How to predict the future? On niches and potential distributions of amphibians and reptiles in a changing climate

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ERKLÄRUNG

Hiermit erkläre ich an Eides statt, dass ich für meine Promotion keine anderen als die angegebenen Hilfsmittel benutzt habe, und dass die inhaltlich und wörtlich aus anderen Werken entnommenen Stellen und Zitate als solche gekennzeichnet sind.

Dennis Rödder

“Geographic distributional areas are the shadows produced by taxa on the geographical screen. To study them one needs to measure ghosts”

A. RAPOPORT

“Most ecologists would agree that niche is a central concept of ecology, even though we do not know exactly what it means”

L. REAL and S. LEVIN

“Of course not. After all, I may be wrong.”

B. RUSSELL

CONTENTS

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AIMS AND OVERVIEW

Predictions of species distributions derived from correlative models can help to understand the spatial patterns of biodiversity and identification of possible threats for populations caused by climate change. The amount of available data and software is rapidly increasing as well as the number of studies applying niche model techniques. However, a discrepancy between increasingly complex studies and the understanding of underlying processes, derivation of valid assumptions, and the development of conceptual backgrounds is still a problem (JIMÉNEZ-VALVERDE et al. 2008). The aim of this thesis at hand is an assessment of the relative importance of macro-climate, biotic interactions and accessibility shaping realized distributions of amphibian and reptile species. The results are comprised in sections each with two or more complementary chapters linked with the research theme but distinct in the questions elucidated. It needs to be noted that the use of slightly different analysis methods used in this thesis mirror the improvements in modelling techniques and the wider availability of GIS data over the period this thesis has been conducted.

Section 1

The first section provides a general overview over the current knowledge concerning impacts of climate change on biota, niche concepts, availability of both climate and species occurrence data and the methods used herein. Additionally, potential ‘pitfalls’ when applying environmental niche models or climate envelope models are highlighted, illustrated and discussed using examples.

Section 2

The second section focuses on the structure of climate niches. Climatic variability within species ranges and habitat choice are analysed and discussed in the context of natural history properties and corresponding constrains on habitat choice of the respective species. In chapter 2.1, the hypothesise that climatic requirements allowing successful egg incubation and balanced sex ratios are the major driver for the geographic distribution of

Trachemys scripta is assessed. It is tested if the observed variation in monthly mean temperatures throughout the native distribution of *T. scripta* can be used as a predictor for its geographic range. The results confirm this hypothesis, although adaptive strategies such as nest site choice by females, plasticity in nesting phenology or regional variation in embryonic temperature sensitivity may exist. However, facing climate change, these adaptive strategies may account only for partial compensation of negative effects.

Recently, several authors observed a climatic mismatch between native and invasive ranges predicted by Climate Envelope Models (CEMs). In chapter 2.2, the issue of possible niche shifts in alien invasive species versus variable choice by deriving CEMs based on multiple variable sets is studied. The main result is that CEMs using variables focusing on the species physiology depicts its worldwide potential distribution better than any other approach. The results indicate that a natural history driven understanding is crucial in developing statistical models.

A necessary assumption when applying CEMs is that climatic niches are rather conservative, but recent findings of niche shifts during biological invasion indicate that this assumption is not valid in every case. As illustrated in chapter 2.2, selection of predictor variables may be one reason for observed shifts. In chapter 2.3, differences in climatic niches in the native and invaded ranges of the Mediterranean Housegecko (*Hemidactylus turcicus*) in terms of commonly applied climate variables in CEMs are assessed. It is analyzed which variables are more conserved versus relaxed (i.e. subject to niche shift) and assess degrees of niche similarity and conservatism per predictor and per set of predictor using both Hellinger distances and Schoener's index. The results indicate that the degree of niche similarity and conservatism varied greatly among predictors and variable sets applied. Shifts observed in some variables can be attributed to active habitat selection whereby others apparently reflect background effects.

Section 3

Section 3 of the thesis at hand focus on the relative importance of dispersal abilities, accessibility and biotic interactions shaping a species' realized distribution. Among reptiles two gecko species, *Hemidactylus frenatus* and *Hemidactylus mabouia*, have considerably increased their range during the last century. Only few sympatric populations are known. The aim of chapter 3.1 is the identification of areas potentially suitable for the geckos using a CEM approach, prediction of their potential distribution under current conditions, and an assessment why sympatric populations of both geckos are apparently rare. The results presented suggest that climatic suitable areas for both species can be found in nearly all tropical regions and allow the conclusion that both competitive exclusion and a non equilibrium in the ranges of the species explain the virtual absence of sympatric populations.

It was suggested that CEMs may be only of limited use if the target species' range is not predominately limited by unsuitable climate. In chapter 3.2, this hypothesis was tested using the alien invasive anuran *Eleutherodactylus coqui* as model species. The Coqui is presently distributed in many Caribbean islands and Hawaiian Islands. Using only native records within Puerto Rico for model training, climate envelope models indicate that the invasive range in the Hawaiian Islands can be predicted with high accuracy if predictors are carefully chosen. In chapter 3.3, the invasive alien Cuban treefrog *Osteopilus septentrionalis* native to Cuba, the Bahamas and some adjacent islands is used as a second example. As in chapter 3.2, the results indicate that the invasive range in Florida can be predicted with high accuracy using only native records within Cuba and the Bahamas for model training using appropriate predictor variables.

Biotic interactions such as competitive exclusion or predation may limit the realized distribution of species in some areas although climatic conditions are well suitable. In chapter 3.4 such a pattern as observed in the Brown tree snake (*Boiga irregularis*) is analyzed. The snake is native to South-East Asia and Australia and has been introduced to Guam. It is considered to belong to the 100 worldwide worst alien invasive species. In the larger vicinity of the snake's known distribution, highest suitability was found for the Northern Mariana and Hawaiian Islands, Madagascar, New Caledonia and Fiji Islands. However, although most East Asian mainland and islands are climatically suitable the invasive populations of this species do virtually not exist. The predicted potential distribution is highly coincident with the general distribution of the genus *Boiga*. Since *B. irregularis* does not coexist with other members of the genus or other potential competitors in its native range, competitive exclusion may be the best explanation for the observed pattern.

Next to macro-climate, anthropogenic habitat alteration has a strong impact on native biota and can significantly shape distribution patterns. *Eleutherodactylus johnstonei*, native to the northern lesser Antilles, has established numerous invasive populations at Caribbean islands and the adjacent Central and South American mainland. The species is a highly successful colonizer, but only able to invade anthropogenic disturbed habitats. In Chapter

3.5, a Climate Envelope Model approach is used to model the geographic distribution of this species and to project that model into other potentially threatened areas. Results obtained from the model are compared with a measure of anthropogenic habitat disturbance (Human Footprint).

Section 4

The focus of the last section is the breadths of climate niches, their evolution and dynamics in space and time. In chapter 4.1, information is provided on the climatic history within the range of *Phelsuma parkeri* native to the relatively flat island of Pemba (elevational range 0 to <100 m a.s.l.). A comparison with paleoclimatic conditions in the Last Glacial Maximum on Pemba revealed that *P. parkeri* and other endemic species of the island survived climatic conditions in the past completely different from the current climatic conditions despite absence of possibilities to compensate these changes by altitudinal range shifts. The results suggest that *P. parkeri* is currently unlikely to be threatened by climate change although projection of its current realized climate niche would suggest a complete range loss. The results of chapter 4.1 illustrate the importance of possible discrepancies between a species' realized nich and its fundamental niche when assessing climate change impacts.

In chapter 4.2 the disturbance vicariance hypothesis (DV) has been proposed to explain speciation in Amazonia and adjacent areas, e.g. in harlequin frogs (*Atelopus*). In this chapter, in concordance with DV predictions the expectations that (i) these amphibians display a natural distribution gap in central Amazonia; (ii) east of this gap they constitute a monophyletic lineage which is nested within in a pre-Andean/western clade; (iii) climatic envelopes of *Atelopus* west and east of the distribution gap are similar with some divergence in precipitation-related parameters; (iv) potential distributions of western and eastern *Atelopus* range into central Amazonia but with limited overlap, are tested.

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Chapter	Published or submitted to	Status
Section 1, in parts	**RÖDDER, D.**, S. SCHMIDTLEIN, S. SCHICK & S. LÖTTERS. Climate Envelope Models in systematics and evolutionary research: theory and practice. *In*: HODKINSON, T., M. JONES, J. PARNELL & S. WALDREN (eds): Systematics and Climate Change. Cambridge University Press. UK.	Submitted
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2.1	**RÖDDER, D.**, A. KWET & S. LÖTTERS. Translating natural history into geographic space: a macroecological perspective on the North American Slider, *Trachemys scripta* (Reptilia, Cryptodira, Emydidae). *Journal of Natural History*.	Submitted
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3.1	**RÖDDER**, **D.**, M. SOLÉ & W. BÖHME. 2008. Predicting the potential distribution of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). *North-Western Journal of Zoology* 4: 236-246.	Published
3.2	**RÖDDER**, **D.** 2009. 'Sleepless in Hawaii' – does anthropogenic climate change enhance ecological and socioeconomic impacts of the alien invasive *Eleutherodactylus coqui* Thomas, 1966 (Anura: Eleutherodactylidae)? *North-Western Journal of Zoology* 5: 16-25.	Published
3.3	**Rödder**, **D.**, & F. WEINSHEIMER. 2009. Will future anthropogenic climate change increase the potential distribution of the alien invasive Cuban treefrog (Anura: Hylidae)? *Journal of Natural History* 43: 1207-1217.	Published
3.4	**RÖDDER**, **D.**, & S. LÖTTERS. 2010. Potential distribution of the alien invasive Brown tree snake, *Boiga irregularis* (Reptilia: Colubridae). *Pacific Science* 64(1).	In press
3.5	**RÖDDER, D**. Human Footprint, facilitated jump dispersal, and the potential distribution of the invasive *Eleutherodactylus johnstonei* Barbour 1914 (Anura: Eleutherodactylidae). *Tropical Zoology*.	Submitted
4.1	**RÖDDER, D.**, O. HAWLITSCHECK & F. GLAW. Environmental niche plasticity of *Phelsuma parkeri* from Pemba Island, Tanzania: implications for conservation. *Tropical Zoology*.	Submitted
4.2	LÖTTERS, S., A. VAN DER MEIJDEN, T. E. KOESTER, T. KRAUS, E. LA MARCA, C. F. B. HADDAD, **D. RÖDDER** & M. VEITH. Testing vicariance *versus* dispersal in Amazonian harlequin frogs: an ecological niche modeling approach. *Biodiversity and Conservation*.	Submitted

SECTION 1: GENERAL INTRODUCTION

1.1. Species in a changing world[1]

The earth's climate has changed since the industrial revolution and future anthropogenic climate change undoubtedly will take place over the next decades (IPCC 2007). Today, the climate is warmer in most regions and extreme events such as excessive rainfall or drought tend to take place more frequent. Globally, the averadge annual temperature has increased by about 0.6-0.7 °C during the 20th century (IPCC 2007) and the rate, at which climate has changed, has almost doubled within the last decades (HOUGHTON et al. 2001). Such warming can not be explained by natural climate variability or factors such as volcanic activity. It may be rather caused by anthropogen activities: mankind is changing the Earth's climate on a global scale due to massive emissions of greenhouse gases and sulphate aerosols (STOTT et al. 2000; HOUGHTON et al. 2001; STOTT 2003; BARNETT et al. 2005).

HULME and VINER (1998) and MACCRACKEN et al. (2001) describe, among many other authors, the potential impacts of climate change. The global temperature is expected to rise globally, whereby the increase in middle and high latitudes and on the continents will be greater. Globally, the amount of annual rainfall will increase. Higher temperatures during the summer will regionally increase evaporation rates and reduce soil moisture, and more frequent storms and heavy rains are expected. In the tropics model projections suggest prolonged dry periods and a greater variability in seasonal rainfall patterns. Recently observed trends in tropical highland areas, where reduced cloud formation hence lower orographic precipitation (e.g. POUNDS et al. 1999), seem to meet these forecasts.

Of particular concern is the high rate of climate change affecting the world's biota (e.g. PARMESAN and YOHE 2003; THOMAS et al. 2004). Meta-analysis comparing responses of a wide range of different taxonomic groups to climate change across several biogeographical regions alredy indicate shifts in phenology and distribution patterns of many plants and animals (e.g. PARMESAN and YOHE 2003). These shifts may have effects on the reproductive success and thus on the survival of the species (e.g. BLAUSTEIN et al. 2001; ROOT et al. 2005). Changes in a species' phenology influencing intra-specific

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[1] Parts of Section 1 are in press as a book chapter to be published in 'Surviving on Changing Climate - Phylogeography and Conservation of Relict Species', Springer, and other parts were submitted as a book chapter to be published in 'Systematics and Climate Change', Cambridge University Press. The work reported in this section was conducted in collaboration with JOHANNES DAMBACH from the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany, SUSANNE SCHICK and STEFAN LÖTTERS from the University of Trier, Faculty of Geosciences, Germany, and SEBASTIAN SCHMIDTLEIN from the Geography Department, University of Bonn, Bonn, Germany.

interactions and thus existing (micro-) niche structures may have serve effects on species communities (PARMESAN and YOHE 2003).

There is much debate about species' responses to global warming which remains largely unknown, however. One assumption is that a high percentage of them may be committed to extinction (THOMAS et al. 2004). Background is that every species occurs within a defined climatic envelope, i.e. part of its fundamental niche, which is expected to lack the ability to adapt as rapid as climate will change (THOMAS et al. 2004). However, only limited robust data on the structure of species' climate niches and their ability to adapt to novel condicitons is currently available, which is often contra indicating and therefore mixed debated (e.g. PEARMAN et al. 2008).

It is well known that distribution patterns of species may vary over space and time. This becomes most evident considering the differences between current and Last Glacial Maximum (LGM, 21,000 y BP) distribution patterns of species in the northern hemisphere (see also e.g. HABEL et al. 2009). Most warm-adapted species experienced reduction and fragmentation of ranges because of intrusion by uninhabitable continental ice sheets causing distributional shifts and fragmentation of primary habitats. On the other hand, cold-adapted species were able to expand their ranges. Today, ranges of those species are restricted to current refugia as can be observed in glacial relict species, respectively. Understanding refugial distributions of species has been a core task in historical biogeography. Before the 1990s, refugia were preliminarily identified based on disjunctions of species distributions, distribution patterns of sister species, and the fossil records (e.g. HOFFMAN 1981). Unfortunately, historical biogeography is often descriptive making future projections difficult. More recently, phylogeographic approaches based on intraspecific molecular analyses and spatial modeling approaches based on ecological properties of species have been developed, but many theoretical concepts and techniques are still in their infanty.

1.2 Climate niches and the spatial distribution of species

The observation of ecological properties of species and their areas of distribution being related is not new (GRINNELL 1917; BÖHME 1978; JAMES et al. 1984), but the increasing availability of information on the variation of environmental parameters in geographic space, species distribution data, and computation capacities during the last decade now allow large scale assessments of relationships between distributions observed and explanatory parameters (KOZAK et al. 2008). Relationships can be assessed by calculating 'environmental' or 'ecological' niches and their subsequent projection into geographic space (GUISAN and ZIMMERMANN 2000). Here, GIS-based environmental data offer huge opportunities to assess variations in environmental factors within the species ranges, especially when combined with spatial modeling techniques (WALTARI et al. 2007; KOZAK et al. 2008; WALTARI and GURALNICK 2009). Such techniques were proposed as a useful supplemental tool despite long time established techniques for the identification of refuges and potential migration pathways (WALTARI et al. 2007; RÖDDER and DAMBACH 2009).

Model techniques can be classified into two different groups: (i) mechanistic models, which predict the potential distribution of a species based on its physiological tolerances measured in laboratory experiments and (ii) spatial model techniques, which derive from the distribution model based on statistical relationships between distribution patterns observed and environmental parameters. In the latter case, Climatic Envelope Models (CEMs) use exclusively climatic variables as predictors whereby a wider range of variables is used in Ecological Niche Models (ENMs) (e.g. soil and vegetation layers or remote sensing data). The development of mechanistic models is just at the beginning (KEARNEY and PORTER 2004; KEARNEY et al. 2008; MITCHELL et al. 2008), but CEMs and ENMs have been applied to predict species' potential distributions (PDs) under current, past, and future climate scenarios for some time now (e.g. ARAÚJO et al. 2004; ARAÚJO and GUISAN 2006; HEIKKINEN et al. 2006; HIJMANS and GRAHAM 2006; PEARMAN et al. 2008), invasive species biology (e.g. PETERSON 2003; PETERSON and VIEGLAIS 2001; RÖDDER et al. 2008; RÖDDER 2009), conservation priority setting (e.g. ARAÚJO et al. 2004; KREMEN et al. 2008; LÖTTERS et al. 2008), and ecology and evolutionary biology (e.g. PETERSON et al. 1999; GRAHAM et al. 2004; KOZAK et al. 2008). Especially CEMs were suggested to be useful for identification of potential Pleistocene refugia with high accuracy suggesting that predictions even across millennia are possible (PETERSON and NYÁRI 2007; WALTARI et al. 2007; WALTARI and GURALNICK 2009).

In CEM approaches, the climate envelope is understood as a part of a species' fundamental or realized niche depending on variables selected and assumptions made (SOBERÓN and PETERSON 2005; SOBERÓN 2007). As defined by HUTCHINSON (1957; 1978) and modified by SOBERÓN and PETERSON (2005), a species' fundamental niche represents the complete set of environmental conditions under which a species can persist, i.e. under which its fitness is greater than or equal to one in the absence of competitors or predators.

Its realized niche in environmental space (= realized distribution in geographic space) is a subset of the fundamental niche considering dispersal limitations and biotic interactions, such as food availability, competition, or interactions with pathogens (Figure 1.2-1). Niche variables can be subdivided concerning specific classes regarding the spatial extent in which they operate and if competition may play a role or not. The Grinnellian class is defined by fundamentally non-interactive variables (e.g. climate) (GRINNELL 1917) whereby the Eltonian class focuses on biotic interactions and resource-consumer dynamics (ELTON 1927). The former operates on a coarse scale and is the main subject in CEM approaches, whereby the latter can principally be measured only at local scales and is commonly not addressed in CEM approaches (SOBERÓN 2007).

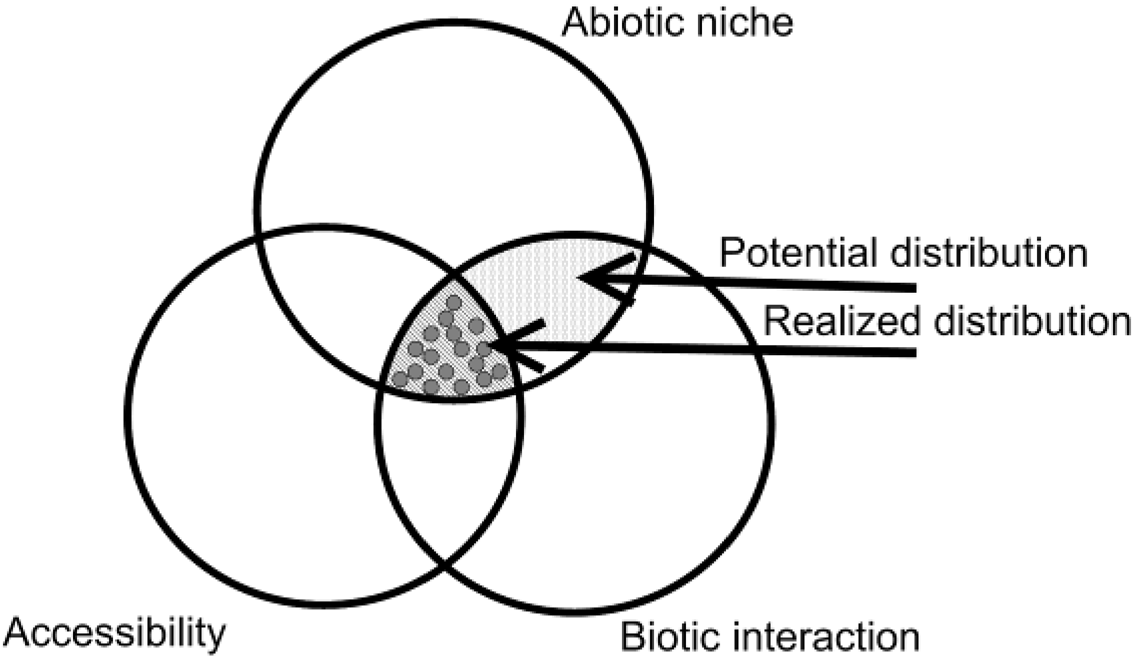

Figure 1.2-1. Relationships between abiotic (= fundamental) niche, biotic interaction and accessibility after HUTCHINSON (1957) as modified by SOBERÓN and PETERSON (2005). The potential distribution is a subset of the abiotic niche considering biotic interactions, whereby the realized distribution is a subset of the potential distribution considering accessibility. Dots represent species records.

It is important to note that Grinnellian (and Eltonian) niches are not always corresponding completely to a species actual range because history and chance are also triggering observed distributions. Remnant populations, source-sink dynamics and incomplete “filling” of a niche due to dispersal limitations or other factors may lead to deviant patterns (PULIAM 2000; GUISAN and THUILLER 2005). This implies that environmental conditions observed at species occurrences may not necessarily cover the entire niche spectrum suitable for the species or may go well beyond the range of conditions suitable for long-term persistence (TILMAN et al. 1994). Species may be in disequilibrium with climate conditions (ARAÚJO and PEARSON 2007; RÖDDER et al. 2008).

1.3. What is needed?

Mapped climate data offer remarkable opportunities to approach variation in environmental factors belonging to the Grinnellian class within the ranges of species, especially when combined with spatial modelling and GIS techniques (KOZAK et al. 2008). Such approaches are known as Climate Envelope Models (CEMs). Before CEMs can be computed it is necessary to compile a set of species occurrence records and a set of suitable predictor variables (e.g. GIS layers containing information on climatic parameters).

Species records

A huge amount of species records are available through the Global Biodiversity Information Facility (GBIF, www.gbif.org) and HerpNet databases (www.herpnet.org). In addition, species records can be obtained from own field trips, museum collections or literature. If necessary, the Alexandria Digital Library Gazetteer Server Client (www.middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp) can be used to georeference records. Despite georeferencing records one-by-one, batch processing has become possible facilitating the procedure (SOBERÓN and PETERSON 2004), e.g. using the BioGeoMancer software (http://biogeomancer.org). The spatial accuracy of the geographical coordinates necessary for robust model building depends on the spatial resolution of the environmental layers used and the algorithm applied (GRAHAM et al. 2008). A minimum amount of at least 10-30 distribution records for the species (or occasionally subspecies, superspecies etc.) under study depending on the algorithm later applied is necessary (e.g. ELITH et al. 2006; PEARSON et al. 2007; WISZ et al. 2008).

The accuracy of coordinates can be assessed with the ‘Check coordinates tool’ provided by DIVA-GIS 5.4 (HIJMANS et al. 2001; HIJMANS et al. 2002). This tool allows testing the accuracy by comparing the species records and an administrative boundaries database on the smallest possible level (state / country / city). This information should be the same, and any mismatches probably reflect errors (HIJMANS et al. 1999). In addition, it is possible to use altitudinal information to spot likely errors in the coordinate data when this information was provided with the museum records. Altitude can be compared with an estimate of the altitude of the locality, using the ‘Extract values by points’ function of DIVA-GIS. When compiling species records it is important to evaluate possible bias (SOBERÓN and PETERSON 2004), which can comprise spatial sample selection bias (JIMÉNEZ-VALVERDE and LOBO 2006), historical (HORTAL et al. 2008) or taxonomical components (SOBERÓN and PETERSON 2004).

Most algorithms build models based on species presence records, but there is also a variety of applications which can, in addition, deal with species absence data. Presence only methods may be preferable since true absence records of species remain difficult to proof (GU and SWIHART 2004), especially for rare or highly mobile species. A problem arises also from the circumstance that it is often unclear whether a species is absent from a given locality because the site is outside of its climate envelope or because of other factors such as biotic interaction, disturbance or dispersal limits. This can lead to misinterpretations, i.e. if the climate at a locality treated as absence locality is within the target species’ climate envelope the model algorithm misinterprets the climate at this site as unsuitable. To construct models for migratory species is a special challenge, since tempo-spatial patterns need to be considered when compiling species records and predictors (MARTINEZ-MEYER et al. 2004; HIRZEL and LE LAY 2008).

Climate data

Climate information can be incorporated into CEMs from various sources, whereby the selection of the most suitable data set depends on the spatial extend of the target area and the goals of the study at hand. Some examples of freely available climate data sets are given in KOZAK et al. (2008). For example, data on current climate from all over the world can be obtained from the Worldclim database, version 1.4, which is based on weather conditions recorded at roughly 50,000 locations for precipitation and 25,000 locations for temperature between 1950 and 2000 (http://www.worldclim.org; HIJMANS et al. 2005), respectively. This grid-based (resolution 30 arc sec) database was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995; 2004). Regional climate data, which is usually preferred for non-global studies if available, is provided by national weather agencies and other local sources.

When projecting species CEMs into past or future climate scenarios it is important to acknowledge that different scenarios will reveal different results and no single 'best' model exists. Hence, strength and weaknesses of different climate models should be considered (BEAUMONT et al. 2008). Evaluation of a variety of scenarios may help to assess variations in outputs. For example, climate change projections for based on the CCCMA, CSIRO and HADCM3 models (FLATO et al. 2000; GORDON et al. 2000) and the emission scenarios reported in the Special Report on Emissions Scenarios (SRES) by the Intergovernmental Panel on Climate Change, IPCC (http://www.grida.no/climate/ipcc/emission/) the years 2020, 2050, 2080 can be obtained via the Worldclim homepage (resolution 30 arc sec). Future projections using other IPCC scenarios are also available from the Climate Research Unit (CRU) of the University of East Anglia, UK (http://www.cru.uea.ac.uk/cru/data/hrg.htm; NEW et al. 1999; NEW et al. 2000). Upcoming regional models are providing spatially more detailed information and take account of regional-scale topographic variability not after the fact as in the Worldclim dataset but from the very beginning.

For paleoclimate during the Last Glacial Maximum (ca. 21,000 years BP), General Circulation Model (GCM) simulations from the Community Climate System Model (CCSM) are available (http://www.ccsm.ucar.edu/; KIEHL and GENT 2004). As second set the Model for Interdisciplinary Research on Climate (MIROC, version 3.2; 115 http://www.ccsr.u-tokyo.ac.jp/~hasumi/MIROC/) can be used, respectively.

Results from each climate scenario include a broad range of variables, with minimum and maximum temperatures and the mean precipitation per month (= 36 climate parameters) as the most commonly used for ecological niche modelling. Based on these monthly layers, 19 bioclimatic parameters can be generated, e.g. with DIVA-GIS 5.4 (http://www.diva-gis.org; HIJMANS et al. 2002). These are often used in CEMs and represent annual seasonality and extreme or limiting climate factors (Table 1.3-1). Bioclimatic parameters are more useful than 'raw' monthly values since they are independent from latitudinal variation. This becomes obvious considering that the 'maximum temperature of the warmest month' is more informative with respect to species biology than the maximum temperature of a specific month because the latter varies with latitude (NIX 1986; BUSBY 1991).

Table 1.3-1 Bioclimatic parameters and their abbreviations representing annual trends, seasonality and extreme or limiting climate factors.

Parameter	**Abbreviated as**
Annual mean temperature	Bio1
Mean monthly temperature range	Bio2
Isothermality	Bio3
Temperature seasonality	Bio4
Maximum temperature warmest month	Bio5
Minimum temperature coldest month	Bio6
Temperature annual range	Bio7
Mean temperature wettest quarter	Bio8
Mean temperature driest quarter	Bio9
Mean temperature warmest quarter	Bio10
Mean temperature coldest quarter	Bio11
Annual precipitation	Bio12
Precipitation wettest month	Bio13
Precipitation direst month	Bio14
Precipitation seasonality	Bio15
Precipitation wettest quarter	Bio16
Precipitation driest quarter	Bio17
Precipitation warmest quarter	Bio18
Precipitation coldest quarter	Bio19

Mulitcolinearity among predictor variables may hamper the analysis of species-environment relationships because ecologically more causal variables may be excluded from models if other inter-correlated variables explain the variation in response variable better in statistical terms (HEIKKINEN et al. 2006). E.g., if two variables are similarly distributed in space both are similarly represented in a species model. Independent variation of the two variables may lead to false predictions when one of them is causally linked to a species distribution and one is not. Therefore, variable selection should be guided by a throughout assessment of the target species' ecology and rather a minimalistic set of predictors should be preferred depending on the focal species. E.g. Bio1, 10, 11, 12, 16 and 17 from the Worldclim dataset reflect the availability and range of thermal energy and humidity and are suitable for CEM projections between different climate scenarios, according to different authors (see CARNAVAL and MORITZ 2008). Specific adjustment of variables according to specific ecological needs of the target species may improve the model output (BEAUMONT et al. 2005). It needs to be noted that negative effects of multicolinearity may vary among algorithms applied.

1.4. How do CEMs work?

Once species records and predictor variables have been compiled, the next step is the development of a multidimensional view of the species' climatic niche. This is a considerable challenge given the complex nature of species' niches (PETERSON and VARGAS 1993). In plain text: in CEM, climatic information for species presence localities are summarized to an 'ideal' climatic niche for the target species (note that this can also be done with reliable absence data) that is afterwards compared to climatic conditions at the query localities, i.e. where the presence/absence of the species is unknown (Figure 1.4-1). The results are geographic maps showing the similarity of an area with the 'ideal' climatic niche. The selection of a suitable algorithm for the computation of the CEM depends on the amount of distribution records available, their quality, and the specific goal of the study (for a brief overview of available algorithms see JESCHKE and STRAYER 2008).

One of the earlier applied algorithms for presence only data are BIOCLIM (NIX 1986; BUSBY 1991) and DOMAIN (CARPENTER et al. 1993), as implemented in DIVA-GIS. Whereas BIOCLIM measures the distance to the midpoint of the training sites in suitable climate space as suggested by conditions at training records, DOMAIN measures the environmental similarity of each grid cell to the most similar training site (NIX 1986; CARPENTER et al. 1993) (Figure 1.4-2). More sophisticated algorithms are GARP (STOCKWELL and NOBLE 1992; STOCKWELL and PETERS 1999) and MaxEnt (PHILLIPS et al. 2004; PHILLIPS et al. 2006). The more recently developed methods derive predictions by developing sets of rules or by machine-learning approaches (GARP, Maxent) and are superior to most other methods (for a comparison of performance quality see ELITH et al. 2006; HEIKKINEN et al. 2006; WISZ et al. 2008). If absence records are available or even abundances, algorithms such as 'artificial neuronal networks', 'classification and regression trees', 'generalized additive models' or 'generalized dissimilarity models' can be applied. These algorithms are implemented in the BIOMOD tool (THUILLER 2003) for example.

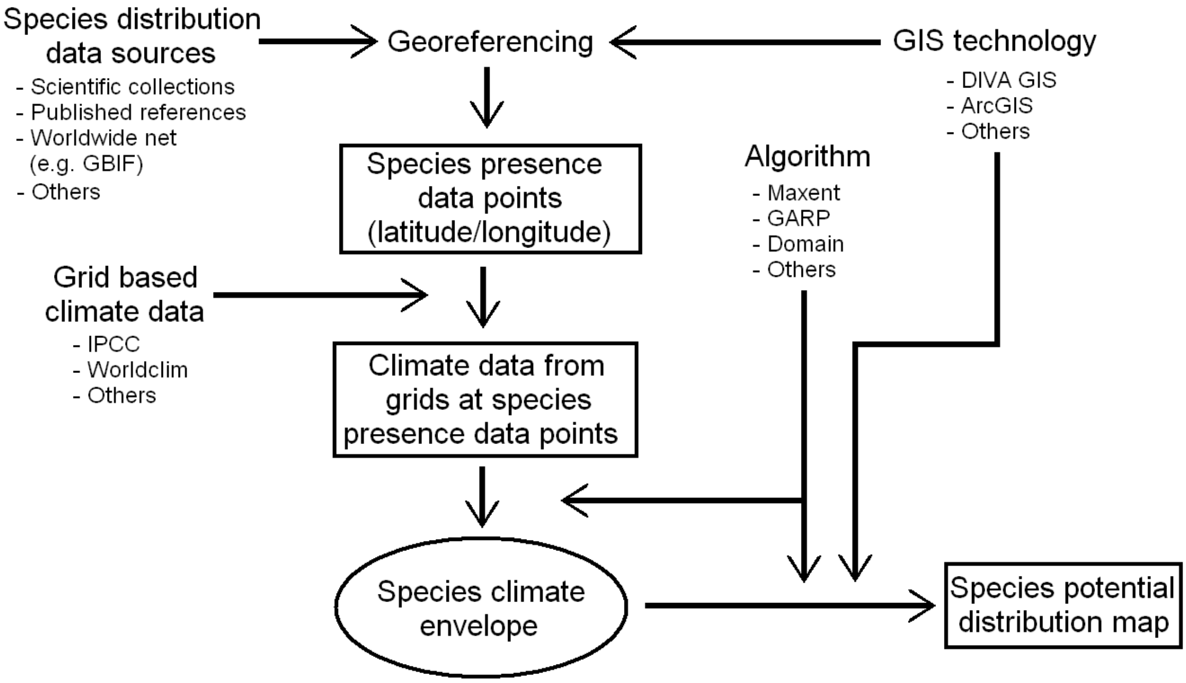

Figure 1.4-1. Flow chart illustrating the main steps for building a Climate Envelope Model.

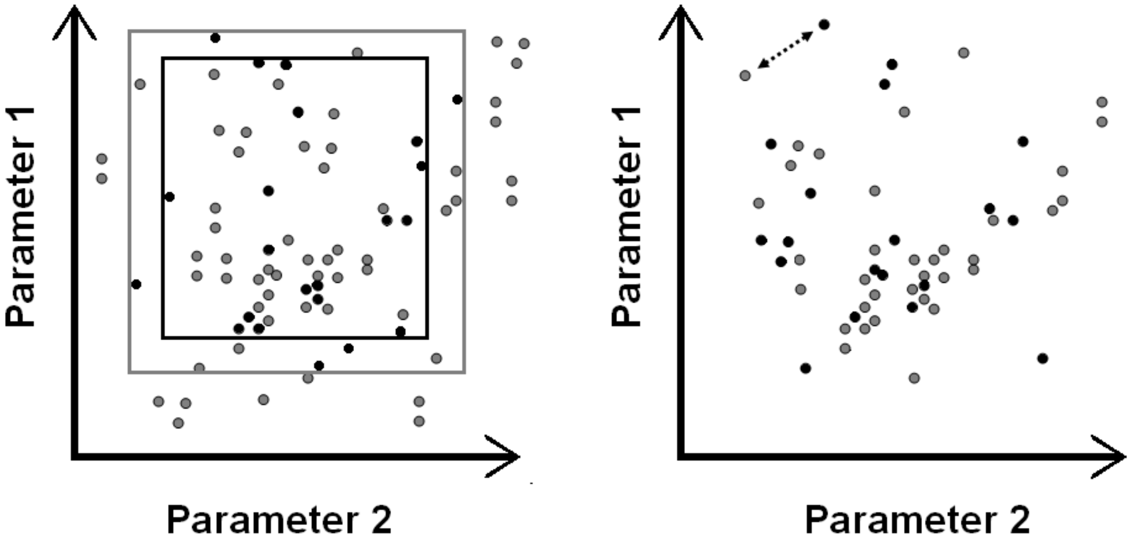

Figure 1.4-2. Assumptions and concepts may vary between different modelling algorithms. In BIOCLIM (left) the environmental niche is defined as a boxcar environmental envelope in climate space, whereby ‘core’ (black box; enclosing 90 % of all species records) and ‘marginal’ areas (grey box; enclosing 100 % of the records) are defined (NIX 1986). All grey dots enclosed by the boxcar envelope are suggested to be suitable for the target species. In DOMAIN (right) the relative distance between conditions as observed at species records (black points) and at locations to be assessed (grey points) is measured in climate space (CARPENTER et al. 1993). Conditions at species records (black points) and conditions at locations in question are indicated (grey points).

1.5. Evaluation of results

One of the most frequently used model tests is an assessment of the Area Under the Curve (AUC) statistics, referring to the ROC (Receiver Operation Characteristic) curve using (Figure 1.5-1) e.g. 25 % of the records as test points and the remaining ones for training (Hanley and McNeil 1982; Phillips et al. 2006). This method is recommended for ecological applications because it is non-parametric (Pearce and Ferrier 2000). Values of AUC range from 0.5 (i.e. random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of Swets (1988) AUC values > 0.9 describe ‘very good’, > 0.8 ‘good’ and > 0.7 ‘useful’ discrimination ability. A second possibility is Cohen’s kappa statistic of similarity (k) (Fielding and Bell 1997; Pearce and Ferrier 2000). Cohen’s kappa yields values ranging from 0.0 (no predictive ability) to 1.0 (perfect predictive ability), whereby k values above 0.7 describe ‘very good’ discrimination ability (Monserud and Leemans 1992). If only few species records for model building are available (e.g. less than 25), a jackknife test can be performed (Pearson et al. 2007). Additionally, in some cases invasive populations of the target species can be used as independent test (Sax et al. 2008).

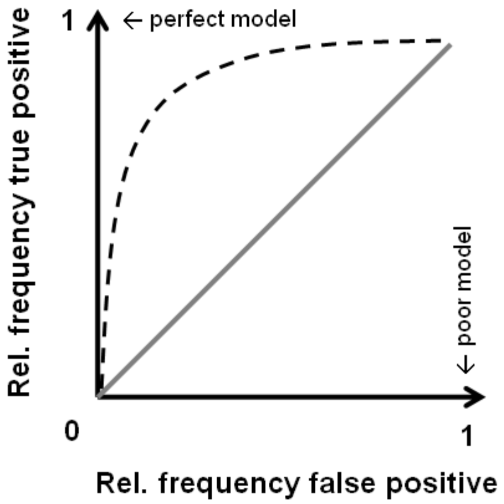

Figure 1.5-1. The Receiver Operating Characteristic (ROC) Curve is formed by plotting values of the relative frequency of true positive records predicted by a given model against the values of the relative frequency of false positive records (Hanley and McNeil 1982). The solid 1:1 line signifies random predictive ability, whereby there is no ability to distinguish occupied and unoccupied sites. The dashed line may be characteristic for a model with good predictive abilities.

It needs to be noted that test statistics, such as AUC or Cohen’s kappa scores are a measure of model fit compared to the observed distribution of a species and must not be interpreted as a measure in the ecological sense of a model. Profound knowledge of a species' natural history is necessary for an evaluation, when a model meets the ecological requirements of the target species.

1.6 CEM applications in taxonomy and ecology: afrotropical reed frogs as examples

Reed frogs (Hyperoliidae: *Hyperolius*) are a monophyletic group of small nocturnal and arborical amphibians which are known from savannahs and forests in sub-Saharan Africa (SCHIØTZ 1999; VEITH et al. in press). More than 130 species have been recognized (FROST 2008). Due to limited inter-specific and remarkable intra-specific morpohological variation, the taxonomy of numerous *Hyperolius* is poorly understood. Certain nominal species may actually represent complexes of distinct taxa. Bioacoustics and DNA barcoding have been proven as useful tools in species discrimination; however, the availability of samples is still sparse (e.g. KÖHLER et al. 2005; VEITH et al. in press). Here are some examples provide provided how CEMs can performs well as a supplement to other methods and outline some potential problems.

Hyperolius cinnamomeoventris sensu lato

This is a reed frog from the Congo Basin and vicinities. LÖTTERS et al. (2004), VEITH et al. (in press) and the own’ unpublished molecular data suggest that several sister species are involved. Samples studied from part of this reed frog’s range in eastern DRC, Uganda and western Kenya are genetically distinct from those from elsewhere within the geographic range encompassed by *H. cinnamomeoventris* sensu lato (Figure 1.6-1). It can be concluded that they represent an 'eastern taxon' within the species complex. However, the relatively few genetic samples do not allow for an appreciation of the species' spatial delimitation. Also it remains unclear how to apply the nomenclature, i.e. the different available names currently in the synonym of *H. cinnamomeoventris* (FROST 2008).

A MaxEnt CEM (Figure 1.6-2A) using 17 presence data points of the 'eastern taxon' and based on Bio1, 10, 11, 12, 16 and 17 (see Table 1.3-1) advocates that this species is potentially distributed in the northern Lake Victoria catchment, part of the northern Congo Basin, the Eastern Arc Mountains and the Ethiopian Highlands (AUC = 0.992). Eastern

Arc and Ethiopia are outside the realized distribution of any *Hyperolius* referable to *H. cinnamomeoventris* sensu lato (Figure 1.6-1) that it can be ignored when analyzing the geographic range of the 'eastern taxon'. Today, all potential junior synonym names are outside of the PD of the ‘eastern taxon’; however it might be possible that they represent glacial relicts. In order to assess this hypothesis I here projected the MaxEnt CEM as shown in Figure 1.6-2A onto paleoclimate data derived from the General Circulation Model (GCM) simulations from the Community Climate System Model (CCSM) as explained above. Figure 1.6-2B indicates how this eastern species was potentially distributed during the Last Glacial Maximum, ca. 21,000 years BP. During this cooler and drier period, the 'eastern taxon' within *H. cinnamomeoventris* sensu lato might have been more widely distributed in the Congo Basin than today. Regarding the type localities of the different junior synonym names, they all are situated outside the potential distribution of the 'eastern taxon' under current and Last Glacial Maximum conditions except that of *H. ituriensis* (Figure 1.6-2A). Therefore, it was concluded that *H. ituriensis* may be the best applicable name.

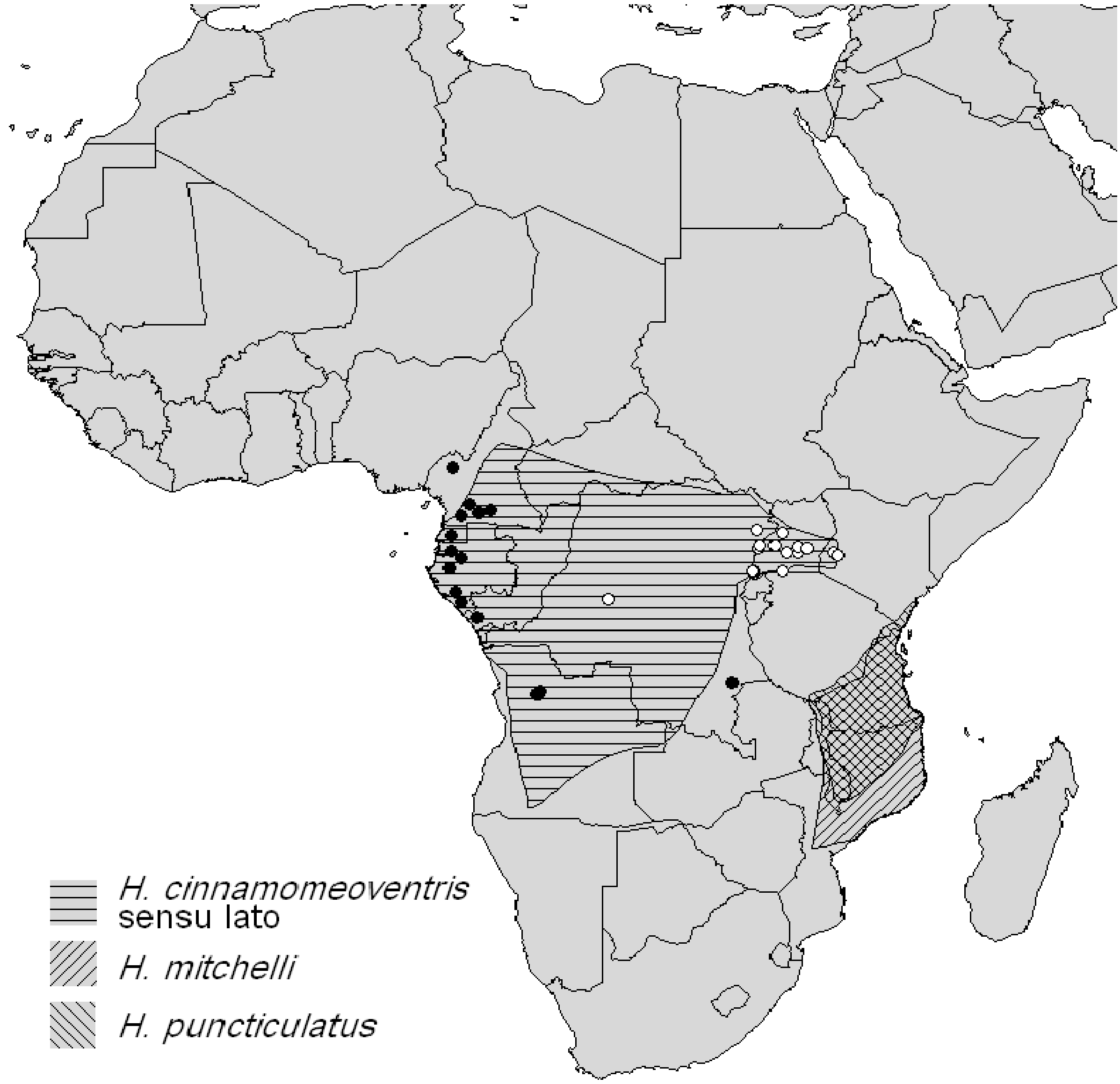

Figure 1.6-1. Distribution of three reed frog species, genus *Hyperolius*, according to the IUCN Red List (http://www.iucnredlist.org). In the case of *H. cinnamomeoventris* sensu lato, DNA barcoding (ca. 550 bp of the 16S mitochondrial rRNA gene) of samples from different localities (all circles, some of which lay outside the geographic range according to the IUCN Red List) revealed that different sibling species are involved; white circles combine samples which belong to an 'eastern taxon' within this species complex (authors' unpubl. data).

Unfortunately distribution data to generate CEMs for other species hidden behind the name *H. cinnamomeoventris* are lacking but genetic evidence (S. LÖTTERS, unpubl. data) supports that at least the 'eastern taxon' does not occur in sympatry with any other species within *H. cinnamomeoventris* sensu lato (Figure 1.6-1). This is well supported by the observation that sister species commonly exhibit allopatric distributions, especially in amphibians (FISHER et al. 2001; GRAHAM et al. 2004). An explanation may be that due to geographic separation it is likely that some degree of shift in climate envelopes as an adaptation to the local environment takes place (GRAHAM et al. 2004).

Hyperolius mitchelli and *H. puncticulatus*

It is not always given that sister species have different climate envelopes. This is the case in two East African reed frogs, *Hyperolius mitchelli* and *H. puncticulatus*, which by their vocalizations and when applying DNA taxonomy can be well distinguished (SCHIØTZ 1999; RÖDDER and BÖHME, in press; authors' unpubl. data). Their known geographic ranges largely overlap (Figure 1.6-1), and a MaxEnt model (using 18 and 27 presence points, respectively, and based on Bio1, 10, 11, 12, 16 and 17; see Table 1.6-1; AUC = 0.903 and 0.952 for the two species, respectively) uncovered that similarity in their climate envelopes is so high (Figure 1.6-2C, E) that the two cannot be separated using CEMs. As expectable, even projecting the MaxEnt models onto CCSM paleoclimate simulations, the potential geographic distributions of *H. mitchelli* and *H. puncticulatus* remained largely similar (Figure 1.6-2D, F).

Apparently, climate niches in these two reed frogs show a high degree of conservatism and have not changed with speciation. This gives an interesting insight into their evolution and poses some questions: Have *H. mitchelli* and *H. puncticulatus* speciated in sympatry? Or have they speciated in allopatry but have retained their climate envelopes because these were overall little specialized? Both patterns are uncommon in amphibians as made clear above. However, sympatric speciation has never been demonstrated in amphibian species. The most likely explanation is that speciation has taken place on isolated refuges during a warm phase allowing isolation. Climatic conditions at these isolates (likely mountains) apparently had shown similar climates, thus explaining the lack of niche divergence during speciation. The examples of *H. mitchelli* and *H. puncticulatus* illustrate also the effects of limited accessibility. Both species may find climatically suitable regions outside their realized distribution in great parts of central Africa and Madagascar. While range expansions to Madagascar are restricted by the sea, apparently the Albertine Rift valley with its numerous lakes prevents westward range extensions. In addition, this lowland region is climatically relatively unsuitable for both species (Figure 1.6-2C, D, indicated in green).

