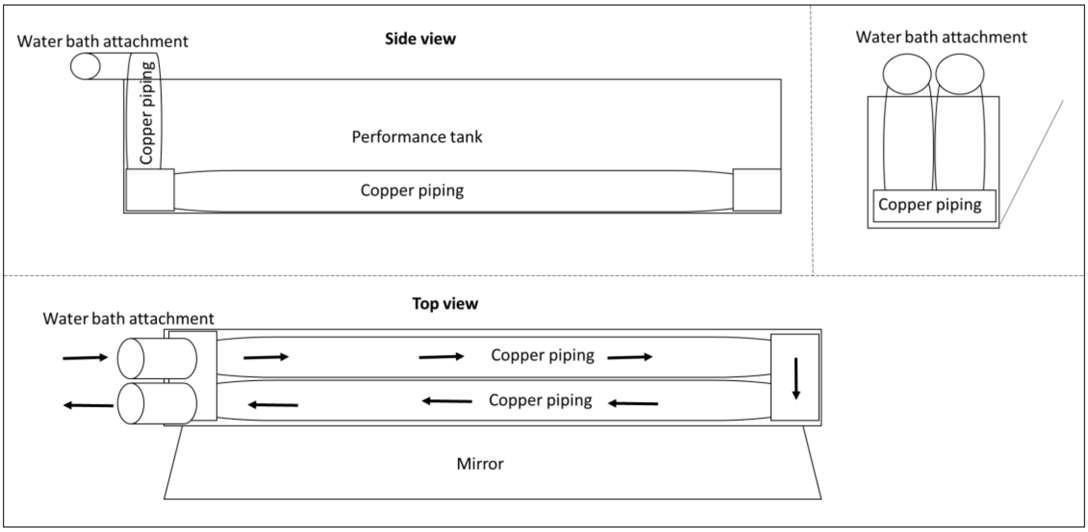
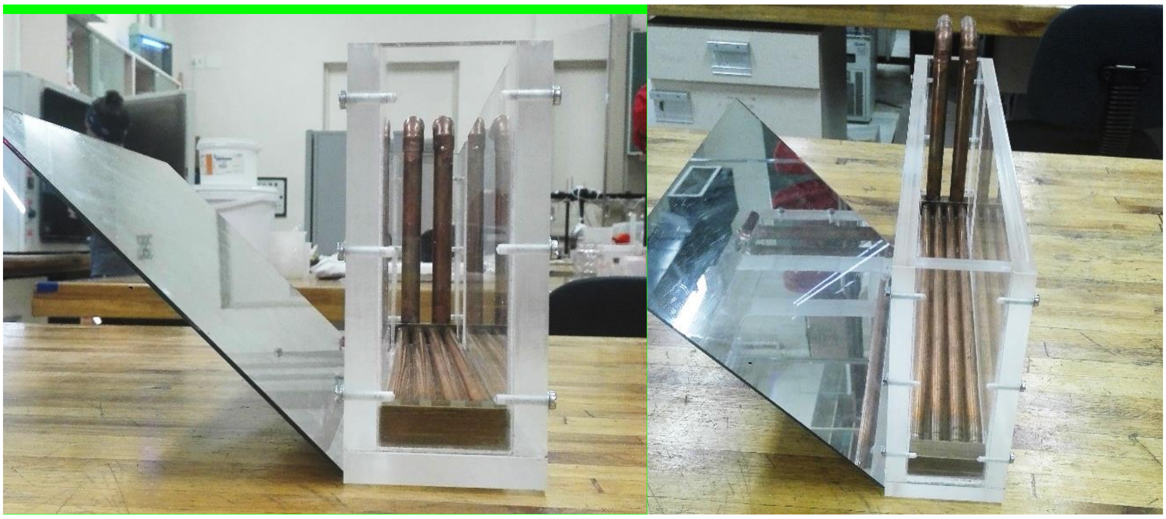
Supplementary Material



Supplementary Material S1: Climate charts showing the monthly temperature [°C] and precipitation [mm] in France (Europe), Western Cape (South Africa) and KwaZulu-Natal (South Africa).



Supplementary Material S2: Schematic figure of the tadpole burst swimming setup.



Supplementary Material S3: Photography of the tadpole burst swimming setup.

Life Stage	Population	CTmin [°C]	EndDist 19°C/ MaxVel 5°C	EndDist 23°C/ MaxVel 10°C	EndDist 27°C/ MaxVel 15°C	EndDist 31°C/ MaxVel 30°C	MaxVel 35°C	CTmax [°C]
Adults	FR	4.26 ± 1.00	2664.75 ± 895.89	2028.25 ± 529.81	1456.60 ± 435.77	1074.25 ± 287.17	-	31.86 ± 1.08
	WC	4.63 ± 1.21	3023.08 ± 1183.82	3197.39 ± 660.01	2375.38 ± 865.46	1507.69 ± 500.34	-	31.69 ± 1.17
	KZN	4.98 ± 1.76	2761.54 ± 593.95	3025.39 ± 726.57	2443.85 ± 443.26	1656.92 ± 351.79	-	31.25 ± 0.88
Tadpoles	FR	3.43 ± 0.41	3.79 ± 2.92	4.86 ± 2.23	6.10 ± 2.57	4.73 ± 2.19	5.50 ± 4.02	35.85 ± 0.57
	WC	4.36 ± 0.40	4.25 ± 2.14	6.81 ± 4.16	13.08 ± 5.22	10.68 ± 3.66	12.23 ± 2.23	38.30 ± 0.48
	KZN	4.18 ± 0.75	2.14 ± 2.02	6.15 ± 1.39	12.84 ± 3.36	13.97 ± 3.34	19.81 ± 3.71	37.83 ± 0.83

Supplementary Material S4: Average performance values ± SD of adults and tadpoles of three populations (France, Western Cape, KwaZulu-Natal) of *Xenopus laevis* tested at different temperature levels. Adults were tested at 19, 23, 27 and 31 °C, while tadpoles were tested at 5, 10, 20, 30 and 35 °C. For adults, performance was measured as endurance distance [cm], while for tadpoles, maximum velocity [MaxVel cm.s^{-1}] was recorded. The average critical thermal limits CT$_{min}$ and CT$_{max}$ for both life-history stages are provided [°C].