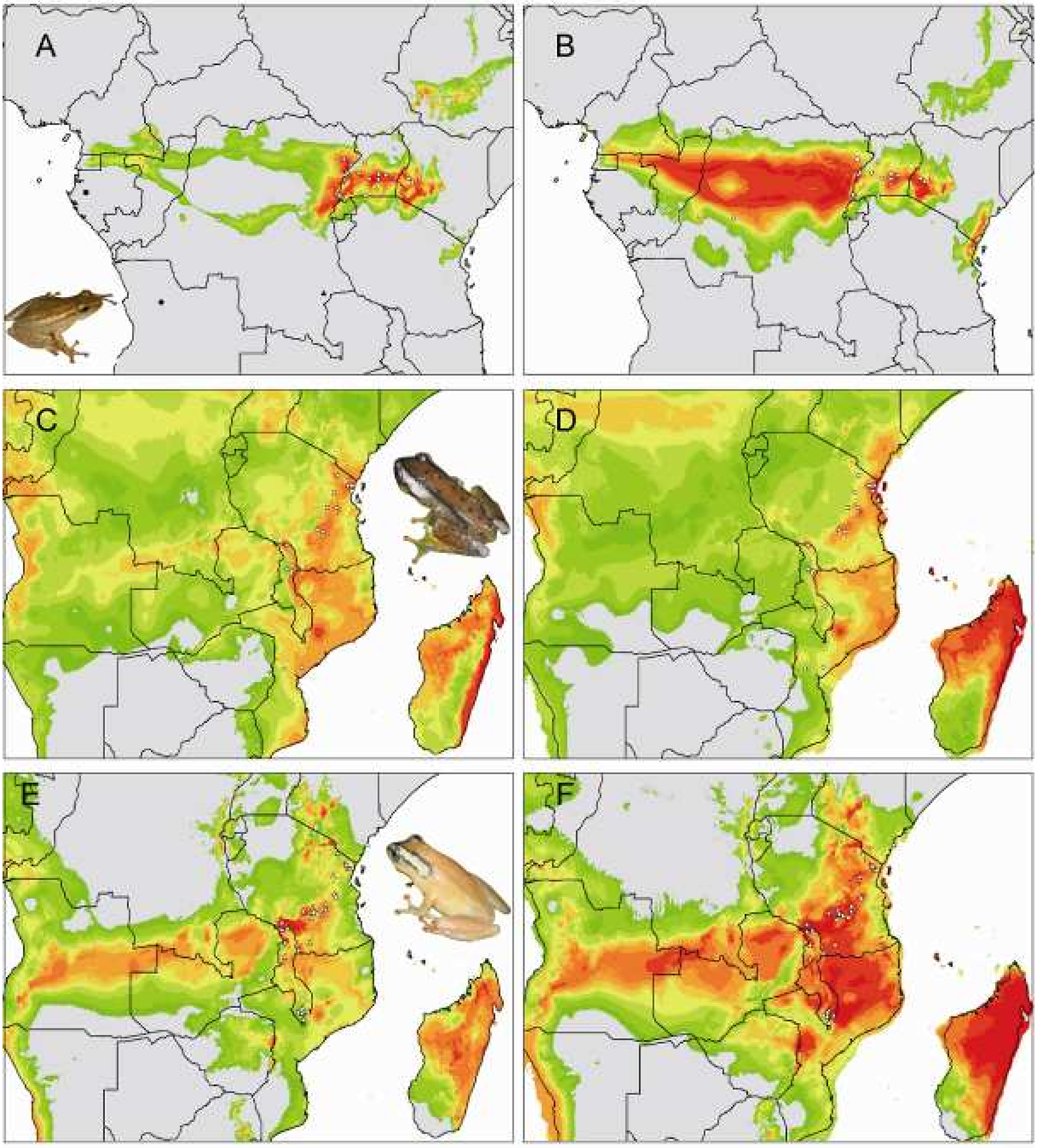

Figure 1.6-2. Climate Envelope Models computed with MaxEnt for different African reed frog species (*Hyperolius*) under current climate (A, C, E) and paleoclimate (B, D, F, considering past sea level fluctuation) conditions. White circles indicate presence data for species used for modelling; other symbols used in A represent type localities of nominal species currently in the synonymy of *Hyperolius cinnamomeoventris* (filled square: *H. fimbriolatus* and *H. olivaceus*, filled circle: *H. cinnamomeoventris* sensu stricto and *H. tristis*, filled triangle: *H. wittei*, grey circle: *H. ituriensis*; for synonym list see FROST 2008).

1.7. Strengths of CEMs and potential ‘pitfalls’ when interpreting results

CEMs are easy to use and inexpensive. A steadily increasing number of studies has been showing that, when CEMs are properly applied, results can have a high quality (e.g. PETERSON 2003; WALTARI and GURALNICK 2009; WALTARI et al. 2007). They have been a rich source of quantitative projections concerning geographic ranges of species with great value in many areas of both basic and applied ecology and conservation. They allow the identification of possible threats due to climate change (e.g. see HABEL et al. 2009) or past migration pathways (Figures 1.7-1, 1.7-2; WALTARI et al. 2007; RÖDDER and DAMBACH 2009; RÖDDER et al. 2009; WALTARI and GURALNICK 2009).

For example, CEM projection of the potential distribution (PD) of the Azure Hawker (*Aeshna caerulea* (STROEM, 1783)) onto palaeo-climatic scenarios reflecting conditions as expected for the LGM 21,000 BP suggest that climatically suitable areas were widely distributed in Europe throughout the LGM (Figure 1.7-1). The PD would have connected current refugia. It is also possible to reconstruct past refugia of currently wide-spread species (WALTARI et al. 2007), e.g. as shown for the yellow-bellied toad *Bombina variegata* (Figure 1.7-2). Furthermore, CEMs can be used as a guideline for efficient further sampling, since phylogeographic studies are expensive in terms of both time and resources. Regarding relict species, CEMs may be useful for the identification of potentially suitable areas which may harbor relict populations unknown so far.

As outlined before, strengths and weaknesses of different climate models should be taken into consideration (BEAUMONT et al. 2008). Evaluation of a variety of scenarios may help to assess output variations. For example, when comparing Figures 1.7-1B, C and 1.7-2B, C the general patterns are similar, but fine scale differences, especially in northward PD limits, can be identified. These can be traced back to different assumptions made in the palaeo-climatic scenarios used, e.g. concerning assumed CO_2 concentrations.

CEMs are derived from a subset of environmental conditions at species records (= variables selected); hence they capture only a more or less extensive part of the climatic niche depending on the variables selected and other factors influencing the distribution of species (see below). They are generally unable to capture the niche completely, and output maps show regions with similar conditions as the testing records according to the predictor variables selected rather than ‘complete’ niches.

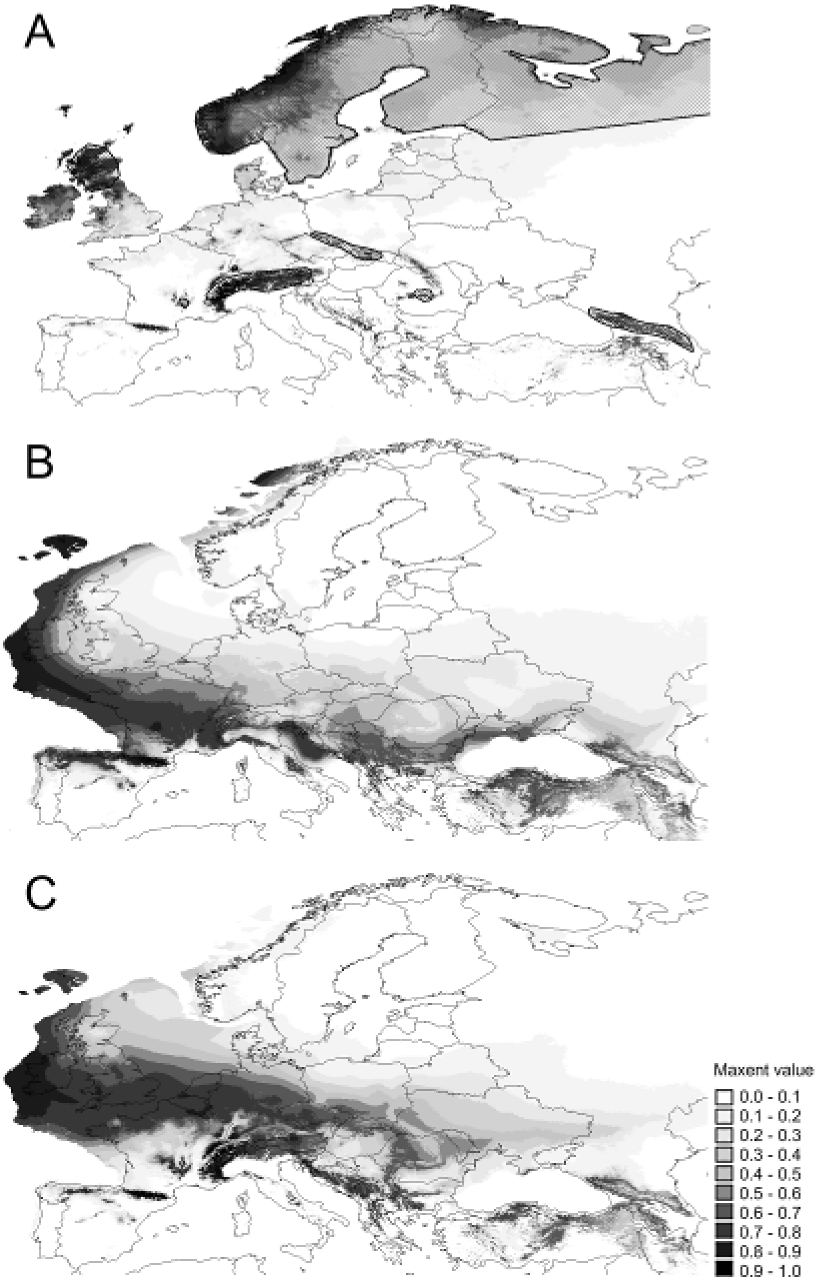

Figure 1.7-1. Today's distribution of *Aeshna caerulea* (A, hatched, source: KUHN and BURBACH 1998; STERNBERG and BUCHWALD 2000) and its potential distribution computed with MaxEnt 3.2.1 derived from current climatic conditions. Higher MaxEnt values suggest higher climatic suitability. Figure B and C show potential distributions of *Aeshna caerulea* assuming two different paleoclimatic scenarios depicting climatic conditions as expected for 21,000 BP (B: CCSM; C: MIROC). Areas of currently known distribution of *A. caerulea* are highly congruent with the proposed potential distribution of the CEM even in small and disjunctive ranges. Projections of the CEM onto palaeoclimatic scenarios suggest potential migration pathways during the LGM connecting most current refugia. Source: RÖDDER and DAMBACH (2009).

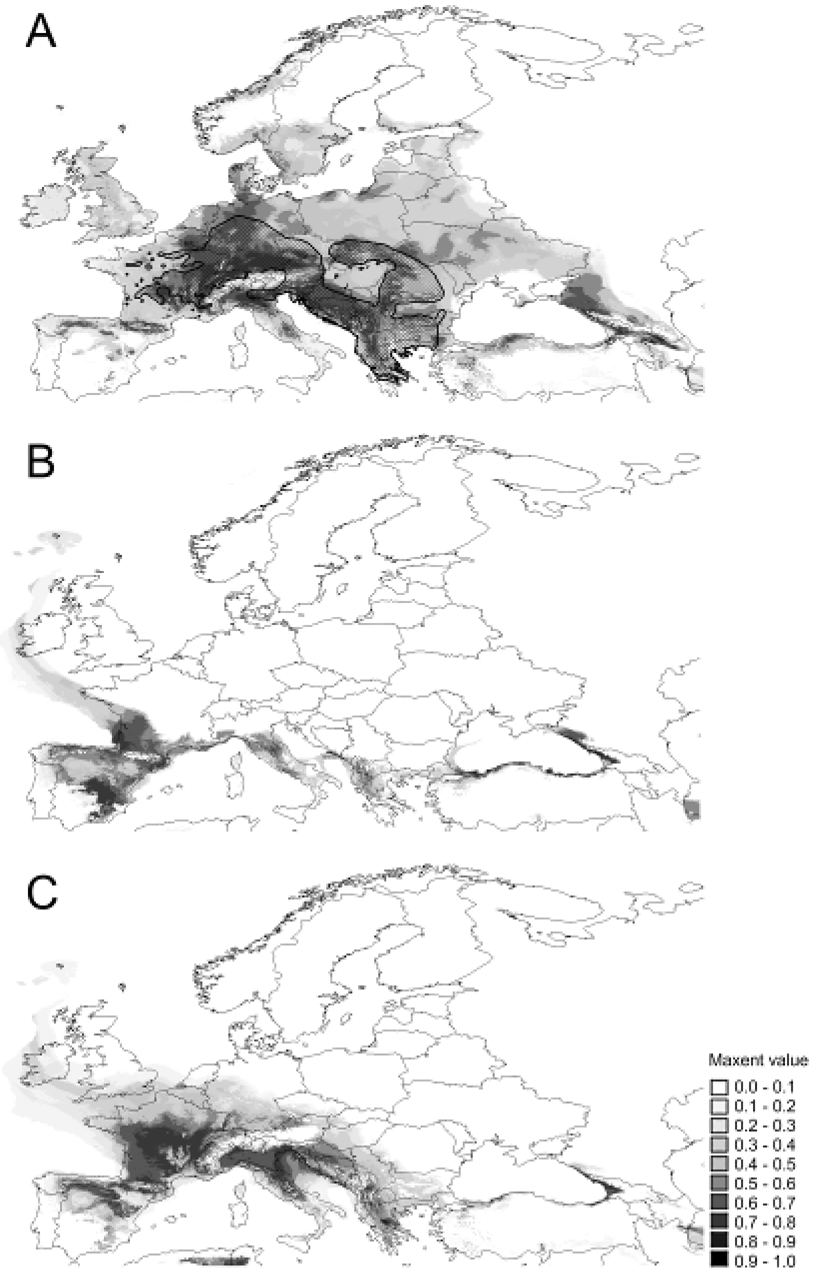

Figure 1.7-2. Today’s distribution of *Bombina variegata* (A, hatched, source: IUCN, 2006) and its potential distribution computed with MaxEnt 3.2.1 derived from current climatic conditions. Higher MaxEnt values suggest higher climatic suitability. Figure B and C show projections of the climate envelope of *B. variegata* assuming two different paleoclimatic scenarios depicting climatic conditions as expected for 21,000 BP (B: CCSM; C: MIROC). Areas of currently known distribution of *B. variegata* are highly congruent with the proposed potential distribution of the CEM even in small and disjunctive ranges, e.g. in France. Projections of the CEM onto palaeoclimatic scenarios suggest potential refugia during the LGM. Source: Rödder and Dambach (2009).

Quality and spatial properties of distribution records used for model building can significantly influence the results, e.g. when samples do not cover the whole climatic niche space suitable of the target species. Another concern is spatial autocorrelation, which is always present in spatial datasets and may bear heavily on models (DORMANN et al. 2007) since some algorithms require that samples are independently distributed of each other, which is seldom the case in biological data. Spatial autocorrelation is basically a lack of independence between observations due to the fact that vicinity in space alters the chance of occurrence. An analogous phenomenon is observed in time if multi-temporal datasets are used. Methods dealing with spatial autocorrelation like SAR models or PCNM approaches are treated in detail by DORMAN et al. (2007).

Unfortunately, most commonly applied methods to reduce sample bias, such as selecting specific distance buffers, and / or spatial autocorrelation, such as SAR or PCNM methods, can not be properly combined with some modelling techniques such as Maxent. In regions exhibiting a steep varieng environmental gradients selection of specific distance buffers may excude species records which may significantly contribute to the feature space. To avoid this drawback I have developed a technique to reduce sample bias by removing duplicate information in climate space from the data set. The genrall idea is that species records situated close by each other should tend to be most similar in feature space. Hence, they can be identified by running a cluster analyses based on their environmental properties and – since 10-30 species records are commonly sufficient for successful model building –records very similar in feature space can be removed from the data set without loosing too much valuable information.

When applying CEMs some key assumptions regarding biological aspects are commonly made: (1) species occur at all locations where the climate is favorable, (2) biotic interactions are unimportant in determining ranges and are constant over space and time and (3) genetic and phenotypic compositions of species are constant over space and time (JESCHKE and STRAYER 2008). (1) Ideally CEMs highlight all areas that are climatically suitable for the target species reflecting its potential distribution regardless dispersal limitations and thus accessibility. When interpreting potential distribution maps it is important to evaluate the dispersal properties of the target species. For example, although *Bombina variegata* (Linnaeus, 1758) could find climatically suitable areas in England today (Figure 1.7-2), the species is unable to colonize the UK due to dispersal limitation by the sea. Genrall methodontologial uncertainities are summarized in Figure 1.7-3.

(2) Biotic interactions are commonly not considered during model building since interactions, such as competition or predation in species assemblages are often too complex to be gathered in a single step during model building. For example, the PD of *Bombina variegata* is considerably wider than its realized distribution in Germany, the Czech Republic, Slovakia and Hungary (Figure 1.7-2A). Here, climate is not the limiting factor since a hybrid-zone between *B. variegata* and its sister species *Bombina bombina* (LINNAEUS, 1761) hamper further dispersal (SZYMURA 1993). Under different climate scenarios, PDs of species can respond spatially in a different manner which can cause strong variations over space and time and result in discrepancies (e.g. as shown by SCHWEIGER et al. (2008) in an ENM approach for a butterfly / host plant system). For simplicity's purpose it may be useful to focus in a first step on the climatic niches of each target species to assess its potential distribution and subsequently compare models for potentially interacting species.

(3) An important point when projecting CEMs onto past or future climate scenarios is that fundamental niches can be subject to evolution. In a recent review, it has been shown that, independent of the taxonomic group, the fundamental niche can remain stable for tens of thousands of years or it can shift substantially within only a few generations (PEARMAN et al. 2008). ‘Niche conservatism’ of closely related species is a phenomenon that has been observed in several different taxonomic groups (e.g., PETERSON et al. 1999; WIENS and GRAHAM 2005), but, on the other hand, niche shifts have also proposed (e.g. GRAHAM et al. 2004; BROENNIMANN et al. 2007; FITZPATRICK et al. 2007; BROENNIMANN and GUISAN 2008; FITZPATRICK et al. 2008; PEARMAN et al. 2008; RÖDDER and LÖTTERS 2009). So evidence for the degree of niche shifts or niche conservatism in closely related species is mixed and debated (PEARMAN et al. 2008; WIENS and GRAHAM 2005). When applying CEMs, it is an important issue if (climatic) niches are rather conservative or not, especially when the aim is an assessment of changes in potential distributions under different climate scenarios. However, in general, there is a considerable lack of knowledge regarding the processes triggering shift in climatic niches as well as in suitable methods to analyze it.

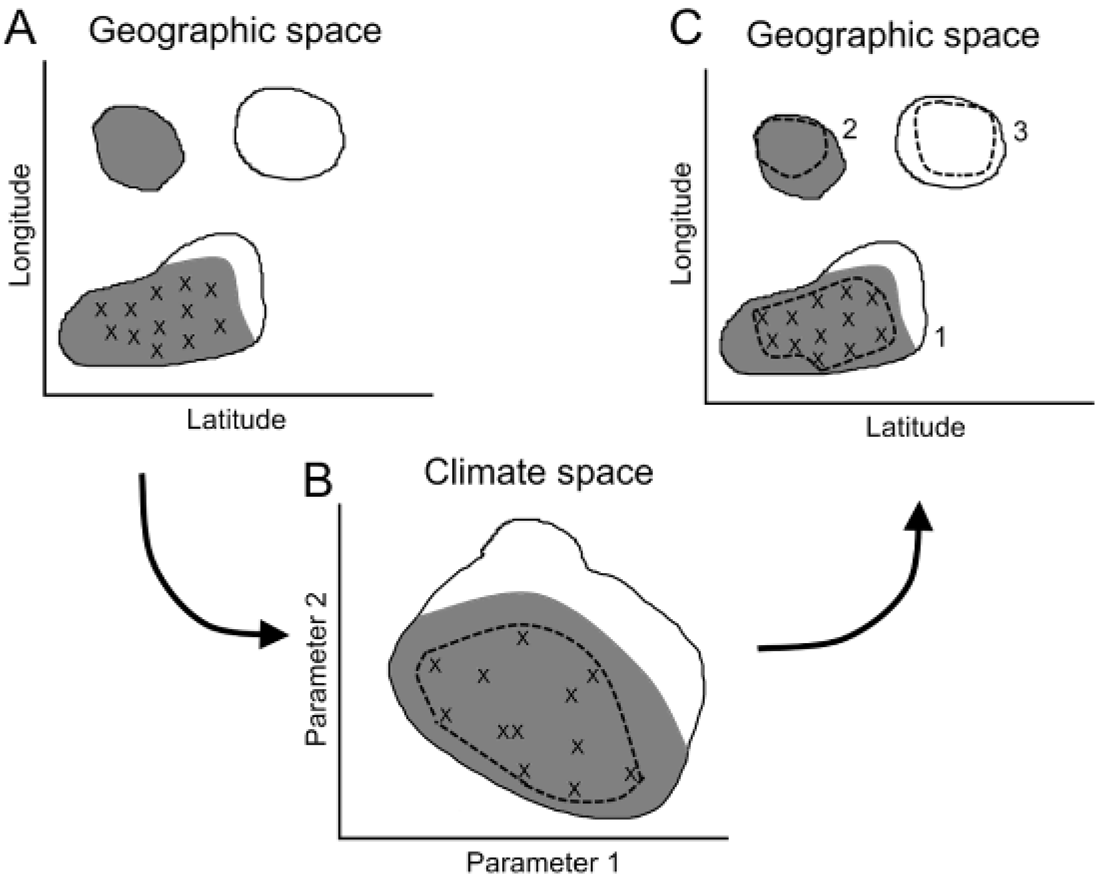

Figure 1.7-3. Potential error sources and uncertainties in CEMs after PEARSON (2007), modified. Species records (x) available for model training commonly reflect neither the species' entire realized distribution (A, C; grey), its potential distribution (solid lines) nor the complete suitable niche space (B: grey). Since CEMs are fitted based on a subset of the suitable niche space (C: dashed line), the model may not identify the whole realized or potential distribution. Subsequent projection of the model in geographic space may identify three different distribution types: projected area 1 identifies the known distribution of the training records, area 2 identifies a part of the realized distribution from which no species records were available, and area 3 identifies a potential distribution that is actually not inhabited, e.g. due to biotic interactions or limited accessibility.

SECTION 2: STRUCTURE OF CLIMATE NICHES

2.1. Translating natural history into geographic space: a macroecological perspective on the North American Slider, *Trachemys scripta* (Reptilia, Cryptodira, Emydidae)[2]

Trachemys scripta ssp.

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[2] This part was submitted to the *Journal of Natural History*.

The work reported in this chapter was conducted in collaboration with AXEL KWET from the Staatliches Museum für Naturkunde, Suttgart, Gemany, and STEFAN LÖTTERS from the Faculty of Geosciences, University of Trier, Germany.

Introduction

It is not new that climate elements and factors have an important influence on the distribution of plant and animal species, as the ecological niche concept has been well discussed over decades (GRINNELL 1917; JAMES et al. 1984). Temperature has a strong impact on physiology, activity and development in most species (PARMESAN 2006). Climatic factors may strongly affect taxa with temperature-dependent sex determination (TDS) such as many crocodiles, turtles and lizards (JANZEN and PAUKSTIS 1991; EWERT et al. 1994). Several studies have suggested that species with TDS may be threatened by anthropogenic global climate change, i.e. mainly warming, affecting sex ratios (JANZEN 1994a; MORJAN 2003). However, a throughout assessment of broad scale geographic variation in climate factors influencing sex ratios of species with TDS is currently lacking, but may be pivotal for an assessment of potential threats caused by climate change.

In recent years, there has been noted a remarkable increase in availability of information on climatic parameters in geographic space, including remote regions and species distribution data. Accompanied by improved computation capacities, these have allowed for an increase of large scale assessments regarding the relationship between observed species distributions and explanatory environmental (climatic) parameters. Such studies can be approached by modelling climate niches (also called climate envelopes) of species and their projection into geographic space (GUISAN and ZIMMERMANN 2000), allowing for a broad-scale assessment of climatic variations throughout a species geographic range.

Herein, we assess broad scale climatic variation in the Slider, *Trachemys scripta* (Reptilia, Cryptodira, Emydidae), distributed in the southern and the southeastern USA and adjacent northeastern Mexico. As all emydids, *T. scripta* lays eggs in subterranean nests. Breeding throughout the whole range takes place from March to July, with nesting in mid-April to mid-July (GIBBONS et al. 1982; ARESCO 2004). The duration between egg deposition and hatching of the neonates takes 60–130 days in the northern range depending on egg incubation temperature, whereby low temperatures cause slower development (e.g. NÖLLERT 1992). In Lousiana, eggs were reported to hatch in approximately 68–70 days (DUNDEE and ROSSMAN 1989). For successful egg development, the soil surrounding the nest has to provide enough moisture (TUCKER et al. 1998) and warmth, ca. 26.0–32.5 °C (WIBBELS et al. 1991; CREWS et al. 1994). Sex determination of *Trachemys* embryos is temperature-dependent, with cooler egg incubation temperatures increasing the number of males and warmer egg incubation temperatures favouring females (EWERT et al. 1994). The differentiation of both sexes is possible within a range of temperature called the transitional range of temperatures (TRT; MOROSOVSKY and PIEAU 1991; CREWS et al. 1994), which spans 2.31 °C (28.3–30.6 °C; CREWS et al. 1994; CADI et al. 2004). Both the initiation date and the length of this period depend on the overall egg incubation temperature, although, in general, the temperature-sensitive phase extends for approximately two weeks (WIBBELS et al. 1991; CADI et al. 2004). Clutch development and sex-ratios are therefore highly influenced by climatic conditions during the breeding season and specific climatic conditions during egg development are essential for establishment and maintenance of populations.

We hypothesise that climatic requirements allowing for successful egg incubation and a balanced sex ratio in *T. scripta* are the major driver for its geographic distribution. In this paper, we (1) evaluate the variation in monthly mean temperatures throughout the native distribution of this species and (2) test if it is a good predictor for its geographic range.

Methods

Presence data points of Trachemys scripta

We found 377 records of *Trachemys scripta* in collections linked to the Global Biodiversity Information Facility (GBIF) and HerpNet databases within the native range of the species following the definition of the Nonindigenous Aquatic Species information resource of the United States Geological Survey (http://nas.er.usgs.gov). All data was checked with DIVA-GIS for bias and errors (HIJMANS et al. 1999; 2002). For georeferencing, we used the Alexandria Digital Library Gazetteer Server Client (http://middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp).

Climate data

Mean soil temperature is largely not available. However, mean air temperature can be used as proxy for mean soil temperature as both are closely correlated, whereby soil temperature is commonly slightly higher than air temperature (e.g. HAYS et al. 2003; HAWKES et al. 2007). The climate information used here goes back to Worldclim, version 1.4 (HIJMANS et al. 2005), which is based on weather conditions recorded between 1950 and 2000 at spatial resolution of 2.5 minutes (about 4 x 4 km in the study area). The dataset was created by interpolation using a thin-plate smoothing spline of observed climate at ~25,000 worldwide weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995; 2004). The climate data set comprising 12 layers describing the monthly mean temperature (TMEAN1–TMEAN12) was downloaded from the Worldclim homepage (http://www.worldclim.org; 15 May 2007). In order to examine the thermal limits of the mean monthly temperature during reproductive period, we extracted at each distribution record the monthly mean temperature and calculated boxplots for comparisons between months (Figure 2.1-1).

We acknowledge that short-term variation in weather conditions may cause change in the sex ratio or even prevent successful breeding in particular years. However, such negative effects may be compensated when such events do occur occasionally accompanied by high longevity in this species (BULL and BULMER 1989). The maximum life span of *Trachemys scripta* may be up to 42 years in the wild (commonly ca. 30 years; HARDING 1997), whereby first reproduction on average can take place at the age of eight years (GIBBONS et al. 1981). Hence, it appears likely that single or even few years with suboptimal reproductive success may not cause extinction of local populations. Mean temperature over a longer time span might be more important for long-term maintenance of populations and hence for a species' geographic distribution.

Assessing the explanative power of variables

In order to evaluate the relative importance of monthly variables, we computed Climate Envelope Models with MaxEnt 3.2.19 (PHILLIPS et al. 2004; 2006; http://www.cs.princeton.edu/~shapire/Maxent; downloaded 15 October 2008). MaxEnt is a machine-learning algorithm for species potential distribution models with environmental predictors. In multiple tests, MaxEnt generally revealed better results than comparable methods (ELITH et al. 2006; HEIKKINEN et al. 2006; WISZ et al. 2008). The general concept behind MaxEnt is to find a probability distribution covering the study area derived from environmental constraints at species presence. The program chooses the distribution that is closest to uniform and therefore maximises entropy (JAYNES 1957) within all distributions (PHILLIPS et al. 2006; PHILLIPS and DUDÍK 2008). Runs used herein were conducted using the default values for MaxEnt settings.

In order to evaluate the predictive performance of the monthly temperature variables, we computed (1) 12 models using the 12 monthly mean temperatures separately as variables (Figure 2.1-2) and (2) a single model based on all 12 variables in combination (Figure 2.1-3).

Maxent allows for model testing by calculation of the ‘Area Under the receiver operation characteristic Curve’ (AUC) based on training and random background data, which represent the ability of the model to distinguish presence data from background (PHILLIPS et al. 2006). This method is recommended for ecological applications because it is non-parametric (PEARCE and FERRIER 2000). Values of AUC range from 0.5 (i.e. random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of SWETS (1988), AUC values > 0.9 describe “very good”, > 0.8 “good” and > 0.7 “useful” discrimination ability.

While a MaxEnt model is being trained with multiple predictors, it is possible to keep track of which environmental variables are making the greatest contribution to the model. During each step of the MaxEnt algorithm, the gain of the model is increased by modifying the coefficient for a single feature. The program subsequently assigns the increase in the gain to the environmental variable(s) that the feature depends on. These are automatically converted into percentages at the end of the training process. These percent contribution values depend on the particular path that the MaxEnt code uses to get to the optimal solution and are therefore heuristically defined (PHILLIPS et al. 2006).

Results and discussion

Monthly temperature variation at Slider records

Variability of mean monthly temperatures within the geographic range of *Trachemys scripta* was highest during winter and lowest during summer (Figure 2.1-1, Table 2.1-1). Highest variation with an amplitude of 22.5 °C was observed in the mean temperature in January (median 3.85 °C; range -7.75–14.75 °C) and lowest with an amplitude of 7.59 °C in the mean temperature in July (median 26.80 °C; range 22.45–30.40 °C). This indicates a high variation throughout the large geographic range encompassed by the Slider in winter and likewise the contrast in summer. We found a strong correlation between the amplitudes of the monthly mean temperature from June to August and the sensitive phase for sex-determination in the Slider (Figure 2.1-1A).

Table 2.1-1 Variation in monthly mean temperature [°C] throughout the realised geographic range of *Trachemys scripta*. Mean monthly temperature data was obtained from 377 species records.

Month	Minimum	Maximum	Amplitude	1. Quartile	Median	3. Quartile
January	-7.75	14.75	22.50	-0.30	3.85	6.85
February	-5.20	16.80	22.00	2.50	5.90	9.15
March	1.10	20.95	19.85	7.55	10.60	13.25
April	8.15	24.55	16.40	13.45	15.65	17.90
May	14.45	27.25	12.80	18.50	20.05	22.15
June	20.10	29.45	9.35	23.35	24.40	25.95
July	22.45	30.40	7.95	25.90	26.80	27.50
August	21.05	30.50	9.45	24.95	25.85	27.05
September	16.65	28.15	11.50	20.80	22.10	23.95
October	10.35	24.15	13.80	14.55	15.90	18.25
November	2.90	19.75	16.85	7.25	10.40	12.65
December	-4.50	15.95	20.45	1.65	5.55	8.10

In the Hawksbill turtle (*Eretmochelys imbricata*), developing nests can increase their temperature for about 3.4 °C so that soil temperature may be raised (GLEN and MROSOVSKY 2004). The authors suggested that increase was attributable to metabolic heat produced by the developing eggs but magnitude of metabolic heating depends on clutch size (BOOTH and ASTILL 2001; BRODERICK et al. 2001). It cannot be ruled out that metabolic heating may also be important in nests of *T. scripta*, which could result in an underestimation of the actual nest temperature when applying mean air temperature as proxy for soil temperature (see above). But clutch size in *E. imbricata* is remarkably larger than in *T. scripta,* likely lowering the available amount of metabolic heat. Furthermore, eggs at the edge of a clutch of the Hawksbill turtle can be cooler than those in the centre (GODFREY et al. 1997; BOOTH and ASTILL 2001) and variation between the top of the clutch and the bottom may also exist (HOUGHTON and HAYS 2001). Therefore, we conclude that nest temperature in the Slider is well reflected by the soil temperature. As a consequence, mean air temperature cannot only be used as a proxy for mean soil temperature (e.g. HAYS et al. 2003; HAWKES et al. 2007) but also for the nest temperature in the Slider.

Which climatic factor best predicts the Slider's geographic range?

Performance of Climate Envelope Models computed with each the single monthly mean temperature as variables largely varied (Figure 2.1-1B), whereby the mean temperature in June and July (summer) had the greatest predictive power. Generally, AUC values obtained from models computed with monthly mean temperatures for winter times were lower than those revealed for summer times. These observations lead us to advocate that the monthly mean temperature during summer months at Slider presence records provide a stronger contrast to random background in MaxEnt approaches. The model received when using the mean June temperature resulted in the highest AUC value suggesting that it is the best predictor (among those studied) for the species’ geographic range (Figure 2.1-1B).

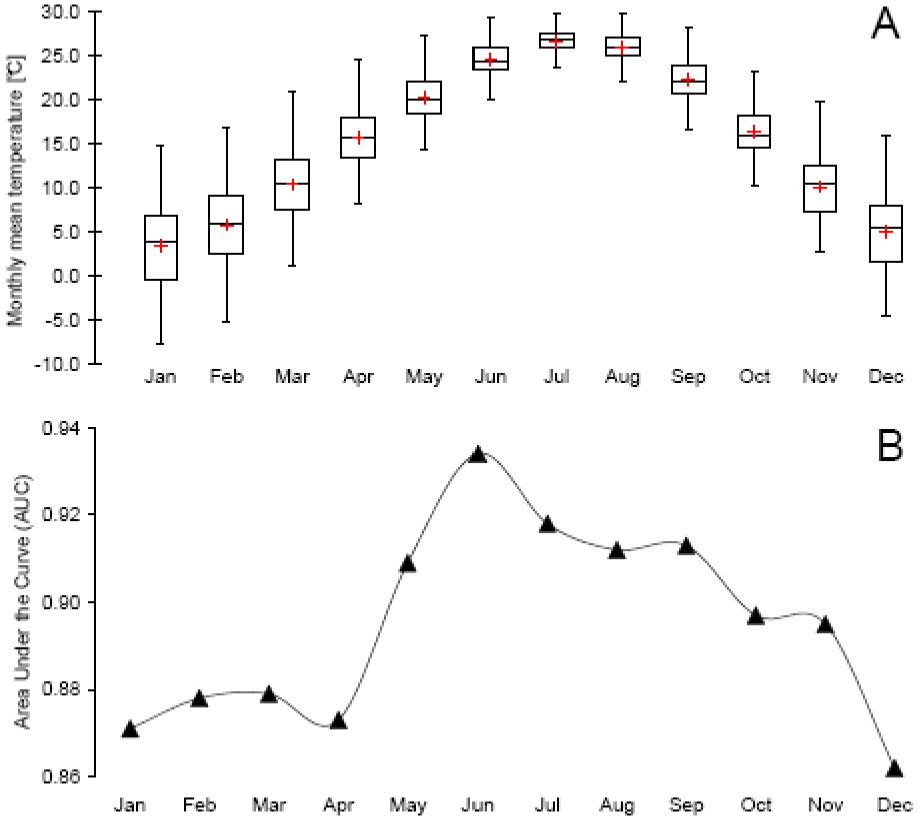

Figure 2.1-1 A: Boxplots illustrating the variability of the monthly mean temperature at 377 distribution records within the native range of *Trachemys scripta*. Note that the variation is lowest during the incubation of eggs (June-August). B: performance of monthly mean temperature observed at the Slider records in models computed with single variables (see text). Higher AUC values suggest that the respective model has a higher ability to distinguish climatic conditions at Slider records from random background.

The model computed with all 12 monthly mean temperatures as variables received a ‘very good’ (see SWEETS 1988) AUC value of 0.957. The known geographic range of *Trachemys scripta* in North America was well matched (Figure 3) which also confirms the predictive power of this model. Maxent's analysis of variable contribution to the model revealed that the mean temperature in August had the highest explanative power, followed by those for June and May, while all others had minor explanative power only (Table 2.1-2).

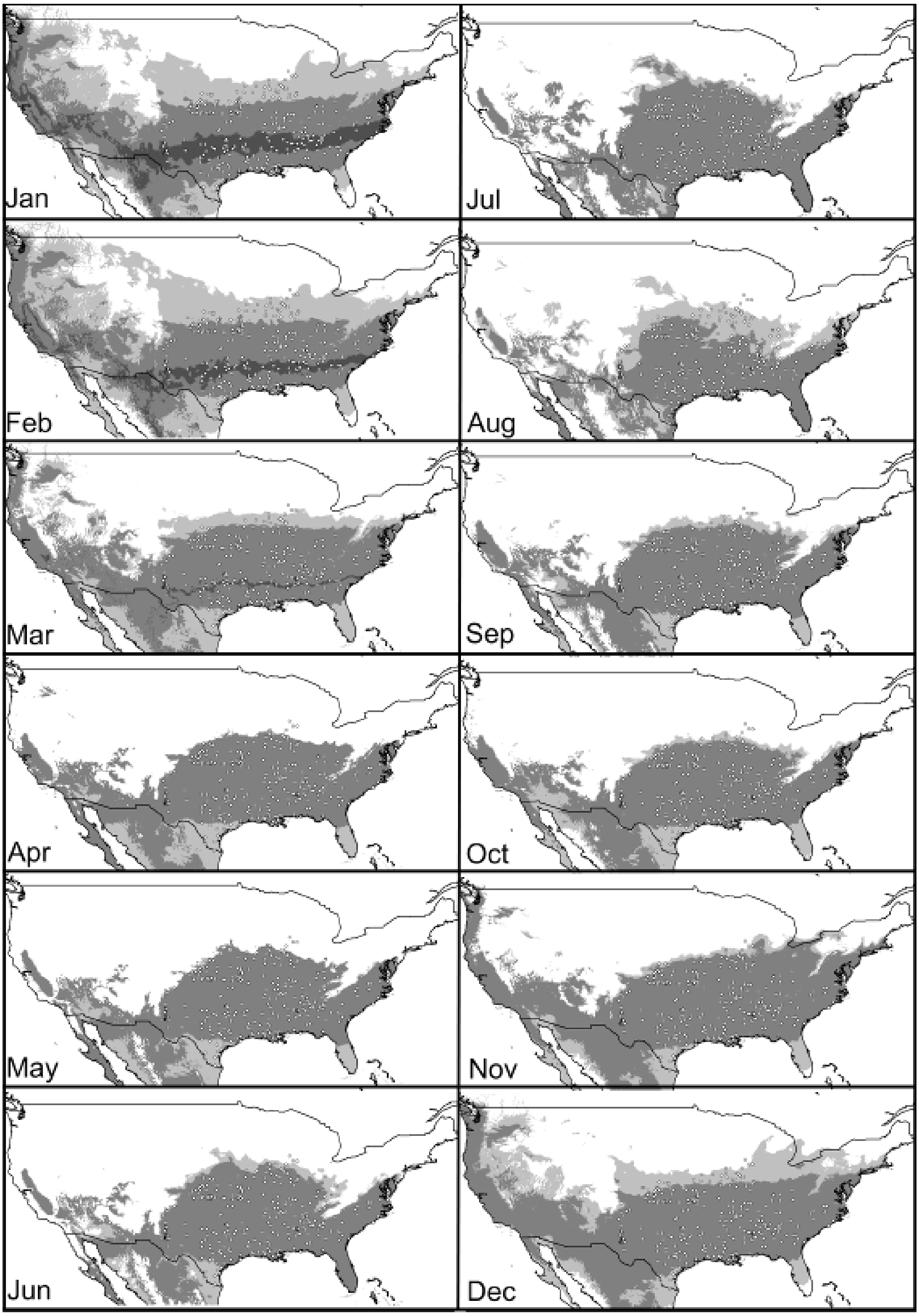

Figure 2.1-2 MaxEnt Climate Envelope Models computed using the mean temperature for each month as single variables. Darker grey-scale suggests higher climatic suitability (same scale as in Figure 3). Species records used for modelling are indicated by white dots.

Table 2.1-2 Heuristic estimate of the explanative power of the mean temperature per month to the MaxEnt Climate Envelope Model. To determine the estimate, in each iteration of the training algorithm, the increase in regularised gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative.

Mean Temperature per Month	Percent Contribution
August	27.7
June	27.1
May	24.3
February	4.8
October	4.6
November	4.5
July	3.3
January	2.1
December	1.0
April	0.2
March	0.2
September	0.1

When computing models with multiple variables, it needs to be noted that multicolinearity among predictor variables may bear the risk of hampering the analysis of species-environment relationships. Ecologically more causal variables may be excluded from the modelling process if other inter-correlated variables explain the variation in response variable better in terms of statistics (HEIKKINEN et al. 2006). We expect such multicolinearity for monthly mean temperatures included in our model, evident through the limited explanative power (in contrast to the single variable approach) of the mean temperature in July suggested by the MaxEnt analysis of variable contribution (Table 2.1-2).

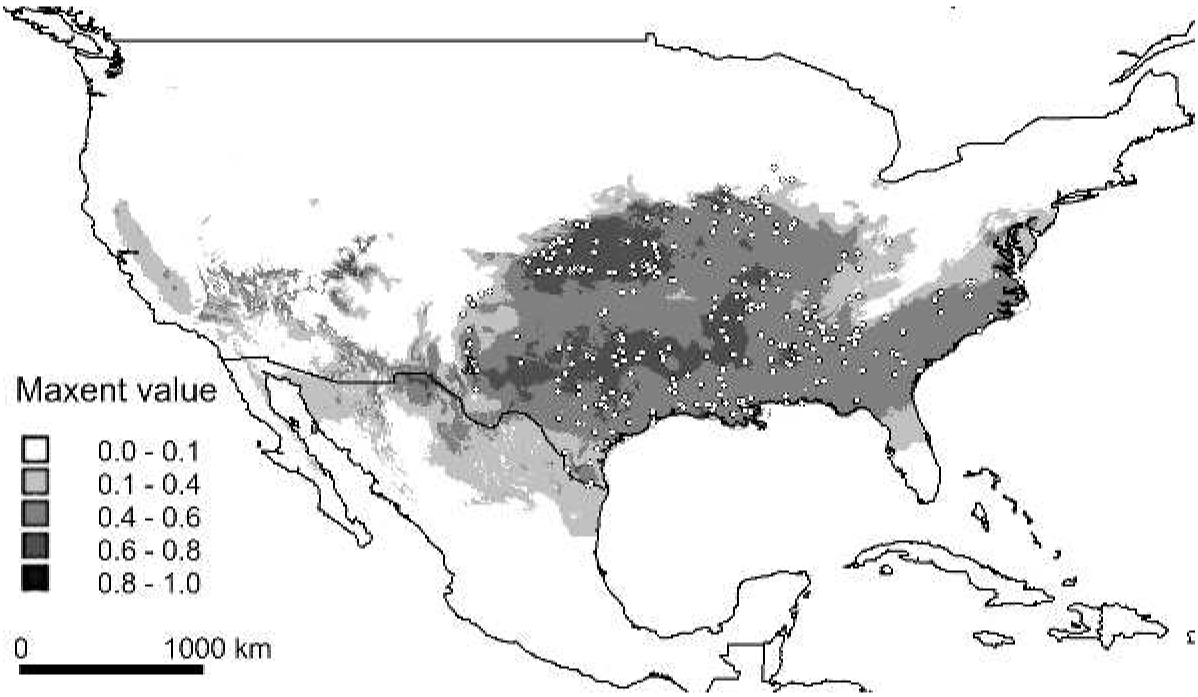

Figure 2.1-3 *Trachemys scripta* records (white dots) used for model training and the species' potential distribution according to a MaxEnt Climate Envelope Model based on mean temperature of all 12 months as variables. Darker grey-scale suggests higher climatic suitability.

Impact of winter temperatures

PACKARD et al. (1997) have suggested that the northern geographic range limit of *Trachemys scripta* may be set ultimately by the inability of hatchlings to tolerate freezing. Slider offspring commonly hibernates inside the nest during the first winter in northern populations and they are sensitive to nest temperatures below -0.6 to -4.0 °C, at which they die (PACKARD et al. 1997; TUCKER and PACKARD 1998; COSTANZO et al. 2008). According to our observations, winter temperatures exhibit the greatest variation throughout the native geographic range (Figure 2.1-1A) and at the same time had the lowest explanative power (Figure 2.1-1B). Although the minimum of the mean monthly temperature was well above 0 °C at the majority of the Slider records studied (Figure 2.1-1A), the mean temperature was lower than -0.6 °C at 88 records in January, at 28 records in February and at 35 records in December. The minimum mean temperature recorded at our records was -7.75 °C in January. We acknowledge that freezing may limit the geographic distribution of *T. scripa* in the North. However, projection of monthly climate envelopes in geographic space illustrates that monthly mean temperatures during December, January and February were not coincident with the species' range limits in the North-East or the West. This makes us believe that low winter temperatures are not the major driver for most of the northern portion of the actual geographic range of the Slider. Summer temperatures may be more important for the geographic distribution of the species as these better meet the native range of the Slider.

Possible strategies for compensation of climatic variation

Although our results argue for a strong relationship between mean temperatures in summer and the spatial distribution of *Trachemys scripta*, the climatic variation throughout this species' range is larger than expected when assuming fixed TRTs. Mechanisms compensating local differences in temperature regimes can comprise either regional differences in behaviours such as nest site choice by females and plasticity in nesting phenology or regional variations in embryonic temperature sensitivity.

For the Painted turtle (*Chrysemys picta*), also native to North America, it has been demonstrated that vegetation cover plays an important role in determining nest temperatures and nest sex ratios over the year (JANZEN 1994b; WEISROCK and JANZEN 1999). However, July mean air temperature determines the average nest sex ratio each year and strongly predicts the cohort sex ratio (SCHWARZKOPF and BROOKS 1987; JANZEN 1994a; 1994b; WEISROCK and JANZEN 1999). In the study of SCHWARZKOPF and BROOKS (1987), sex ratios were not correlated with any nest parameters except temperature which, on the other hand, was more dependent on annual climatic variation than on variation in site characteristics. The authors concluded that Painted turtle females selected nest sites to maximise the probability for their eggs to hatch rather than to influence the offspring sex ration. If this is also the case in *T. scripta*, the Slider may not be able to compensate variation in summer temperatures throughout its range.

Comparing geographic variation in timing of nesting, ARESCO (2004) found little variation in *T. scripta*. He concluded that it is unrelated to regional temperature differences and fixed as a result of stabilizing selection. Even if phenotypic plasticity of timing of nesting will be possible, it might not be sufficient, like it has been suggested by SCHWARZ and JANZEN (2008) for the Painted turtle. The authors underlined that phenotypic plasticity of labile nesting dates depended on the climate of the previous winter, but argued that this plasticity appears to be insufficient to prevent potentially negative effects of climate warming on offspring sex ratios. Even a minor increase in the summer temperature had a much stronger effect on nest sex ratios than, alternatively, laying eggs earlier in the season (SCHWARZ and JANZEN 2008).

If environmental temperature differs between populations, then sex-ratio selection is expected to adjust either maternal behaviour (as discussed above) or embryonic temperature sensitivity to maintain balanced sex-ratios in different populations (BULL 1982). Physiological studies suggest that seasonal shifts in hormone levels, affecting the sex ratio may buffer extreme ratios in some species (BOWDEN et al. 2000). Such effects were uncovered in *T. scripta* by SHEEHAN et al. (1999), who artificially treated eggs with hormones. However, BULL (1982) found no evidence for natural differences in embryonic temperature sensitivity between northern and southern Slider populations.

Conclusion

Our study indicates that freezing during the winter may regionally but not generally limit the Slider's geographic distribution. It appears to be more likely that climatic requirements allowing for successful egg incubation and balanced sex ratios in *T. scripta* are the major driver for the Slider’s spatial range. Although adaptive strategies such as nest site choice by females, plasticity in nesting phenology or regional variation in embryonic temperature sensitivity may account for partial compensation of negative effects caused by local differences or climate change, they might be insufficient for entire compensation.

Acknowledgments

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2.2. Alien invasive Slider in unpredicted habitat: a matter of niche shift or variables studied?[3]

Trachemys scripta elegans

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[3] This part was submitted to *PLoS ONE*.

The work reported in this chapter was conducted in collaboration with SEBASTIAN SCHMIDTLEIN from the Geography Department, University of Bonn, Bonn, Germany, and MICHAEL VEITH and STEFAN LÖTTERS from the Faculty of Geosciences, University of Trier, Trier, Germany.

Introduction

Alien invasive species are a concern in nature conservation as they may have a negative impact on native biodiversity (LOWE et al. 2000). Potential distribution maps of invasive species based on Climate Envelope Models (CEM) have been shown to represent a powerful tool to identify areas climatically suitable for alien invasive species (e.g. PETERSON and VIEGLAIS 2001; WELK et al. 2002; GIOVANELLI et al. 2007; RÖDDER et al. 2008; RÖDDER 2009). In these approaches, the climate envelope can be understood as a part of a species' fundamental niche (e.g. SOBERÓN and PETERSON 2005; but see also PULLIAM 2000), which is the entirety of abiotic and biotic conditions under which it can survive. According to HUTCHINSON (1957, 1978) as modified by SOBERÓN and PETERSON (2005), the portion of the fundamental niche exploited by a species is commonly limited by biological interaction with other species (e.g. competition, predation) and by spatial accessibility (e.g. physical barriers) (Figure 2.2-1A). Fundamental niches are subject to evolution: in a recent review, it has been shown that, independent of the taxonomic group, the fundamental niche can remain stable for tens of thousands of years or it can shift substantially within only a few generations (PEARMAN et al. 2008). However, in general, there is a considerable lack of knowledge regarding the processes triggering niche shifts.

SAX et al. (2007) pointed out that alien invasive species can provide unexpected experiments providing valuable insights into ecological and evolutionary processes. Indeed, some recent studies have addressed the question of rapid niche shifts during invasion processes. Using CEMs, BROENNIMANN et al. (2007) found that in the Spotted knapweed (*Centaurea maculosa*) the climate envelopes in its native range (western North America) differed from its invasive range in Europe. Similarly, FITZPATRICK et al. (2007) demonstrated in a CEM approach that Fire ants (*Solenopis invicta*) can be ascribed to climate envelopes in their invaded range (North America) from which they are absent in their native South American range. These observations made by BROENNIMANN et al. (2007) and FITZPATRICK et al. (2007) could represent a shift either in the fundamental (Figure 2.2-1B) or realized niche (Figure 2.2-1C). Since alien invasive species, by definition, access areas they were absent from before, the "new" climate envelope might most likely simply represent a better exploitation of the existing fundamental niche (Figure 2.2-1C). To the best of our knowledge, information on the physiological limits of *Centaurea maculosa* and *Solenopis invicta* is sparse. Hence, it cannot be ruled out that the climate variables chosen by BROENNIMANN et al. (2007) and FITZPATRICK et al. (2007) are not physiologically limiting for the native range borders of these species.

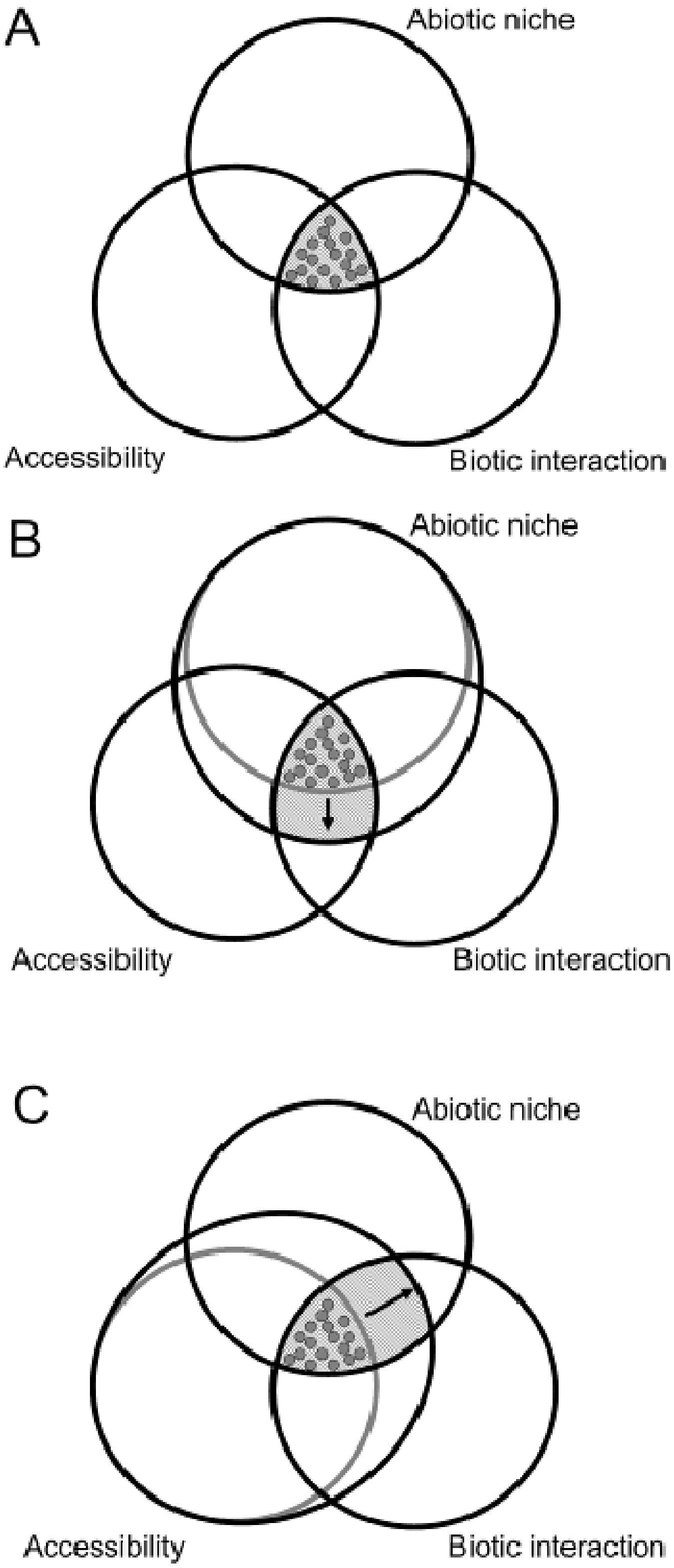

Figure 2.2-1 (A) Relationships between fundamental niche, biotic interaction and accessibility after Hutchinson (1957) as modified by Soberón and Peterson (2005); (B) fundamental niche shift; (C) better exploitation of the fundamental niche after access into new areas. Dots represent native species records.

We think that this striking question – i.e. genetic novelty (niche evolution) versus a better insight into the existing fundamental niche breadth – should be addressed when applying CEM.

Some authors have argued that CEM approaches using observed distributions for model computation per se rather reflect realized than fundamental niches (e.g. PULLIAM 2000). That may cause errors when projecting CEMs into new areas, since suitable areas may be excluded although being physiologically suitable for the target species. Modeling should thus focus on the physiological limits of species for optimal predictions. Without this information, many of the observed mismatches (or "niche shifts") might simply be artifacts caused by a choice of unsuitable variables. We hypothesize that a selection of predictors aiming at a description or even at a complete depiction of the climatic conditions in the native range may be less useful for statistical model training than predictor selections based on a mechanistic understanding of physiologically limiting factors.

So far, only a few studies have tried to model the fundamental niche of a species without using distribution records. In a comprehensive study, KEARNEY and PORTER (2004) combined physiological measurements of the Australian gecko *Heteronotia binoei* and high-resolution climatic data to calculate its climate envelope and to project it onto geographic space. KEARNEY et al. (2008) undertook a similar study in Cane toads, *Chaunus marinus*, which is an invasive alien species in Australia. Such a mechanistic approach, as suggested by these authors, seems to be clearly superior to the commonly used empirical methods. However, detailed information on the physiology and natural history traits required to fully address the fundamental niches from a mechanistic point of view will remain unavailable for most of our planet's species (KEARNEY and PORTER 2004; KEARNEY et al. 2008). However, at least the variables with physiological relevance are often known. Accordingly, empirical records and statistical models will remain a starting point, with predictor sets based on natural history providing the most successful calibrations - a hypothesis to be tested here.

In order to test this hypothesis, the Slider (*Trachemys scripta* SCHOEPFF, 1792) may be a suitable study organism. It is an alien invasive species in many parts of the world and its ecology has been thoroughly studied. Between 1989 and 1997, about 52 million individuals were produced in the United States for the foreign pet trade (TELECKY 2001). Released by pet owners, it has established feral populations in many different regions of the world (e.g. OTA et al. 2004; PERRY et al. 2007; RAMSAY et al. 2007; IUCN Invasive Species Specialist Group: "*Trachemys scripta elegans*" under: www.issg.org). At the same time, the natural history (including thermal tolerance, reproduction and physiology) of the slider has been the object of numerous studies (e.g. HUTCHISON et al. 1966; HUTCHISON 1979; GARSTKA et al. 1991; WIBBELS et al. 1991; CREWS et al. 1994; BACCARI et al. 1993; BAILEY and DRIEDZIC 1995; LAMB et al. 1995; PACKARD et al. 1997; TUCKER et al. 1998; TUCKER and PACKARD 1998), providing the basis for a natural history-driven modeling approach.

Methods

Slider record data

We used 375 Slider records available through the Global Biodiversity Information Facility (GBIF; www.gbif.org) and HerpNet databases (www.herpnet.org) within the native range of the species, as defined by L. A. SOMMA, A. FOSTER and P. FULLER (2008): "*Trachemys scripta*" in the USGS Nonindigenous Aquatic Species Database (http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=1259). In addition, 205 records of invasive populations were obtained from the source by SOMMA and colleagues, the Delivering Alien Invasive Species Inventories for Europe database (DAISE; www.europe-aliens.org), the IUCN Invasive Species Specialist Group (www.issg.org), the Brazilian Instituto Hórus (www.instutohorus.org.br) and additional published references (JONES 1988; SCHWARTZ and HENDERSON 1991; DA SILVA and BLASCO 1995; DEGENHARDT et al. 1996; MCKEOWN 1996; PLATT and SNYDER 1996; LUISELLI et al. 1997; MARTÍNEZ-SILVESTRE et al. 1997; NOVOTNY 1997; ARVY and SERVAN 1998; SAENZ and COLLINS 1999; DIXON 2000; MINTON 2001; FICETOLA et al. 2002; TOWNSEND et al. 2002; EMER 2004; OTA et al. 2004; STITT et al. 2004; EHRET and PARKER 2005; ARESCO and JACKSON 2006; BRUEKERS and BROUWER 2006; CHEN 2006; PIEH and LAUFER 2006; PRÉVOT-JULLIARD et al. 2007). For georeferencing we used the Alexandria Digital Library Gazetteer Server Client (www.middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp). The accuracy of coordinates processed by us was assessed with DIVA-GIS (HIJMANS et al. 1999; 2001). In doing so, we only included invasive records with confirmed successful reproduction.

Climate data

Our climate information stems from Worldclim 1.4 (HIJMANS et al. 2005), which is based on climate conditions in the period 1950-2000 at a spatial resolution of about 1 x 1 km. It was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995; 2004). The climate data set was downloaded from the DIVA-GIS homepage (http://www.diva-gis.org), i.e. 36 monthly mean variables (minimum temperature, maximum temperature and precipitation). Based on these data, we calculated 19 ‘bioclimate’ variables for further processing with DIVA-GIS 5.4 (see Figure 2.2-2 and Appendix 2.2-S1; HIJMANS et al. 2001). DIVA-GIS provide the opportunity to plot the cumulative frequency of distribution records according to ‘bioclimate’ variables. This allowed us to compare the climatic tolerance between the native and invasive distributions of the Slider for all 19 ‘bioclimate’ variables.

Selection of climate variables

We chose three sets of variables: ‘comprehensive’ set: all 19 ‘bioclimate’ layers depicting the most comprehensive climatic pattern following the approach of different authors running CEM (e.g. BROENNIMANN et al. 2007; GIOVANELLI et al. 2007); ‘minimalistic’ set: a subset of seven variables out of the ‘comprehensive’ data set defining the availability of thermal energy and water (e.g. the minimum, maximum and mean values at the species records) as applied to different taxa by HIJMANS and GRAHAM (2006), PETERSON and NYÁRI (2007), FITZPATRICK et al. (2007) and FICETOLA et al. (2007); ‘natural history’ set: a subset of five variables out of the ‘comprehensive’ set aiming at reflecting the physiological limits of the Slider’s climate envelope (see results for details). To be clear, we did not use these variables to map the known physiological limits. The variables were used as predictors in the same way as the other sets. In addition, we analyzed random subsets of seven and five ‘bioclimate’ variables, respectively, to test the null hypotheses that our selected variable sets ’minimalistic’ and ’natural history’ do not predict the potential distribution of invasive populations better than any random set consisting of the same number of variables. All sets, including the ‘minimalistic’ and ‘natural history’ sets, were extracted from the same set of 19 Worldclim variables

Selection of the ‘natural history set’ of variables: The Slider strongly depends on continuous availability of water throughout the year, whereby almost any kind of water body is suitable (SOMMA et al. 2008). Therefore, it is not surprising that the south-western limit of its native range border is found in the North American deserts, which are characterized by low precipitation throughout the year (SOMMA et al. 2008). To take this into account, we included the 'annual precipitation' and the 'precipitation of the driest quarter' in our data set for CEMs. It has been demonstrated that the feeding behavior and digestive turnover rates in the Slider are strongly temperature-dependent. At body temperature < 10 °C the species does not feed anymore (PARMENTER 1980; RAMSAY et al. 2007). Hence, in accordance with a positive energetic balance over the year, we added the 'annual mean temperature' into our modeling approaches. The physiologically determined minimum equates with the minimum value recorded within the native range (8.3 °C; see Appendix 2.2-S1). HUTCHISON (1979) has shown that the upper avoidance temperature is around 37 °C which is remarkably similar to the upper limit of the 'maximum temperature of the warmest month' recorded within the native range (i.e. 37.4 °C; see Appendix 2.2-S1). To account for this we included the 'maximum temperature of the warmest month' in CEM approaches.

Adult Sliders commonly hibernate at the bottom of icebound water bodies being largely insulated against cold air. They maintain a body temperature of approximately 4 °C, which makes the species insensitive to cold winters. Nevertheless, PACKARD et al. (1997) compared Slider records from Illinois and eastern Iowa with contours identifying locations where frost penetrates to a depth of 12 cm in 11 out of 14 winters and found a strong relationship. In colder parts of the native range, Slider neonates hibernate inside their nests and are sensitive to temperatures below -0.6 °C, at which they die (see also TUCKER and PACKARD 1998). As a consequence, adult Sliders hibernating in water may tolerate frost, but neonates in nests may be negatively affected by frost. The native range of our study species to the north is therefore reasonably defined by minimum temperatures during winter. Considering this relationship, we included 'minimum temperature of the coldest month' when computing CEM.

Computation of CEM

For the CEM calculation we used MaxEnt 3.2.1 (PHILLIPS et al. 2006; http://www.cs.princeton.edu/~shapire/maxent), a machine-learning algorithm following the principles of maximum entropy. It has been shown to reveal better CEM results than other comparable methods (e.g. ELITH et al. 2006; JESCHKE and STRAYER 2008; WISZ et al.

2008). A disadvantage of MaxEnt is that it is a ‘black box’ method. Since results can remarkably vary between different algorithms, we compared MaxEnt results with those obtained from a second algorithm BIOCLIM (NIX 1986; BUSBY 1991), as implemented in DIVA-GIS. BIOCLIM develops climate envelope models by intersecting the ranges inhabited by the species along each environmental axis. An advantage of this method is that results are completely transparent for interpretation.

Clumped records can violate the statistical independence of observations and therefore assumptions of CEMs (e.g. DORMANN et al. 2007). To account for this we extracted all ‘bioclimate’ values from the native distribution records and performed a cluster analysis with XLSTAT 2008 (Addinsoft; www.xlstat.com) in order to remove redundant information in the data set. XLSTAT allows to blunt cluster classes at a predefined threshold of similarity (herein 99.9 %), and calculates mean values for each resulting class. These class means were used for further processing in CEMs.

DIVA-GIS allows for model testing by calculation of the Area Under the Curve (AUC), referring to the ROC (Receiver Operation Characteristic) curve by using a subset of data (commonly 25-30 %) as test points and the remaining ones as training points (ELITH et al. 2006; PEARCE and FERRIER 2000). Independent validation (i.e. with invasive records) was suggested to be superior to data splitting (e.g. JESCHKE and STRAYER 2008); therefore, we used all invasive Slider records as subsets and in a second run 25 % of the native records. Because absence data are lacking, DIVA-GIS uses a set of random pseudo absence points (HIJMANS et al. 2001). AUC calculation is recommended for ecological applications because it is non-parametric. Values of AUC range from 0.5 for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of SWETS (1988), AUC values > 0.9 describe ‘very good’, > 0.8 ‘good’ and > 0.7 ‘useable’ discrimination ability.

For thresholds derived from the natural history and physiological traits describing the climate envelope of the Slider, it is important to reduce the contribution of variables to their upper or lower tails, respectively. This is reasonable considering the limiting function of the ‘minimum temperature of the coldest month’, which may kill neonates. Here, only the lower tail has a biological meaning, but warmer temperatures may provide no disadvantage for the species. In BIOCLIM this kind of function is implemented directly, but is unfortunately absent in Maxent. Therefore, we used grids of each variable containing categorical classes between the upper or lower limits and the mean of the variables within the native range of the Slider for MaxEnt runs. For parts of a grid representing the biologically meaningless tail, values greater or smaller than the mean of the variable within the native range were combined into a single category. These procedures remove the influence of meaningless tails during MaxEnt runs.

The logistic output of MaxEnt is a continuous map which allows fine distinctions to be made between the modeled suitability of different areas. MaxEnt calculates a threshold value at each run (PHILLIPS et al. 2006). Values greater than this threshold may be interpreted as reasonable approximation of a species' potential distribution, but the higher a MaxEnt value, the better the prediction and therefore the climatic suitability for a species.

Six types of areas are mapped in the BIOCLIM output: areas outside the 0-100 percentile climatic envelope of the species for one or more 'bioclimate' variables are considered unsuitable, grid cells within the 0-2.5 percentile have a 'low' climatic suitability, those within the 2.5-5 percentile a 'medium', those within the 5-10 percentile a 'high', those within the 10-20 percentile a 'very high' and cells within the 20-100 percentile an 'excellent' climatic suitability (HIJMANS et al. 2001).

Results

Figure 2.2-2 compares each of the 19 'bioclimate' variables of the native and invasive ranges of the Slider, respectively. Ranges of variables observed in invasive populations which exceed those observed in native ones can be interpreted as shifts in niche dimension. Ranges in the following variables were most similar in native and invasive ranges: 'annual mean temperature', 'mean temperature of the wettest quarter', 'mean temperature of the driest quarter', 'annual precipitation', 'precipitation of the driest month', 'precipitation of the driest quarter' and 'precipitation of the coldest quarter'. The highest dissimilarity was found in 'isothermality', 'temperature seasonality', 'annual temperature range', 'minimum temperature of the coldest month' and 'mean temperature of the coldest quarter'. Lower temperature limits in the native and invasive ranges were almost equal for 'annual mean temperature', 'isothermality', 'minimum temperature of the coldest month', 'mean temperature of the wettest quarter' and 'mean temperature of the driest quarter', but the upper limits within the invasive range frequently exceeded those of the native range.

Areas meeting all climatic requirements of the species according to the expected physiological limits of the Slider are mapped in Figure 2.2-3. Areas where any of the proposed climatic variables are outside the physiological limit of the species were excluded. The remaining area is highly coincident with the native range as well as records of native and invasive populations (AUC_{native} = 0.849; $AUC_{invasive}$ = 0.795).

Applying the ’comprehensive set’ of ‘bioclimate’ variables to CEM calculation predicted the native range in a way which matched the known natural distribution of the Slider in both MaxEnt and BIOCLIM models. However, the models largely failed to predict populations elsewhere in the world due to overfitting (Figure 2.2-4A, also see Appendix 2.2-S2; MaxEnt AUC_{native} = 0.991; $AUC_{invasive}$ = 0.716; BIOCLIM AUC_{native} = 0.990; $AUC_{invasive}$ = 0.547). Using the ’minimalistic’ subset of ‘bioclimate’ variables, CEM accuracy within the native range was reasonably met. However, predictions for invasion of the Slider outside North America remained poor (Figure 2.2-4B; also see Appendix 2.2-S2; MaxEnt AUC_{native} = 0.989; $AUC_{invasive}$ = 0.702; BIOCLIM AUC_{native} = 0.988; $AUC_{invasive}$ = 0.535). In contrast, only the results for the ‘natural histroy’ subset of variables met both native and invasive potential distributions of the Slider (Figures 4C; also see Appendix 2.2-S2; MaxEnt AUC_{native} = 0.974; $AUC_{invasive}$ = 0.861; BIOCLIM AUC_{native} = 0.974; $AUC_{invasive}$ = 0.757).

The randomly selected subsets of five and seven ‘bioclimate’ variables revealed that all models were ‘very good’ in describing the native range ($AUC_{\text{seven variables}}$ 0.987 – 0.994; $AUC_{\text{five variables}}$ 0.977 – 0.994; Figures 2.2-5, 2.2-6), which is slightly better then our models derived from the ‘natural history’ set. Comparing the predictive performance of the models outside the Slider’s native range, selection of a lower number of variables was associated with a broader area classified as suitable in a limited number of models (< 10 %). The AUC value of our model for invasive records derived from natural history criteria was higher than all AUC values obtained from random variable selection confirming a better prediction ability (AUC ranges seven random variables: native: 0.987–0.994, invasive: 0.587–0.847, AUC ranges five random variables: native: 0.977–0.994, invasive: 0.569–0.855; AUC data set ‘natural history’ = 0.861). In both random iterations, invasive records were less frequently captured than invasive records at the same latitudes as the native records (Figures 2.2-6A, B). This applies especially to records situated at lower latitudes (between 26° N and S corresponding to the southernmost known native records). This latitudinal decrease in predictive performance was confirmed when testing the models using only invasive records between 26° N and S as test points (n = 62; Figures 2.2-6D, E; AUC range seven random variables: 0.356–0.708; AUC range five random variables: 0.279–0.749), whereas our model derived from natural history criteria performed well here

(Figure 2.2-6C, AUC = 0.795). Thus, the vast majority of models did not capture the Slider’s actual climate envelope.

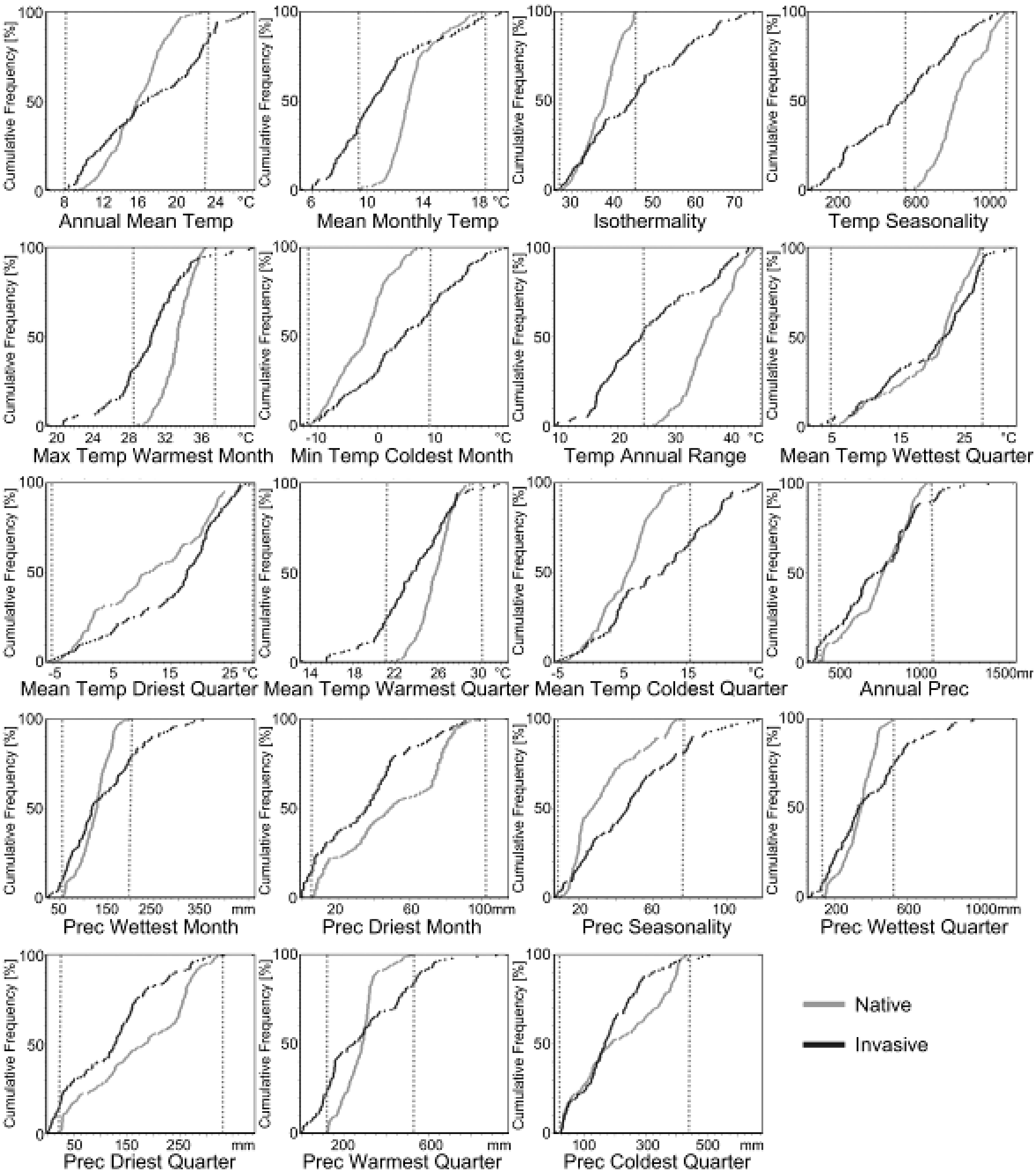

Figure 2.2-2 Comparison of 19 ‘bioclimate’ variables at 375 native and 205 invasive records of the Slider. Ranges of variables within the native records are indicated with vertical dashed lines. Note that some upper and lower limits of both native and invasive records are highly congruent.

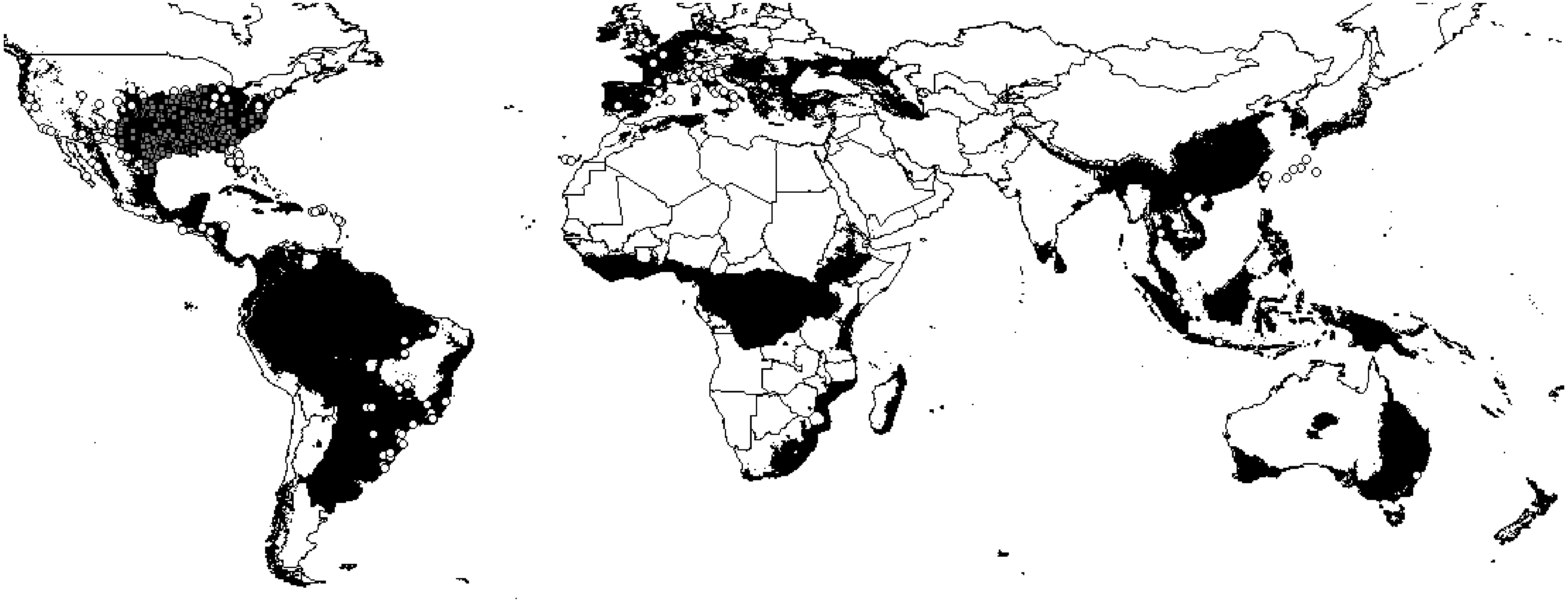

Figure 2.2-3 Presence of the Slider in its native range (grey dots) and in its invasive range where it is known to reproduce (white dots). Areas considered as suitable for the Slider with respect to physiological limits as described in the text are indicated (black).

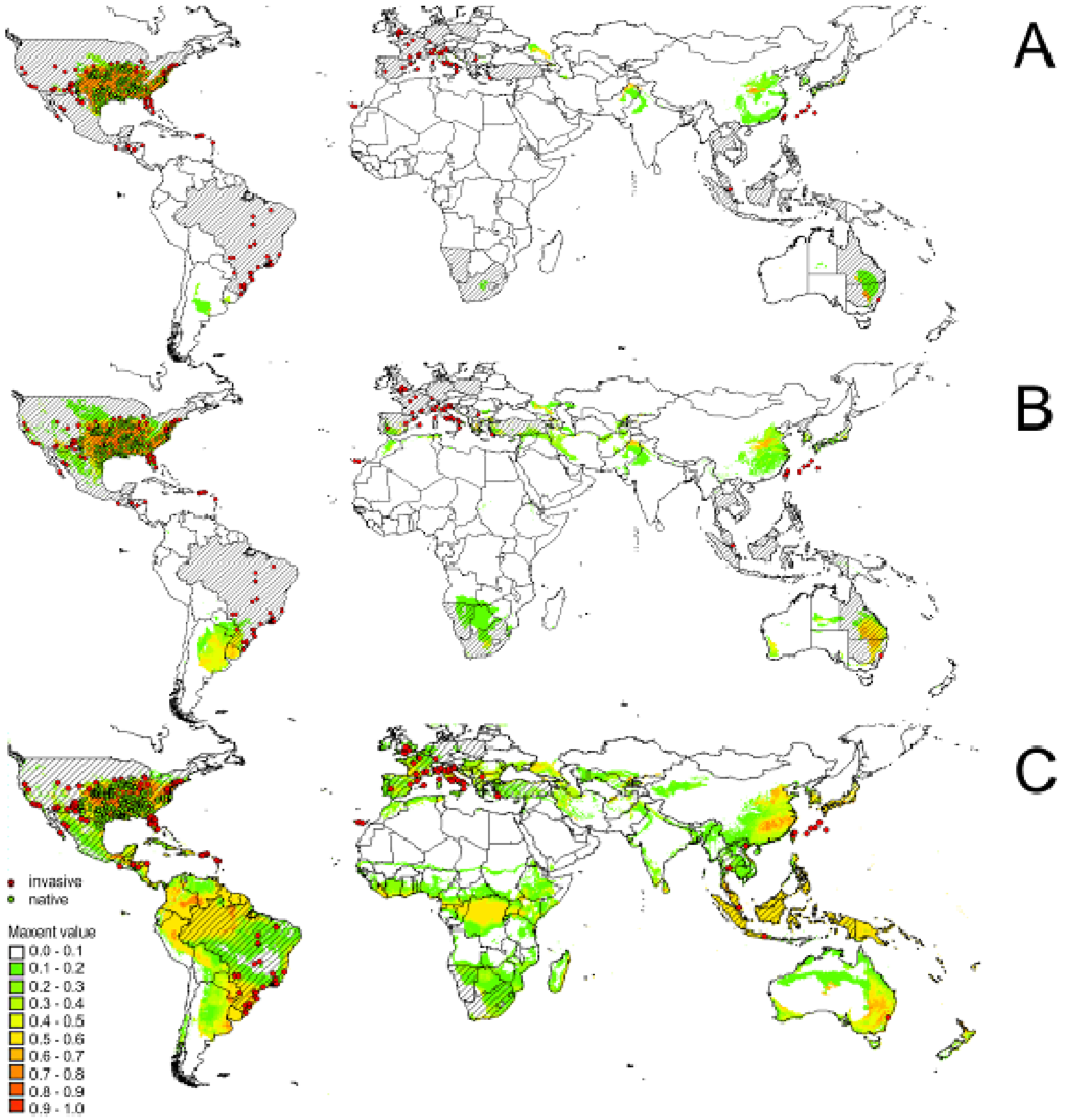

Figure 2.2-4 Presence of the Slider in its native range (green dots) and invasive range where it is known to reproduce (red dots), countries from which reproducing populations are known but no specific localities are available (hatched) and potential distribution derived from MaxEnt climate envelope (colored): (A) using 19 'bioclime' variables, approach 'comprehensive'; (B) using 7 'bioclime' variables, approach 'minimum'; (C) using 5 'bioclime' variables derived from physiological and natural history traits of the Slider, approach 'natural history'.

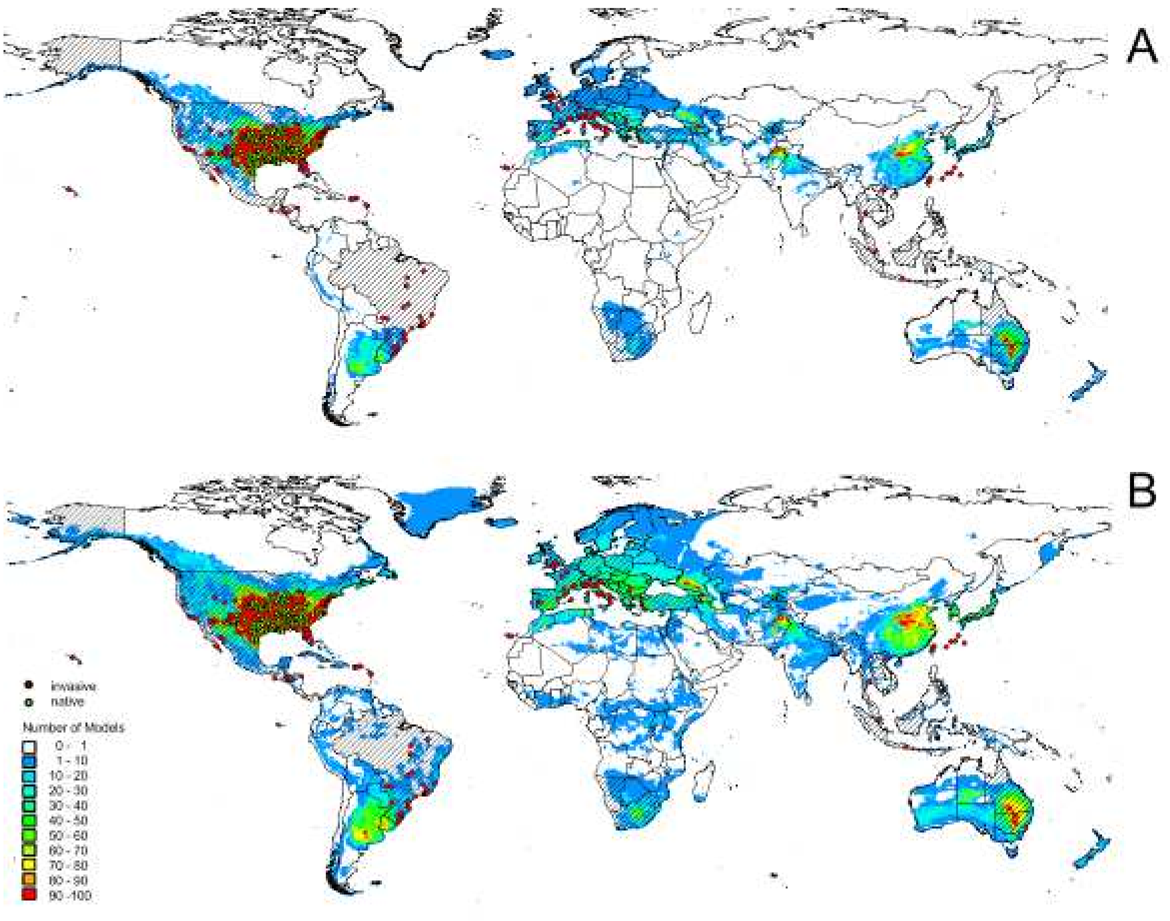

Figure 2.2-5 Prediction accuracy of 2 × 100 MaxEnt models calculated with a random selection of seven (A) and five (B) variables out of the complete set of 19 ‘bioclimate’ variables. Note that the native range is well captured by each model whereby the invasive populations, especially between 26.0° N and S longitude, are not.

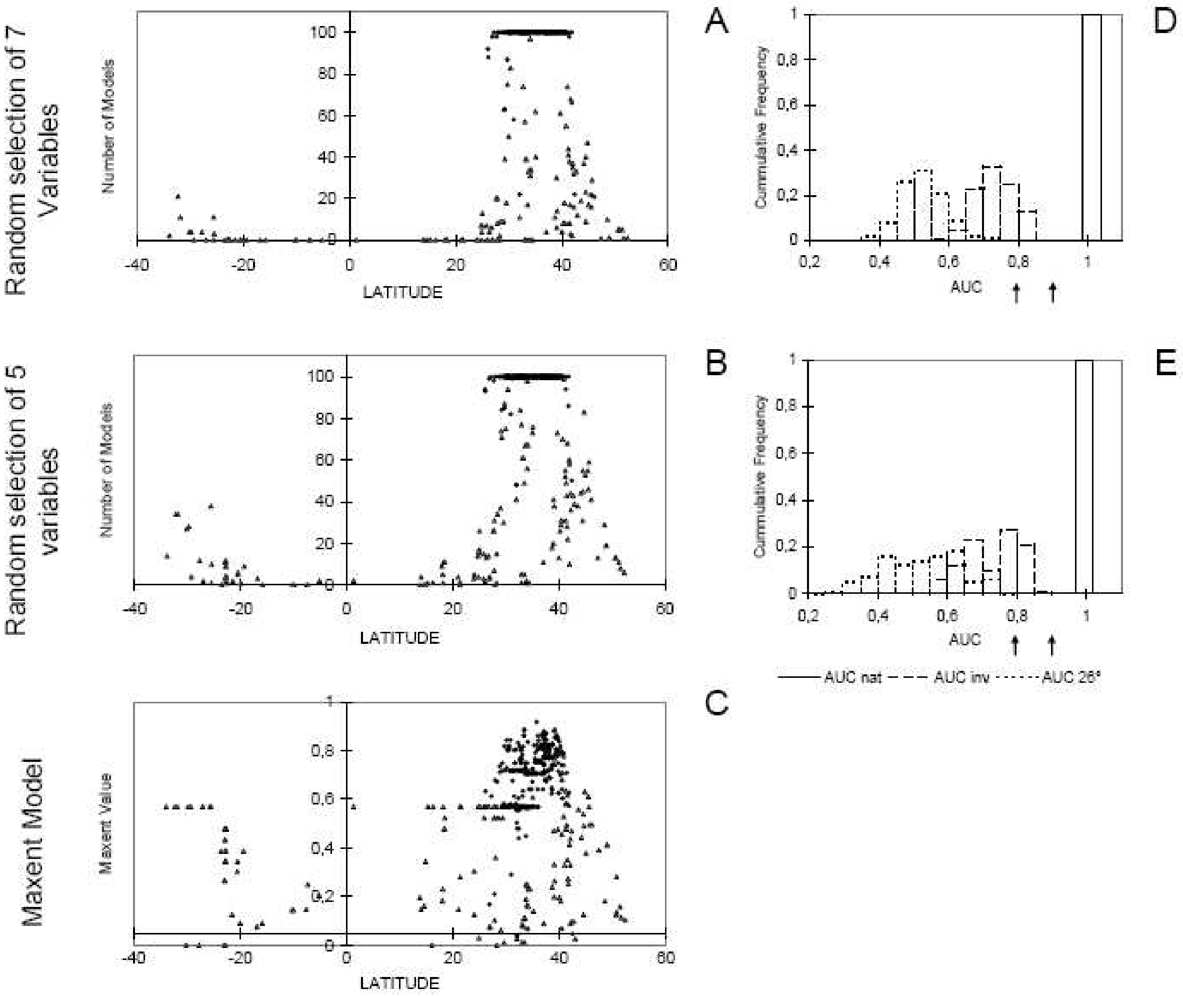

Figure 2.2-6 The predictive performance for invasive populations largely decrease at lower Latitudes in models computed with random subsets of variables (A, B), but not in a MaxEnt model derived from natural history criteria (C) (filled dots: native records; open triangles: invasive records). Test statistics of 100 MaxEnt models based on random selection of each seven (D) and five variables (E) out of the complete set of 19 ‘bioclimate’ variables. Model accuracy was tested with native (AUC nat), invasive (AUC inv) and ‘tropical’ invasive records (AUC 26°; 26° latitude N and S; n = 62). Note that the native range is well captured by each model whereby the invasive populations, especially in the tropics, are not. Arrows indicate AUC inv values of the MaxEnt model derived from natural history criteria (AUC inv = 0.861; AUC 26° = 0.795).

Discussion

Our results provide evidence that the observation of an apparent 'niche' (i.e. climate envelope) shift in the Slider strongly depends on the choice of the variables applied during modeling. The observed range of a species reflects multiple determinants, including climatic tolerances, biotic interactions, equilibrium with climate and dispersal limitation. Hence, niche-based models derived from distribution alone will predict the geographic equivalent of the realized niche rather than the potential range of a species (PULLIAM 2000). A CEM derived from the realized niche may therefore under-predict a species' fundamental niche because it does not consider biotic interactions and abiotic factors which may limit distributions. In our study species, one such abiotic factor is probably the ocean, which limits the native range south- and eastwards. This illustrates that not all range limits can be explained by climate alone what strongly affects the models herein by frequently excluding areas between 26° N and 26° S.

Furthermore, when applying a data set depicting the complete climatic variation within the realized distribution of a species, the limits of all dimensions of its fundamental niche are unlikely to be reached because some niche dimensions may have a wide-reaching impact defining a large part of the native range border (as the 'minimum temperature of the coldest month' in the Slider). Likewise, others may have no impact. However, the parameters without an actual limiting function could be treated as limiting in CEM and may exclude areas suitable for the target species outside the native range from a natural history point of view.

Although the CEM approach may provide insight into the fundamental niche of a species (PETERSON 2001; PETERSON and VIEGLAIS 2001), it cannot provide a complete picture and might be poor in choosing the relevant determinants of distribution patterns. Our results imply that parameters, which are unrelated to a species' natural history and physiology albeit congruent with its range limits, are frequently used by the models as proxies for a species' climatic envelope. This becomes evident in comparing the predictive performance of our models in the invaded range computed with a random selection of variables and a model derived from natural history criteria (Figures 2.2-5A, B). Only the model considering explicit natural history traits performed significantly better than models based on an equal number of randomly chosen variables (Figures 2.2-4C, 2.2-6C; also see Appendix 2.2-S2). The vast majority of random models did not capture the Slider's actual climate envelope although test statistics may suggest a reasonably high model quality. Hence, the observed mismatches may be misinterpreted as range shifts rather than as errors in the selection of variable (Figures 2.2-4A, B, 2.2-5A, B; also see Appendix 2.2-S2). PETERSON and NAKAZAWA (2008) also found that the predictive power of models in respect of native and introduced distributions is strongly affected by the different environmental data sets applied. These findings are congruent with our results, since different sets of predictor variables have a different chance of capturing a greater or smaller part of the niche dimensions restricting a species' native range, thus explaining their different prediction success.

Assuming a shift in the sliders' fundamental niche is not necessary to explain the range of invasive populations in CEM, as mismatches between climate envelopes in native and invasive ranges can simply be explained by the choice of variables in CEM. Before any conclusions on niche shifts are made, an assessment of a species' fundamental niche should be addressed based on a mechanistic understanding of the limiting factors of its range. Our results indicate that such an understanding of causal factors is essential when assessing the climatic suitability of a geographic area or potential range shifts in past or future scenarios.

Our study does not aim at a principle rejection of a fundamental niche shift occurring during invasion processes (e.g. as suggested by BROENNIMANN et al. 2007; FITZPATRICK et al. 2007). If in fact a niche shift had occurred in invasive populations of the Slider, our conclusions would be based on the false assumption of no niche shift. However, assuming inappropriate model selection instead of niche shift (evolutionary response) in a successful invader that has conquered large areas in different parts of the world within about 30 years is a more parsimonious assumption, especially in the light of all the methodological uncertainties accompanying with CEM (ELITH et al. 2006). This raises some concerns about the simplistic approach of applying 'standard datasets' of predictors in climate envelope modeling.

Conclusions

The mismatch between 'very good' (as defined by SWETS, 1988) model performance in a mere statistical sense and the model's ability to capture the climatic niche of an organism is of particular concern. Selection of variables must be conducted carefully and needs to be fitted to the ecological and physiological characteristics of each species. Unfortunately, the lack of physiological data for the vast majority of species and the application of 'standard' sets of environmental variables make predictions for whole species' communities and biodiversity loss questionable (e.g. MALCOM et al. 2006; THOMAS et al. 2004). Thus, future research should place more emphasis on the evaluation of the physiological and ecological important characteristics which are important for each single species instead of being content with deductions from distributional information.

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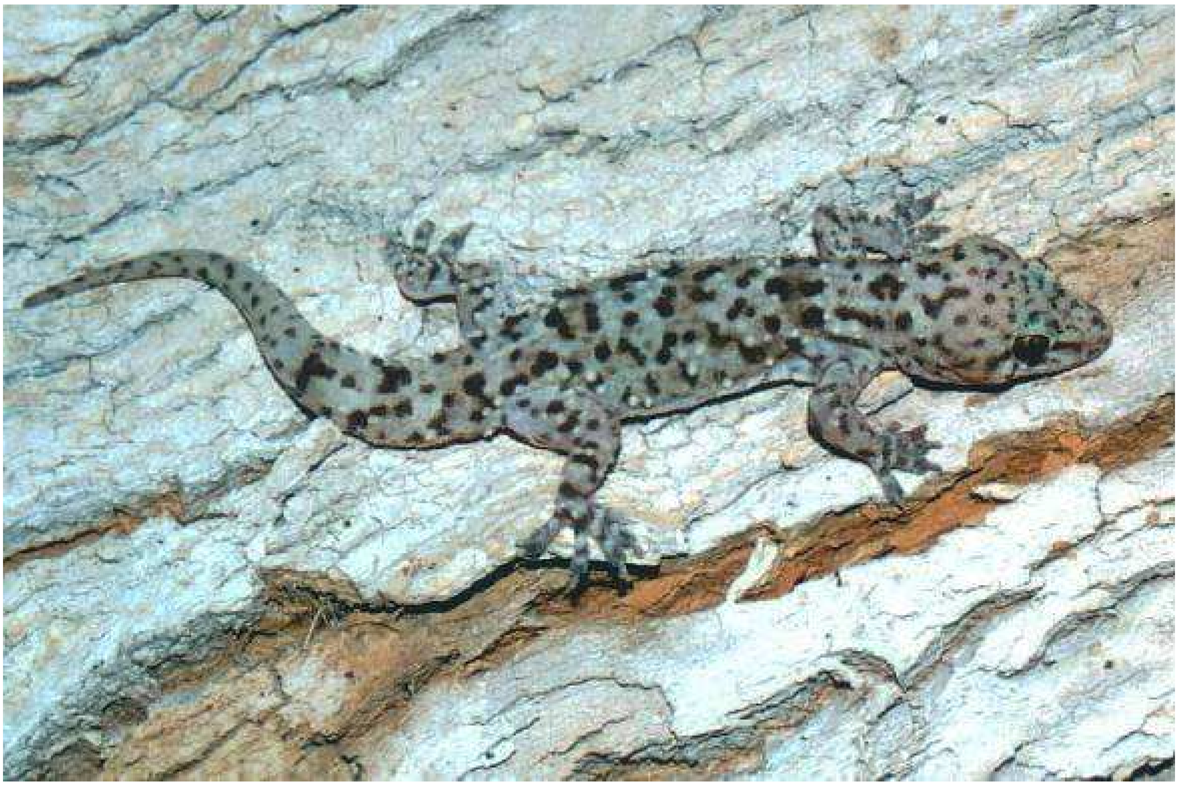
2.3. Niche shift versus niche conservatism? Climatic characteristics within the native and invasive ranges of the Mediterranean Housegecko (*Hemidactylus turcicus*)[4]



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Hemidactylus turcicus

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[4] This part is accepted for publication in *Global Ecology and Biogeography*.

The work reported in this chapter was conducted in collaboration with STEFAN LÖTTERS from the University of Trier, Faculty of Geosciences.

Introduction

Invasive species, as unanticipated experiments, may provide valuable insights for ecology and evolutionary biology including niche characteristics (KOZAK et al. 2008; SAX et al. 2008). Successful establishment of a non-indigenous species into a species community depends on existing species richness, competitors, predators, food availability and human footprint on its climatic similarity compared to the source ecosystem (EHRLICH 1989; WILLIAMSON 1996). Here, GIS-based Climate Envelope Models (CEMs) can provide an easy-to-use method to assess the potential distribution (PD) of species derived from their climatic niches (i.e. climate envelopes). In recent years, the number of studies using CEMs to assess PDs of species has exploded; they address past, present and future distributions applying different climate scenarios (e.g. JESCHKE and STRAYER 2008). Also it has been demonstrated how useful CEMs can be for the identification of climatically suitable regions to species and hence for predicting the potential of invasive species (e.g. PETERSON and VIEGLAIS 2001; GIOVANELLI et al. 2007; JESCHKE and STRAYER 2008; RÖDDER et al. 2008; RÖDDER 2009).

When applying CEMs to project PDs of invasive species in new regions, one has to distinguish between the fundamental and realized niches. As defined by HUTCHINSON (1957; 1978), a species’ fundamental niche represents the complete set of environmental conditions under which it can persist. The realized niche in environmental space is a subset of the fundamental niche considering physical dispersal limitations and biotic interactions (e.g. competition, predation; Figure 2.3-1). Generally, niche variables can be subdivided concerning specific classes regarding the spatial extent in which they operate and if competition may play a role or not (SOBERÓN 2007). The Grinnellian class is defined by fundamentally non-interactive variables, as climate-related ones (GRINNELL 1917), whereby the Eltonian class focuses on biotic interactions and resource-consumer dynamics (ELTON 1927). The former operates on a coarse scale and is the main subject in CEM approaches, while the latter can be measured at local scales only and is commonly not addressed in CEMs (SOBERÓN 2007).

When calculating CEMs, it is assumed that the range of the target species is in equilibrium with climate (ARAÚJO and PEARSON 2005) and that the climate envelope of the studied species is conservative across space and time (WIENS and GRAHAM 2005; PEARMAN et al. 2008). Evidence to which degree climate envelopes are conservative is ambiguous why the entire issue is currently under debate. Several studies have tried to assess the degree of niche conservatism, but momentarily general conclusions are lacking

(PEARMAN et al. 2008). One reason might be that strikingly different comparative methods and null hypothesis were used to quantify and define niche conservatism (WARREN et al. 2008). PETERSON et al. (1999), for example, assessed niche similarity, which asks whether CEMs derived from occurrences of one species predict occurrences of a second better than expected under a null hypothesis that they provide no information about one another's range. On the other hand, GRAHAM et al. (2004) performed a test of niche equivalency asking whether the niches of two species are effectively indistinguishable, i.e. more similar than random (see also KNOUFT et al. 2006; PFENNINGER et al. 2007). Both tests of niche similarity and equivalency contrast extremes within a spectrum of niche conservation which might cause conflicting conclusions when applying one or the other (WARREN et al. 2008).

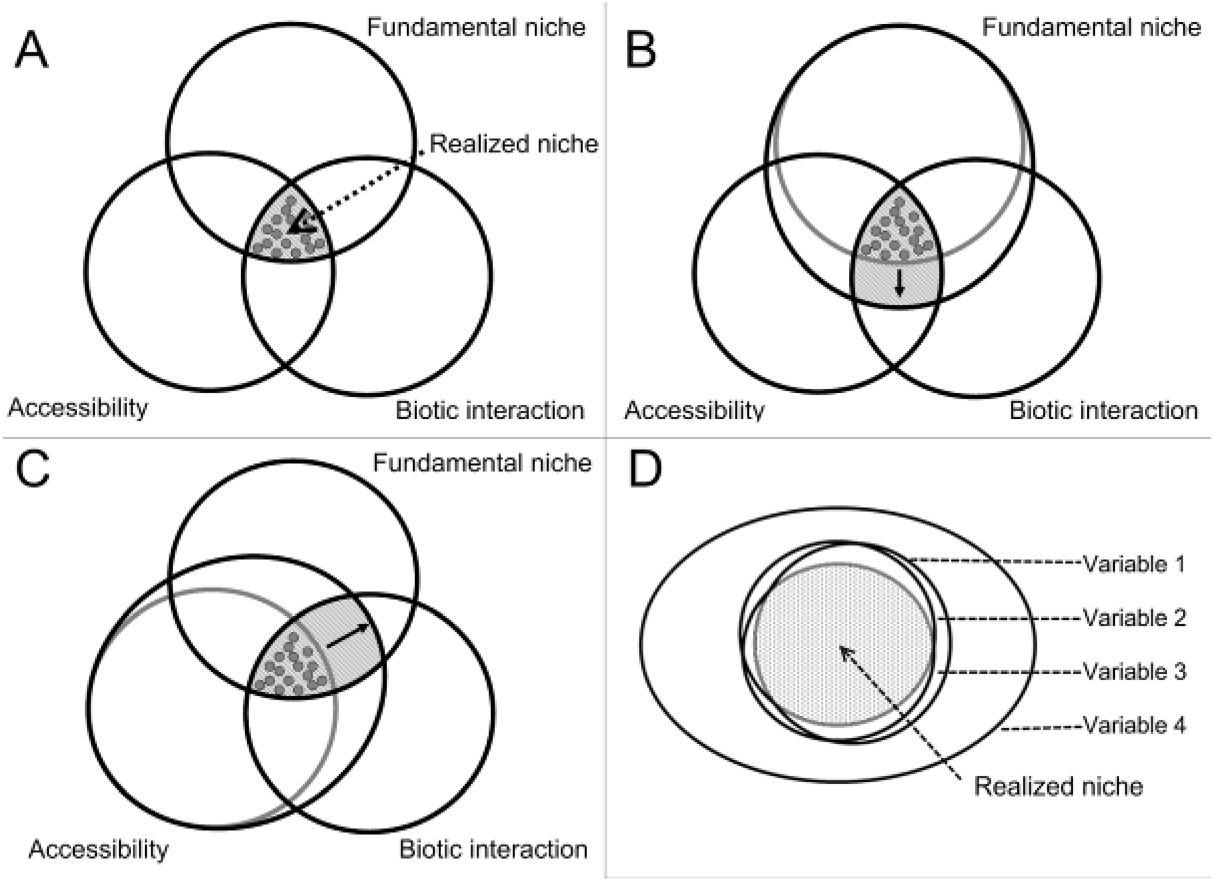

Figure 2.3-1 (A) Relationships between fundamental niche, biotic interaction and accessibility in ecological space (after HUTCHINSON 1957 as modified by SOBERÓN and PETERSON 2005); the realized niche (= conditions as observed within the realized distribution) is indicated in grey and native species records as dots; (B) increase of fundamental niche space resulting a an shift in the realized niche; (C) better exploitation of the fundamental niche after access into new areas; (D) different degrees in limitation of the realized niche between variables: variables 1-3 are actually limiting the realized niche, whereby the limits of the 'relaxed' variable 4 is not reached within the realized niche.

Recently, several authors have found a mismatch between species' native and invasive ranges in terms of climate envelopes (e.g. BROENNIMANN et al. 2007; FITZPATRICK et al. 2007; BROENNIMANN and GUISAN, 2008). It was suggested that niche shifts during biological invasion may have taken place what would seriously violate basic assumptions behind many CEM applications. However, PETERSON and NAKAZAWA (2008) showed that differences in predictive abilities of CEMs for invasive species are correlated with the choice of environmental data sets involved. The authors pointed out that variable selection is a crucial step, which can highly influence CEM output. Climatic conditions in different geographic regions may show variation in many parameters including some biologically meaningful ones actually restricting the range of a species under study and some variables, which may have a weak or no impact (termed 'relaxed' hereafter; Figure 2.3-1). Since different variable sets are likely to cover different parts of the environmental niche space suitable to a species, differences in predictive abilities of models are most likely if a species occupies a different niche space in its native and invasive ranges regarding some (relaxed) variables involved (FITZPATRICK et al. 2008).

In this paper, we assess differences in climatic niches in the native and invaded ranges of the Mediterranean Housegecko (*Hemidactylus turcicus*) in terms of commonly applied climate variables in CEMs. We analyze which variables are more conserved versus relaxed (i.e. subject to niche shift). Furthermore, we study the predictive power of different sets of climate variables aiming at either comprehensiveness or minimalism of temperature, precipitation and both temperature and precipitation combined.

Methods

Studied species

Some Old World House Geckos, genus *Hemidactylus* (Reptilia; Gekkonidae), have remarkably extended their distributions since the last century (e.g. CARRANZA and ARNOLD, 2006). There are more apparent cases of large range extensions in these squamate reptiles than in any other reptile group. Today, *Hemidactylus turcicus*, which has its native range in the Mediterranean basin (BÖHME 1981), is considered a widespread species outside this region species and has also been introduced into the New World (CARRANZA and ARNOLD 2006).

The population density of *H. turcicus* within the invasive range is generally high (e.g., 544-2210 geckos ha^{-1} in Edinburg, Texas (SELCER 1986), and 478 geckos ha^{-1} in

Edmond, Oklahoma (LOCEY and STONE 2006)), but genetic exchange between populations may be limited since diffusion dispersal abilities are restricted in this species (about 5-20 m per year; LOCEY and STONE 2006). On the other hand, jump dispersal caused by accidental transport of adult geckos or their eggs by humans is suggested to occur frequently since high population densities are often associated with highway arteries (DAVIS 1974). The species is suggested to be highly adaptive and a successful colonizer (e.g. SELCER 1986; MESHAKA 1995).

First records of the Mediterranean Housegecko in the New World were documented in 1910 in Key West, Florida (FOWLER 1915). In 1950, it had arrived at Brownsville, Texas (DAVIS 1974). Today, this House Gecko is widespread in the southern USA including Alabama, Arizona, Arkansas, southern California, Florida, Georgia, Louisiana, Maryland, Mississippi, Missouri, New Mexico, Nevada, Oklahoma, South Carolina, Texas, and Virginia (Appendix 2.3-S1). In addition, *H. turcicus* has been introduced into Panama and Mexico (COLLINS and IRWIN 2000) and to Cuba (SCHWARTZ and HENDERSON 1991).

Species records

We used 1,400 (1,173 native, 227 invasive; Figure 2.3-2) georeferenced records of *Hemidactylus turcicus* situated in unique grid cells from collections linked to the Global Biodiversity Information Facility (GBIF, 2007) and the HerpNet (2007) databases; literature data were added for complementation purposes. However, for model computation, only those records within areas with confirmed reproduction were considered (see Appendix 2.3-S1). Georeferencing was conducted when necessary with the Alexandria Digital Library Gazetteer (http://middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp).

We used DIVA-GIS 5.4 (http://www.diva-gis.org; HIJMANS et al. 2002) to test the accuracy of coordinates (Check Coordinates tool) by comparing the species records and an administrative boundaries database at the smallest possible level (state/country/city). This information should be the same, and any mismatches probably reflect errors (HIJMANS et al. 1999). In addition, we used altitudinal information to spot likely errors in the coordinate data when this information was provided with the record data used. Altitude was compared with an estimate of the altitude of the locality, using the Extract Values by Points function in DIVA-GIS.

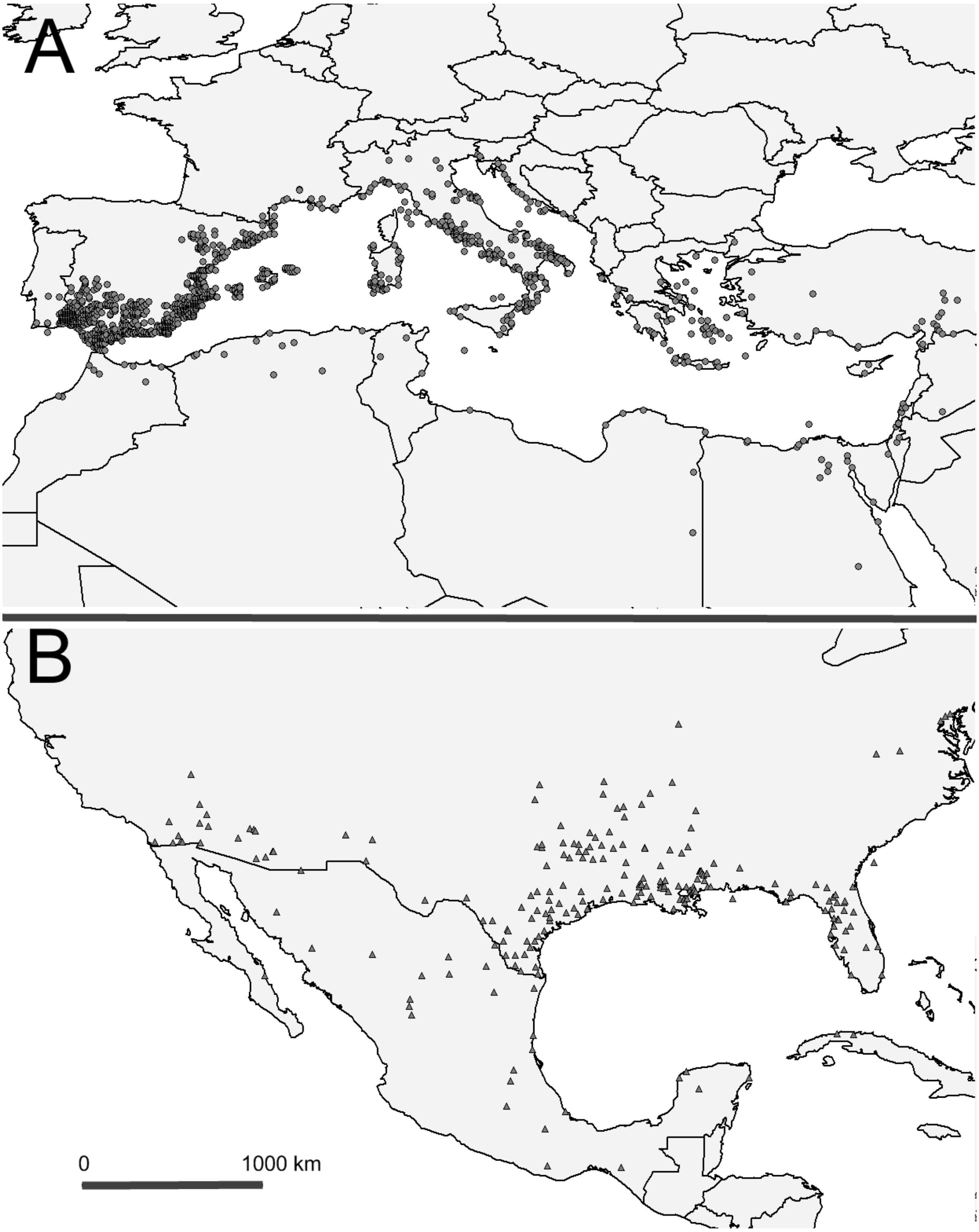

Figure 2.3-2 *Hemidactylus turcicus* records in native European (A) and invasive American ranges (B), used for model training.

Climate data

Information on current climate was obtained from the Worldclim database (version 1.4), which is based on weather conditions recorded between 1950 and 2000 with grid cell resolution 5 minutes (HIJMANS et al. 2005; http://www.worldclim.org). It was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995; 2004). Climate data include monthly mean variables of minimum and maximum temperature and precipitation. Based on these data, 19 so called 'bioclimate' variables (Table 2.3-1) were calculated with DIVA-GIS 5.4. Bioclimate variables have been proven to be useful for CEM approaches (e.g. FITZPATRICK et al. 2007, 2008; PETERSON and NAKAZAWA 2008; WARREN et al. 2008) and are more useful than monthly values, since they are independent from latitudinal variation. This becomes obvious when considering that the 'maximum temperature of the warmest month' is more informative to a warmth-dependent species than the 'maximum temperature' of a specific month, since the same month at the same time might not be the warmest within the entire geographic range of a species. With the goal to compare conditions at native and invasive House Gecko records, we extracted all 19 bioclimate variables at each record and visualized them using stripe plots computed with XLSTAT 2008 (http://www.addinsoft.com).

Multi-co-linearity among predictor variables, e.g. as expectable for the 'minimum temperature of the coldest month' and the 'minimum temperature of the coldest quarter', may hamper the analysis of species-environment relationships because ecologically more causal variables can be excluded from models if other correlated variables explain the variation in response variable better in statistical terms (HEIKKINEN et al. 2006). To account for this, we selected in each set of variables either monthly or quarterly variables if *a priori* we expected co-linearity.

CEMs derived from climatic conditions as observed at native and invasive gecko records were separately computed for each bioclimate variable. Further, we selected nine different sets of variables (Table 2.3-1): two sets comprising most bioclimatic variables with exclusion of highly collinear ones (Comprehensive $_{\text{month}}$; Comprehensive $_{\text{quarter}}$), two extreme minimalistic sets of variables (Minimum $_{\text{month}}$; Minimum $_{\text{quarter}}$), which aim on the availability of water and energy, two sets describing temperature related parameters (Temperature $_{\text{month}}$; Temperature $_{\text{quarter}}$), two sets describing precipitation related parameters (Precipitation $_{\text{month}}$; Precipitation $_{\text{quarter}}$), one set comprising variables which combine temperature and precipitation characteristics (Combined variables).

Climate Envelope Models

For CEM computation we used MaxEnt 3.2.19 (http://www.cs.princeton.edu/~shapire/Maxent; PHILLIPS et al. 2006), a machine learning algorithm for species PD models with environmental predictors. In multiple tests, MaxEnt generally revealed better results than comparable methods (ELITH et al. 2006; HEIKKINEN et al. 2006; WISZ et al. 2008). The general concept behind MaxEnt is to find a probability distribution covering the study area that satisfies a set of constraints derived from conditions at species presence. Each constraint requires that the expected value of an environmental variable or a function thereof must be within a confidence interval of its empirical mean over the presence records. The program chooses the distribution that is closest to uniform and therefore maximizes entropy (JAYNES 1957) within all distributions that satisfy the constraints as any other choice would represent constraints on the distribution that are not justified by the data (PHILLIPS et al. 2006).

Runs used herein were conducted using the default values for all program settings. Background points were randomly chosen within the area enclosed by a minimum convex polygon comprising all native (likewise invasive, respectively) records. MaxEnt allows for model testing by calculation of the area under the receiver operation characteristics curve (AUC) based on training and test data, which represent the ability of the model to distinguish presence data from background data (PHILLIPS et al. 2006).

Niche overlap, similarity and equivalency

We compared climate envelopes in terms of potential distributions quantitatively with SCHOENER'S (1968) index for niche overlap (*D*) (e.g. WARREN et al. 2008). This index allows for a quantification niche similarity between two probability distributions over geographic space:

$$D(p_x, p_y) = 1 - \frac{1}{2}\sum_i \left| p_{x,i} - p_{y,i} \right|,$$

whereby $p_{x,i}$ and $p_{y,i}$ each denote the probability assigned in the CEM for species X and Y to grid cell *i*. *D* values range from 0 (niche models have no overlap) to 1 (niche models are identical). Schoener's *D* was originally developed for values reflecting relative use of particular microhabitats or prey items. Although it has been proposed to be useful in comparisons of potential distributions there is no assurance that $p_{x,i}$ (and $p_{y,i}$) are proportional to local species density or any other measure of relative use in CEMs

(WARREN et al. 2008). For this reason, these authors proposed the Hellinger distance (*H*) to be used in addition, defined as

$$H(p_x, p_y) = \sqrt{\sum_i (\sqrt{p_{x,i}} - \sqrt{p_{y,i}})^2} .$$

Since *H* ranges from 0 to 2, a modification approaching the *D* range, i.e. from 0 (no overlap) to 1 (identical), according to

$$I(p_x, p_y) = 1 - \frac{1}{2} H(p_x, p_y)$$

was suggested by WARREN et al. (2008). We evaluated the significance of *D* and *I* values with null models regarding niche similarity and equivalency (WARREN et al. 2008).

For niche equivalency we applied a randomization test as proposed by WARREN et al. (2008) that relies on the metrics *D* and *I*. For the native (n_{nat}) and invasive occurrences (n_{inv}) we created 100 pseudoreplicate datasets by randomly partitioning the pooled sets of n_{nat} + n_{inv} occurrences into sets of size n_{nat} and n_{inv}. CEMs were created from each pseudoreplicate and compared using *D* and *I*. The observed *D* and *I* values were compared to the percentiles of these null distributions in a one-tailed test to evaluate the hypothesis that niche models for native and invasive records were not significantly different. The test allows for an assessment of niche conservatism in a strictest sense: i.e. the effective equivalency of the climate niche in the native and invasive ranges. It is expected to be only met if native and invasive populations of one species tolerate exactly the same set of climatic conditions and have the same set of environmental conditions available to them.

In order to assess niche similarity, we again used a randomization test of WARREN et al. (2008). This test compares the actual similarity of CEMs based on native records in terms of *D* and *I* values to the distribution of similarities obtained by comparing them to a CEM obtained by randomly choosing n_{inv} cells from among the cells in the study area of the invasive records. The same procedure was performed in both directions (invasive <-> native records) 100 times to construct an expected distribution of *D* and *I* values between a CEM generated using actual occurrences and one generated from random background data points. As background, we defined the area within a minimum convex polygon comprising all native (or invasive) records, respectively. These null distributions served as two-tailed test to assess the following null hypothesis: measured niche overlap between native and invasive ranges is explained by regional similarities or differences in available habitat. This hypothesis is rejected if the actual similarity falls outside the 95 % confidence limits of the null distribution. Significantly higher values suggest that CEMs are more similar than expected by chance and lower values indicate greater differences, whereby the difference between the observed and closest value in the null distribution may be a quantitative measure. Computations of *D*, *I*, niche similarity and equivalency were performed with a Perl script also used by WARREN et al. (2008).

Results

Bioclimatic conditions at native and invasive records

Figure 2.3-3 summarizes bioclimatic conditions at native and invasive records of *Hemidactylus turcicus*. The ranges of the 'mean temperature of the wettest quarter', 'precipitation seasonality', and 'precipitation of the coldest month' at invasive records completely fell within the ranges observed at native records. Ranges of the 'annual mean temperature', 'mean monthly temperature range', 'maximum temperature of the warmest month', 'mean temperature of the warmest quarter', 'annual precipitation', 'precipitation of the wettest month' and 'precipitation of the wettest quarter' exceeded the conditions as observed at native records only slightly or the number of exceeding records was relatively low. High proportions of the ranges of 'isothermality', 'temperature seasonality', 'minimum temperature of the coldest month', 'temperature annual range', 'mean temperature of the wettest quarter', 'mean temperature of the coldest quarter', 'precipitation of the driest month', 'precipitation of the driest quarter' and 'precipitation of the warmest quarter' at invasive records well exceeded those observed at the native records.

Single variables: niche overlap, similarity and equivalency

Table 3.2-2 provides results of the niche overlap, similarity and equivalency tests. *D* values ranged from 0.38 to 0.76 and *I* values from 0.60 to 0.84 (i.e. always higher the *D* values). Highest niche overlap ($D \geq 0.70$; $I \geq 0.80$) was found in the 'minimum temperature of the coldest month', 'precipitation seasonality' and 'precipitation of the coldest quarter'. Lowest overlap ($D \leq 0.50$; $I \leq 0.70$) was detected in the 'annual mean temperature', 'mean temperature of the wettest quarter', 'mean temperature of the warmest quarter' and 'precipitation of the warmest quarter'. Values of the other variables were intermediate. The hypothesis of niche equivalency was rejected in all cases.

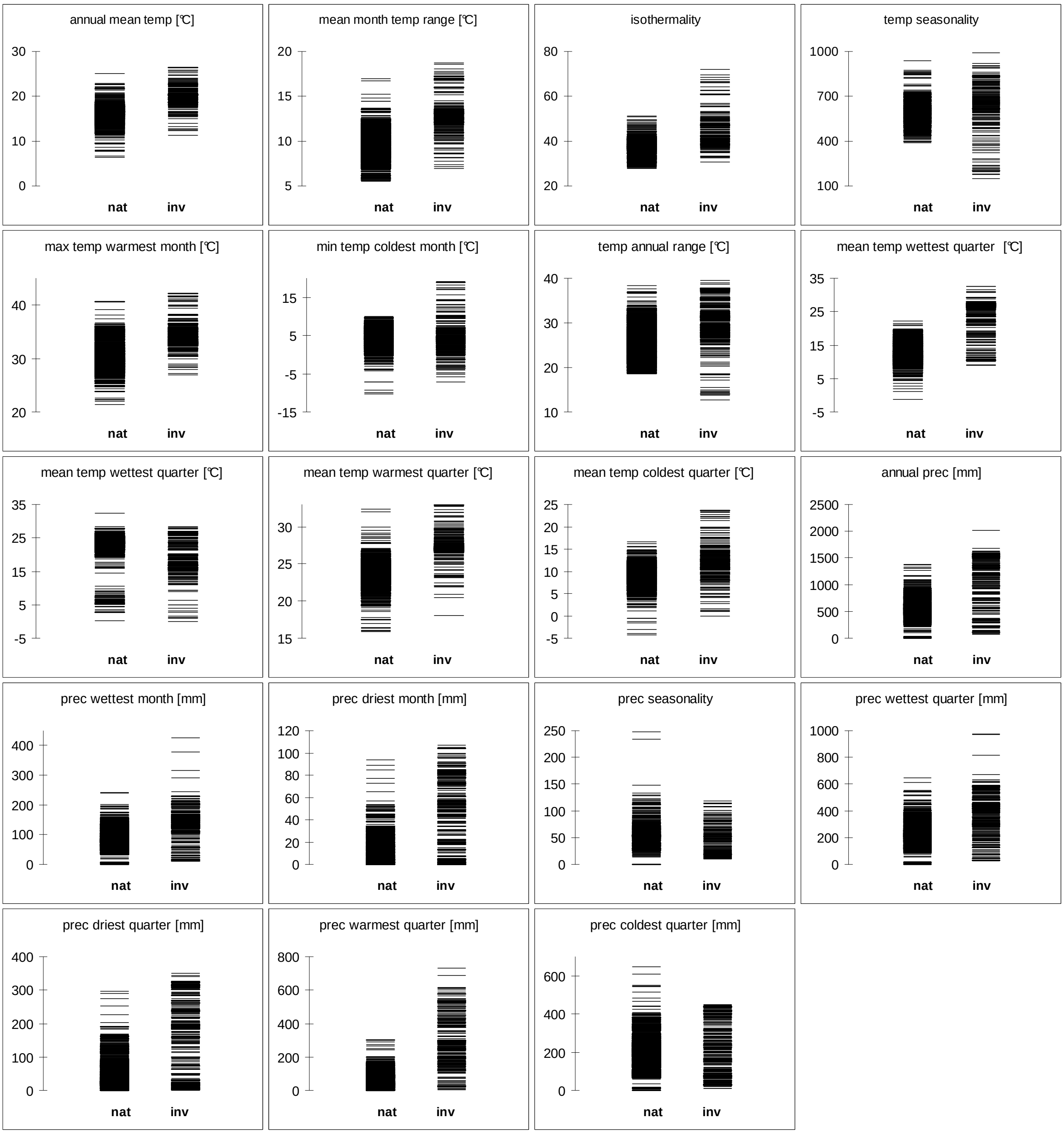

Figure 2.3-3 Comparison of bioclimate variable scores as observed at native (nat) and invasive (inv) records of *Hemidactylus turcicus*.

Results from the niche similarity test based on native records compared to the invasive background revealed that climatic conditions described by nine parameters were more different and eight more similar to those expected by chance when applying both *D* and *I* measures (Table 3.2-2). Two tests applying *D* and three applying *I* revealed no significant results. Greatest differences (*D* ≥ ± 0.20; *I* ≥ ± 0.10) to the null distributions were found in the ‘minimum temperature of the coldest month’ and a small differences only ($D \leq \pm$ 0.02; $I \leq \pm$ 0.02) in the ‘mean temperature of the coldest quarter’. Results based on invasive records compared to the native background revealed that climatic conditions described by nine parameters were more different and only three more similar to those expected by chance when applying both measures (Table 3.2-2). One test applying D and four applying I revealed no significant results and in three cases the background tests revealed contraindicating results for D and I. Greatest differences ($D \geq \pm$ 0.20; $I \geq \pm$ 0.10) to the null distributions were found in the ‘mean monthly temperature range’ and the ‘mean temperature of the warmest quarter’. Small differences only ($D \leq \pm$ 0.02; $I \leq \pm$ 0.02) were detected in the ‘mean temperature of the wettest quarter’, ‘precipitation of the driest month’, ‘precipitation of the wettest quarter’ and ‘precipitation of the coldest quarter’. Those variables showing a relatively high degree of similarity of native and invasive ranges were tentatively more similar to those expected by random (e.g. ‘minimum temperature coldest month’, ‘precipitation coldest quarter’; Table 2.3-2) when compared to those showing low overlap (Figure 2.3-4), although this relationship was not significant ($R^2 < 0.1$).

CEMs computed with sets of variables

Figures 2.3-5 and Appendix 2.3-S2 show crosswise projections of climate envelopes developed with the nine sets of variables, and Table 2.3-1 summarizes the importance of variables in each set of variables. We received excellent AUC values in all models following the classification accuracy of SWETS (1988) (Table 3.2-2). Models computed with monthly and quarterly temperature and precipitation variables were highly coincident (see Figures 2.3-5 and Appendix 2.3-S2; Table 2.3-3). Models obtained from the data sets ‘Comprehensive’ and ‘Combined variables’ widely failed to predict the invasive (likewise native) range in crosswise projections. Those computed with the data sets ‘Minimum’ captured comparatively higher proportions when trained with native records, but not when trained with invasive records. Models resulting from the variable sets ‘Precipitation’ and ‘Temperature’ performed intermediated, but frequently over-predicted the ranges.

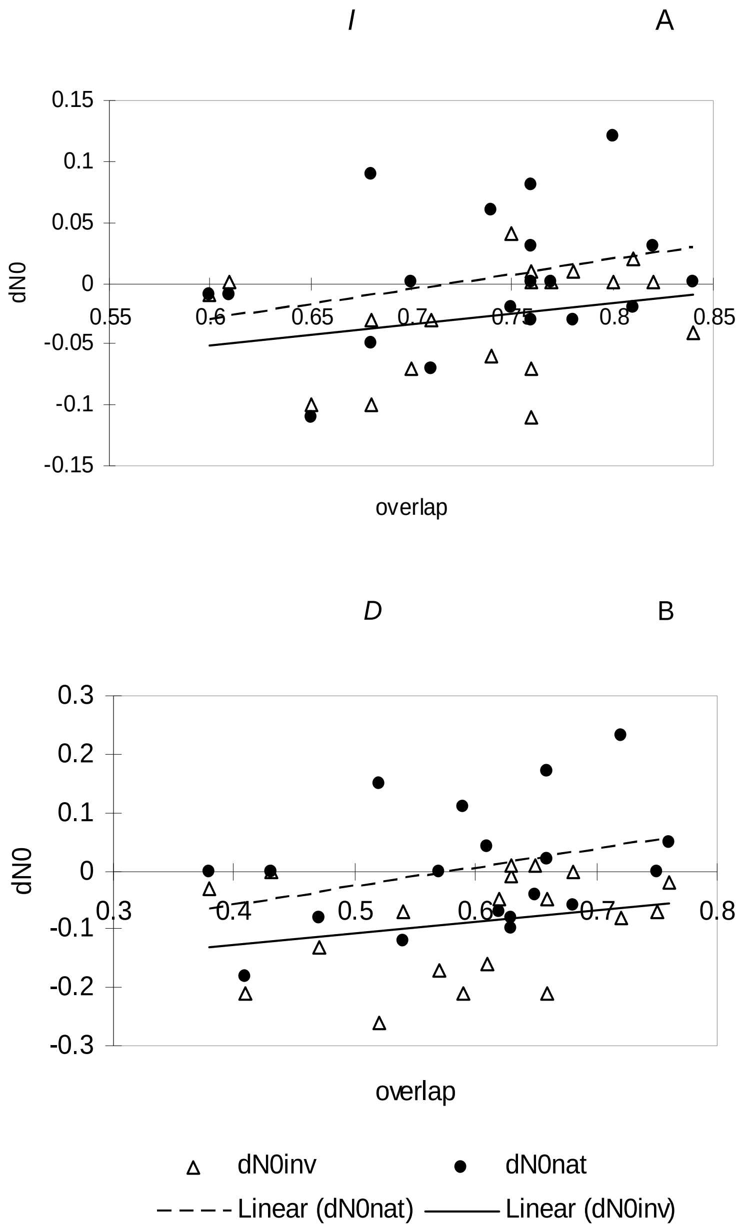

Figure 2.3-4 Niche overlap in terms of *D* and *I* values and distance to expected null distribution of the 19 bioclimate parameters analyzed (for details see Table 2.3-1).

Sets of variables: niche overlap, equivalency and similarity

D Values observed in models computed with nine sets of variables ranged from 0.12 to 0.55 and *I* values from 0.44 to 0.71 (i.e. higher than *D* values; Table 2.3-3). High niche overlap (*D* ≥ 0.50; *I* ≥ 0.70) was observed between CEMs received from the two ‘Precipitation’ data sets, whereby lowest overlap (*D* ≤ 0.15; *I* ≤ 0.45) was detected using the ‘Comprehensive’ data sets. The hypothesis of niche equivalency was rejected in all cases.

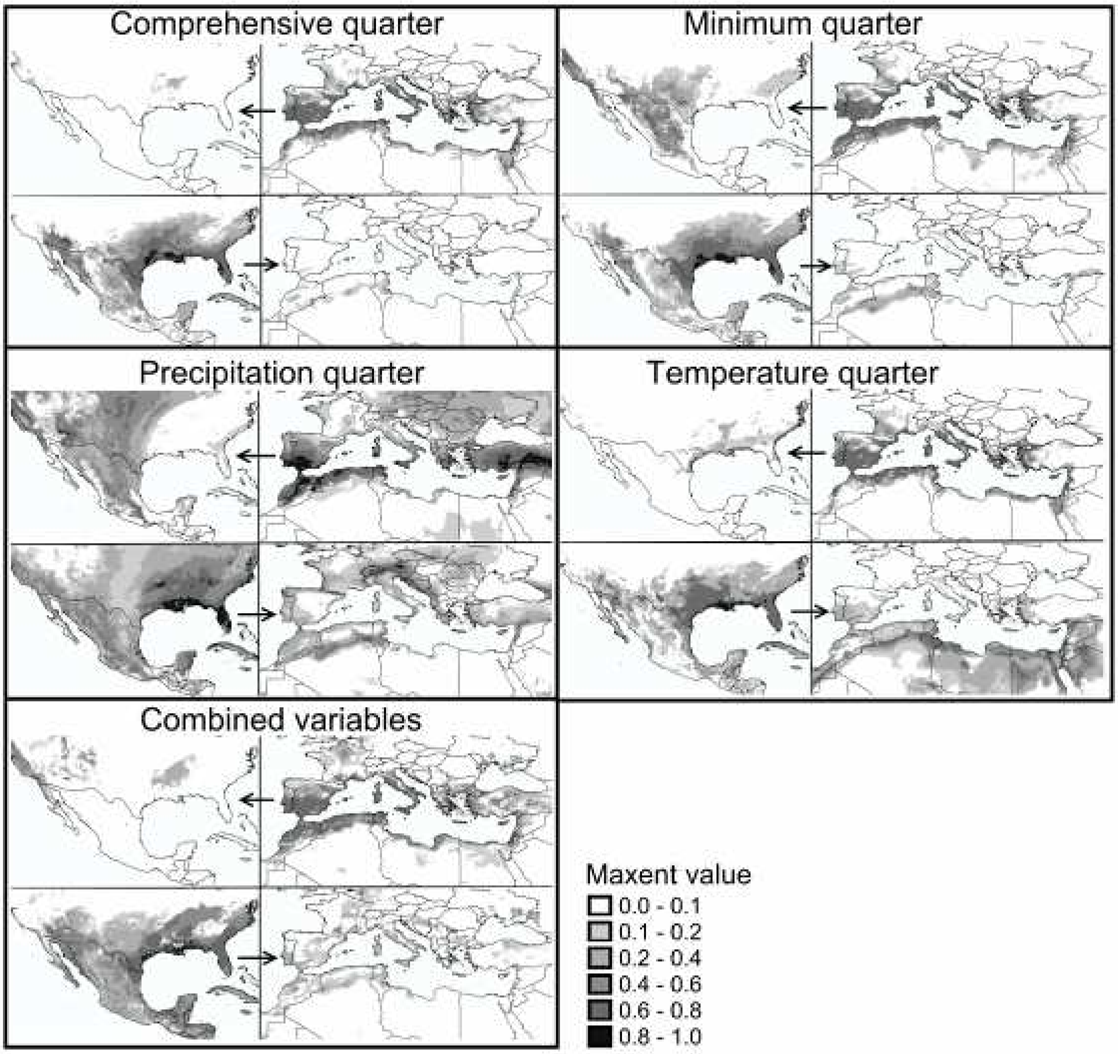

Figure 2.3-5 Crosswise projections of climate envelopes developed with variable sets ‘Comprehensive’, ‘Minimum’, ‘Precipitation’, ‘Temperature’ and ‘Combined variables’. Arrows indicate direction of projections, i.e. climate envelopes were developed based on records within one area and projected into the other.

Table 2.3-1 Bioclimatic parameters, sets used for Climate Envelope Model generation and relative contribution of parameters in final models [%]. Data sets are referred to as Comprehensive $_{\text{month}}$ (1), Comprehensive $_{\text{quarter}}$ (2), Minimum $_{\text{month}}$ (3), Minimum $_{\text{quarter}}$ (4), Temperature $_{\text{month}}$ (5), Temperature $_{\text{quarter}}$ (6), Precipitation $_{\text{month}}$ (7), Precipitation $_{\text{quarter}}$ (8), Combined variables (9) in the text.

Source of variation	Abbreviation	Data set, nat									Data set, inv								
		1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
annual mean temperature	Bio 1	10.8	13.3	38.7	29.9	30.7	26.1				41.6	40.7	49.3	42.1	60	59.1			
mean monthly temperature range	Bio 2	21.6	22.1			25.5	28.4				0.5	0.7			13.1	17			
isothermality	Bio 3	1.7	1.4			7.9	6.6				0.1	0.2			0.5	1.5			
temperature seasonality	Bio 4	12.9	13.1			13.8	18.4				1.9	1.4			2	2.4			
max temperature warmest month	Bio 5	1.1		12.7		2.7					4.2		2.7		19.9				
min temperature coldest month	Bio 6	4.5		42.2		15.9					0.5		0.7		1.8				
temperature annual range	Bio 7	1.8	3.4			3.5					0.6	0.7			2.7				
mean temperature wettest quarter	Bio 8	9.6	9.6							19.6	1.9	1.9							18.5
mean temperature driest quarter	Bio 9	10.8	10.4							40.9	0.7	1							32.5
mean temperature warmest quarter	Bio 10		1.7		25.2		5.6					10.5		12.8		19.8			
mean temperature coldest quarter	Bio 11		0.1		35.6		15					0.6		1.6		0.3			
annual precipitationipitation	Bio 12	0.4	0.3	4.1	6.9			29.1	27.5		0.6	4	4.9	8.6			20.6	37.7	
precipitation wettest month	Bio 13	0.2		2				8.6			13.5		11.6				51.9		
precipitation direst month	Bio 14	0.2		0.2				41.9			15.3		30.8				20		
precipitation seasonality	Bio 15	0.1	0					20.4	22.3		1.2	0.6					7.4	8	
precipitation wettest quarter	Bio 16		0.1		1.7				12.2			1.3		1				10.4	
precipitation driest quarter	Bio 17		0.2		0.7				39			22.6		33.9				44	
precipitation warmest quarter	Bio 18	12.5	12.9							15.2	5.8	6.7							26.3
precipitation coldest quarter	Bio 19	11.9	11.4							24.3	11.5	7.1							22.6

Table 3.2-2 AUC values per model, niche overlap in terms of *I* and *D* values and assessment of niche similarity and equivalency via randomization tests (see text). Significant values of niche equivalency are indicated with asterisks; ns = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; obs = observed significance level; nat = native; inv = invasive; dN0 = minimum difference between null distribution and observed overlap; values where overlap > dN0 are bolt, values where overlap < dN0 are italicized.

Source of variation	Model fit	*D*					*I*				
	AUC_{nat}, AUC_{inv}	Overlap	Similarity				Overlap	Similarity			
			obs_{nat}	dN0_{nat}	obs_{inv}	dN0_{inv}		obs_{nat}	dN0_{nat}	obs_{inv}	dN0_{inv}
annual mean temperature	0.935, 0.898	0.47**	< *0.01*	-0.08	< *0.01*	-0.13	0.68**	< *0.01*	-0.05	< *0.01*	-0.03
mean monthly temperature range	0.786, 0.757	0.52**	**< 0.01**	0.15	< *0.01*	-0.26	0.68**	**< 0.01**	0.09	< *0.01*	-0.10
isothermality	0.850, 0.770	0.57**	ns	-	< *0.01*	-0.17	0.70**	ns	-	< *0.01*	-0.07
temperature seasonality	0.894, 0.746	0.59**	**< 0.01**	0.11	< *0.01*	-0.21	0.74**	**< 0.01**	0.06	< *0.01*	-0.06
max temperature warmest month	0.858, 0.886	0.54**	< *0.01*	-0.12	< *0.01*	-0.07	0.71**	< *0.01*	-0.07	< *0.01*	-0.03
min temperature coldest month	0.877, 0.804	0.72**	**< 0.01**	0.23	< *0.01*	-0.08	0.80**	**< 0.01**	0.12	ns	-
temperature annual range	0.867, 0.746	0.66**	**< 0.01**	0.17	< *0.01*	-0.21	0.76**	**< 0.01**	0.08	< *0.01*	-0.11
mean temperature wettest quarter	0.819, 0.830	0.43**	< *0.05*	-	< *0.05*	-	0.60**	< *0.01*	-0.01	< *0.01*	-0.01
mean temperature driest quarter	0.903, 0.798	0.61**	**< 0.01**	0.04	< *0.01*	-0.16	0.76**	**< 0.01**	0.03	< *0.01*	-0.07
mean temperature warmest quarter	0.917, 0.902	0.41**	< *0.01*	-0.18	< *0.01*	-0.21	0.65**	< *0.01*	-0.11	< *0.01*	-0.10
mean temperature coldest quarter	0.923, 0.844	0.66**	**< 0.01**	0.02	< *0.01*	-0.05	0.76**	**< 0.05**	-	**< 0.05**	-
annual precipitationipitation	0.750, 0.820	0.62**	< *0.01*	-0.07	< *0.01*	-0.05	0.76**	< *0.01*	-0.03	**< 0.01**	0.01
precipitation wettest month	0.705, 0.840	0.63**	< *0.01*	-0.08	< *0.01*	-0.01	0.78**	< *0.01*	-0.03	**< 0.01**	0.01
precipitation direst month	0.817, 0.800	0.65**	< *0.01*	-0.04	**< 0.01**	0.01	0.77**	ns	-	ns	-
precipitation seasonality	0.747, 0.676	0.75**	ns	-	< *0.01*	-0.07	0.84**	ns	-	< *0.01*	-0.04
precipitation wettest quarter	0.722, 0.800	0.68**	< *0.01*	-0.06	ns	-	0.81**	< *0.01*	-0.02	**< 0.01**	0.02
precipitation driest quarter	0.818, 0.836	0.63**	< *0.01*	-0.10	**< 0.01**	0.01	0.75**	< *0.01*	-0.02	**< 0.01**	0.04
precipitation warmest quarter	0.872, 0.782	0.38**	**< 0.05**	-	< *0.01*	-0.03	0.61**	**< 0.01**	-0.01	ns	-
precipitation coldest quarter	0.817, 0.785	0.76**	**< 0.01**	0.05	< *0.01*	-0.02	0.82**	**< 0.01**	0.03	ns	-

Table 2.3-3 AUC values per model, niche overlap in terms of *I* and *D* values and assessment of niche similarity and equivalency via randomization tests (see text). Significant values of niche equivalency are indicated with asterisks; ns = p > 0.05; * = p < 0.05; ** = p < 0.01; obs = observed significance level; nat = native; inv = invasive; dN0 = minimum difference between null distribution and observed overlap; values where overlap > dN0 are bolt, values where overlap < dN0 are italicized.

Variable set	Model fit	*I*					*D*				
	AUC_{nat}, AUC_{inv}	Overlap	Similarity				Overlap	Similarity			
			obs_{nat}	dN0_{nat}	obs_{inv}	dN0_{inv}		obs_{nat}	dN0_{nat}	obs_{inv}	dN0_{inv}
Comprehensive $_{\text{month}}$	0.990, 0.982	0.44**	**< 0.01**	0.01	**< 0.01**	0.03	0.12**	**< 0.05**	-	**< 0.01**	0.01
Comprehensive $_{\text{quarter}}$	0.989, 0.983	0.44**	**< 0.01**	0.01	**< 0.01**	0.03	0.13**	**< 0.05**	-	**< 0.01**	0.02
Minimum $_{\text{month}}$	0.981, 0.973	0.56**	*< 0.01*	-0.01	**< 0.01**	0.02	0.29**	*< 0.01*	-0.03	ns	**-**
Minimum $_{\text{quarter}}$	0.980, 0.973	0.57**	*< 0.01*	-0.07	**< 0.01**	0.04	0.31**	*< 0.01*	-0.17	**< 0.01**	0.02
Temperature $_{\text{month}}$	0.985, 0.959	0.57**	**< 0.01**	0.01	*< 0.01*	-0.04	0.32**	**< 0.01**	0.02	*< 0.01*	-0.11
Temperature $_{\text{quarter}}$	0.985, 0.950	0.58**	**< 0.01**	0.02	*< 0.01*	-0.07	0.38**	**< 0.01**	0.07	*< 0.01*	-0.22
Precipitation $_{\text{month}}$	0.927, 0.918	0.70**	ns	-	**< 0.01**	0.01	0.52**	*< 0.05*	-	ns	**-**
Precipitation $_{\text{quarter}}$	0.902, 0.918	0.71**	ns	-	**< 0.01**	0.01	0.55**	*< 0.05*	-	**< 0.01**	0.05
Combined variables	0.983, 0.962	0.51**	**< 0.01**	0.01	**< 0.01**	0.03	0.26**	**< 0.01**	0.02	**< 0.01**	0.02

Results from the niche similarity test based on native records compared to the invasive background revealed that climatic conditions described by the ‘Comprehensive’, ‘Temperature’ and ‘Combined variables’ sets were more similar and those described by the ‘Minimum’ variable sets were more different to those expected by chance when applying both *D* and *I* measures (Table 3.2-3). The ‘Precipitation’ data sets revealed no significant results regarding *I* values, but were more different regarding *D* values at a significance of $P < 0.05$. Greatest differences to the null distributions were found in the data set ‘Minimum $_{\text{quarter}}$’, whereas only small differences were observed in the others. Results based on invasive records compared to the native background revealed that climatic conditions described by the variable sets ‘Temperature’ are more different than expected by chance when applying both measures (Table 3.2-3). Two tests applying *D* values revealed no significant results (Minimum $_{\text{month}}$, Precipitation $_{\text{month}}$) but were significantly different with respect to *I* values. The greatest differences to the null distributions were found in the variable sets ‘Temperature’. Only small differences ($D \leq \pm 0.05$; $I \leq \pm 0.03$) were detected among the other sets.

Discussion

Our results clearly indicate that the degree of conservatism of the climate niches of *Hemidactylus turcicus* varies among predictors and variable sets applied. The study was based on comprehensive occurrence data from all regions in which this gecko is present in Europe and North and Central America, providing a robust basis. Results presented herein have important implications for studies on biological invasion, impact of climate change and niche evolution.

Which circumstances may facilitate establishment of invasive populations and subsequent shifts in ecological niches? Release from competitors, pathogens or predators is one of the most commonly invoked explanations for the establishment and proliferation of invasive populations (e.g. COLAUTTI et al. 2004). Although some native species have been observed to predate on the Mediterranean Housegecko in its invasive range, the gecko generally occupies a niche that offers little competition with native species (SELCER 1986). Therefore, reduction of biotic stress may have facilitated initial establishment of invasive populations. However, today several other, more recently introduced geckkonid species compete with *H. turcicus* in some regions. For instance, at Port of Galveston, Texas, *H. turcicus* apparently has been replaced by the recently introduced lizard *Cyrtopodion* *scabrum* (KLAWINSKI et al. 1994). *Hemidactylus turcicus* is also declining in southern Florida due to interspecific competition with the congenerics *H. garnotti* and *H. mabouia* (MESHAKA et al. 1994).

It was suggested that climatic suitability may have a strong impact on competition success, especially in ectotherms (e.g. RÖDDER et al. 2008). Our CEMs based on the variable sets suggest a relative low climatic suitability for *H. turcicus* in Florida, mainly caused by higher precipitation compared to its native range. Climatic suitability for *H. mabouia* is much higher than for *H. turcicus* in Florida, making it more vulnerable to interspecific competition (RÖDDER et al. 2008). This well supports the findings of MESHAKA et al. (1994).

Niche conservatism versus niche shift

HOLT et al. (2005) theorized that evolution of environmental tolerance may be most likely if a species is introduced into a novel environment marginal to its tolerance. Interestingly, earliest observations of established populations of the Mediterranean Housegecko were reported from Key West, Florida (FOWLER 1915), which is characterized by our models computed with sets of variables as an area with the most different climate as present in the native distribution. Differences are mainly caused by Florida being wetter what may indicate that parameters related to precipitation are biologically less important than those related to temperature. On the other hand, possible lack of competition during initial establishment may have caused advantages allowing for population establishment despite adverse circumstances.

Our results clearly indicate varying degrees of conservatism of climatic niches among predictors and variable sets applied in *H. turcicus*. Given the complex nature of climatic niches, it might be reasonable to assume varying degrees of conservatism among predictor variables. Niches may be conserved along some environmental axes but not along others (FITZPATRICK et al. 2008). Observed niche shifts may be either assigned to shifts in both the fundamental and the realized niches (PEARMAN et al. 2008; Figure 2.3-1B) or to shifts in the realized niche only (e.g. due to extended accessibility or due to relaxation of biotic constraints; Figure 2.3-1C). Since the realized niche is a subset of a species' fundamental niche (HUTCHINSON 1957; 1978), the likelihood of a given variable to be classified by our approach as conservative is expected to depend on the degree its realization covers the species' fundamental niche (Figure 2.3-1D). If the realized niche covers the entire fundamental niche, shifts per se have to be considered as an evolutionary response accompanied by novel adaptations. Shifts in the realized niche may occur more easily if the fundamental niche is only in part realized in a species' actual geographic range (relaxed variables; Figure 2.3-1 D).

Habitat selection versus background effects

Rejection of the null hypothesis in the niche similarity test indicate that the observed niche difference between native and invasive populations is a function of habitat selection and/or suitability rather than an artifact of the underlying environmental difference between the suit of the habitats available. If one assumes that the degree of difference between the observed overlap and the null distribution is correlated with the degree of habitat selection, it is possible to identify an interesting tendency: those variables showing a relatively high degree of similarity within the native and invasive range are also tentatively more similar than expectable by chance (e.g. 'minimum temperature coldest month', 'precipitation coldest quarter') compared to those showing limited overlap (Figure 2.3-4). This may indicate that these variables are biologically more important for *H. turcicus*.

Methodical caveats

Generally, relaxed variables should be a poor predictor for a species' realized distribution in statistical terms. Environmental conditions, as observed at the training records, should exhibit minor contrast to background points only (if any), whereby such contrast is expected to be high when applying conserved variables. In turn, this should result in lower AUC values in CEMs computed with relaxed variables compared to those derived from conserved ones. However, our results obtained from models developed with single variables indicate right the opposite pattern. AUC values slightly decreased with increasing *D* and *I* values (Table 3.2-3, Appendix 3.2-S3).

The fit of models based on our data sets including multiple predictors was generally superior to models computed with single variables. Novel machine-learning algorithms for presence-only applications, such as Maxent, assess the explanatory power of each variable used for model building (i.e. the ability to distinguish conditions observed at presence records form those obtained from random background points). Thereby, they address the issue of possible over-restriction of PDs by lowering the importance or excluding variables from the model, which are less suitable for a characterization of the observed distribution pattern compared to other variables. However, we noted that variable importance varied remarkably in our CEMs trained with native or invasive records as well as the data sets applied (Table 3.2-1). There may be two explanations: (1) the different sets of background data available within the native and invasive ranges each provide different contrasts during model training and (2) poorer models may tentatively characterize a relatively large area as suitable in contrast to highly accurate models. That, in turn, may result in a better chance to detect a high degree of conservatism in terms of *D* and *I* values comparing poor models.

Conclusions

Our results indicate that the selection of variables involved can highly influence CEM results. When analyzing niche conservatism with CEM approaches, as proposed by WIENS and GRAHAM (2005) and WARREN et al. (2008), different sets of conservative predictors should be applied in order to evaluate variability. Results need to be critically evaluated and interpreted with caution, whereby assessments of models developed with single variables may facilitate their interpretation of results.

It was suggested by BROENNIMANN and GUISAN (2008) that training models with records from both the native and invasive ranges can improve the model output by incorporating more information on the target species' fundamental niche. Although this approach clearly provides some advantages, still there may be one major drawback: the possible incorporation of relaxed variables. This may limit the predictive ability of the model when projected into different areas or climate scenarios. Therefore, for invasive species, we recommend a throughout assessment of the species' ecology and degree of conservatism among predictor variables by comparing climatic properties of the native and invasive range. Final models should be based on biologically important and more conserved variables to avoid over-restrictive predictions. A set of rather few variables should be preferred.

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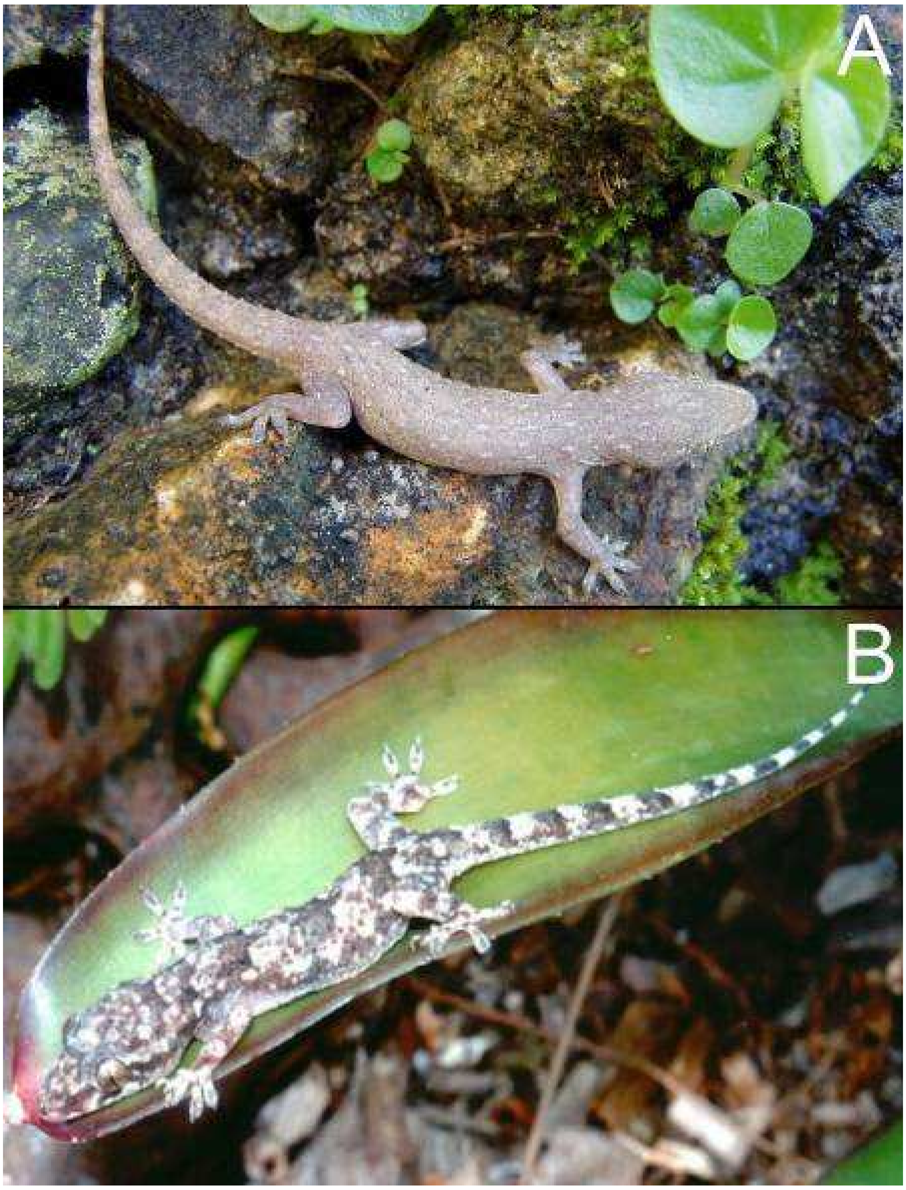
SECTION 3: HOW DO ACCESSIBILITY AND BIOTIC INTERACTIONS SHAPE REALIZED DISTRIBUTIONS?

3.1. Predicting the potential distributions of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus, Hemidactylus mabouia*)[5]



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Hemidactylus frenatus (A) and *H. mabouia* (B)

The work reported in this chapter was conducted in collaboration with MIRCO SOLÉ from the Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Ilhéus, BA, Brazil, and WOLFGANG BÖHME from the Herpetology Department, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

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Introduction

Globalization has led to a heightened spread of alien invasive species, a leading anthropogenic disturbance with far-reaching implications (NAEEM et al. 1995). Invasive species can alter mutualistic relationships, community dynamics, ecosystem function and resource distributions (MOONEY and CLELAND 2001). They can cause extinctions affecting thereby local and global diversity (COLLINS et al. 2002; VITOUSEK et al. 1996).

Within the Squamata, some *Hemidactylus* geckos (*Hemidactylus mabouia* (MOREAU DE JONNÈS, 1818), *H. turcicus* LINNAEUS, 1758, *H. brookii* GRAY, 1845, *H. frenatus* SCHLEGEL 1836, *H. garnotii* DUMÉRIL and BIBRON, 1836, *H. persicus* ANDERSON, 1872, *H. flaviviridis* RÜPEL, 1835 and *H. bowringii* GRAY, 1845) have largely extended their ranges during the last century (e.g. CARRANZA and ARNOLD 2006). They have more apparent cases of larger range extensions than any other reptilian group. *Hemidactylus frenatus*, which has its native range in tropical Asia and the Indo-Pacific (CASE et al. 1994), and *Hemidactylus mabouia,* which has its native range in Central and East Africa, are especially widespread (CARRANZA and ARNOLD 2006). *Hemidactylus frenatus* has already colonized many pacific islands, Florida, Central America and the Venezuelan coast (e.g. CASE et al. 1994; MESHAKA et al. 2004). Invasive populations of *Hemidactylus mabouia* are currently well distributed in West Africa, all over the Caribbean (VAN BUURT 2006), South America (COLLI 2005; FUENMAYOR et al. 2005) and Florida (MESHAKA et al. 2004). Although most common in urban areas, it is also abundant in natural environments of several biomes, e.g. within Brazil (COLLI 2005; VANZOLINI 1968a,b; ZAMPROGNO and TEIXEIRA 1997). Both species are very adaptive and effective colonizers (e.g. BONFIGLIO et al. 2006; CASE et al. 1994; FUENMAYOR et al. 2005), widely distributed in tropical regions and may have reached South America by both natural transmarine colonization (KLUGE 1969) and human-mediated colonization (CARRANZA and ARNOLD 2006). The latter is suggested by virtually no genetic variation over their huge range and their presence in many coastal urban areas (CARRANZA and ARNOLD 2006). Sympatric populations of both are rare and known only from Florida (MESHAKA 2000; KRYSKO et al. 2003), Colombia, Costa Rica (GBIF 2007), and Madagascar (GBIF 2007; GLAW and VENCES 2007).

On occasion, the introduction of *H. frenatus* and *H. mabouia* had devastating consequences for native species independent from ecotypes such as small and large species, diurnal and nocturnal taxa, as well species with parthenogenetic and sexual reproduction. *Hemidactylus frenatus* is displacing *Lepidodactylus lugubris* DUMÉRIL and BIBRON, 1836 and *H. garnotii* on a global scale (CASE et al. 1994; PETREN et al. 1993;

PETREN and CASE 1995; DAME and PETREN 2006), and *H. mabouia* is competing with *Hemidactylus angulatus* HALLOWELL, 1852 in Cameroon (BÖHME 1975), *Gymnodactylus darwinii* (GRAY, 1845) in Brazil (TEIXEIRA 2002; ZAMPROGNO and TEIXEIRA 1997), with *Phyllodactylus martini* LIDTH DE JEUDE, 1887 and *Gonatodes antillensis* LIDTH DE JEUDE, 1887 in Curaçao and Bonaire (VAN BUURT 2006), and with *Gonatodes vittatus* (LICHTENSTEIN, 1856) and *Thecadactylus rapicauda* (HOUTTUYN, 1782) in Venezuela (FUENMAYOR et al. 2005), respectively. The arrival of *H. frenatus* in the Mascarene Island decimated six species of *Nactus* geckos, and three of them are now considered to be entirely extinct (ARNOLD 2000; COLE et al. 2005). Considering these possible consequences of invasion, an assessment and identification of regions with a high invasion potential is necessary for effective conservation planning.

Ecological niche-modelling is a good tool to assess potential geographic distributions of species derived from their climatic niches (‘climate envelope’; GUISAN and THUILLER 2005; ELITH et al. 2006), providing in some cases additional information for conservation planning strategies and selection of protection areas (e.g. JEGANATHAN et al. 2004; YOUNG 2007). Ecological niche modelling has also been applied to the prediction of the invasive potential of non-native species (e.g. PAPES and PETERSON 2003; PETERSON and VIEGLAIS 2001; FICETOLA et al. 2007). Such approaches relay on the assumption that climatic tolerances of species are the primary determinants of their current distributions and that climatic niches are rather conservative, at least within evolutionary relatively short time frames (e.g. some hundreds to thousands of years) (e.g. WIENS and GRAHAM 2005).

Herein, we want to (1) identify areas potentially suitable for the geckos using a climate envelope approach, (2) predict their potential distribution (PD) for 2100 under a climate change scenario, and (3) try to assess why sympatric populations of both species are rare.

Material and methods

Species records

We used 456 georeferenced records of *H. frenatus* and 279 georeferenced records of *H. mabouia* taken from collections linked to the Global Biodiversity Information Facility (GBIF 2007), the HerpNet (2007) database, and listed by the Instituto Hórus (2007). Literature data was added for complementation purposes (BÖHME 1975; GLAW and VENCES 2007; FUENMAYOR et al. 2005). Georeferencing was conducted when necessary with the Alexandria Digital Library Gazetteer (http://middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp). All data was checked in the DIVA-GIS software (HIJMANS et al. 1999; 2002) for bias and errors.

Climate data

For information on current climate, we used the Worldclim database, version 1.4, based on weather conditions recorded 1950-2000, with spatial resolution approximately 1 x 1 km (HIJMANS et al. 2005). It was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995; 2004).

Projected climate data we used go back to DUFFY et al. (2003) and GOVINDASAMY et al. (2003) who ran the Community Climate Model 3 (CCM3) developed by the National Center for Atmospheric Research (NCAR) at about 50 x 50 km² spatial resolution to simulate conditions at doubled atmospheric levels of CO_2 compared to pre-industrial conditions, as is expected for approximately the year 2100. These future data were rescaled to a spatial resolution of approximately 1 x 1 km² by HIJMANS and GRAHAM (2006) and presently represent the highest available spatial resolution for future global climate data (HIJMANS et al. 2005). Both present-day and future climate data sets were downloaded from the DIVA-GIS homepage (http://www.diva-gis.org; accessed 15 May 2007) and included the following 36 monthly mean variables: minimum temperature and maximum temperature, and precipitation.

Based on the climate data mentioned, so called ‘bioclimate’ variables can be calculated with DIVA-GIS 5.4 (http://www.diva-gis.org; downloaded 15 May 2007; HIJMANS et al. 2001). For our models we selected the annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of wettest month, and precipitation of the driest month representing a set of parameters, which describe the availability of water and energy and the species tolerances regarding these parameters.

Climate Envelope Models

For CEMs, MaxEnt 3.2.1 (PHILLIPS et al. 2004, 2006; http://www.cs.princeton.edu/~shapire/Maxent; downloaded 15 March 2008) was used, a machine learning algorithm for species PD models with environmental predictors (e.g. climatic layers), which reveals better results than comparable methods (ELITH et al. 2006; HEIKKINEN et al. 2006), especially when the number of data points is relatively few (HERNANDEZ et al. 2006).

Maxent allows for model testing by calculation of the area under the ROC (receiver operation characteristic) curve (AUC) (PHILLIPS et al. 2006). Therefore, we (1) selected 25 % random test points out of each data set for the native distribution and we (2) run the model using all records within the native distribution of the species as training points and used the records where they are invasive as test points. The second approach allowed us to test for the predictive power for invasiveness of our models. The MaxEnt results were imported into DIVA-GIS as *asc files for further analysis.

We assessed the degree of overlap in the climate envelope between *H. frenatus* and *H. mabouia* comparing the MaxEnt probabilities at each record crosswise, e.g. we extracted the MaxEnt probabilities of *H. frenatus* at the locations where *H. mabouia* was recorded, respectively. This procedure allowed us to assess if the two species can occur in microsympatry and if they can, the identification of which species can cope with a broader climatic diversity within the PD of the other. The Mann-Whitney-U test was used to compare the results and box plots to visualize them. All calculations were conducted with XLSTAT 2007 (www.adinsoft.com).

Results

Using 25 % random test points out of each data set for testing we received excellent AUC values (*H. frenatus*: test AUC = 0.969; training AUC = 0.966; *H. mabouia*: test AUC = 0.955; training AUC = 0.938), following the classification accuracy of SWETS (1988). Running the model using only records within the native distribution of the species and using the records where the species are invasive as test points, we received also ‘excellent’ AUC values (*H. frenatus*: test AUC = 0.941; training AUC = 0.967; *H. mabouia*: test AUC = 0.959 ; training AUC = 0.942). PD maps predicted by our models are presented in Figure 3.1-1 and 3.1-2.

Our CEMs suggest that *H. frenatus* can find climatically optimal habitats under current conditions in tropical Asia, at the Australian east coast, Central America, within the Amazon basin, the Guiana Region, the West African coast (Figure 3.1-1). Therefore, a further spread of the species is most likely in large parts of South America and tropical Africa. *Hemidactylus mabouia* can find climatically optimal habitats mainly throughout the Congo basin towards the Kenyan coast, in southern India, coastal regions in tropical Asia, Central America, the Guiana Region, northern parts of the Amazon basin and at the eastern Coast of Brazil in Bahia (Figure 3.1-2). In most regions it is already invasive. Risk of further invasion is highest in Central America and tropical Asia.

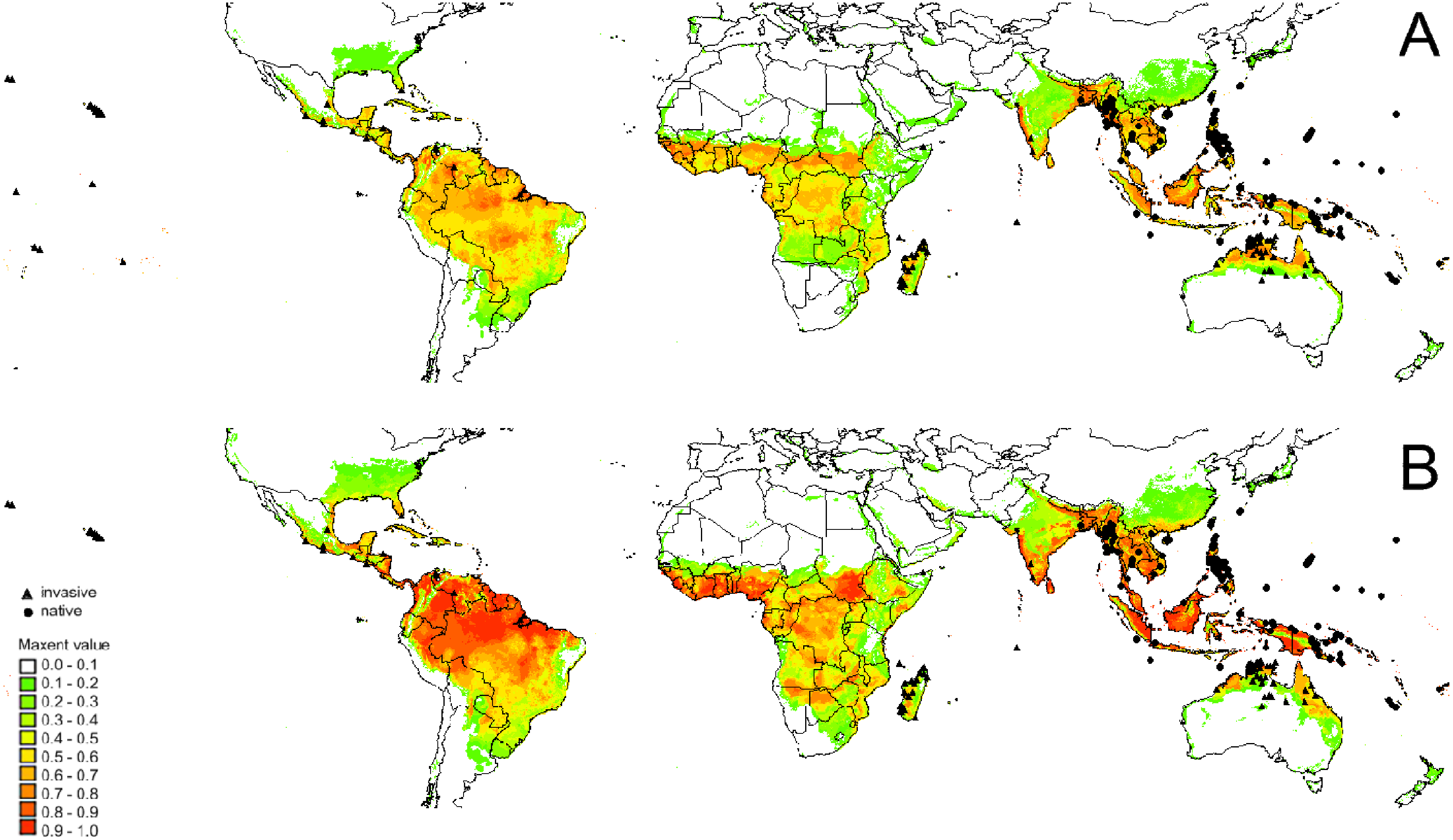

Figure 3.1-1. Predicted potential distribution for *Hemidactylus frenatus* under current (A) and future (B; CCM3) conditions. Higher MaxEnt values reflect a higher climatic suitability for the species.

Under CCM3 conditions, there will be more regions with suitable climate for *H. frenatus* and less for *H. mabouia* (Figure 3.1-1, 3.1-2). Major improvements for *H. frenatus* will occur in the native range of the species in Asia, northern parts of Australia, in the Amazon basin and the Guiana Highlands, eastern parts of Colombia and Peru, along the West African coast and in Botswana and Namibia. Reductions will occur in Burma, Bangladesh and eastern parts of India. Better climatic conditions within the Amazon basin might enhance the spread of *H. frenatus* in northern and central parts of South America. For *H. mabouia* our predictions suggest only small improvements, which would be situated in our scenario at the coast of Somalia, the Central African Republic, South Africa, eastern parts of Madagascar, and southern Brazil. Reductions of climatic suitability will occur in the Congo basin, along the West African coast, in Mozambique, in Central America, in the Amazon basin, eastern parts of Columbia, Peru, Bolivia, Paraguay, and within the Guiana Highlands.

On a global scale, a crosswise comparison between the MaxEnt probabilities at the records revealed, that the climatic suitability for *H. frenatus* at *H. mabouia*'s records is higher than the climatic suitability of *H. mabouia* at *H. frenatus'* records under current conditions (Figure 3.1-3). This difference was significant (Mann-Whitney-U test: P = 0.046). However, the climatic suitability for the species is much lower in crosswise comparisons than within the known ranges of each species (Figure 3.1-3).

Discussion

Although there are different patterns of climatically optimal regions, our PD maps suggest that both species can occur nearly everywhere in the tropics. Looking at the PD maps of both species, huge overlaps become obvious and it is surprising that they apparently only occasionally co-occur. *Hemidactylus frenatus* seems to be absent in Africa and main parts of South America although the climatic conditions are suitable for the species, since we found no records in the data bases and literature. For Brazil, its absence is further supported because it is not listed by the Brazilian invasive species data base (INSTITUTO HÓRUS 2007). There are two possible explanations for this pattern: (1) *H. frenatus* and *H. mabouia* are still spreading and could simply not have reached their maximal distribution and/or (2) factors related to different climatic conditions and/or interspecific interactions such as competition and predation could hamper successful invasion in some areas.

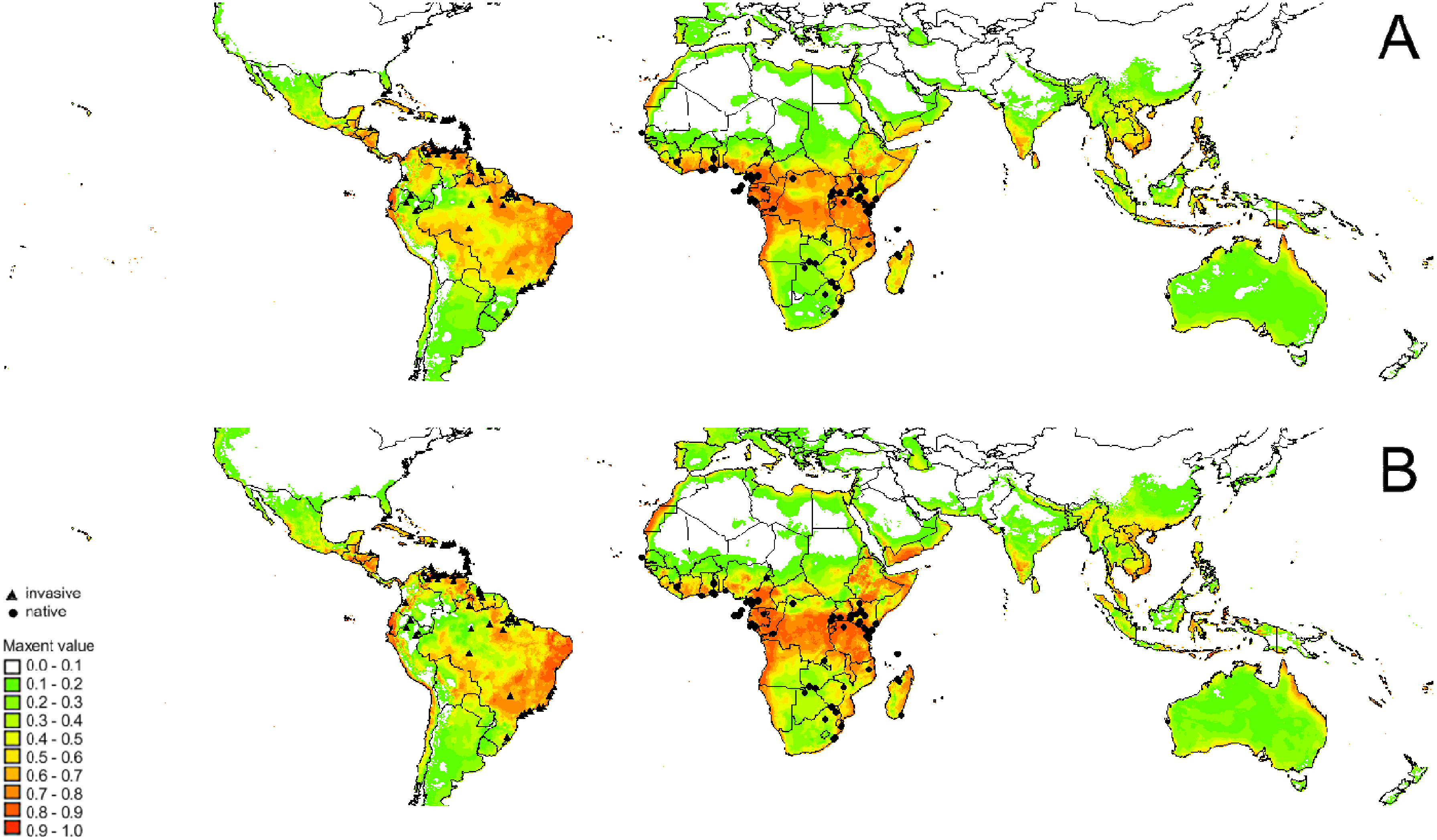

Figure 3.1-2. Predicted potential distribution for *Hemidactylus mabouia* under current (A) and future (B; CCM3) conditions. Higher MaxEnt values reflect a higher climatic suitability for the species.

Do the current ranges of the two geckos reflect equilibrium or are they still spreading?

Facilitated due to human travel and trade activities, *H. frenatus* has spread to all the major islands in between tropical Asia and Hawaii during the 20th century, where it was first recorded short after World War II (CASE et al. 1994). Its colonization success is very high; in 1971 it was absent in Vanuatu (MEDWAY and MARSHALL 1975), but in 1986 ”it was virtually the only urban gecko seen in the city of Port Vila on Efaté and is by far the most common gecko in the town of Santo on Espiritu Santo” (CASE et al. 1992). In their 1994 review, CASE et al. do not report from records in Australia, where it is common today (Figure 3.1-1). The summary given by the authors supports the hypothesis that *H. frenatus* could be still spreading eastward from its native range. When it has reached Central and South America remains unclear, but it was suggested that the species is established in Venezuela since more than 10 years (FUENMAYOR et al. 2005). Recent dispersal is supported by genetic studies, since specimens of *H. frenatus* from Hawaii and Colombia are genetically identical (CARRANZA and ARNOLD 2006).

Time series illustrating the dispersal of *H. mabouia* in the Americans remain widely unknown. *Hemidactylus mabouia* was recorded in Curaçao in the late 1980’s, in Bonaire around 2000, an in Aruba in 2002 for the first time (VAN BUURT 2006). KLUGE (1969) suggested that a natural colonization of the Americas by *H. mabouia* could be also possible, but the uniformity of genetic samples of *H. mabouia* from Central and South America and Africa indicates it at least too has spread comparatively rapidly and recently (CARRANZA and ARNOLD 2006). In tropical America, recent records indicate that it is still spreading (e.g. VAN BUURT 2006; CARRANZA and ARNOLD 2006; FUENMAYOR et al. 2005).

We think that, today, (1) can explain the apparently absence of *H. mabouia* in tropical Asia and the rarity of *H. frenatus* in South America only in parts. Both *H. frenatus* and *H. mabouia* were introduced to nearly all tropical regions including even smallest islands, where they have established themselves rapidly. Thus the chance that specimens of *H. frenatus* were transported by human beings to either Africa or South America (or specimens of *H. mabouia* to tropical Asia) should be great. Furthermore, their high colonization success in urban areas together with their high population densities should enhance the chance to detect them and therefore enhance their chance to be present in collections. This would suggest that the pattern is not likely to be a collection bias.

Competitive exclusion

It is known that *Hemidactylus* species can replace each other because many are ecologically analogous (MESHAKA 2000; DAME and PETREN 2006). Habitat features such as structure have an effect on successful competition (e.g. PETREN and CASE 1996), but ability of successful competition may be related to climatic suitability of a region, too. Rather pessimal climatic conditions may cause environmental stress, which can reduce a species' fitness and its ability for successful competition.

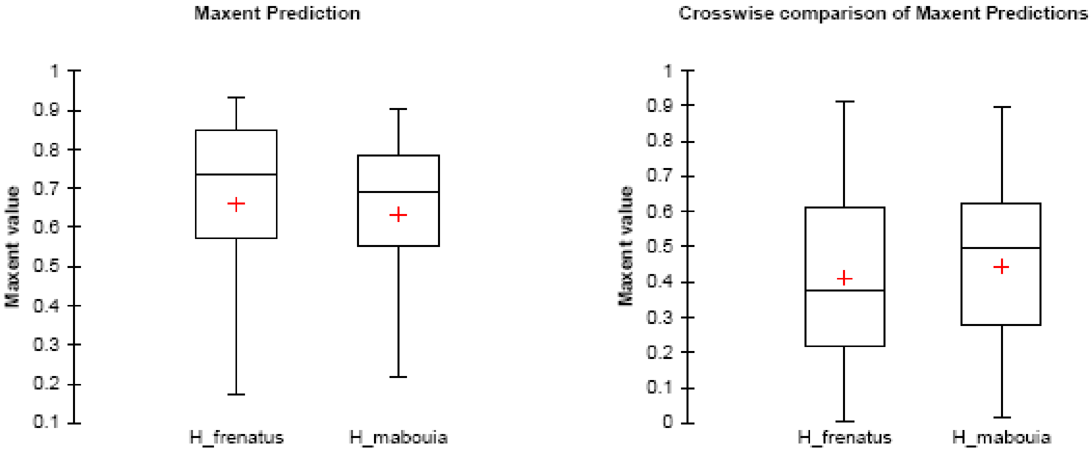

Figure 3.1-3. MaxEnt values at the records for each species (left) and crosswise comparison between the MaxEnt values per species record (right). For the crosswise comparison, MaxEnt values of one species were extracted at records where the other was found.

MESHAKA et al. (2004) reported that *H. frenatus* and *H. garnotii* were replaced by *H. mabouia* in Key West, Florida. On the other hand, POWELL et al. (1998) suggested that *H. frenatus* has displaced *H. mabouia* in Veracruz, México. Comparison of the MaxEnt scores of the two species in this regions revealed, that MaxEnt scores in Key West, Florida are much higher for *H. mabouia* (0.72) than for *H. frenatus* (0.50), but MaxEnt scores for *H. mabouia* (0.61) are nearly equal to scores of *H. frenatus* (0.59) in Veracruz. This could be a possible explanation of the different observations, but is pending further studies. On a global scale, the crosswise comparison between the MaxEnt probabilities at the records revealed, that the climatic suitability for *H. frenatus* at *H. mabouia*'s records is significantly higher than the climatic suitability for *H. mabouia* at *H. frenatus*' records

(Figure 3.1-3). As a consequence, the ability of *H. mabouia* for successful competition should be more restricted than in *H. frenatus*. However, the climatic suitability for the species is much lower in crosswise comparisons than within the known ranges of each species (Figure 3.1-3). The better climatic suitability of Africa and South America for *H. mabouia* compared to *H. frenatus* may favour *H. mabouia* here. The opposite might be true for Asia and Central America explaining the virtually absence of *H. mabouia*.

Conclusions

We conclude that both competitive exclusion and a non equilibrium in the ranges of the species explain the virtual lack of sympatric populations, although the impact of climate on competition success is pending further testing in the field. The raised climatic suitability for *H. frenatus* combined with the reduced suitability for *H. mabouia* within the Amazon basin and the Guiana Highlands in our future scenario may alter the abundances of the species here, what might provide an interesting possibility for field studies. Further research is needed to start understanding the dynamics of competitive exclusion, climate and competition success.

Acknowledgements

This work was funded by the “Graduiertenförderung des Landes Nordrhein-Westfalen”.

3.2. ‘Sleepless in Hawaii’ – does anthropogenic climate change enhance ecological and socioeconomic impacts of the alien invasive *Eleutherodactylus coqui* Thomas 1966 (Anura: Eleutherodactylidae)?[6]

©Wilfredo Falcón-Linero

Eleutherodactylus coqui

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[6] This part was published in *North-Western Journal of Zoology* 5 (1): 16-25.

Introduction

Alien invasive species are a concern in nature conservation as they may have negative impact on native biodiversity (LOWE et al. 2000). Furthermore, they can have major socioeconomic impacts as reported for the coqui (*Eleutherodactylus coqui*; KRAUS and CAMPBELL 2002). This species is a small (33-57 mm), brown or grey-brown, arboreal frog, which has been accidentally introduced into several tropical areas and was listed as one of the 100 worst alien invasive species (LOWE et al. 2000).

In its native range, Puerto Rico, *E. coqui* is found in more habitat types than any other eleutherodactylid species (JOGLAR 1998). It is ecologically a generalist utilizing the entire vertical spectrum of their habitat from forest floor to canopy (GOSNER and WOOLBRIGHT 1995). *Eleutherodactylus coqui* utilize internal fertilization and fertilized eggs undergo direct development making them independent from stagnant water (TOWNSEND and STEWART 1994). The species is highly fertile; females deposit 4-6 clutches of about 28 eggs each (min = 16, max = 41) per year in subterranean nests, which develop within 17-26 days (KRAUS et al. 1999). Time between generations (i.e. from egg to egg-laying adult) is about eight months (TOWNSEND and STEWART 1994; KRAUS et al. 1999). Densities of *E. coqui* are with around 20 000 individuals ha^{-1} in its native range and around 50 000 individuals ha^{-1} in its invasive range - on the Island of Hawaii - among the highest known for any amphibian in the world (STEWART 1995; STEWART and WOOLBRIGHT 1996; WOOLBRIGHT et al. 2006). Population densities are also known to increase after hurricane disturbances which define the structure and function of an ecosystem (WOOLBRIGHT 1991; 1996). Diet of the frog varies depending on age and size but is primarily composed of arthropods. Juveniles consume smaller prey such as ants while adults consume a more varied diet that includes spiders, moths, crickets, snails, and small frogs. As a nocturnal predator occurring in such high densities 114 000 to 350 000 invertebrates ha^{-1} can be consumed each night (BREAD 2007; STEWART and WOOLBRIGHT 1996). That may have a major ecological impact.

One of the major ways in which *E. coqui* spreads is the nursery and ornamental plant trade where clutches or frogs accidently hitchhike on plants (KRAUS 2003; KRAUS and CAMPBELL 2002; KRAUS et al. 1999). Travelling by plants has been reported from several regions including Guam and mainland United States including California and Connecticut (Joglar 1998), and the Hawaiian Islands (KRAUS et al. 1999). Many accidently exported specimens have subsequently established nonindigenous feral populations as reported for the Bahamas (KAIRO et al. 2003), Culebra and Vieques (JOGLAR 1998; JOGLAR and RIOS-

LÓPEZ 1998), Dominican Republic (CAMPBELL 2000), Maui, the Island of Hawaii, Kauai, Oahu (KRAUS et al. 1999), the Galapagos Islands (SNELL and REA 1999), Florida, and the US Virgin Islands (CAMPBELL 2000; KAIRO et al. 2003). One single specimen was reported for Guam, Mariana Islands, but has since been eradicated and no further records are known (MCCOID 1993), so it was not included herein. Records for New Orleans, Louisiana as reported by CONANT and COLLINS (1991) are most likely erroneous (DUNDEE 1991).

Eleutherodactylus coqui has a loud, piercing call that can measure 90–100 decibels at a distance of 0.5 meters from a frog. In the Hawaiian Islands, the calls are a serious problem for local residents and hotel guests who complain about the noise keeping them awake at night (KRAUS et al. 1999; KRAUS and CAMPBELL 2002). Residents are encountering reduced property values and increased difficulty selling property (KRAUS and CAMPBELL 2002). This is also a problem for other areas where *Eleutherodactylus* species have been introduced outside their native ranges. For example, in French Guiana in South America, the calls of introduced *E. johnstonei* BARBOUR, 1914 are disturbing the sleep of local residents (LEVER 2003). The coqui can also be a serious problem for international trade: according to KRAUS and CAMPBELL (2002), frogs on the Island of Hawaii may lead to rejection by trading partners of goods that may be infested with the frogs or their eggs. In April 2004, the coqui situation was declared by the Mayor of Hilo as a state of emergency because ‘the threat that excessive noise emitted by the coqui frogs poses to human health and welfare, the unknown impact of the coqui frogs on the Island of Hawaii ecosystems as well as its threat to the economic welfare of the Island of Hawaii’ (BEARD and PITT 2005). Multimillion US dollar campaigns were launched to eradicate the species. However, no spatial assessment of areas climatically suitable for the species is available. Therefore, I assess (i) the potential distribution of the coqui under current climate conditions in order to identify regions with high potentials for coqui invasions and (ii) possible changes within its invasive Hawaiian range applying future climate change scenarios herein.

Material and methods

Climate and computation of Climate Envelope Models

GIS-based Climate Envelope Models (CEMs) may provide an easy-to-use method to assess the potential distribution of species. In recent times, there have been several examples using CEMs for species potential distributions under past, present and future climate scenarios (e.g. HIJMANS and GRAHAM 2006; MALCOM et al. 2006; PETERSON and

NYÁRI 2007; CARNAVAL and MORITZ 2008). Such approaches rely on the assumption that climatic tolerances of species are the primary determinants of their current distributions and that specific climatic niches are conservative, at least within an evolutionary short time frames of some hundreds to thousands years (e.g. WIENS and GRAHAM 2005; but see also PEARMAN et al. 2007). Herein, MaxEnt 3.2.1 (PHILLIPS et al. 2004; 2006; http://www.cs.princeton.edu/~shapire/maxent) was used for CEM calculation in order to assess the potential distribution of the coqui. MaxEnt is a machine-learning algorithm following the principles of maximum entropy (JAYNES 1957). It has been shown to reveal better results than other comparable methods such as BIOCLIM, DOMAIN or GARP (e.g. ELITH et al. 2006).

Information on current climate was obtained from the Worldclim database, version 1.4, which is based on weather conditions recorded between 1950 and 2000 with grid cell resolution 30 arc seconds (HIJMANS et al. 2005; http://www.worldclim.org). It was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995; 2004).

For future climate scenarios, I used climate change projections with a spatial resolution of 2.5 minutes based on the CCCMA, CSIRO and HADCM3 (FLATO et al. 2000; GORDON et al. 2000) models and the emission scenarios reported in the Special Report on Emissions Scenarios (SRES) by the Intergovernmental Panel on Climate Change, IPCC (http://www.grida.no/climate/ipcc/emission/). A set of different families of emission scenarios was formulated based on future production of greenhouse gases and aerosol precursor emissions. The SRES scenarios of A2a and B2a were used in this study. Each scenario described one possible demographic, politico-economic, social and technological future as expected for the years 2020, 2050 and 2080. Scenario B2a emphasizes more environmentally conscious, more regionalized solutions to economic, social and environmental sustainability. Compared to B2a, scenario A2a also emphasizes regionalized solutions to economic and social development, but it is less environmentally conscious.

For the models I selected the ‘annual mean temperature’, ‘maximum temperature of the warmest month’, ‘minimum temperature of the coldest month’, ‘annual precipitation’, ‘precipitation of wettest month’, and ‘precipitation of the driest month’ as variables representing a set of parameters, which describe the availability of water and energy and the species tolerances regarding these parameters.

Species records

A total number of 198 unique records of *E. coqui* within its native range of were available through the Global Biodiversity Information Facility (GBIF; www.gbif.org) and HerpNet databases (www.herpnet.org), 31 of them were situated in unique grid cells and used for model building. In addition, 41 records of invasive populations were obtained from the Nonindigenous Aquatic Species information resource of the United States Geological Survey (SOMMA 2008), the IUCN Invasive Species Specialist Group (www.issg.org), and additional published references. For georeferencing Alexandria Digital Library Gazetteer Server Client (www.middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp) was used. The accuracy of coordinates processed was assessed with DIVA-GIS (HIJMANS et al. 1999; 2001). In doing so, only invasive records within areas with confirmed reproduction were included. Land use maps were downloaded from the State of Hawaii Land Use Commission (http://luc.state.hi.us/luc_maps.htm) in order to evaluate the overlap between urban, rural and protected areas and the potential distribution of *E. coqui*.

Results

Maxent allows for model testing by calculation of the Area Under the Curve (AUC), referring to the ROC (Receiver Operation Characteristic) curve using the invasive records as test points and the native records for training (HANLEY and MCNEIL 1982; PHILLIPS et al. 2006). This method is recommended for ecological applications because it is non-parametric (PEARCE and FERRIER 2000). Values of AUC range from 0.5 (i.e. random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of SWETS (1988) AUC values > 0.9 describe 'very good', > 0.8 'good' and > 0.7 'useful' discrimination ability. I received 'very good' AUC values in the model ($AUC_{training} = 0.997$; $AUC_{test} = 0.996$). All known invasive ranges of *E. coqui* are situated within higher MaxEnt classes (> 0.6) confirming the predictive power of the model.

Under current climatic conditions, *E. coqui* can find suitable areas nearly everywhere in the tropics (Figure 3.2-1). Especially the South American Andes, the Venezuelan Pantepui region, Eastern Brazil, the Congo basin and most Asian Islands may be potentially suitable for the species. Within the Caribbean, major parts of the Bahamas, Cuba, the Dominican Republic, Haiti, Jamaica, and the Antilles are highlighted by the MaxEnt model (Figure 3.2-2). On Hawaii and Maui, areas suitable for *E. coqui* are restricted to lower elevations mainly at the coast, whereas climatic conditions at Honolulu and Kauai are suitable throughout the whole islands (Figure 3.2-3). These areas are highly overlapping with urban areas, whereas the species finds proportionally less suitable areas within reserves (Figure 3.2-4).

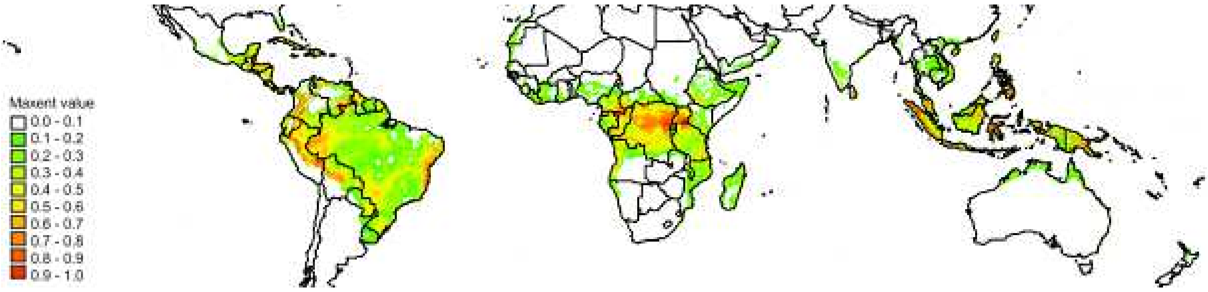

Figure 3.2-1. Potential distribution of *Eleutherodactylus coqui* under current climate conditions. Higher MaxEnt values suggest higher climatic suitability.

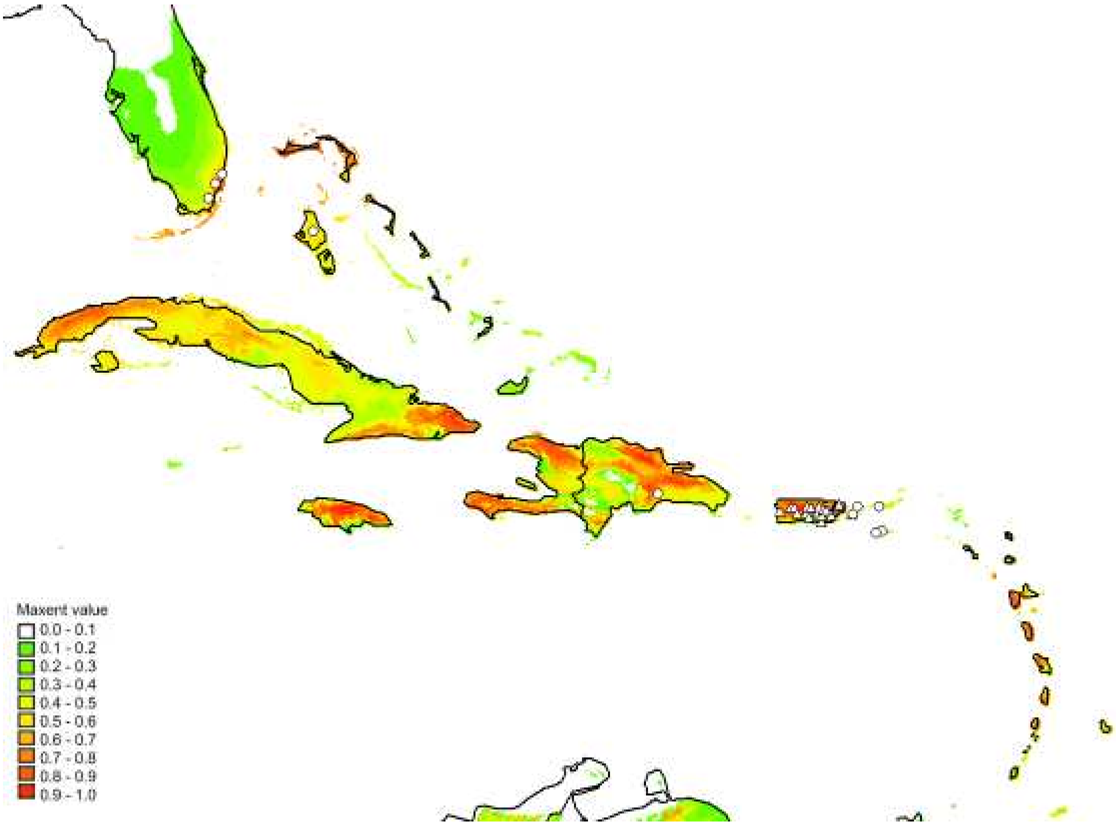

Figure 3.2-2. Potential distribution of *Eleutherodactylus coqui* under current climate conditions within the Caribbean. Higher MaxEnt values suggest higher climatic suitability. Native records are indicated as triangles and invasive as points.

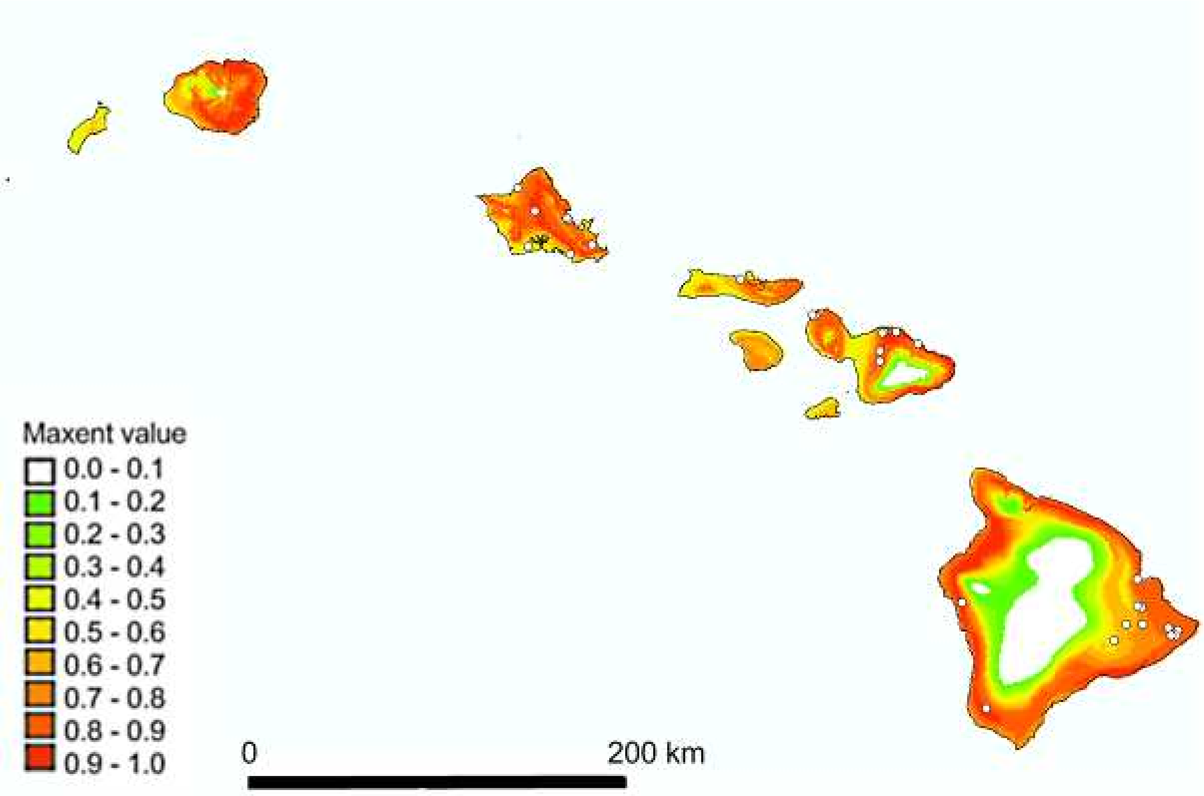

Figure 3.2-3. Potential distribution of *Eleutherodactylus coqui* under current climate conditions within Hawaii. Higher MaxEnt values suggest higher climatic suitability.

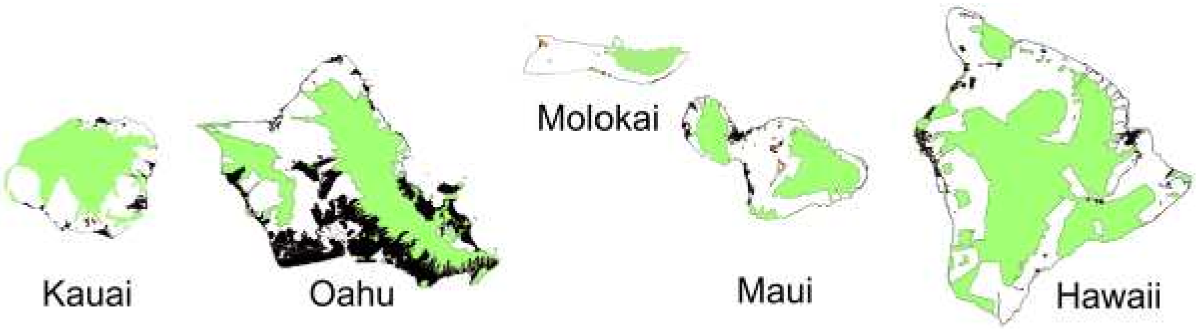

Figure 3.2-4. Land use patterns on the major Hawaiian Islands in 2007. Urban areas are indicated in black and reserves in green. Source: Land Use Commission of the State of Hawaii.

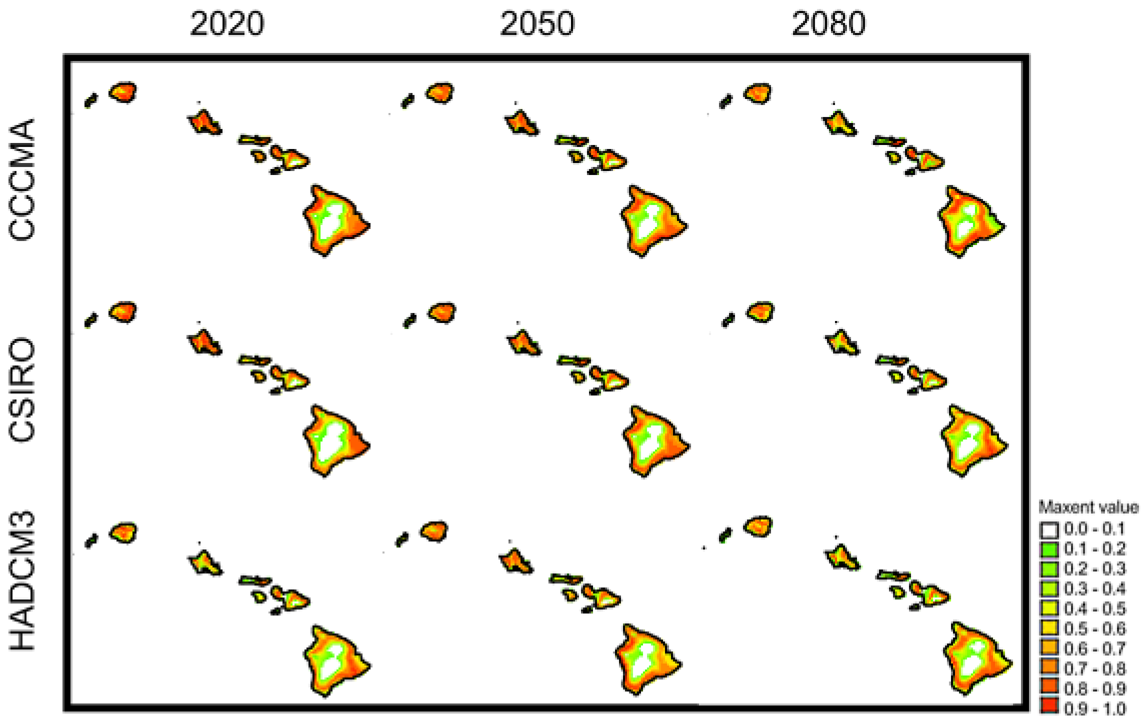

Figure 3.2-5. Potential distribution of *Eleutherodactylus coqui* under future climate change scenarios assuming A2a conditions. Higher MaxEnt values suggest higher climatic suitability.

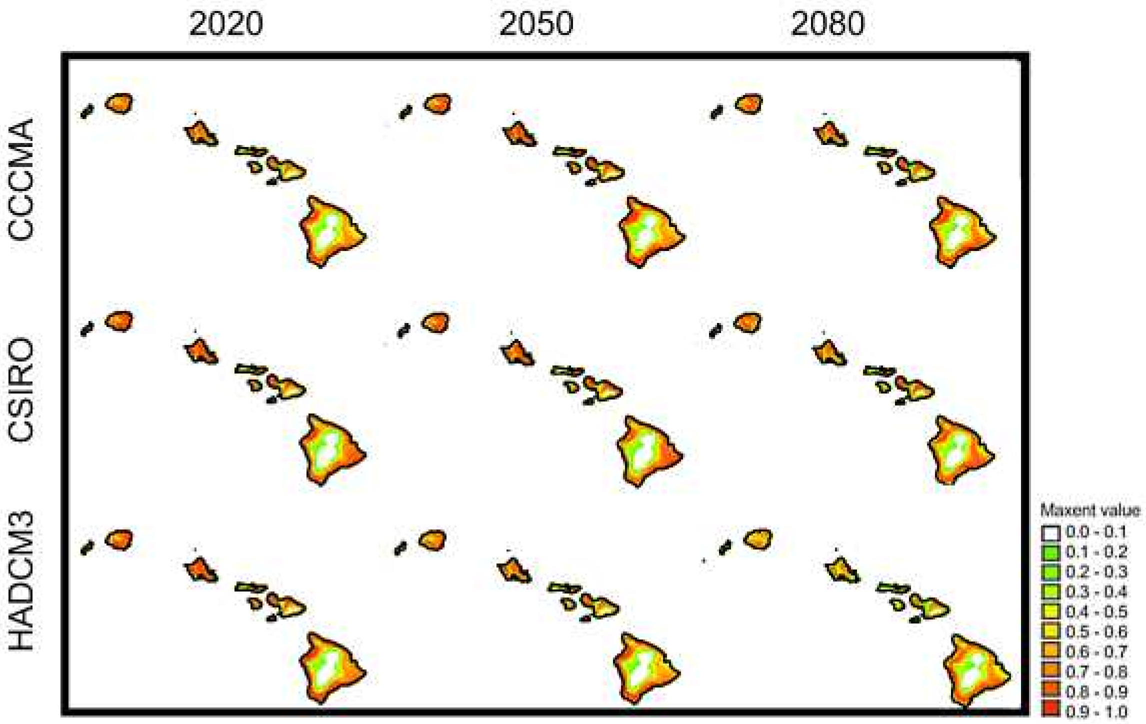

Figure 3.2-6. Potential distribution of *Eleutherodactylus coqui* under future climate change scenarios assuming B2a conditions. Higher MaxEnt values suggest higher climatic suitability.

Projections of the CEM of *E. coqui* onto the future climate change scenarios revealed that, over all, the amount of suitable grid cells remain roughly stable (i.e. changes are less than 10 % relative to current conditions, Table 3.2-1) within the Hawaiian Islands. Generally, the B2a scenarios suggested a greater range expansion than the A2a scenarios. Looking at the spatial patterns at the Islands of Hawaii and Maui, *E. coqui* may be able to expand its range towards higher elevations (Figures 3.2-5, 3.2-6). On the other hand, decreases in climatic suitability around Cape Kumukahi, situated at the east coast of the Island of Hawaii, may also occur. Potential distribution patters on the smaller islands Oahu and Kauai remain roughly stable.

Table 3.2-1 Changes in climatically suitable areas for *Eleutherodactylus coqui* relative to current conditions at the Hawaiian Islands assuming climate change scenarios A2a and B2a.

Model	**Climate Change Scenario**					
	A2a			B2a		
	2020	2050	2080	2020	2050	2080
CCCMA	101.4 %	103.1 %	98.9 %	100.2 %	103.6 %	104.1 %
CSIRO	98.4 %	102.2 %	90.4 %	101.4 %	101.4 %	102.5 %
HADCM3	102.3 %	102.7 %	98.3 %	102.1 %	102.3 %	102.7 %

Discussion

The spatial modelling approach suggests that *E. coqui* may find climatically suitable regions throughout all major tropical areas. Although all islands and most parts of adjacent continents provide climatically suitable conditions for *E. coqui*, only a few have been invaded. One reason may be that all of these islands are inhabited by a diverse anuran fauna which is rich in ecologically similar *Eleutherodactylus* species (HEDGES et al. 2008). Adjacent areas in Central and South America harbour a diverse fauna of Craugastoridae and Strabomantidae of which many are also ecologically similar (HEDGES et al. 2008). This would most likely make a successful establishment *E. coqui* difficult. However, care need to be taken to prevent further spread towards the Pacific and Asian islands lacking such potential competitors.

In the Hawaiian Islands the situation is different because a native amphibian fauna is absent (KRAUS 2003) and potential predators are rare (BEARD and PITT 2006; WOOLBRIGHT et al. 2006). This lack of competition and predators was also assumed to have caused the extraordinary high population densities of *E. coqui* here. It was suggested that *E. coqui* can reduce endemic invertebrates in the Hawaiian Islands (SIN et al. 2008). A comparison between the potential distribution of the coqui under current conditions (Figure 3.2-3) and protected areas on the major Hawaiian Islands (Figure 3.2-4) revealed that main parts of the reserves on Hawaii and Maui are outside the climatic envelope of *E. coqui*. Within these areas, winters are too cold to maintain feral populations (KRAUS and CAMPBELL 2002). So, endemics inhabiting these areas may be not threatened by the invader yet. Unfortunately, the whole islands Kauai, Molokai, and Oahu, including all protected areas, provide suitable climatic conditions.

Applying future anthropogenic climate change scenarios the models suggest an extension of the potential distribution of *E. coqui* towards higher altitudes in the Hawaiian Islands, and thereby into uninfected nature reserves. The range alternation may already have started since such a trend was recently observed by KRAUS and CAMPBELL (2002). The authors reported that *E. coqui* has expanded its altitudinal range on the Island of Hawaii form previously 0-670 m to 1170 m, where it maintained feral populations which successfully survived at least the winters of 1999-2000 and 2000-2001. KRAUS et al. (1999) and KRAUS and CAMPBELL (2002) pointed out that *E. coqui* may cause serious ecological problems if they invade mid-elevation native forests situated between 900 and 1200 m at the Island of Hawaii.

Looking at the socioeconomic impact it becomes obvious that all urban and rural areas of the Hawaiian Islands are within the climatic optimum of *E. coqui*. In the future scenarios, this pattern remains stable and the potential distribution of the frog may even increase. This threatens the multimillion dollar floriculture and nursery industries because of quarantine restrictions and de-infestation measures that are required before plants can be exported (KRAUS and CAMPBELL 2002). This is especially important since *E. coqui* densities on the Island of Hawaii are the highest in the world (STEWART 1995; STEWART and WOOLBRIGHT 1996; WOOLBRIGHT et al. 2006). Populations of *E. coqui* are expanding (KRAUS and CAMPBELL 2002) and this trend will most likely continue. During the next decades many residents and hotel guests may stay ‘sleepless in Hawaii’.

Acknowledgements

I am grateful to AARON BAUER for valuable comments on the manuscript. This work was funded by the “Graduiertenförderung des Landes Nordrhein-Westfalen”.

3.3. Will future anthropogenic climate change increase the potential distribution of the alien invasive Cuban treefrog (Anura: Hylidae)?[‡‡]

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Osteopilus septentrionalis

[‡‡] This part was published in the *Journal of Natural History 43: 1207-1217*.

The work reported in this chapter was conducted in collaboration with FRANK WEINSHEIMER from the the Herpetology Department, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Introduction

Invasive alien species are a concern in nature conservation as they may have negative impacts on native biodiversity and can have major socioeconomic impacts (VITOUSEK et al. 1996), e.g. as reported for the Cuban treefrog (*Osteopilus septentrionalis* (DUMÉRIL and BIBRON, 1841)), a tropical, mostly arboreal and nocturnal hylid with a snout-vent-length of 28-165 mm (MESHAKA 2001; VARGAS-SALINAS 2006). In addition to Cuba, the natural distribution of *O. septentrionalis* includes the Bahamas, Isla de la Juventud, San Salvador, the Acklins Islands and the Cayman Islands (DUELLMAN and CROMBIE 1970; MESHAKA 2001). During recent decades, this hylid has been introduced to Anguilla (TOWNSEND 2000), the Bahamas (FRANZ et al. 1993), the British Virgin Islands (MASHAKA 2001; OWEN et al. 2005; 2006), Curaçao (VAN BUURT 2007), Florida (SCHWARZ 1952), the French Antilleans (BREUIL and IBÉNÉ 2008), Puerto Rico (SCHWARTZ and HENDERSON 1991), and the Virgin Islands (MESHAKA 2001) where it has become invasive. A population introduced to Hawaii has reportedly been extinguished (BANKS et al. 2004).

The first reports of the Cuban treefrog occurring in the United States came from Key West in 1931, although the species was likely already established well before it was reported (JOHNSON 2007). Introduction was most likely accidental, maybe as undetected stowaways in import vegetables from Cuba (BEHLER 1979; MESHAKA 1996). By the early 1950s, *O. septentrionalis* was present in most of the Keys, and by 1952 the first specimens were detected in Miami (SCHWARTZ 1952). During subsequent years, northward range expansion continued. Feral populations of the species were detected in Broward County by 1960, and in St. Lucie and Indian River counties less than 20 years later (KING 1960; MYERS 1977). Range expansion continued on the Gulf coast of Florida such that the species reached Naples about 1970 and Fort Meyers and Sanibel Island by the early 1980s (DUELLMAN and CROMBIE 1970; WILSON and PORRAS 1983). Established populations have existed in Marion County since at least 2002 (Florida Museum of Natural History, Herpetology Collection, voucher No. 145041) and in 2003 specimens were collected in Duval County (Florida Museum of Natural History, Herpetology Collection, voucher No. 133206, 137173). Today, Cuban treefrogs are found throughout peninsular Florida, with breeding populations found as far north as Jacksonville on the east coast and Cedar Key on the Gulf Coast (JOHNSON 2007; MCGARRITY and JOHNSON 2008). Some scattered individuals have been reported in the Florida panhandle and also from coastal Georgia and South Carolina, but these do not represent breeding populations (JOHNSON 2007; MCGARRITY and JOHNSON 2008). Further unintended introductions of *O. septentrionalis* to new locations appear to be most likely still facilitated through the transportation of individuals hidden in shipping crates or on potted plants and transplanted shrubs (BEHLER 1979; JOHNSON 2007).

Important natural history properties accounting for the high invasiveness of *O. septentrionalis* include its high fecundity, short larval period, broad diet, and broad habitat and dietary niches (MESHAKA 2001; VARGAS-SALINAS 2006). Females are continuously fertile, laying very large clutches of 1,200 to over 16,000 eggs in any warm, shallow bodies of water lacking predators such as fish (MESHAKA 2001). In its native range, reproduction takes place year round (MESHAKA 2001); its spawning season is more restricted in its invasive range in Florida (May through October; BEHLER 1979).

Cuban treefrogs can have major impacts on native species. It is the biggest hylid in the USA and is larger than other anuran species on Caribbean Islands (with exception of the Cane toad *Rhinella marina*; e.g. SMITH 2005), which might confer competitive advantage. For example, in Florida the gecko *Hemidactylus mabouia* is the only competitor of adult Cuban treefrogs (MASHEKA 2001). SMITH (2005) showed that Cuban treefrog tadpoles compete with indigenous anuran larvae in Florida and have a negative impact on their growth and development. Furthermore, tadpoles of *O. septentrionalis* are omnivorous, cannibalistic, and could potentially eat the eggs of indigenous frogs (MESHAKA 2001). Because of its large size and its broad trophic niche, *O. septentrionalis* can have a strong impact on ecosystems since it can consume huge amounts of small arthropods and vertebrates including even lizards and other frogs (CARMICHAEL and WILLIAMS 1991; CONANT and COLLINS 1991; WYATT and FORYS 2004).

Successful establishment of a non-indigenous species into an ecosystem depends on the presence of competitors and predators, food availability, and human footprint (EHRLICH 1989; WILLIAMSON 1996). Additionally, the climatic similarity of the novel ecosystem compared to the source ecosystem is an important issue (BOMFORD et al. 2008), and therefore anthropogenic climate change is expected to affect range-size patterns of invasive species (e.g. HELLMANN et al. 2008). Here, GIS-based Climate Envelope Models (CEMs) can provide an easy-to-use method to assess the potential distribution of species derived from their climatic niches (‘climate envelope’). In recent times, there have been several examples using CEMs to assess potential distributions of species under past, present and future climate scenarios (e.g. PETERSON 2001; PETERSON and VIEGLAIS 2001; CARNAVAL and MORITZ 2008; RÖDDER et al. 2008). CEMs can be helpful for the identification of climatically suitable areas and have been widely applied to the prediction of the invasive potential of non-native species (e.g. PETERSON and VIEGLAIS 2001; GIOVANELLI et al. 2007; JESCHKE and STRAYER 2008; RÖDDER et al. 2008, RÖDDER 2009). Such approaches rely on the assumption that climatic tolerances of species shape major parts of their current distributions and that specific climatic niches are conservative, at least within an evolutionary short time frame of some hundreds to thousands years (e.g. WIENS and GRAHAM 2005; but see also PEARMAN et al. 2007). Herein, we aim to assess (i) the potential distribution under current climate conditions in order to identify regions with high potential for invasions within the Caribbean and (ii) possible changes in the potential distribution of *O. septentrionalis* due to anthropogenic global warming.

Material and Methods

Species records

In total, 6,665 records of *O. septentrionalis* were available through the Global Biodiversity Information Facility (GBIF; www.gbif.org) and HerpNet databases (www.herpnet.org). Of these, 72 records were situated within unique grid cells in its native range and used for model building. In addition, 68 records of invasive populations were obtained from the US Geological Survey data base (www.nas.er.usgs.gov) and the IUCN Invasive Species Specialist Group (www.issg.org). For georeferencing, Alexandria Digital Library Gazetteer Server Client (www.middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp) was used. The accuracy of coordinates processed was assessed with DIVA-GIS (HIJMANS et al. 1999; 2001).

Climate data

Information on current climate was obtained from the Worldclim database, version 1.4, which is based on weather conditions recorded between 1950 and 2000 with grid cell resolution of 30 arc seconds (HIJMANS et al. 2005; http://www.worldclim.org). It was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995, 2004). For future climate scenarios, we used climate change projections based on the CCCMA, CSIRO and HADCM3 models (FLATO et al. 2000; GORDON et al. 2000) and the emission scenarios reported in the Special Report on Emissions Scenarios (SRES) by the Intergovernmental Panel on Climate Change; IPCC (http://www.grida.no/climate/ipcc/emission/). A set of different families of emission scenarios was formulated based on future production of greenhouse gases and aerosol precursor emissions. The SRES scenarios of A2a and B2a were used in this study. Each scenario described one possible demographic, politico-economic, social and technological future as expected for 2020, 2050 and 2080. Scenario B2a emphasizes more environmentally conscious, more regionalized solutions to economic, social and environmental sustainability. Compared to B2a, scenario A2a also emphasizes regionalized solutions to economic and social development, but it is less environmentally conscious.

For model computation we selected the ‘annual mean temperature’, ‘mean maximum temperature of the warmest quarter’, ‘mean minimum temperature of the coldest quarter’, ‘annual precipitation’, ‘mean precipitation of wettest quarter’, and ‘mean precipitation of the driest quarter’ as variables representing a set of parameters, which describe the availability of water and energy. In order to compare bioclimatic conditions between native and invasive records, the cumulative frequency of bioclimatic parameters was plotted with DIVA-GIS.

Computation of Climate Envelope Models

In this study MaxEnt 3.2.1 (PHILLIPS et al. 2004; 2006; http://www.cs.princeton.edu/~shapire/maxent) was used for CEM computation in order to assess the potential distribution of the Cuban treefrog. MaxEnt is a machine-learning algorithm following the principles of maximum entropy (JAYNES 1957). It has been shown to produce more reliable results than other comparable methods such as BIOCLIM, DOMAIN or GARP (e.g. ELITH et al. 2006; WISZ et al. 2008). The reliability of the results obtained from MaxEnt models has been confirmed by its good capacity to predict novel presence localities fo less well known species (PEARSON et al. 2007) and the outcome of introductions of invasive species outside the native range (FICETOLA et al. 2007; RÖDDER et al. 2008; RÖDDER 2009). Herein, 10, 000 random background points were automatically selected by MaxEnt within a minimum convex polygon covering and including the native records. The logistic output format with suitability values ranging from 0 (unsuitable) to 1 (optimal) (PHILLIPS and DUDÍK 2008) was used.

Maxent allows for model testing by calculation of the Area Under the Curve (AUC), referring to the Receiver Operation Characteristic (ROC) curve using either the invasive records as test points and the native records for training (AUC_{test}) or all native records for training and background points for testing ($AUC_{training}$) (HANLEY and MCNEIL 1982; PHILLIPS et al. 2006). This method is recommended for ecological applications because it is non-parametric (PEARCE and FERRIER 2000). Values of AUC range from 0.5 (i.e. random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of SWETS (1988), AUC values > 0.9 describe ‘very good’, > 0.8 ‘good’ and > 0.7 ‘useful’ discrimination ability. We acknowledge that there is currently some discussion about the suitability of this method (LOBO et al. 2008) but, in the absence of a more useful method and because AUC has been and is still widely used (e.g. ELITH et al. 2006; PHILLIPS et al. 2006; JESCHKE and STRAYER 2008; WISZ et al. 2008), we have continued to use it here.

Results

We received ‘very good’ AUC values in the model ($AUC_{training}$ = 0.959; AUC_{test} =0.914). Analysis of variable contributions in the model revealed that the ‘mean minimum temperature of the warmest quarter’ had, with 42.1%, the highest explanatory power followed by ‘mean precipitation of the wettest quarter’ (21.4%), ‘mean temperature of the coldest quarter’ (15.2%), ‘annual mean temperature’ (13.7%), ‘mean precipitation of the driest quarter (6.5%) and ‘annual mean precipitation’ (1.2%). Climatic conditions observed at the invasive records are mainly coincidental with the conditions at the native records, with exception of the ‘mean temperature of the coldest quarter’ which is lower at some northern records in the invasive range (Figure 3.3-1).

Under current climatic conditions, *O. septentrionalis* could find suitable areas in most of the coastal regions adjacent to its native range around the Gulf of Mexico and in the Caribbean Islands (Figure 3.3-2). On the American mainland, the borderland between the United States and Mexico, and the Yucatan Peninsula, are at especially high risk of invasion. Most islands of the Bahamas are colonized by this big hylid and the remaining islands which are not colonized at present show good climatic conditions for the survival of this species. In Florida, *O. septentrionalis* covers the whole climatically-suitable area already. Here, the known invasive range of *O. septentrionalis* is highly coincidental within suitable areas predicted by our model, additionally confirming its predictive power (Figure 3.3-3).

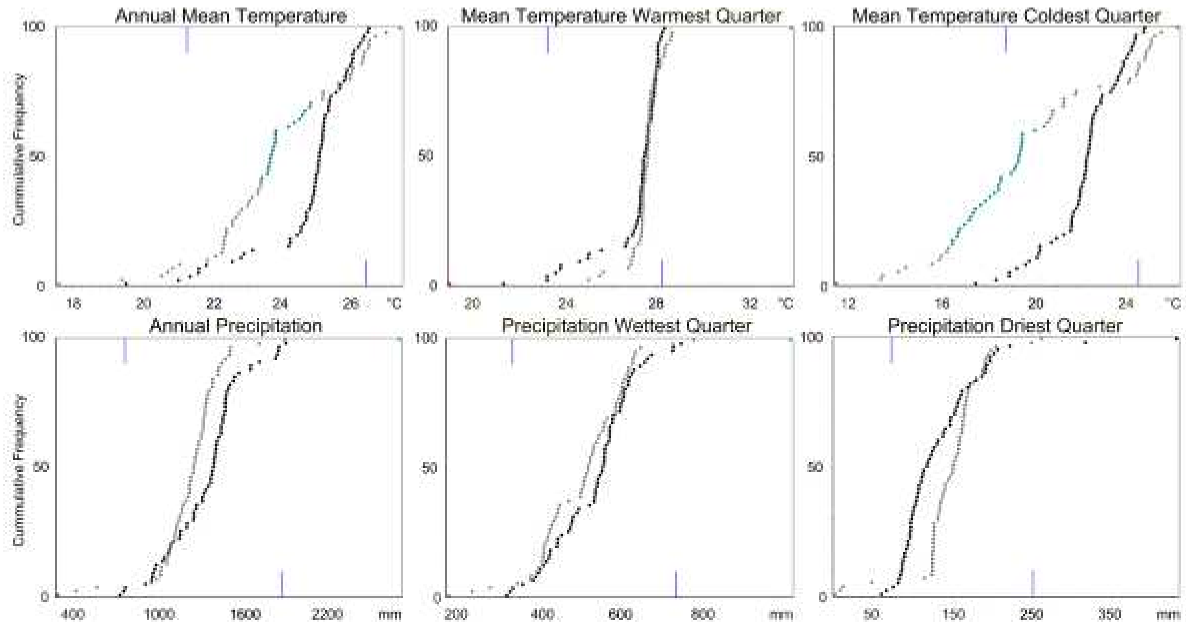

Figure 3.3-1 Comparison of climatic conditions at native and invasive records of *Osteopilus septentrionalis*. Native records used for model building are indicated in black, invasive records in grey.

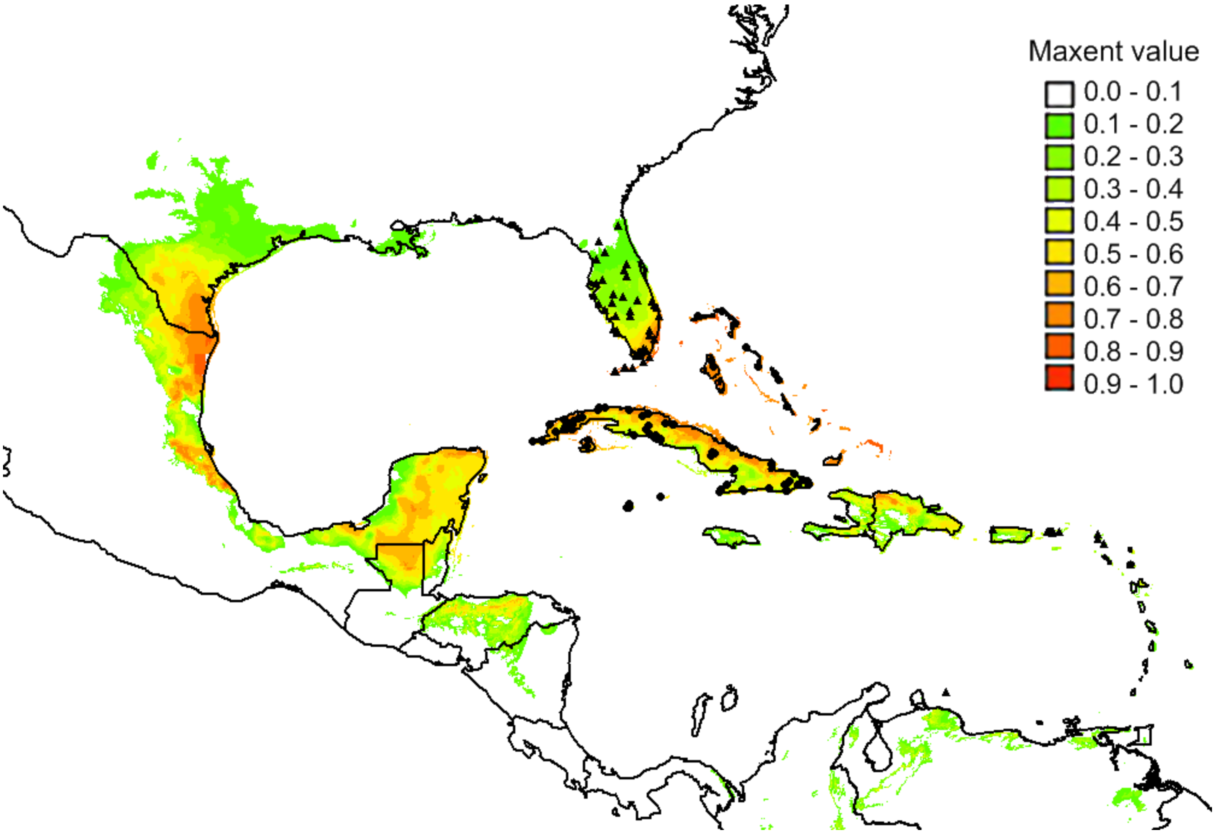

Figure 3.3-2 Potential distribution of *O. septentrionalis* under current climate conditions within the Caribbean. Higher MaxEnt values suggest higher climatic suitability. Native records are indicated as points and invasive records as triangles.

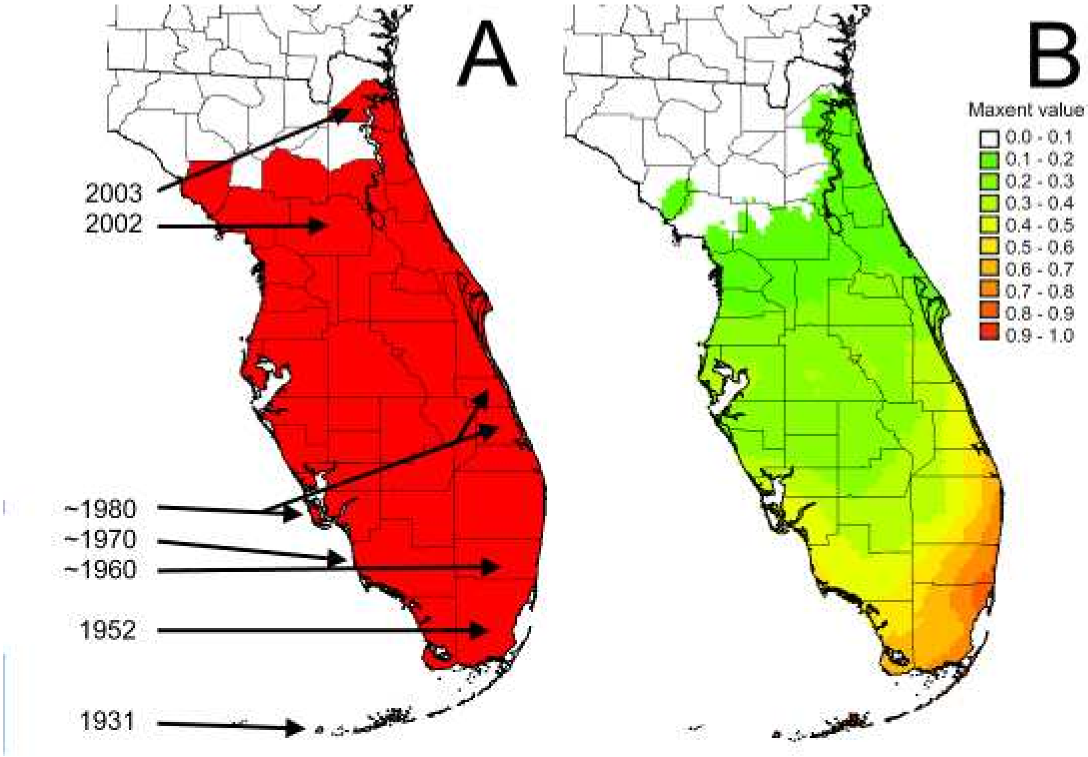

Figure 3.3-3 Comparison between the known distribution of *O. septentrionalis* (A; Source: JOHNSON 2007; MCGARRITY and JOHNSON 2008) and model prediction for Florida (B). Spread history of *O. septentrionalis* is indicated.

Projections of the CEM of *O. septentrionalis* onto the future climate change scenarios indicate that climatically-suitable areas may become more widespread overall (Figure 3.3-4). These areas include the whole Atlantic coastline from the Mexican border to North Carolina, which may connect suitable areas with today's potential distribution. In contrast the climatic suitability in its native range, as well as on the Yucatan Peninsula, will decrease. Only minor differences were observed in model projections onto climate change scenarios derived from CCCMA, CSIRO and HADCM3 scenarios, therefore only mean values are presented. Between the A2a and B2a prediction families, a greater extension of the potential distribution in family A2a compared with B2a was suggested by our models.

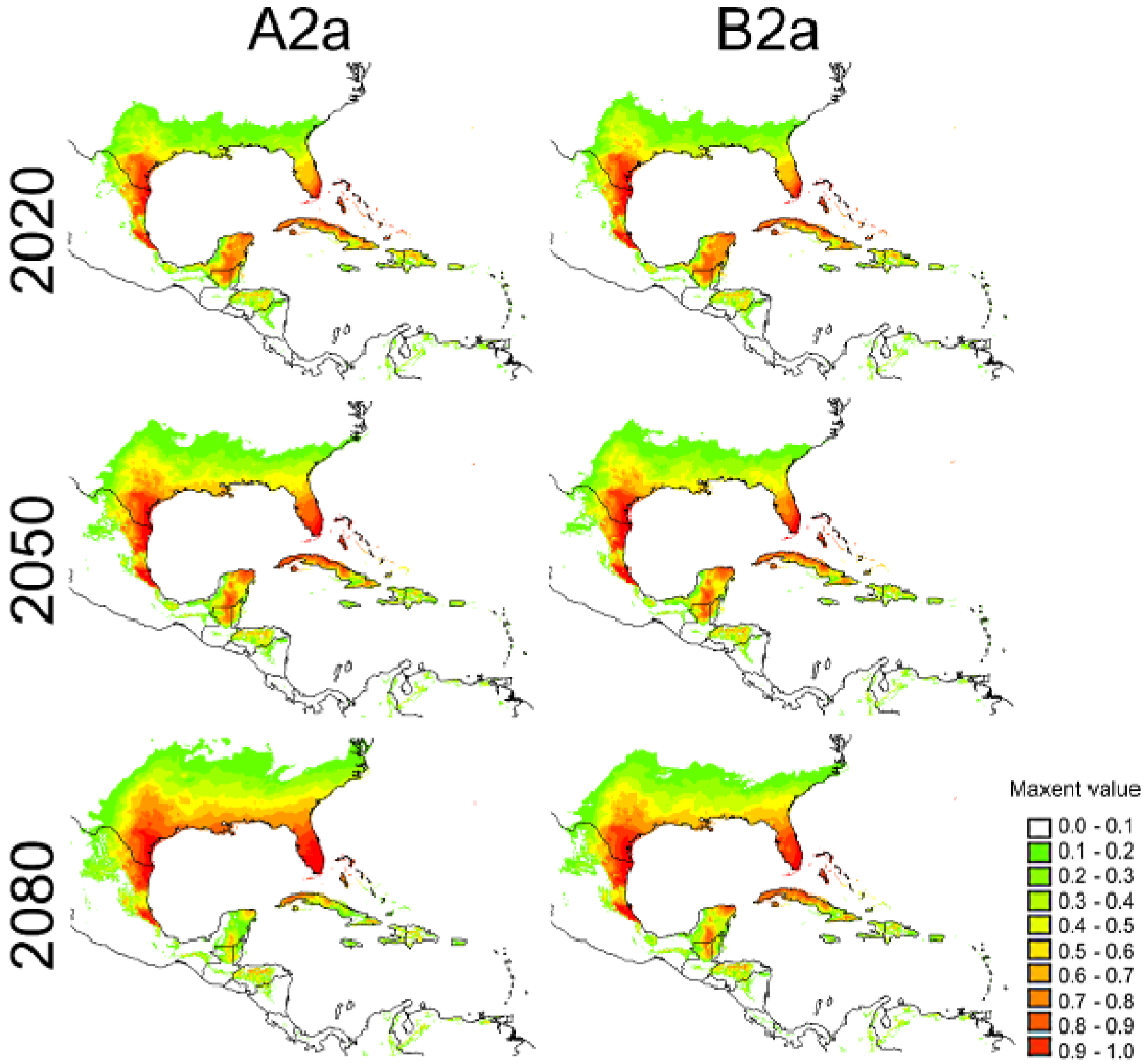

Figure 3.3-4 Maps of the potential distribution of *O. septentrionalis* as expected for 2020, 2050 and 2080 assuming A2a and B2a conditions. Maps show mean values of MaxEnt values derived from models projected onto CCCMA, CISRO and HADCM3 scenarios.

Discussion

Our climate envelope modeling approach suggests that *O. septentrionalis* may find climatically suitable regions all over the Caribbean and the countries adjacent to the Gulf of Mexico. In Florida, our model accurately depictes its current invasive range with decreasing climatic suitability with increasing degrees in north latitude. Recently, McGarrity and Johnson (2008) detected a significant gradient in sexual size dimorphism decreasing with increasing degrees north latitude paralleling our results. This gradient is largely driven by a pronounced decrease in female mean snout to vent length

(McGarrity and Johnson 2008). The authors argued that this gradient may be traced back to reduced growth rates, increased time to maturity and reduced life expectancy whereby all of these possible explanations may be closely tied to climatic variation. Furthermore, they suggested that the decreasing female mean size toward the northernmost extent of the current non-indigenous range may be associated with diminished impacts and invasive success.

Comparison between climatic conditions at the native and invasive records revealed that they are roughly similar with the exception that ‘mean temperature of the coldest quarter’ is lower than the observed minimum of the native records (Figure 3.3-1). This may indicate that temperature limits as present it its native range might not reflect the total range of the physiological tolerance of *O. septentrionalis*, which may be reached in its northern limit of its invasive range as suggested by McGarrity and Johnson (2008). On the other hand *O. septentrionalis* might be able to endure cold snaps in microclimatically-suitable places (e.g. inside houses or old roof trusses) - at least within short time frames. This appears to be reasonable since it is well known that Cuban treefrogs frequently utilize man-made structures (Meshaka 2001).

Our projections onto anthropogenic climate-change scenarios indicate a possible extension of the current potential distribution of the Cuban treefrog in Northern America. However, successful colonization of newly arising suitable areas may depend on the propagation speed of *O. septentrionalis*. Time series suggest that the frog was able to expand its range at about 10 km y^{-1} in Florida (e.g., Key West-Miami, ~250 km / 21 y; Miami-Indian River Country, ~250 km/ 28 y; Miami-Duval Country: 570 km / 51 y) and, assuming this spread rate, it could reach Louisiana and Virginia within the next 80 years. Assuming that *O. septentrionalis* might be able to increase its invasive range as suggested by the models, it might compete with native species such as *Hyla cinerea*, *H. squirella* and *H. femoralis* within much larger proportions of their ranges than today, increasing its negative effects as reported by Wyatt and Forys (2004).

Next to its natural propagation rate, human facilitated propagation is an important factor, e.g. national (and international) plant trade. Here the species can be displaced uncontrollably and may reach remote areas rapidly (Meshaka 2001; Owen et al. 2005; 2006). Therefore, means of control have to focus on prevention to avoid a further spreading through human activities, campaigns to sensitize the urban population to this ecological threat as well as strict regulation of the plant trade. The selection and prospect of success of eradication and containment measures may depend on the stability and demographic structure of the target population. It should therefore be guided by a thorough assessment of the relationships between population density and intraspecific competition (e.g. GOVINDARAJULU et al. 2005). Unsuitable eradication methods may even increase population densities, e.g. as shown by American bullfrogs (*Rana catesbeiana*) by GOVINDARAJULU et al. (2005). The authors demonstrated that control efforts for bullfrogs by removing tadpoles and breeding adults may not be optimal, since (1) partial removal of tadpoles may lead to higher tadpole survival and development rates and higher postmetamorphic survival due to decreased density-dependent competition and (2) removal of adults may lead to higher survival of early metamorphic stages through reduced cannibalism. For American bullfrogs, culling of metamorphs in fall may be the most effective method of decreasing bullfrog population growth rate (Govindarajulu et al. 2005). However, a similar assessment for the Cuban treefrog is currently lacking.

In addition, regional differences in population structure and fitness may require different regulation or eradication approaches. At the edge of the potential distribution, populations of Cuban treefrogs are expected to be more vulnerable to eradication methods; here more sustainable methods can be applied. This may include culling of metamorphs, collecting adult frogs or removal of clutches by hand as well as attempts to avoid creating unintended breeding sites (e.g. open rain barrels). Increased climatic suitability may be accompanied by increased survival rates, fecundity and numbers of generations per year making more aggressive control strategies necessary, e.g. establishing fish at breeding sites or application of chemical agents. However, selection of appropriate methods guided by an assessment of relationships between population densities and regulating mechanisms such as intraspecific competition or predation may improve their efficiency.

Acknowledgements

We are grateful to LOUISE ALLCOCK and two anonymous reviewers for suggestions and improvements of the manuscript. The work of DR was funded by the “Graduiertenförderung des Landes Nordrhein-Westfalen”.

3.4. Potential distribution of the alien invasive Brown tree snake, *Boiga irregularis* (Reptilia: Colubridae)[8]

©David Fischer

Boiga irregularis

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[8] This part is accepted for publication in *Pacific Science* 64(1).

The work reported in this chapter was conducted in collaboration with STEFAN LÖTTERS from the Faculty of Geosciences, University of Trier, Germany.

Introduction

Alien invasive species are a concern in nature conservation as they may have negative impact on native biodiversity and can have major socioeconomic impacts. A remarkable example is the Brown tree snake, *Boiga irregularis* MERREM, 1802 (SAVIDGE 1987; RODDA and FRITTS 1992; FRITTS and RODDA 1998; WILES et al. 2003). This venomous, 1-3 m long arboreal colubrid snake is native to Papua New Guinea, the Solomon Islands and the northern and eastern coasts of Australia (Figure 3.4-1, RODDA et al. 1999). Its status in Sulawesi (Indonesia) is uncertain. RODDA et al. (1999) listed populations from Sulawesi as ‘native’, while ISKANDAR and TJAN (1996) suggested that *B. irregularis* may have reached the island only via trade. Ecologically, this snake can be regarded a ‘generalist’ concerning habitat requirements and prey selectivity. *Boiga irregularis* is known from natural forest and grass land as well as agricultural and urban areas and does not show particular food preferences (RODDA et al. 1999).

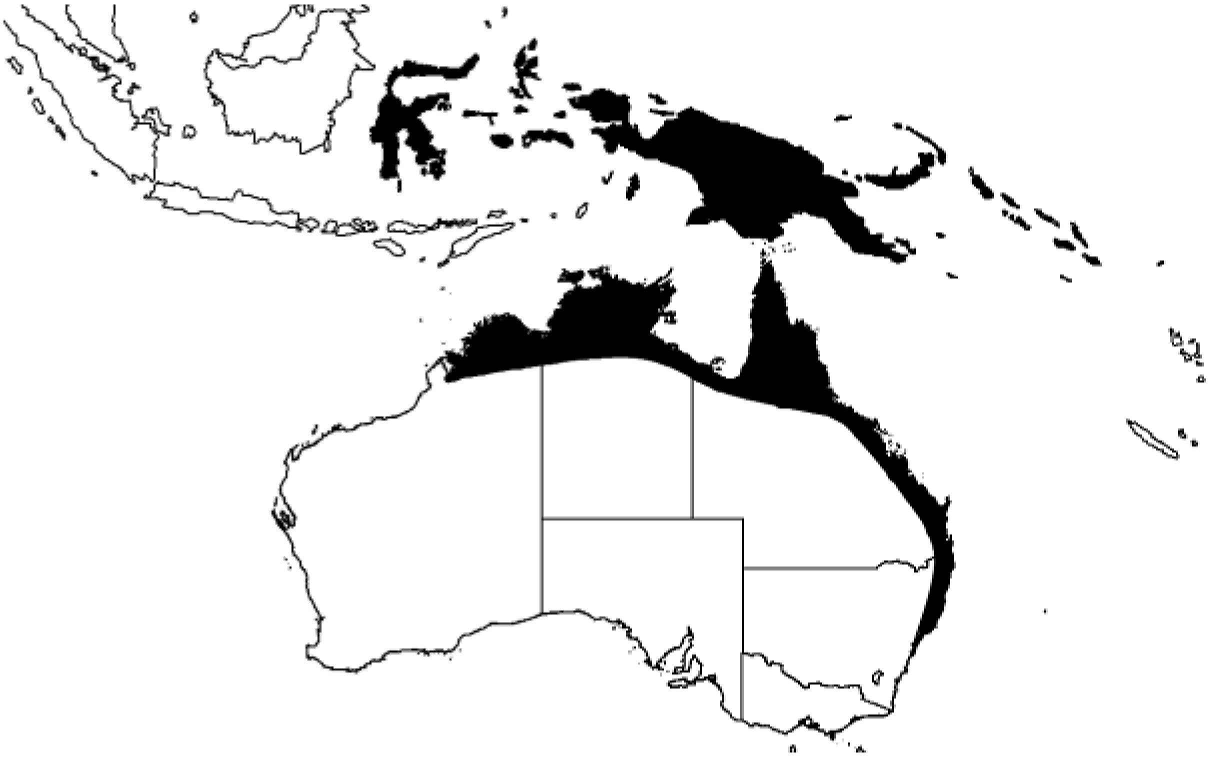

Figure 3.4-1 Native distribution of *B. irregularis*. Source: RODDA 1999.

The Brown tree snake has been accidentally brought to several islands in the Pacific shortly after World War II where it successfully established local populations due to obviously un-occupied niches and plenty of naïve prey (RODDA et al. 1992). As a result, *B.*

irregularis today is listed among the 100 worldwide worst alien invasive species (LOWE et al. 2000). The most devastating consequences of its introduction are known from Guam where it has led to decimation of vertebrate species including flying foxes, several small terrestrial mammals and lizards as well as the extinction of eight out of 11 endemic bird species in the 1980s (SAVIDGE 1987; WILES et al. 2003). It is suggested that here *B. irregularis* has significantly altered food web structures enhancing its effect on native biota and explaining its extraordinarily devastating effect (D'ANTONIO and DUDLEY 1995; FRITTS and RODDA 1998). One of the major means of spread of *B. irregularis* is as a stowaway in military equipment and cargo (FRITTS 1987; KRAUS 2007). Currently, anthropogenic dispersal is more associated with large-scale exercises and personal cargo of people moving from Guam to other duty posts. Also sea freight (container/bulk) may play a role in dispersal (KRAUS 2007) and several tree snakes translocated by aircraft cargoes have been detected at Honolulu airport in recent years (e.g. ATKINSON and ATKINSON 2000). During the last decades, the Brown tree snake has arrived to Cocos Islands, Diego Garcia, Hawaiian Islands (Honolulu, Oahu), Indonesia (Java), Japan, New Zealand, Northern Mariana Islands (Saipan, Tinian), Malaysia (Singapore), Marshall Islands (Kwajalein), Micronesian Islands (Pohnpei), Ryukyu Islands (Okinawa), Spain (Rota), Taiwan, USA (Texas, Corpus Christi) and Wake Island (MITO and UESUGI 2004; IUCN Invasive Species Specialist Group 2007, www.issg.org). Although, it apparently has so far not become residential at any of these places, this list of geographic sites and their distances from the native occurrence demonstrate the snake’s ‘efficiency’ in dispersal. A result is that this clearly demands for special concern with regard to conservation (BUDEN et al. 2001; GILL et al. 2001; KRAUS and CARVALHO 2001; RODDA et al. 2002). In the USA, incursions by *B. irregularis* have been repeatedly intercepted (MCCOID et al. 1994), but eradication of established populations are expensive and difficult (RODDA et al. 2002).

It appears to be a question of time until the Brown tree snake will establish additional invasive populations. FRITTS and RODDA (1998) studied the risk of invasion by the species using biological and natural history information. They concluded that the Mariana, Hawaiian and Caroline Islands are most at risk because a native snake fauna is absent and potential prey density is high. Invasion risk will depend next to the arrival of founder individuals over time, also on environmental conditions making areas more perfect for the ectothermic species. We see an urgent need to identify those regions in which this species finds suitable conditions for successful establishment of invasive populations. Climate Envelope Models (CEMs) are a useful tool to study potential distributions of species both under past, current and future climatic scenarios (e.g. HIJMANS and GRAHAM 2006; MALCOM et al. 2006; PETERSON and NYÁRI 2007; CARNAVAL and MORITZ 2008; RÖDDER et al. 2008; RÖDDER 2009). The scope of the present study is to assess the worldwide potential distribution of *B. irregularis* under current climatic conditions in order to identify regions with high potential for invasions.

Material and Methods

Species records and climate data

A total of 2,679 *Boiga irregularis* records were available through the Global Biodiversity Information Facility (GBIF, www.gbif.org) and HerpNet databases (www.herpnet.org). In addition, records of invasive populations were obtained from the IUCN Invasive Species Specialist Group (www.issg.org), whereby only records within areas with confirmed reproduction were included. For georeferencing, the Alexandria Digital Library Gazetteer Server Client (www.middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp) was used.

We used DIVA-GIS 5.4 (HIJMANS et al. 2001) to test the accuracy of coordinates (Check Coordinates tool) by comparing information accompanying the species records and locality data extracted from an administrative boundaries database at the smallest possible level (state/country/city). This information should be the same, and any mismatches may reflect errors (see HIJMANS et al. 1999). In addition, we used altitudinal information to spot likely errors in the coordinate data when this information was provided with the records used. Altitude was compared with the altitude of the locality in a digital elevation model, using the Extract Values by Points function of DIVA-GIS. Of the total records available, 337 were situated in unique grid cells within the species' native range, classified as being accurate and hence suitable for model building (see below).

Information on current climate was obtained from the Worldclim database, version 1.4, which is based on weather conditions recorded between 1950 and 2000 with a grid cell resolution of 2.5 minutes (HIJMANS et al. 2005, www.worldclim.org). It was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995, 2004).

Variable selection

RODDA et al. (2007) approached the climate envelope of the Brown tree snake in its native geographic range regarding annual mean monthly temperature and precipitation. They found that the amount of precipitation was a good predictor for its distribution. Such a relationship appears to be further supported by natural history observations since the seasonal activity of the Brown tree snake is limited to the warmer and wetter summer months in its Australian range (COVACBVICH and LIMPUS 1973; SHINE 1991*a*). It was also observed that the snake is unable to shed properly when the relative humidity is lower than 60 % (RODDA et al. 1999). Within the native distribution of the target species, this dependency is reflected in the geographic range in Australia where *B. irregularis* inhabits mainly humid areas close to the sea. Therefore, next to the mean annual values, minimum and maximum annual values may be important suggesting that 'annual precipitation', 'precipitation of wettest month' and 'precipitation of the driest month' are suitable predictor variables.

Temperature is a key factor influencing ectothermic species; therefore the 'annual mean temperature' is a significant variable related to energetic balances and digestive turn over rates. MATHEIS and MILLER (2002) showed that temperature seasonality is physiologically important influencing reproduction. These authors investigated the effect of two different temperature regimes for eliciting reproduction in male and female *B. irregularis*. They found that specimens maintained at 24 °C followed by a 60-day cool period at 19 °C exhibited substantial reproductive activity. Clutches were produced by females shortly after returning to 24 °C. In contrast, individuals maintained at 28 °C followed by an identical 19 °C cooling period exhibited relatively little reproductive activity and none of the females had produced eggs. Considering these effects we added the 'maximum temperature of the warmest month', 'minimum temperature of the coldest month' as predictor variables for model computation.

Climate Envelope Models

Maxent 3.2.1 (PHILLIPS et al. 2006, www.cs.princeton.edu/~shapire/maxent) was applied for CEM calculation in order to assess the potential distribution of the Brown tree snake and to map it into geographic space. MaxEnt is a grid-based machine-learning algorithm following the principles of maximum entropy (JAYNES 1957). The general concept is to find a probability distribution covering the study area that satisfies a set of constraints derived from occurrence data. Each constraint requires that the expected value of an environmental variable or a function thereof must be within a confidence interval of its empirical mean over the presence records. The program chooses the distribution that is closest to uniform and therefore maximizes entropy within all distributions that satisfy the constraints as any other choice would represent constraints on the distribution that are not justified by the data. MaxEnt is able to incorporate complex dependencies between predictor variables and has been shown to reveal better results than other comparable methods (e.g. ELITH et al. 2006; WISZ et al. 2008). The reliability of the results obtained from MaxEnt models has been confirmed by its capacity to predict novel presence localities for poorly known species (PEARSON et al. 2007) and the outcome of introductions of alien invasive species outside the native distribution (e.g. PETERSON and VIEGLAIS 2001; FICETOLA et al. 2007; JESCHKE and STRAYER 2008; RÖDDER et al. 2008; RÖDDER 2009).

Runs used herein were conducted using the default values for all program settings, whereby randomly chosen background points were restricted to an area defined by a minimum convex polygon including all native records. Herein, the logistic output format with suitability values ranging from 0 (unsuitable) to 1 (optimal) was used and areas where ‘clamping’ (i.e. nonanalogous climatic condition as present in the training area) occurred during projections were subsequently excluded (PHILLIPS and DUDÍK 2008).

Maxent allows for model testing by calculation of the Area Under the Curve (AUC), referring to the ROC (Receiver Operation Characteristic) curve; herein we assessed the ability of the model to distinguish background points from training points (HANLEY and MCNEIL 1982; PHILLIPS et al. 2006). This method is recommended for ecological applications because it is non-parametric (PEARCE and FERRIER 2000, but see LOBO et al. 2008). Values of AUC range from 0.5 (random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of SWETS (1988), AUC values > 0.9 describe ‘very good’, > 0.8 ‘good’ and > 0.7 ‘useful’ discrimination abilities. MaxEnt allows for an assessment of the relative contribution of variables included using a jackknifing approach.

Results

Current potential distribution

We received ‘very good’ AUC values in the model (AUC = 0.971), and the known invasive range of *Boiga irregularis* at Guam is situated within higher MaxEnt classes (> 0.780), also confirming the predictive power of the model. The lowest observed MaxEnt value at the presence point used for model training was 0.201. Analyses of variable contributions in the model revealed that ‘annual precipitation’ with 33.3 % has the highest explanative power, followed by ‘maximum temperature of the warmest month’ (28.5 %), ‘annual mean temperature’ (13.8 %), ‘precipitation of the driest month’ (11.7 %), ‘precipitation of the wettest month’ (7.7 %) and the ‘minimum temperature of the coldest month’ (4.9 %). The relative variable importance obtained via jackknifing from the MaxEnt model appears to be consistent with natural history observation (see above). ‘Clamping’ occurred only at very few sites such as at a very small ridge at the west coast of India. Those areas were excluded from further analyses.

Under current climatic conditions, the Brown tree snake performs a geographically wide potential distribution almost all over the Tropics and adjacent subtropical regions, especially widespread within the southern hemisphere, but also extending to Northern Armerica including Florida and coastal areas next to the Gulf of Mexico (Figure 3.4-2). Regarding the general region, in which the Brown tree snake occurs, i.e. South-East Asia and Australia, major parts of New Caledonia, New Zealand, the Fiji Islands and Vanuatu were uncovered as highly suitable to *B. irregularis* by the CEM (Figure 3.4-3). Guam, the Caroline Islands and the Northern Mariana Islands including Saipan are entirely suitable to *B. irregularis* (Figure 3.4-3, Table 3.4-1). Apart from regions in the vicinity of the species’ native geographic range in South-East Asia, its climate envelope is elsewhere mirrored in both lowland (e.g. Congo and Amazon basins) and montane (e.g. southern coastal Brazil, Ethiopian Highlands) regions. Apart from this, high suitability was found on the Hawaiian Islands (lower elevations) (Figure 3.4-4) and Madagascar (mainly east coast and higher elevations, Figure 3.4-5).

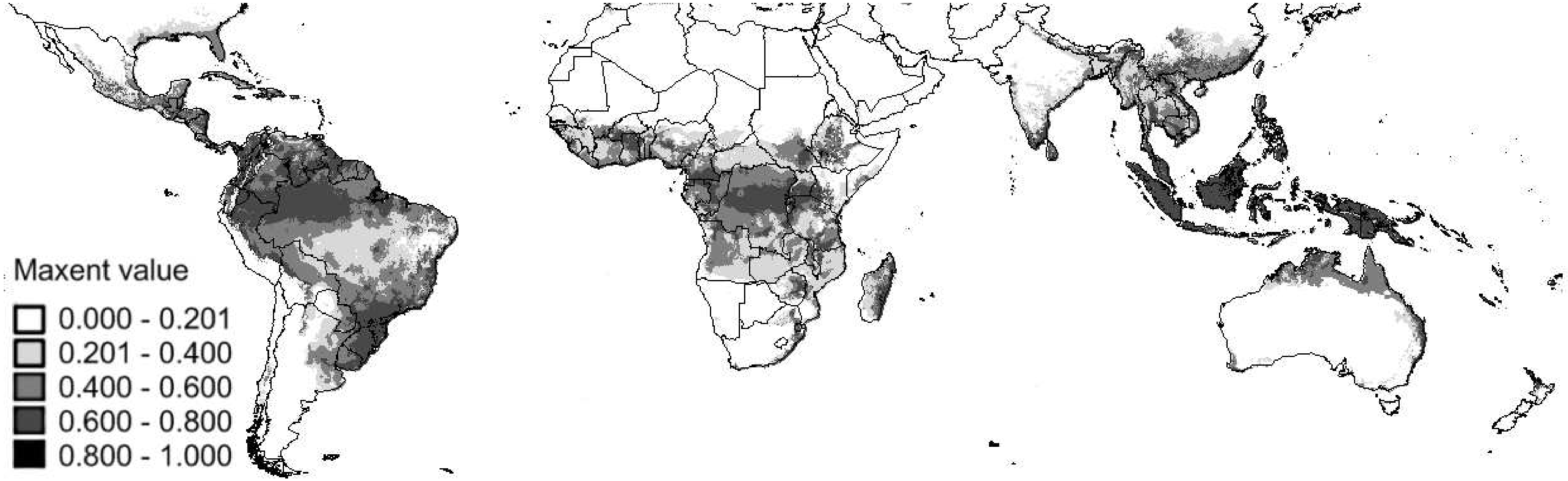

Figure. 3.4-2 Potential distribution of *Boiga irregularis* under current climate. Any area with a MaxEnt value above 0.201 may be climatically suitable for *B. irregularis*, although higher MaxEnt values suggest higher climatic suitability.

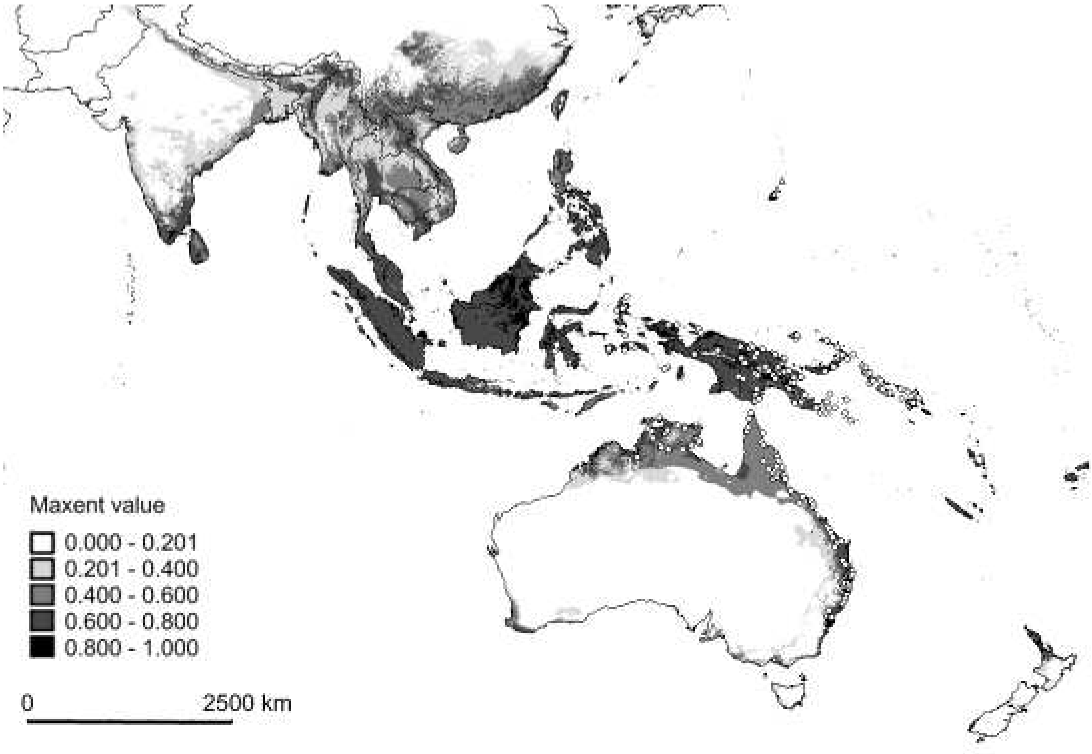

Figure 3.4-3 Potential distribution of *Boiga irregularis* under current climate within South-East Asia and Australia. Higher MaxEnt values suggest higher climatic suitability. Native records are indicated as open circles and invasive ones as triangles.

Discussion

When interpreting the results and assessing an invasion risk, it is important to evaluate possible discrepancies between the realized and fundamental climatic niche of *B. irregularis* and the relative contribution of ecological factors other than climate, which may limit the species' current distribution. Next to a species' climate envelope these are accessibility limitations and/or biotic interactions such as competition or predation (see also SOBERÓN and PETERSON 2005).

Biotic interactions and/or accessibility

Although, the modeled potential distribution in the eastern portion of the native range of *Boiga irregularis* is coincident with the realized distribution (i.e. current species records), western is not (Figure 3.4-3). Climatically, the Brown tree snake can find suitable areas on Borneo, Java and Sumatra west of the Wallace line, but none of these islands has been successfully invaded, as far known (RODDA et al. 1999; IUCN Invasive Species

Specialist Group 2007, www.issg.org). Possible explanations could be a non equilibrium of the actual range with climate due to limited accessibility or ongoing spreading, limited prey availability or the presence of predators or competitors (e.g. ARAÚJO and PEARSON 2005; RODDA et al. 1999; RÖDDER et al. 2008).

Accessibility highly influences the number of jurisdictions where a species is introduced, which is a significant predictor of the probability a species can establish invasive populations (BOMFORD et al. 2008). Limited accessibility appears to be an unlikely explanation for the absence of *B. irregularis* west of the Wallace line. Although faunal exchange between the westernmost populations in Sulawesi and New Guinea and adjacent Indonesian islands in geological times was rather restricted (e.g. INGER and VORIS 2001), cargo traffic within Indonesia and adjacent islands increased during the last century and is generally high today (ESPADA and KUMAZAWA 2005). Therefore, the chance for accidentally introduced specimens is expected to be high considering that cargo is one of the major spread ways (KRAUS 2007).

In the case of the Brown tree snake, presence of competitors perhaps explains best the observed pattern. SHINE (1991*a*, *b*) suggested that colubrid snakes such as *B. irregularis* are not in significant competition with the endemic elapid snakes and pythons in Australia because they have invaded the continent with ecological specializations that are rare amongst the endemics. Especially differences in foraging habitats and in the preferred prey spectrum in comparison to the endemic Australian snakes may have enhanced their success (SHINE 1991*b*). This might not be true for the snake fauna west of the Wallace line. The genus *Boiga* currently comprises 34 species and 11 of them inhabit allopatric ranges adjacent to the native range of *B. irregulatis* (*B. angulata*, *B. bengkuluensis*, *B. cynodon*, *B. dendrophila*, *B. drapiezii*, *B. jaspidea*, *B. multimaculata*, *B. nigriceps*, *B. philippina*, *B. schultzei*, *B. tanahjampeana*, UETZ et al. 2007), but none of them is known to be invasive (www.issg.org). It is remarkable that although other snakes occur in sympatry with the Brown tree snake, other *Boiga* species do commonly not. Only at Sulawesi *B. dendrophila* and *B. multomaculata* occur together with the Brown tree snake, but here *B. irregularis* was only reported from the immediate neighborhood of sea ports where it might have been introduced (ISKANDAR and TJAN 1996). It is unclear if actually at Sulawesi inland populations do exist or not (INGER and VORIS 2001).

Interestingly, the Brown tree snake is the only member of the genus known to have established invasive populations. Differences in behavioral traits, which might provide superior abilities to establish invasive populations, are not known. For us, the most likely explanation is that the native range of Brown tree snake is much closer to areas lacking a native terrestrial snake fauna enhancing the chance of translocation.

Climate

MATHIES and MILLER (2002) showed that a period of cool temperatures elicits reproductive activity in both sexes. The authors pointed out that temperatures experienced during the artificial hibernation were much lower than the snakes would experience on Guam, where temperature seasonality is relatively invariant throughout the year (± 1 °C, RODDA et al. 1999). Comparing native populations in Australia and invasive populations at Guam, MOORE et al. (2005) found that snake specimens from Guam exhibited significantly reduced body conditions compared to individuals from Australia. The authors suggested that Brown tree snakes on Guam were living under stressful conditions, possibly due to overcrowding and overexploitation of food resources, resulting in decreased adult size/weight and suppressed reproduction. The findings of MATHIES and MILLER (2002) might provide an additional explanation for their finding since environmental stress may cause absence of hibernation and disturbed seasonal reproductive cycles. However, although reproductive activity at Guam may be suppressed and desynchronized reproductive activity, only minor enhanced fluctuations in temperature throughout the year may be sufficient to elicit reproduction; therefore fluctuations and / or extreme weather events due to anthropogenic climate change might enhance the snake problem. Furthermore, the observation that a moderate hibernation enhances the reproductive cycle allows the hypothesis that *Boiga irregularis* may find climatically suitable habitats also in more temperate regions with a higher degree of seasonality, such as the northern parts of New Zealand, Japan or Taiwan. Generally, climatic similarities of a novel environment compared to the native range enhance the probability of successful establishment of alien invasive species (BOMFORD et al. 2008).

Which regions are at high risk of invasion by the Brown tree snake?

FRITTS and RODDA (1998) studied the risk of invasion by the Brown tree snake using biological and natural history information. They concluded that the Northern Mariana, Hawaiian and Caroline Islands are most at risk because a native (competing) snake fauna is absent and prey is available. Since the Mariana and Caroline Islands are comparable in terms of faunal composition to Guam, an invasion in these islands may have similarly dramatic ecological consequences. The faunal composition of the Hawaiian Islands might also generally support the establishment of *Boiga irregularis* (KRAUS and CARVALHO 2001). However, predictions based on natural history and biological information appears to bear a higher degree of uncertainty here, because the faunal composition of the Hawaiian Islands is distinctly different from that found at Guam (FRITTS and RODDA 1998).

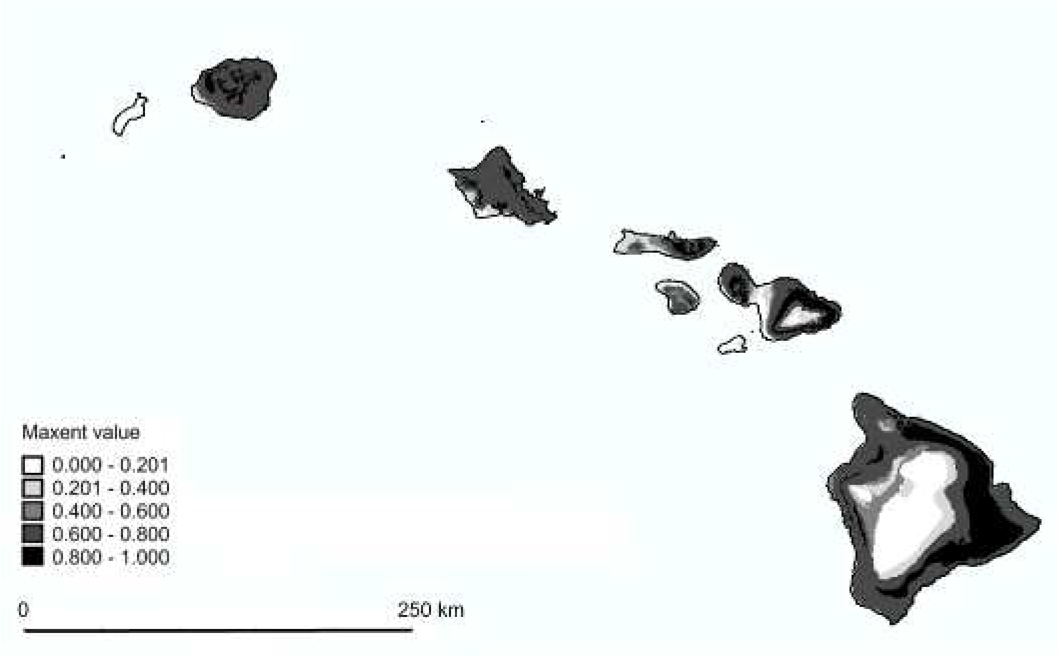

Figure 3.4-4 Potential distribution of *Boiga irregularis* under current climate on the Hawaiian Islands. Higher MaxEnt values suggest higher climatic suitability.

CEM predictions obtained in this paper confirm the expected climatic suitability of the Northern Mariana, Hawaiian and Caroline Islands. Additionally, our models highlight major parts of Central Africa, Central and Southern America and a broad swath of the southeastern US coastal plain (coincident with the prediction presented by RODDA et al. (2007)) New Caledonia, New Zealand and Madagascar as having high climatic suitability to *B. irregularis.* Records of Brown tree snakes which were accidentally imported to Hawaii and New Zealand do already exist (GILL et al. 2001, IUCN Invasive Species Specialist Group 2007, www.issg.org) and it may be feared that the Brown tree snake will establish here. Impacts may be enhanced due high availability of prey affecting population dynamics of the invader. Establishment of *B. irregularis* in New Zealand, in addition, may be facilitated due to the absence of competitors, since exclusively sea snakes occur there (Hydrophiidae). Similarly, for New Caledonia and the Fiji Islands only 19 and seven snake species are known respectively (UETZ et al. 2007). Sixteen of the New Caledonian species again are hydrophiids, two are fossorial thyphlopida while *Candoia bibroni* (Boidae) could be a potential competitor to the Brown tree snake. At Fiji, there are each three hydrophiids and thyphlopids plus *Candoia bibroni*.

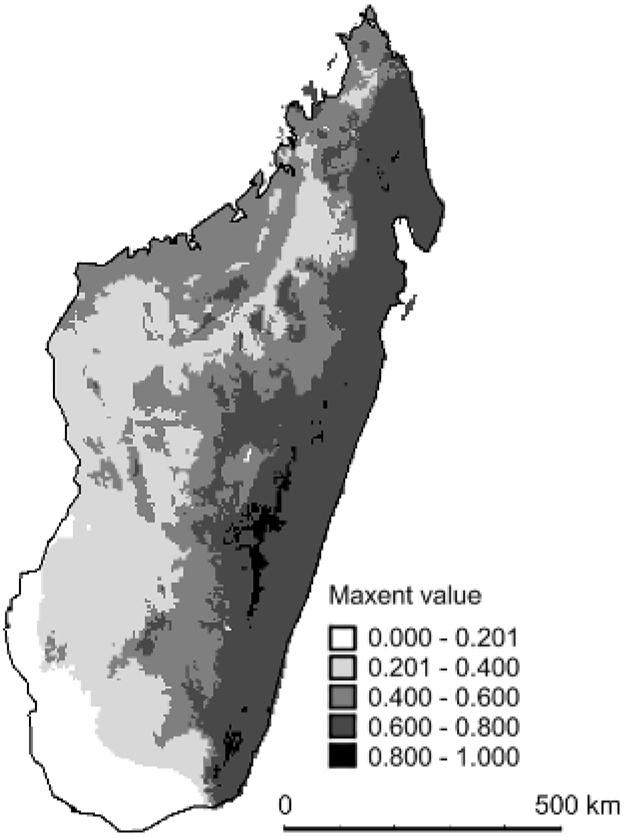

Figure 3.4-5 Potential distribution of *Boiga irregularis* under current climate conditions in Madagascar. Higher MaxEnt values suggest higher climatic suitability.

It needs to be noted that possible discrepancies between the realized climatic niche (= climatic conditions within realized distribution) and the fundamental climatic niche of *B. irregularis* may lead to an underestimation of threat in some regions. Unfortunately, the relationship between realized and fundamental niche can only be addressed experimentally but not with CEM approaches leaving some degree of uncertainty. However, interestingly the potential distribution of *B. irregularis* derived from our model is remarkably coincident with the realized distributions of all other members of the genus *Boiga*, implying that climatic niches are rather conservative within the genus - at least regarding the variables chosen herein - and that we captured a great part of its fundamental niche with our model. However, areas outside the potential distribution proposed may exhibit different climatic conditions as present within the realized distribution of *B. irregularis*, but they may not necessarily be unsuitable.

Conclusions

We conclude that the *Boiga irregularis* is a species causing a high extinction risk to endemic faunas in regions where specimens are frequently translocated via military shipment and cargo (FRITTS 1987; KRAUS 2007; BOMFORD et al. 2008) and which at the same time are suitable under current climate and lack competitors, namely the Northern Mariana and Hawaiian Islands, New Caledonia and Fiji Islands. Climatically suitable regions harboring minimal or lacking native snake species are likely to be most impacted. Here, availability of resources may be enhanced compared to an ecosystem already harboring competing snakes.

Under future anthropogenic climate change, the situation will not change essentially but climatic suitability for *B. irregularis* will generally remain high in Madagascar and New Caledonia and even increase in New Zealand (D. RÖDDER, unpublished data). Possible spread routes to Madagascar, New Caledonia and Fiji Islands include sea cargo, military equipment (FRITTS 1987; KRAUS 2007) and also accidentally translocations via aircraft cargoes (ATKINSON and ATKINSON 2000). Preventing further spread to the areas highlighted may depend on maintaining very strict cargo checks of boats and searches at airports.

Acknowledgements

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3.5. Human Footprint, facilitated jump dispersal, and the potential distribution of the invasive *Eleutherodactylus johnstonei* Barbour 1914 (Anura: Eleutherodactylidae)[9]

Eleutherodactylus johnstonei

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[9] This part was submitted to *Tropical Zoology*.

Introduction

Alien invasive species are a concern in nature conservation as they may have a broad range of negative impacts. These can comprise various aspects such as extinction of species, biotic homogenization, alteration of community structure, disruption of food-webs, losses to agriculture, damage to human structures, disease epidemics and degradation of human quality of life (KRAUS 2008), respectively. *Eleutherodactylus johnstonei* is a small (17-35 mm), dull-coloured, nocturnal frog, most likely native to the Lesser Antilles (Antigua, Barbuda, Nevis, Monserrat, Saba, St. Martin, St. Eustatius, St. Kitts, St. Lucia, St. Vincent; LEVER 2003). The geographic distribution of *E. johnstonei* has been continuously expanding during the last centuries (KAISER 1992; KAISER & WAGENSEIL 1995). Its exact origin, however, remains unclear although many hypotheses have been formulated (e.g. KAISER 1997). As a highly adaptive species, the frog has established invasive populations in several Caribbean islands including Aruba, Barbados, Bonaire, Curaçao, Jamaica (HARDY and HARRIS 1979; KAISER 1997; LEVER 2003; BUURT 2006) and Bermuda, as well at the Central and South American mainland (Colombia, Costa Rica, French Guiana, Guyana, Panama, Venezuela; KAISER et al. 2002; LEVER 2003). Today, it is the most widely distributed frog in the eastern Caribbean.

Eleutherodactylus johnstonei disperses by a variety of means, whereby the major ways are human facilitated jump dispersal via ornamental plant trade, transportation of roadside litter, merchandise and man made irrigation schemes (BARBOUR 1930; CHENSKY 1989; LEVER 2003). Subsequent accidental or intentional introductions by residents is indicated by its predominate presence in upscale urban areas such as private residences and areas where transportation of goods is centred (KAISER et al. 2002; BUURT 2006). The key of the success of *E. johnstonei* in establishing invasive populations may be its broad ecological versatility, tolerance of xeric conditions (POUGH et al. 1977) and independence of standing water due to direct developing eggs (KAISER et al. 2002). It is apparently more successful in occupying even heavily anthropogenic disturbed habitats than other members of the genus (STEWART 1977; STEWART and MARTIN 1980; GERMANO et al. 2003) and a highly successful colonizer once introduced (BOMFORD et al. 2009).

It was shown that *E. johnstonei* frequently outcompetes native species in disturbed habitats, but it is commonly unable to establish itself in undisturbed areas occupied by ecologically similar species (e.g. POUGH et al. 1977; KAISER and HENDERSON 1994; KAISER and WAGENSEIL 1995; KAISER 1997; KAISER et al. 2002; KRAUS 2008). For example, KAISER et al. (1994) suggested that introduced *E. johnstonei* in Grenada may have led to the decline of the native *E. euphronides* through interspecific competition. Similar interactions between *E. johnstonei* and other native species were reported from Antigua (SCHWARTZ 1967), Dominica (KAISER and HENDERSON 1994), and Jamaica (POUGH et al. 1977), respectively. Therefore, in combination with rapidly progressing habitat destruction, it may be a catalyst for the disappearance of other species (HARDY and HARRIS 1979).

Next to competition with native species, further possible impacts of introduced *Eleutherodactylus* include transmission of diseases (e.g. of *Batrachochytrium dendrobatidis* as reported for *Eleutherodactylus coqui* THOMAS, 1966; BEARD and O´NEILL 2005)) or of parasites (e.g. *Leptospira interrogans*; EVERARD et al. 1990) and socioeconomic damages (KRAUS and CAMPBELL 2002; LEVER 2003). In French Guiana, the calls of introduced *E. johnstonei* are disturbing the sleep of local residents (LEVER 2003). This is also a problem for other areas where *Eleutherodactylus* species have been introduced outside their native ranges. In the Hawaiian Islands, the calls of *E. coqui* are a serious problem for local residents and hotel guests who complain about the noise keeping them awake at night (KRAUS et al. 1999, KRAUS and CAMPBELL 2002). In Hawaii, residents are encountering reduced property values and increased difficulty selling property (KRAUS and CAMPBELL 2002).

A risk assessment identifying regions in which *E. johnstonei* can find suitable conditions for successful establishment of invasive populations may be helpful to prevent further introductions and to coordinate effective conservation measurements. Successful establishment of a non-indigenous species into an ecosystem depends on the presence of competitors and predators, food availability, and human footprint (EHRLICH 1989; WILLIAMSON 1996). Additionally, the climatic similarity of the novel ecosystem compared with the source ecosystem is an important issue (BOMFORD et al. 2008). For such an assessment, GIS-based analyses such as Climate Envelope Models (CEMs) can be a powerful tool (e.g. PETERSON and VIEGLAIS 2001; RÖDDER et al. 2008; BOMFORD et al. 2009; RÖDDER 2009). Herein, I compare the potential distribution of *E. johnstonei* under current climate conditions and the spatial distribution of anthropogenic modified habitats in order to identify regions with high potentials for *E. johnstonei* invasions.

Material and methods

Species records

For model building 3,362 species records were obtained from through the Global Biodiversity Information Facility (GBIF; www.gbif.org) and HerpNet databases (www.herpnet.org), and additional published references (SCHWARTZ and HENDERSON 1991; KAISER et al. 2002; LEVER 2003; BUURT 2006). A total number of 124 records were situated in unique grid cells and used for model building (39 native and 85 invasive records). If necessary, the Alexandria Digital Library Gazetteer Server Client (www.middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp) was used for georeferencing. The accuracy of coordinates processed was assessed with DIVA-GIS 5.4 (HIJMANS et al. 1999; 2002).

Variable selection

POUGH et al. (1977) showed that climatic conditions are directly correlated with activity patterns and habitat choice in *E. johnstonei*, whereby temperature and moisture conditions of its preferred habitats are closely related to its physiological properties. According to laboratory experiments conducted by these authors, the preferred temperature of *E. johnstonei* is 25.7 ± 0.67 °C (n= 49), whereby its critical maximum temperature ranges between 36.2 – 40.8 °C (acclimated to 20°C: mean= 39.2 ± 0.47 °C, range= 36.2-40.8 °C, n= 10; acclimated to 30°C: mean= 38.6 ± 0.19 °C, range= 38.0-40.0 °C, n= 10). Although *E. johnstonei* is apparently more tolerant to dehydration than most other *Eleutherodactylus* (POUGH et al. 1977), a continuous availability of water may be necessary for its persistence. Therefore, I selected the ‘annual mean temperature’, ‘maximum temperature of the warmest month’, ‘minimum temperature of the coldest month’, ‘annual precipitation’, ‘precipitation of wettest month’, and ‘precipitation of the driest month’ as variables representing a set of parameters, which describe the availability of water and energy and their minimum and maximum. Information on current climate was obtained from the Worldclim database, version 1.4, which is based on weather conditions recorded between 1950 and 2000 with grid cell resolution 30 arc seconds (HIJMANS et al. 2005; http://www.worldclim.org). It was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995, 2004). In order to compare bioclimatic conditions between native, invasive records and published data provided by

POUGH et al. (1977), I plotted the cumulative frequency at the records per bioclimatic parameter with DIVA-GIS.

It was shown that successful establishment of invasive populations of *E. johnstonei* is often facilitated by anthropogenic habitat disturbance (e.g. POUGH et al. 1977; KAISER and WAGENSEIL 1995; KAISER 1997; KAISER et al. 2002), which can be quantified by the Human Footprint (HF; SANDERSON et al. 2002). Therefore, I compare the results obtained from the potential distribution map derived from the CEM with the HF values describing the human influence within a given area. HF values range from 0 to 100 and can be understood as the sum total of ecological footprints of human populations including population density, land transformation, access, electric power infrastructure, and biome normalization (SANDERSON et al. 2002). Higher HF values suggest a higher anthropogenic impact.

Computation and evaluation of the Climate Envelope Model

For CEM calculation I used MaxEnt 3.2.19 (PHILLIPS et al. 2004; 2006; http://www.cs.princeton.edu/~shapire/maxent), a machine-learning algorithm following the principles of maximum entropy (JAYNES 1957). It has been shown to reveal better results than other comparable methods such as BIOCLIM, DOMAIN or GARP (e.g. ELITH et al. 2006). The reliability of the results obtained from MaxEnt models has been confirmed by its good capacity to predict novel presence localities of less well known species (e.g. PEARSON et al. 2007) and the outcome of introductions of invasive species outside the native range (e.g. RÖDDER et al. 2008; RÖDDER 2009). Both native and invasive *Eleutherodactylus johnstonei* records were pooled for model building following BROENNIMANN and GUISAN (2008). The records were not randomly distributed over its native and invasive range (Figure 3.5-1), leaving the problem of clumped records due to biased sampling which may violate CEM assumptions (e.g. DORMANN et al. 2007). To account for this, I extracted all bioclimatic values at the records and performed a cluster analysis based on Euclidean distances, whereby resulting classes were blunted at a threshold leaving 60 classes. The mean values of the bioclimatic variables per class were used for further processing. This method reduces the amount of duplicate information in the data set and thereby the impact of clumped records due to biased sample selection. Calculations were performed with XLSTAT 2008 (Addinsoft, http://www.xlstat.com; downloaded 1 July 2008). For model building, 10,000 random background points were automatically selected by MaxEnt within a minimum convex polygon covering and including both native and invasive records. The logistic output format with suitability values linear ranging from 0 (unsuitable) to 1 (optimal) was used (PHILLIPS and DUDÍK 2008). CEM predictions may become unreliable if the model is predicted onto climate parameters outside the training range (termed ‘clamping’; PHILLIPS et al. 2006); therefore such areas were removed from the final potential distribution map.

Maxent allows for model testing by calculation of the Area Under the Curve (AUC), referring to the ROC (Receiver Operation Characteristic) curve (HANLEY and MCNEIL 1982; PHILLIPS et al. 2006). I used the class means of the bioclimatic variables as described above for model training and (1) all original species records as test points (referred to as AUC_{test}) and (2) random background points within the training area as test points (referred to as $AUC_{training}$). This method is recommended for ecological applications because it is non-parametric (PEARCE and FERRIER 2000). Values of AUC range from 0.5 (i.e. random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of SWETS (1988) AUC values > 0.9 describe ‘very good’, > 0.8 ‘good’ and > 0.7 ‘useful’ discrimination ability. Furthermore, MaxEnt offers the option to perform a jackknife analyses to determine the relative importance of the variables in the final model.

Results

I received ‘good’ to ‘very good’ AUC values in the model ($AUC_{training} = 0.897$; $AUC_{test} = 0.921$). Clamping occurred only in a small stripe along the western Coast of Southern America from northern Peru to central Chile, which was excluded from further analyses. Analysis of variable contributions in the model revealed that the ‘maximum temperature of the warmest month’ had with 40.2 % the highest explanative power followed by ‘precipitation of the wettest month’ (35.1 %), the ‘annual mean temperature’ (9.5 %), ‘mean temperature of the coldest quarter’ (6.8 %), the ‘precipitation of the driest month’ (6.1 %) and the ‘annual mean precipitation’ (2.3 %). Climatic conditions observed at the invasive records frequently exceed conditions at the native records, with exception of the ‘maximum precipitation of the wettest quarter’ (Figure 3.5-1). The by POUGH et al. (1977) experimentally determined preferred temperature of *E. johnstonei* corresponds well with the annual mean temperature at the native records (median= 25.7 °C, range= 23.0 – 26.7 °C; Figure 3.5-1), but the upper and lower values are frequently exceeded the invasive range (median= 26.0 °C, range= 17.8 – 27.7 °C; Figure 1). Upper and lower values of the maximum temperature of the warmest month within the native range (median= 30.4 °C, range= 27.6 – 31.4 °C; Figure 3.5-1) are also frequently exceeded in the invasive range (median= 31.1 °C, range= 23.8 – 34.1 °C; Figure 3.5-1), but still much lower than the critical maximum temperature (as reported by POUGH et al. 1977).

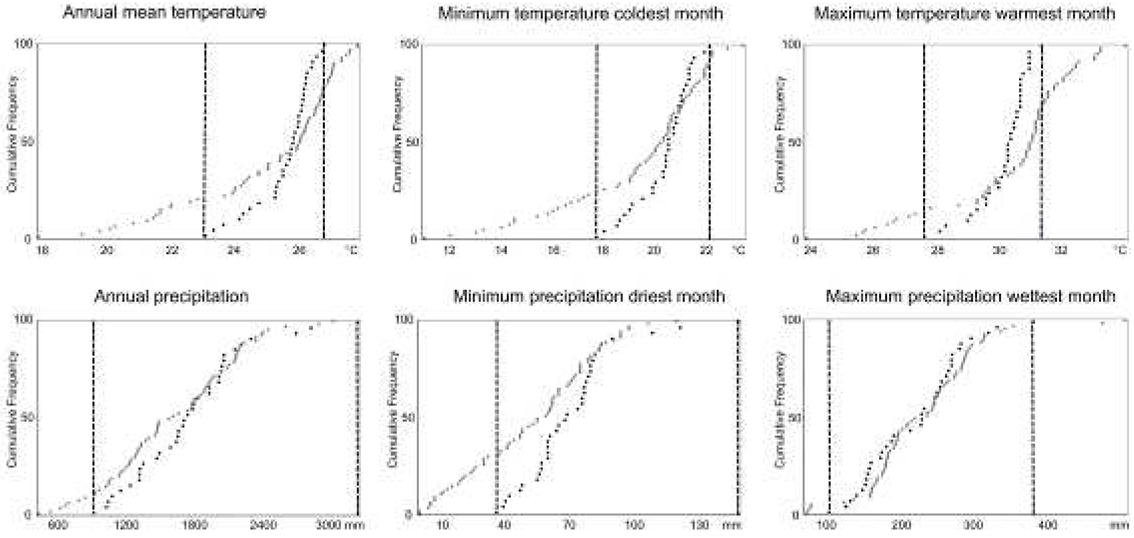

Figure 3.5-1 Comparison of climatic conditions at native and invasive records of *Eleutherodactylus johnstonei*. Native records are indicated in black, invasive records in grey.

Under current climatic conditions, *E. johnstonei* can find suitable areas everywhere in the Antilles, coastal parts of the Dominican Republic and Haiti, Jamaica, Puerto Rico and coastal parts of Panama, Columbia, Venezuela and Guyana (Figure 3.5-2). In the South American mainland, the Iquitos region in Peru, upper parts of the Amazon basin and coastal parts of north-eastern Brazil are highlighted by the model. Looking at fine scale patterns within the invasive range, further spread of *E. johnstonei* may be hampered by climatically unsuitable areas within the inlands of Colombia and Venezuela. However, climatically suitable potential dispersal routes along the Andes and eastern parts of the pantepui region may exist (Figure 3.5-2).

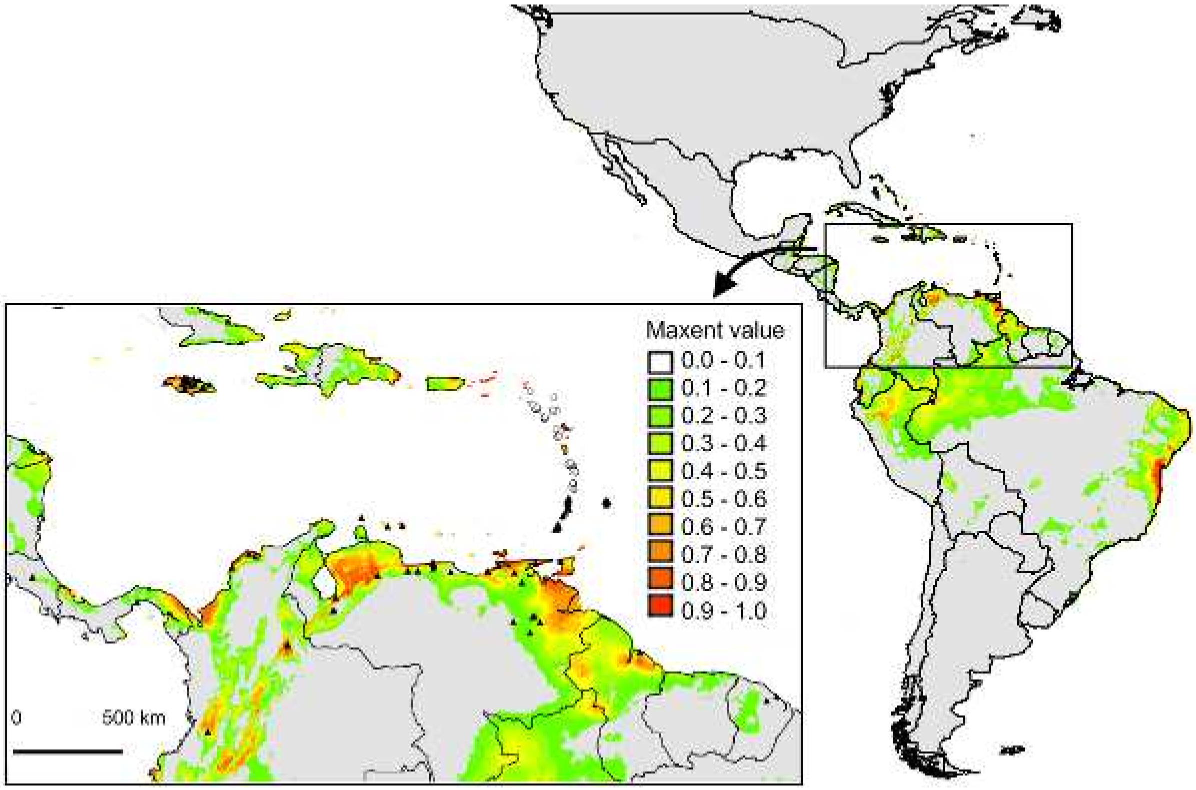

Figure 3.5-2 Potential distribution of *Eleutherodactylus johnstonei* under current climate conditions. Higher MaxEnt values suggest higher climatic suitability. Native records are indicated as white points, invasive records as black triangles.

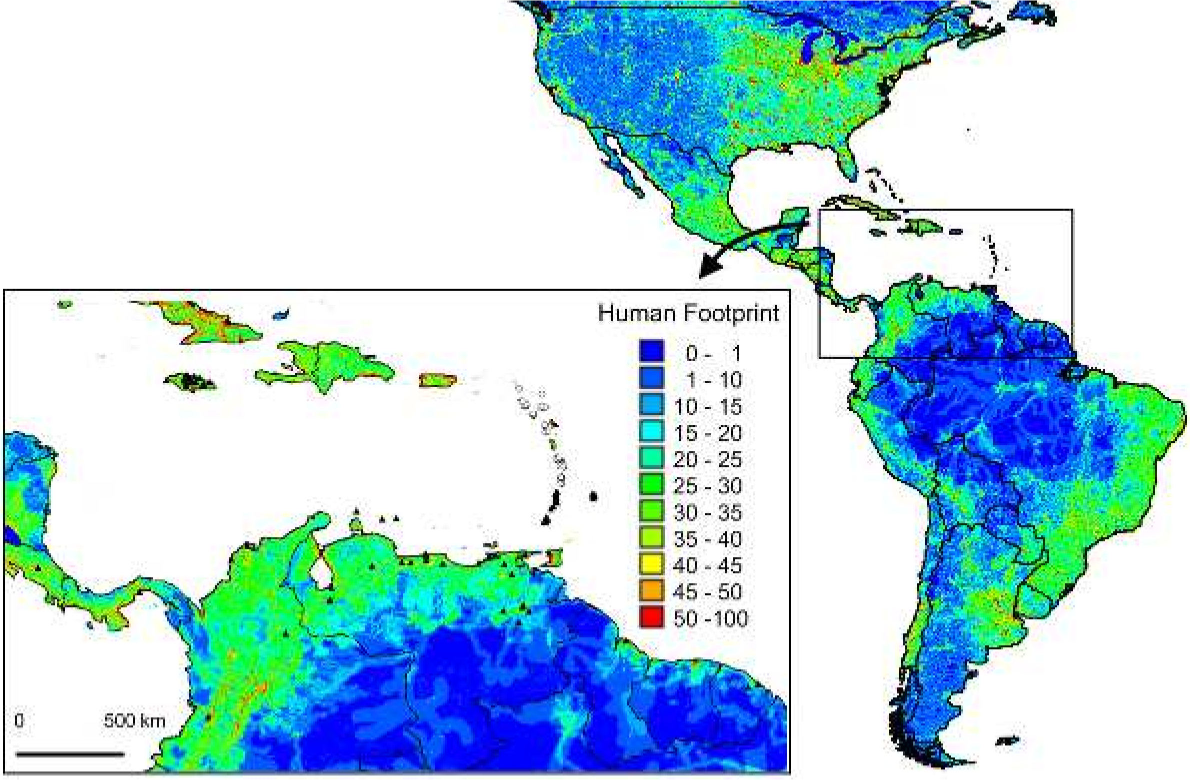

Figure 3.5-3 Human Footprint (HF), a quantitative evaluation reflecting the continuum of human influence across terrestrial biomes. Higher values suggest a stronger anthropogenic habitat disturbance. Native records of *Eleutherodactylus johnstonei* are indicated as white points, invasive records as black triangles. Source: SANDERSON et al. (2002).

Most known populations of *E. johnstonei* are situated in areas characterized by high HF values (native range: mean= 50.9 ± 9.6, range= 34 – 73; invasive range: mean= 49.3 ± 15.5, range= 12 – 93; Figure 3.5-3). Comparing the spatial patterns of *E. johnstonei*'s potential distribution (Figure 2) and HF values (Figure 3.5-3) it becomes evident that Costa Rica, Panama, the North coast of South America including major parts of the Andes in Colombia, Ecuador and Venezuela and coastal parts of north-eastern Brazil are highly suitable in terms of climatic conditions and anthropogenic habitat disturbance. Although climatically suitable, the Iquitos region in Peru and parts of the Amazon basin are characterized by low HF values probably hampering an invasion.

Discussion

My results indicate that almost all Caribbean islands and most parts of adjacent continents provide suitable conditions for *E. johnstonei* and invasive populations are already known from most of them. However, a few islands situated within already invaded islands (i.e. Haiti, the Dominican Republic, Puerto Rico and the US Virgin Islands) have not been invaded yet. One reason may be that all of these islands are inhabited by a diverse anuran fauna which is rich in ecologically similar *Eleutherodactylus* species (HEDGES et al. 2008). A possible competitor in Puerto Rico and the US Virgin Islands may be *Eleutherodactylus coqui*. Within its native range in Puerto Rico, densities of *E. coqui* are with around 20,000 individuals ha^{-1} among the highest known for any amphibian in the world (STEWART 1995; WOOLBRIGHT et al. 2006). *Eleutherodactylus coqui* is ecologically a generalist, highly adaptive and tolerates habitat modifications (as *E. johnstonei*) (WOOLBRIGHT 1991; 1996). The presence of *E. coqui* would most likely make a successful establishment *E. johnstonei* difficult.

Despite harbouring an anuran fauna diverse in ecologically similar species, *E. johnstonei* has established numerous invasive populations at the Colombian and Venezuelan coast. KAISER et al. (2002) suggested that one of the potential barriers hampering its further dispersal in Colombia and Venezuela may be temperature decrease with increased altitude. The highest known population occurs in Mérida, Venezuela at up to 1400 m a.s.l. and the authors argued that this altitude is the maximum possible for the species. The influence of altitude is also highlighted by the CEM in the Andes of Colombia and Venezuela, whereby the potential distribution of *E. johnstonei* is disrupted (Figure 3.5-2). However, invasive populations are already known from these patchy suitable sites and, since human facilitated dispersal is the main spread way, the lack of continuous suitable areas may finally not prevent further spreadings.

In the capital city of Georgetown, Guyana, *E. johnstonei* has remained confined to the urban area although agricultural land and anthropogenic disturbed forests were close by (KAISER et al. 2002). Hence, KAISER et al. (2002) concluded that in may cause no harm to native species because its expansion ability is limited by the availability of disturbed habitats. This may hold true for Georgetown since the area around the city is characterized by comparatively low HF values (Figure 3.5-3), but not necessarily for invasive populations in Colombia, Costa Rica, Panama and Venezuela where HF values in surrounding areas are overall high. The Andes of Colombia, Ecuador and Venezuela are therefore most suitable for *E. johnstonei* in terms of climate and habitat modification (Figure 3.5-3). This Andean region harbours a highly diverse amphibian fauna which is highly threatened due to anthropogenic habitat alteration (e.g. STUART et al. 2008) and the emerging infectious disease Chytridiomycosis (e.g. LIPS et al. 2008). The high number of ecologically similar Strabomantid species (HEDGES et al. 2008; STUART et al. 2008) may prevent the spread of *E. johnstonei* in natural habitats. However, *E. johnstonei* may be able to compete with them in the next future. Many of those species have very restricted ranges, most likely a low adaptation capacity to environmental stress and are vulnerable to the rapidly progressing anthropogenic habitat alteration (STUART et al. 2008). Facing the rapidly progressing habitat destruction in this area, *E. johnstonei* may be a catalyst for the disappearance of other species.

Methodical caveats

CEM approaches rely two basic the assumptions: (1) that climatic tolerances of species are the primary determinants of their current distributions and (2) that specific climatic niches are conservative, at least within an evolutionary short time frames of some hundreds to thousands years (e.g. WIENS and GRAHAM 2005; but see also PEARMAN et al. 2008). In the case of species inhabiting islands such as *E. johnstonei*, climate is not the primary limiting factor for the geographic distribution violating assumption (1). Hence, climatic conditions potentially suitable for the species but not present in its native range may be unintentionally excluded from the CEM leading to an underestimation of its potential distribution. However, several examples have shown that CEMs can successfully predict invasive populations of species originating from islands (e.g. RÖDDER 2009;

RÖDDER and WEINSHEIMER 2009) if the problem of possible underestimation is taken into account. To minimize this problem, I used climatic conditions as present in both *E. johnstonei*'s native and invasive distribution for model building herein, e.g. as suggested by BROENNIMANN and GUISAN (2008), including all information currently available. However, it needs to be noted that the climatic niche breadth of *E. johnstonei* may still be broader than suggested by the model.

Conclusions

It took several centuries of presumably human-mitigated introductions until *E. johnstonei* as established invasive populations in all currently known regions (KAISER 1992; 1996). First specimens at the South America mainland were detected in Georgetown, British Guyana prior 1919; it was introduced in the late 1950s to Caracas, Venezuela, from where it most likely expanded its range to Colombia (HARDY and HARRIS 1979) and was introduced with plants from Venezuela to Curaçao in the late 1970s and later to Aruba and Bonaire (BUURT 2005, 2006). These spatial and temporal patterns suggest that it can establish invasive populations more rapidly today then in the past. KAISER et al. (2002) suggested that *E. johnstonei* will continue to expand its range by chance without a possibility of stopping it. The progressing anthropogenic habitat disturbance and enhanced transportation of goods during the last decades may even enhance its spread rate.

Acknowledgements

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SECTION 4: NICHE DYNAMICS IN SPACE AND TIME

4.1. Environmental niche plasticity of the endemic gecko *Phelsuma parkeri* from Pemba Island, Tanzania: a case study of extinction risk on flat islands by climate change[10]

Phelsuma parkeri

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[10] This part was submitted to *Tropical Zoology*

The work reported in this chapter was conducted in collaboration with OLIVER HAWLITSCHEK and FRANK GLAW from the Herpetology Department, Zoologische Staatssammlung München, München, Germany.

Introduction

Habitat loss, overexploitation and climate change are among the most serious threats for species (STUART et al. 2004; THOMAS et al. 2004), whereby species inhabiting islands with restricted ranges are at greater risk of extinction than those found on continents (Frankham, 1998). The greater risk for island endemics can be traced back to (1) their greater susceptibility to perturbation from invasive species or pathogens, (2) their commonly fewer and smaller populations caused by the small range size, and (3) their greater vulnerability to changes in environmental conditions due to small genetic variability allowing often only little adaptation capacity. Additionally, their small range size makes them more vulnerable to habitat fragmentation since even moderate fragmentation may prevent gene flow among populations.

A great part of the geographic distribution of a species is determined by its fundamental niche, i.e. those environmental conditions under which populations can persist. As defined by HUTCHINSON (1957; 1978), a species' climatic niche or climate envelope is part of its fundamental niche (Figure 4.1-1). The realized niche of a species is understood to represent a subset of the fundamental niche considering dispersal limitations and biotic interaction such as competition, or interaction with pathogens (SOBERÓN and PETERSON 2005; Figure 4.1-1). It was shown that climatic factors directly affect the distribution, abundance and life cycles of species. Anthropogenic climate change has already caused shifts in geographic distribution of numerous taxa (PARMESAN and YOHE 2003; PARMESAN 2006). If climate changes, island endemics may be restricted in their ability to conduct range shifts depending on the topographic variability and the size of the island. Species inhabiting islands characterized by low altitudinal variation might be most strongly affected by climate change due to the lack of possibilities for horizontal or upward range shifts. On the other hand only a small part of the fundamental niche may be realized since climate is commonly not the major factor limiting the distribution of island species. In order to assess the relative proportion of the fundamental niche and the realized niche, a comparison between conditions tolerated in the present and in the past may be helpful.

One species meeting these characteristics is *Phelsuma parkeri*, a medium sized (total length up to 165 mm), green day gecko endemic to Pemba Island which is - like all species in the genus - listed on CITES Appendix II (HALLMANN et al. 2008). According to recent molecular analyses *P. parkeri* is the sister species to the much larger *Phelsuma grandis* and has reached the island by oversea dispersal from Madagascar (RAXWORTHY et al. 2007; ROCHA et al. 2007). Although the genetic distance between *P. parkeri* and its next relative

P. grandis is comparatively low in comparison to other *Phelsuma* species, there is no doubt that this difference predates the Pleistocene period. Assuming that the ancestor of *P. parkeri* has arrived immediately from Madagascar (i.e. excluding the possibility of step stone dispersal followed by subsequent extinction) the species has most likely maintained feral populations on Pemba during the climatic fluctuations in the Pleistocene.

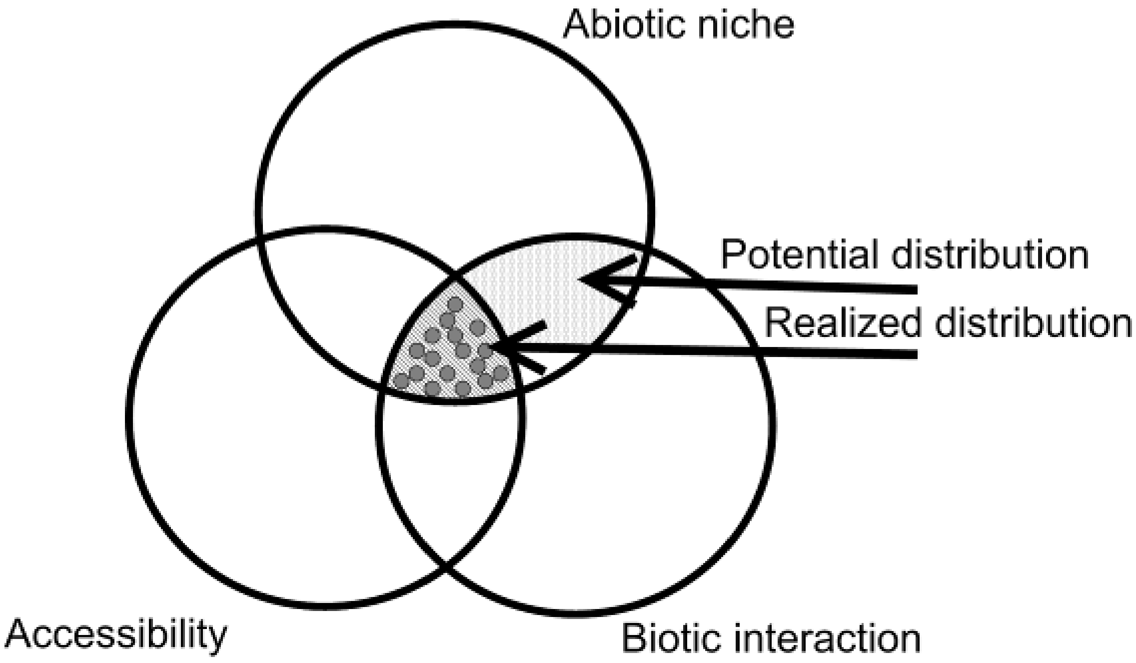

Figure 4.1-1 Relationships between abiotic (= fundamental) niche, biotic interaction and accessibility after HUTCHINSON (1957) as modified by SOBERÓN and PETERSON (2005). The potential distribution is a subset of the abiotic niche considering biotic interactions, whereby the realized distribution is a subset of the potential distribution considering accessibility. Dots represent species records.

Pemba Island is situated ca. 50 km off the African coast in the Indian Ocean and part of the Zanzibar archipelago that includes the islands of Zanzibar and Pemba. Pemba Island, with a length of ca. 67 km and a breadth of ca. 22 km, covers an area of approximately 1040 km^2 (PAKENHAM 1979). Compared to the Tanzanian interior, climate on the Zanzibar archipelago is characterized by high humidity (JUMA 2004), whereby south-western Pemba receives with a maximum of 1940 mm y^{-1} the highest mean annual rainfall in East Africa (JUMA 2004; Table 4.1-1). Pemba's driest area is situated in eastern parts of central Pemba

(1117 mm y^{-1}; Figure 4.1-S1). The temperature throughout the island is relatively invariant throughout the year (Table 4.1-1; Figure 4.1-2).

Pemba Island is a network of small valleys and hills, whereby only few exceed 90 m a.s.l. (Figure 4.1-2). Western and central parts of the island are covered by hygrophilous tropical vegetation. In contrast, along most of the eastern seaboard of Pemba, a band of bushland of varying width can be found. This unique, xerophytic vegetation grows on the old outcropping coral rock, named coral-rag (PAKENHAM 1983) – a soil type having much lower water capacity compared to the western soils.

Pemba Island is part of the East African coastal forest mosaic according to SPAWLS et al. (2002). A comparative species diversity analysis comprising 29 East African coastal forests based on distributions of birds, mammals and reptiles revealed that Pemba harbours one of the most unique faunas with only very limited overlap with other coastal forests (AZERIA et al. 2007). Pemba Island is - unlike its neighbour Zanzibar - thought to have been isolated from the continent by a 700 - 800 m deep oceanic channel for several millions of years and can be considered a true oceanic island (ARCHER and TURNER 1993; JUMA 2004). The island is characterized by a remarkable number of endemic species, some of which have their closest relatives in the Madagascan region such as plants (*Aloe pembanum*), mammals (*Pteropus voeltzkowi*), and several reptiles (*Lygosoma pembanum*, *Natriciteres pembana*, *Lycophidion pembanum*, *Leptotyphlops pembae*, *Phelsuma parkeri*) (PAKENHAM 1983; NAHONYO et al. 2005).

The goal of the present study is (i) to evaluate the current distribution of *Phelsuma parkeri* on Pemba Island; (ii) to assess its environmental niche plasticity in terms of microhabitat utilization and macroclimatic factors as actually present and as expected during the last glacial maximum; (iii) to discuss its conservation status facing invasive species, changing climate and land use. Inspired by a recent proposal of the CITES commission / Tanzanian Government for commercial use, we also discuss the potential impact of sustainable use for pet trade.

Material and methods

We conducted visual encounter surveys on Pemba Island between 9th and 22nd January 2009 in a period of sunny weather and almost no rain. Study plots distributed all over the island were mainly restricted to easily accessible areas and therefore more often situated along the existing road network (Figure 4.1-2). Specimens were determined visually and captured only occasionally. For each specimen encountered we recorded exact locality information including longitude, latitude and altitude using a Garmin Etrex Venture HC GPS. Microhabitat data included perch site (plant species) and estimated elevation above ground to the nearest 0.5 m. Additional locality data was taken from literature and georeferenced with Google Earth (http://earth.google.de/) (five sites; PAKENHAM 1983).

Climate data

Information on current climate (annual mean temperature and precipitation as well as minimum and maximum temperature / precipitation of the warmest / coldest and wettest / driest month) was obtained from the Worldclim database, version 1.4, which is based on weather conditions recorded between 1950 and 2000 with a grid cell resolution of 30 arc sec (HIJMANS et al. 2005, www.worldclim.org). It was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude and elevation as independent variables (HUTCHINSON 1995; 2004).

For paleoclimate as expected for Pemba Island during the Last Glacial Maximum (LGM), General Circulation Model (GCM) simulations from the Community Climate System Model (CCSM; http://www.ccsm.ucar.edu/; KIEHL and GENT 2004) and the Model for Interdisciplinary Research on Climate (MIROC, version 3.2; 115 http://www.ccsr.u-tokyo.ac.jp/~hasumi/MIROC/) were provided by R. J. HIJMANS. Original GCM data were downloaded from the PIMP2 website (http://www.pimp2.cnrs-gif.fr/) with spatial resolution of roughly 300 x 300 km. Surfaces were created as described by PETERSON and NYÁRI (2007).

For future climate scenarios, we used climate change projections based on the CCCMA, CSIRO and HADCM3 (FLATO et al. 2000; GORDON et al. 2000) models and the emission scenarios reported in the Special Report on Emissions Scenarios (SRES) by the Intergovernmental Panel on Climate Change, IPCC (www.grida.no/climate/ipcc/emission/). A set of different families of emission scenarios was formulated based on future production of greenhouse gases and aerosol precursor emissions. The SRES scenarios of A2a and B2a were used in this study. Each scenario described one possible demographic, politico-economic, social and technological future as expected for 2080. Scenario B2a emphasizes more environmentally conscious, more regionalized solutions to economic, social and environmental sustainability. Compared to

B2a, scenario A2a also emphasizes regionalized solutions to economic and social development, but it is less environmentally conscious.

Modelling algorithm

Maxent 3.2.19 (PHILLIPS et al. 2004; 2006, www.cs.princeton.edu/~shapire/maxent) was applied for Climate Envelope Model (CEM) calculation in order to assess the potential distribution of *P. parkeri* and to map it into geographic space. MaxEnt is a grid-based machine-learning algorithm following the principles of maximum entropy (JAYNES 1957). The idea behind MaxEnt is to find a probability distribution covering the study area that satisfies a set of constraints derived from the environmental conditions at the species records. MaxEnt is able to incorporate complex dependencies between predictor variables and has been shown to reveal better results than other comparable methods (e.g. ELITH et al. 2006; WISZ et al. 2008). The reliability of the results obtained from MaxEnt models has been confirmed by its capacity to predict novel presence localities for poorly known species (PEARSON et al. 2007) and the outcome of introductions of alien invasive species outside the native distribution (e.g. PETERSON and VIEGLAIS 2001; RÖDDER et al. 2008; RÖDDER 2009). Runs used herein were conducted using the default values for all program settings. The logistic output format with suitability values ranging from 0 (unsuitable) to 1 (optimal) was used (PHILLIPS and DUDÍK 2008).

Maxent allows for model testing by calculation of the Area Under the Curve (AUC), referring to the ROC (Receiver Operation Characteristic) curve; herein we assessed the ability of the model to distinguish background points from training points (HANLEY and MCNEIL 1982; PHILLIPS et al. 2006). This method is recommended for ecological applications because it is non-parametric (PEARCE and FERRIER 2000). Values of AUC range from 0.5 (random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of Swets (1988), AUC values > 0.9 describe ‘very good’, > 0.8 ‘good’ and > 0.7 ‘useful’ discrimination abilities. In the case of MaxEnt AUC values reflect the model’s ability to distinguish presence records from random background points (PHILLIPS et al. 2006).

Results

During our surveys we encountered *P. parkeri* in a total number of 39 localities distributed all over the island with exception of the dry coral-rag region (Figure 4.1-2) and the offshore islets which were not surveyed. Preferred perch sites of *P. parkeri* included coconut trees (*Cocos nucifera*; n= 23; n%=71.88), banana plants (*Musa* sp.; n= 6; n%= 18.75) and palm trees (*Raphia* sp.; n= 3; n%= 9.38). One specimen was encountered on a jacktree (*Artocarpus heterophyllus*), and two specimens on unidentified trees (one dead, one alive). Perch sites varied in estimated elevation between 1.5 m and 12 m (mean= 3.7 m; SD= 3.1 m). The number of encountered specimens greatly varied during the day, whereby most specimens were observed in the afternoon (~ 15 – 18 hrs). No specimens were encountered at night. With exception of one hatchling, all other geckos apparently had a similar size and were therefore classified as adults.

Potential distribution and changes in climatic conditions

The ability of our model to distinguish presence from random background records was ‘good’ (AUC = 0.821) according the classification of SWETS (1988). The minimum MaxEnt value observed at the training points was 0.306 and the lowest 10 percentile was 0.447. Our CEM approach suggest that *P. parkeri* can find climatically suitable conditions almost on the whole island (Figure 4.1-3) what meets our impression during field work. The region with lowest MaxEnt scores is coincident with the coral-rag area and characterized by much lower annual mean, minimum and maximum precipitation compared to the rest of the island.

Comparison of current climatic conditions and those as suggested by CCSM and MIROC simulations for 21,000 BP revealed that no analogous climate to today’s conditions has existed during the LGM (Table 4.1-1). Main differences are related to climatic parameters comprising decreases between 1.4 to 2.8 °C in the maximum temperature of the coldest month and 2.1 to 3.4 °C in the minimum temperature of the warmest month throughout the island (Table 4.1-1). Suggested changes in precipitation patterns are inconsistent among models whereby CCSM suggest decreases and MIROC suggest increases (Table 4.1-1).

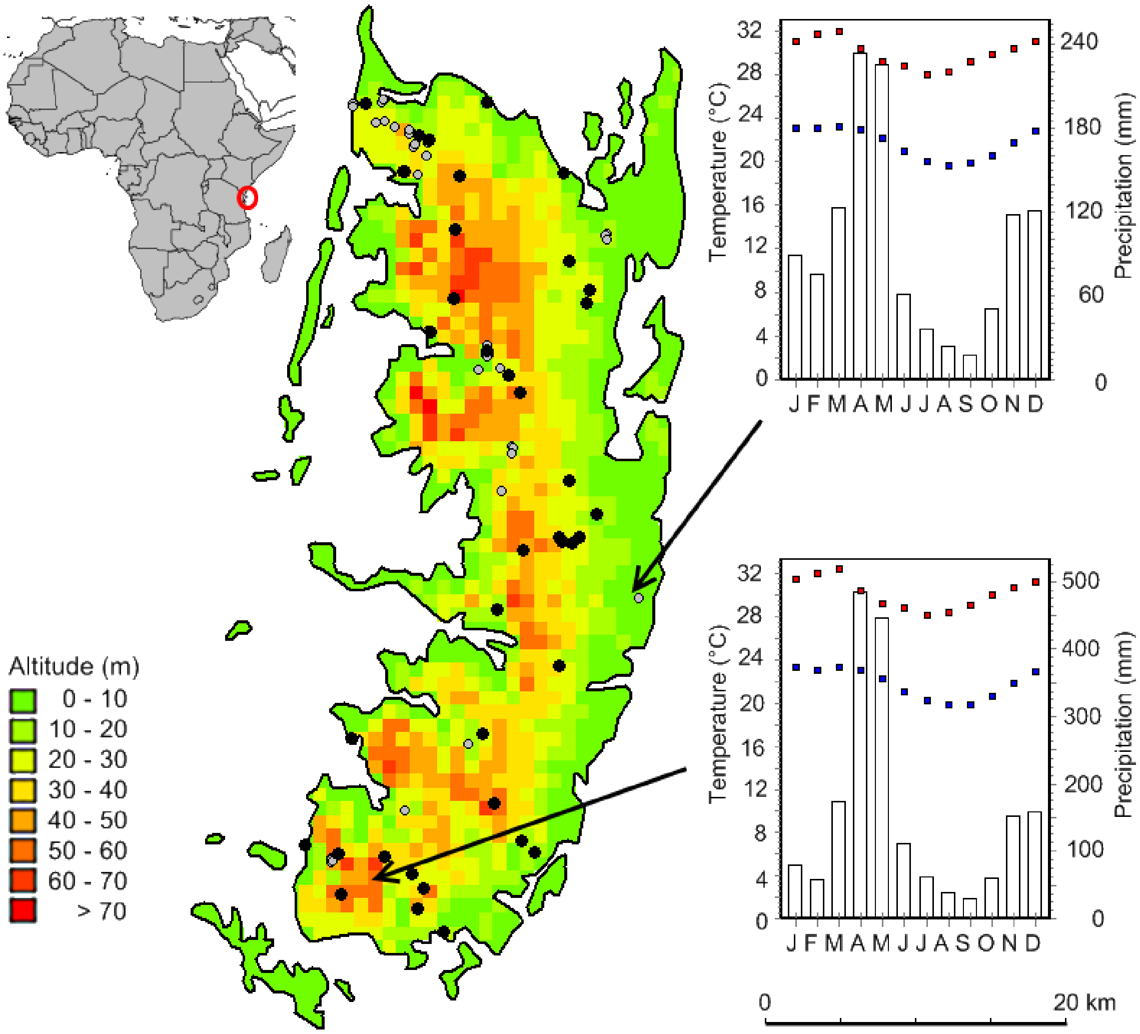

Figure 4.1-2 Distribution of sampled localities (grey dots) and *Phelsuma parkeri* records on Pemba Island (black points) and climatic variability throughout the island, exemplified on two selected grid cells (right).

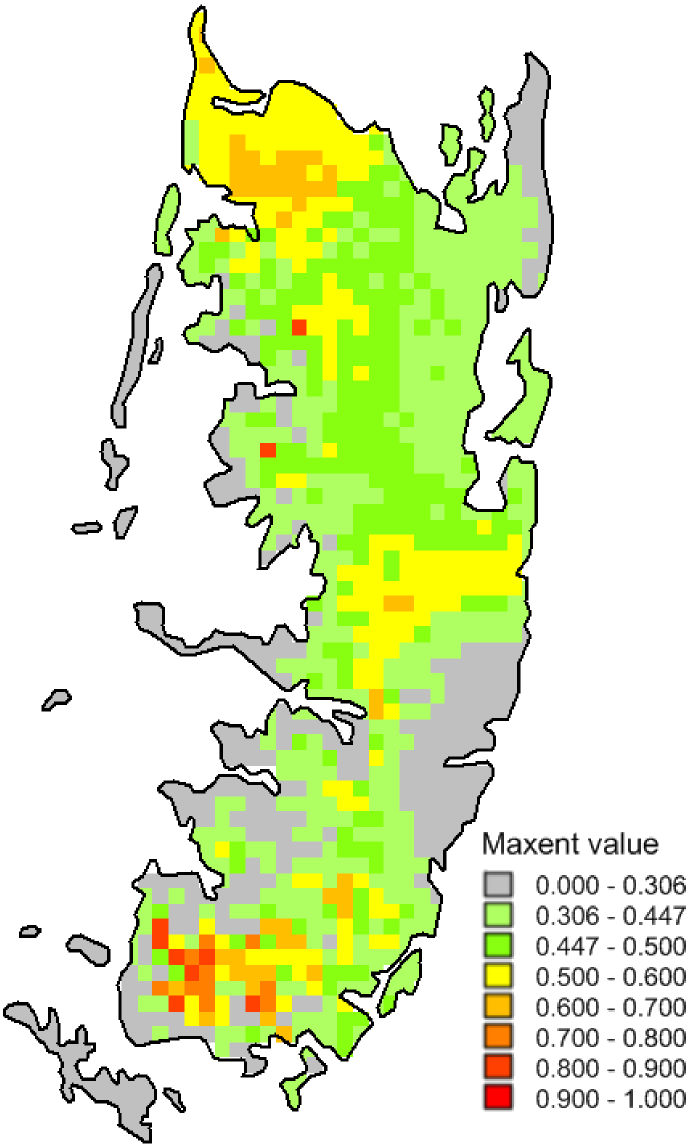

Figure 4.1-3 Potential distribution of *Phelsuma parkeri* in Pemba Island. Warmer colours suggest higher climatic suitability. The minimum MaxEnt value observed at the training points was 0.306 and the lowest 10 percentile was 0.447.

Future anthropogenic climate change as proposed by CCCMA, CSIRO and HADCM3 simulations assuming A2a and B2a conditions suggest overall increases in the annual mean temperature between 2.0 and 4.2 °C throughout the island relative to current conditions. The minimum temperature of the coldest month may increase about 1.2 to 3.8 °C and the maximum temperature of the warmest month at about 2.0 to 3.7 °C (Table 4.1-1). Suggested changes in precipitation patterns are inconsistent among scenarios; annual mean precipitation may vary between -168 and +427 mm y^{-1}, precipitation of the driest month between -15 and +4 mm and precipitation of the wettest month between -175 and +142 mm (Table 4.1-1).

Discussion

Possible threats

When assessing risks caused by habitat modification, biotic interactions and changing climate, it is important to evaluate possible discrepancies between the realized and fundamental climatic niches and the relative contribution of each ecological factor which may limit a species' distribution. Next to a species' climate envelope these are accessibility limitations caused by habitat fragmentation and/or biotic interactions such as competition or predation (see also SOBERÓN and PETERSON 2005).

Our results imply that *P. parkeri* was hitherto not negatively affected by anthropogenic habitat modifications since it is currently widespread and abundant on Pemba Island. The only exceptions are the drier, savannah like east coast (coral-rag region), the coastal natural dry forest in the northeast (Msitu Mkuu), clove plantations and mangroves. During our survey the species was most abundant in cultivated areas such as coconut and / or banana plantations which currently cover large parts of the island. In the remaining natural forest habitats, we encountered only few specimens. These observations may indicate that *P. parkeri* may even have taken advantage of the deforestation and the transformation of natural vegetation to cultivation. The situation might change if higher proportions of the island are transformed into rice fields or clove plantations. Enhanced use of biocides in agriculture may be also a potential threat. However, no such tendencies are evident at present.

Table 4.1-1 Comparison of current climatic conditions and those as expected during the Last Glacial Maximum 21,000 y BP (MIROC, CCSM) and assuming future anthropogenic climate change scenarios A2a and B2a. Minimum and maximum values reflect the variation within Pemba Island.

Variable	**Current**		**Paleoclimate**			
			MIROC		CCSM	
	min	max	min	max	min	max
annual mean temperature	25.1	26.4	22.0	24.8	22.1	24.8
max. temperature warmest month	31.4	33.0	28.0	30.8	28.1	30.9
min. temperature coldest month	18.9	20.3	16.1	18.9	16.1	18.8
annual precipitation	1117	1940	1022	1662	1454	2392
precipitation of the wettest month	204	505	199	434	283	625
precipitation of the driest month	16	46	14	39	21	56

	Future climate as expected in 2080 assuming A2a conditions					
	CCCMA		CSIRO		HADCM3	
	min	max	min	max	min	max
annual mean temperature	28.3	29.5	28.5	29.6	29.3	30.3
max. temperature warmest month	34.1	35.5	33.8	35.1	35.2	36.0
min. temperature coldest month	22.3	23.6	22.6	23.8	21.9	23.1
annual precipitation	1266	2018	1527	2367	1095	1550
precipitation of the wettest month	293	600	277	586	180	330
precipitation of the driest month	15	47	13	43	11	31

	Future climate as expected in 2080 assuming B2a conditions					
	CCCMA		CSIRO		HADCM3	
	min	max	min	max	min	max
annual mean temperature	27.2	28.4	27.8	29.0	27.6	28.7
max. temperature warmest month	32.6	34.0	33.9	35.2	33.3	34.6
min. temperature coldest month	21.1	22.4	21.4	22.7	21.0	22.3
annual precipitation	1316	2128	1342	2164	1190	1772
precipitation of the wettest month	311	647	272	577	214	448
precipitation of the driest month	15	45	11	40	15	50

Invasive species may have negative effects on native taxa, whereby island endemics can be especially affected (ATKINSON 1989; TOWNS et al. 2006). It was shown that gecko species can be effective competitors (e.g. DAME and PETREN 2006) leading in extreme cases to the extinction of endemic species (e.g. introduction of *Hemidactylus frenatus* has caused the extinction of three *Nactus* species in the Mascarene Islands; COLE et al. 2005). On Pemba Island, five other gecko species are known. Two diurnal geckos (*Lygodactylus capensis pakenhami* and *Lygodactylus viscatus*) occurring in the same microhabitat are much smaller in adult size and are therefore not likely to compete with *P. parkeri*. Predominately nocturnal geckos known from Pemba include *Hemidactylus angulatus*, *H. mercatorius*, *H. platycephalus* and *Ebenavia* sp. (PAKENHAM 1983). *Hemidactylus platycephalus* is widely distributed on Pemba Island and has much overlap in microhabitat use with *P. parkeri*. However, we failed to find any evidence for strong competition since both *H. platycephalus* and *P. parkeri* frequently occupied the same coconut tree. The other three are much smaller than *P. parkeri* in adult size and therefore most likely no effective competitors. Another potential competitor for *P. parkeri* might be *P. dubia*. This species, originating from Madagascar, was introduced to parts of the East African coast, including Zanzibar (ROCHA et al. 2007). In contrast to the gecko species mentioned above, *P. dubia* is only slightly smaller than *P. parkeri* and shares its diurnal, tree-dwelling habits. Therefore, in case of its introduction to Pemba, it might prove an important threat to the native *Phelsuma* species. However, competition success may be highly influenced by climatic suitability for (ectotherm) competitors such as geckos (RÖDDER et al. 2008). Since climate change is likely to alter competition success in ectotherm species we recommend a monitoring program regularly evaluating the population status of *P. parkeri*.

Are *P. parkeri* and other species endemic to the rather flat Pemba Island likely to be affected by climate change? According to our CEM, the breadth of currently realized climatic niche of *P. parkeri* is rather small (Table 4.1-1) and climatic conditions as currently present on Pemba Island will most likely not be present in the near future. Assuming a complete coverage of the gecko’s currently realized climate niche and its fundamental, extinction may be most likely. However, paleo-climatological models suggest a climate which was quite different from today’s conditions observed at Pemba Island. Although potential refuges with conditions equivalent to today’s environment were most likely absent, *P. parkeri* and other terrestrial endemics persisted. Possible explanations of the survival of *P. parkeri* may comprise: (1) compensation of macroclimatic variations by microclimate, allowing shifts in phenology, such as thermoregulation, activity patterns and / or microhabitat use, (2) pre-adaptation due to a broader fundamental climatic niche than currently realized, and (3) evolutionary responses causing shifts in the fundamental climatic niche. Future climate change scenarios suggest overall a rapid temperature increase. An evolutionary response (3) may be unlikely due to the short timeframe available. Explanation (1) appears to be most likely for short term responses to changing climates, whereby the compensation capacity of the microhabitat may depend on the magnitude of changes. We expect that *P. parkeri* will be able to compensate the moderate climate warming in the near future e. g. by earlier begin of daily activity, earlier retreat into shaded perch sites, and preference of habitats with denser vegetation. Shifts in phenological patterns as response to anthropogenic climate change were already shown for many species (PARMESAN 2006). Additionally, inhabiting an island, climate is not the range limiting factor in *P. parkeri,* hence it is most likely that the realized climate niche is smaller than it's fundamental. In conclusion we do not expect that the anthropogenic climate change of the near future will be an important threat to *P. parkeri* and other endemic species on Pemba.

IUCN status and potential sustainable use

Recently, a discussion about the actual conservation status and potential sustainable use of *P. parkeri* has emerged (K. HOWELL, pers. comm.). Our results indicate that *P. parkeri* is distributed over the largest part of the island in high abundances, is well adapted to current land use and most likely not threatened by climate change. As discussed above, however, potential future threats to *P. parkeri* might arise from the introduction of invasive species, especially *P. dubia* and shifts in land use. As none of these potential threats are evident at present to justify inclusion in the categories Critically Endangered, Endangered or Vulnerable according to the criteria defined in IUCN (2001), the status Near Threatened (NT) is proposed for *P. parkeri*. A further potential threat could arise from over-exploitation of *P. parkeri* for pet-trade. Until present, *P. parkeri* was virtually absent from pet-trade and apparently only few specimens are bred in captivity (HALLMANN et al. 2008). Recently, it was suggested to export live specimens of *P. parkeri* for captive breeding and pet trade (K. HOWELL, pers. comm.). According to our results, we are confident that annual export of a limited number of specimens (up to 1,000 specimens / year) would not significantly affect the population size. To ensure sustainability, we propose that (1) the population of *P. parkeri* is monitored continuously to assess the impact of the removal of specimens and to detect possible upcoming threats, as discussed above, and that (2) the maximum number of animals exported per year is limited pending on the population status.

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4.2. Reinforcing the predictions of the disturbance vicariance hypothesis in Amazonian harlequin frogs: a molecular phylogenetic and climatic envelope modelling approach[11]

© Stefan Lötters

Atelopus pulcher

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[11] This part was submitted to *Biodiversity and Conservation.*

The work reported in this chapter was conducted in collaboration with STEFAN LÖTTERS, ARIE VAN DER MEIJDEN and MICHAEL VEITH from the Faculty of Geoscience, University of Trier, Germany, TIMO E. KÖSTER from the Department of Zoology, University of Mainz, Mainz, Germany, TANJA KRAUS from the Department of Remote Sensing, Institute of Geography, University of Würzburg, Würzburg, Germany, ENRIQUE LA MARCA from the Laboratorio de Biogeografía, Escuela de Geografía, Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes, Venezuela, and CELIÓ F.B. HADDAD from the Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, SP, Brazil.

Introduction

There is a lot of ongoing debate regarding the explanation of plant and animal diversification and distributions in the Amazon basin and adjacent Guianas. Several historical biogeographic scenarios have been suggested (e.g. HAFFER 1997, 2008; HALL and HARVEY 2002; NOONAN and WRAY 2006). This paper deals with the disturbance vicariance hypothesis (DV), applicable to speciation in the Pleistocene (BUSH 1994; NOONAN and GAUCHER 2005; HAFFER 2008). Prolonged but slight cooling prior to this, in late Miocene (Huayquerian, 5.4-9 mya), allowed plant and animal taxa from the eastern Andean versant to occupy altitudinal ranges several hundred meters lower. Forest species dispersal into the lower Amazon basin eastward up to the eastern Guiana Shield was possible (Figure 4.2-1A). With comparatively warmer conditions during most of the Pliocene cool-adapted species were locally retracted to higher elevations and regional vicariant speciation processes started (Figure 4.2-1B). With every Pleistocene glacial (starting only ca. 500,000 years BP), this retraction was 'disturbed' as again cooling allowed for lowland dispersal (Figure 4.2-1C-D). Dispersal abilities were limited, however, as glacial cooling was accompanied by forest loss due to the reduction of precipitation of up to 20 %. Glacial lowland forest fragments remained in western Amazonia (pre-Andean region) and on the eastern Guiana Shield (Figure 4.2-1C). Examples which fit DV include caesalpinioid trees (*Vouacapoua americana*, DUTECH et al. 2003) or poison frogs (*Dendrobates tinctorius*, NOONAN and GAUCHER 2006).

Harlequin frogs (*Atelopus*) are a species-rich bufonid genus of Andean origin, with more than 80 species occurring in forest habitats in the Andes (LÖTTERS 1996; LA MARCA et al. 2005). In this paper we focus on the less than 10 (depending on the taxonomy applied; see LÖTTERS et al. 2002) *Atelopus* occurring exclusively in forest habitats in the Amazon basin and on the eastern Guiana Shield. In an earlier molecular genetic study, NOONAN and GAUCHER (2005) showed that the five nominal species of the Guianan harlequin frogs are genetically little differentiated and that they apparently interbreed in nature (in fact they may represent one or two species only; first author's unpubl. data). Supported by divergence time estimates, the authors suggested that their observed phylogeographical patterns fit DV predictions, i.e. that with change of Pleistocene glacial and interglacial phases divergence processes on the eastern Guianan Shield were 'disturbed' going back to a single Andean ancestor, likely of late Miocene origin.

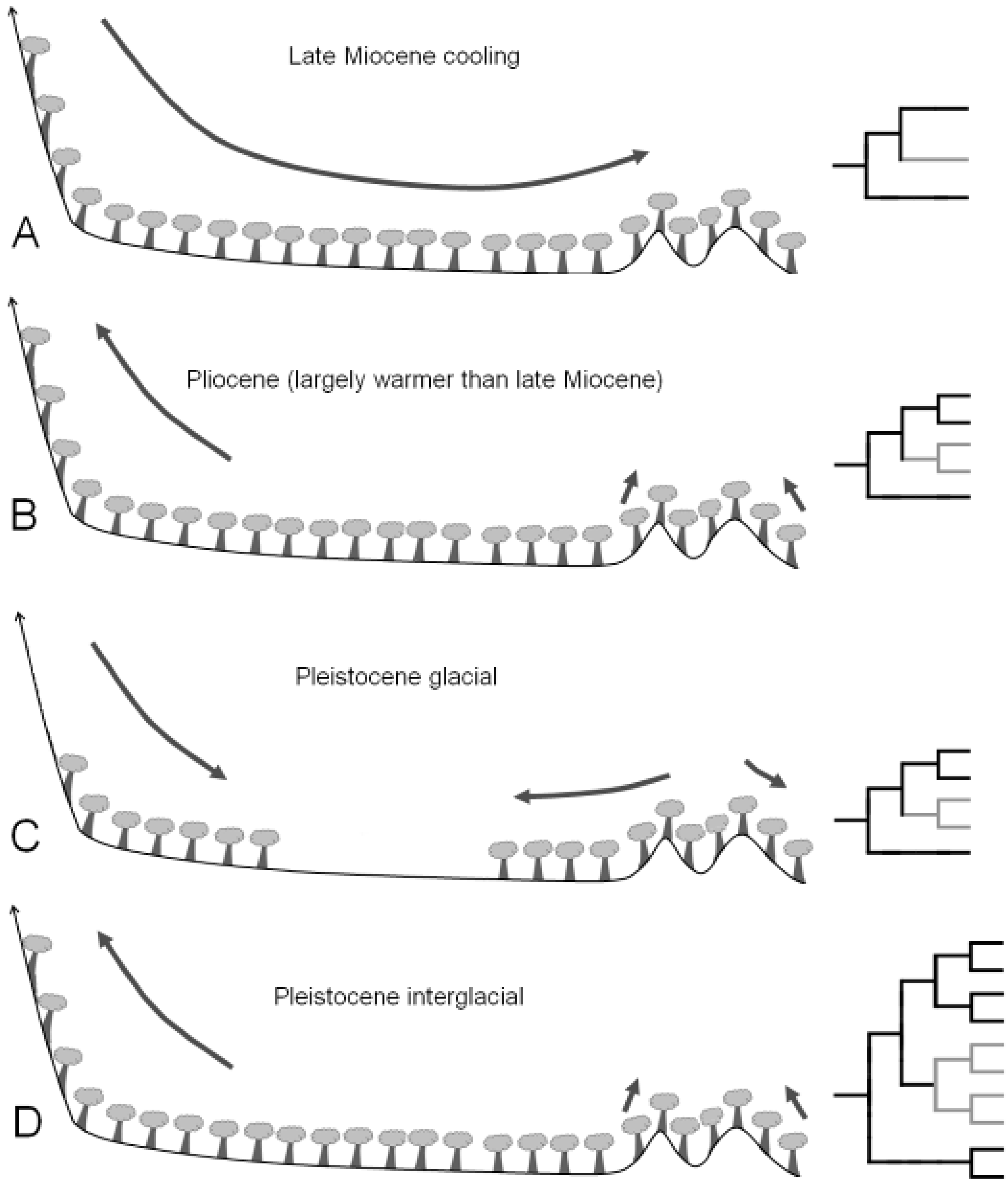

Figure 4.2-1 Schematic illustration of DV with Andes in the West (left) and the eastern Guiana Shield in the East: (A) cooling during the late Miocene allowed for dispersal (arrow in drawing, grey in phylogenetic tree) of cool-adapted forest taxa from the Andean versant eastward up to the eastern Guiana Shield; (B) due to subsequent warming (Pliocene) cool-adapted species were retracted to higher elevations (arrows) resulting in vicariant speciation (Guiana Shield species indicated in grey in phylogenetic tree); (C) speciation is 'disturbed' during Pleistocene glacials cool-adapted species as lowland dispersal was possible again (with limitations due to forest loss and the development of a western and an eastern forest fragment); (D) retraction to higher elevations and speciation continued during warmer interglacials (Guiana Shield species indicated in grey in phylogenetic tree). Scenario (D) was followed by (C) for several times. Scheme not to scale.

To their molecular phylogeny, NOONAN and GAUCHER (2005) added only four *Atelopus* species from outside the Guiana Shield. As a result, the validity of their study is pending additional corroboration. This is especially significant because our knowledge on the current-day distribution of harlequin frogs in central Amazonia is poorly understood: LESCURE and GASC (1986) proposed a continuous distribution of harlequin frogs from the Andes to the eastern Guiana Shield, whereas LÖTTERS et al. (2002), in a taxonomic study, were unable to trace *Atelopus* material in scientific collections from a large part of central Amazonia, casting some doubt on a continuous distribution. Such a hiatus could be well explainable by DV predictions, since the recolonisation of central Amazonia should not be possible during the current interglacial (Figure 4.2-1D). If DV is applicable to harlequin frogs, we expect that nowadays they display a natural distribution gap in central Amazonia. From a phylogenetic point of view, according to DV predictions and the results of NOONAN and GAUCHER (2005), we expect that harlequin frogs from east of this distribution gap in central Amazonia constitute a clade nested within those from the Andes and the adjacent Amazonian lowlands (Figure 4.2-1D) when expanding the genetic samples by inclusion of more species from outside Amazonia than available to NOONAN and GAUCHER (2005).

Species can respond to climate change in two ways. One is horizontal or vertical change of geographic range (i.e. increase, decrease up to extinction, shift) and maintenance of the specific climate envelope (also termed niche conservancy; WIENS and GRAHAM 2005). In the other the geographical range is retained, necessarily accompanied by climate envelope shift (PEARMAN et al. 2007). In DV, species change their geographic ranges (Figure 4.2-1A-D). Hence, there is reason to generally assume climate envelope maintenance. Vertical range shift of cool-adapted species along the Andean versant was up to 800 m (BUSH 1994). However, maximum altitudes found on the eastern Guiana Shield have been about 300 m above today's sea level only. Therefore, it is obvious that within the eastern glacial forest fragment (Figure 4.2-1C) climate envelopes have shifted in those cool-adapted species which have survived warmer periods. As a consequence, when comparing current-day *Atelopus* populations from western and eastern Amazonia (i.e. the former western and eastern forest fragments; Figure 4.2-1C), their climate envelopes under today's macroclimate, although overall similar, are expected to show some divergence.

The current interglacial reached its climate optimum about 8,000-4,500 years BP and temperature has decreased since then. According to DV, harlequin frog species should currently expand their distributions into lower areas. When mapping climate envelopes of current-day *Atelopus* populations from both western and eastern Amazonia under macroclimatic conditions into geographic space, they should range into central Amazonia. However, because of the expected climate envelope shift in eastern Amazonian *Atelopus*, mapped climate envelopes are expected to be rather allopatric than sympatric.

With the goal to reinforce DV predictions we combined different methodical approaches to study (i) if extant harlequin frogs display a central Amazonian distribution gap; (ii) if eastern Amazonian *Atelopus* constitute a single clade nested in a phylogeny comprising an enlarged data set from the Andes and adjacent lowlands; (iii) if climate envelopes of western versus eastern Amazonian populations are divergent under today's macroclimate; (iv) if allopatry is the result rather than sympatry when mapping these climate envelopes into geographic space.

Methods

A central Amazonian distribution gap

In order to determine the extant distribution of *Atelopus* in Amazonia, 87 presence data points from all over Amazonia were employed in this study (Figure 4.2-2). They were taken from published references and obtained through interviews with seven experts (see Appendix 4.2-S1). Interviews were open, non-standardized, as described by ATTESLANDER (1974). Only acknowledged experts in anuran taxonomy and with field experience in Amazonia or the Guiana Shield were interviewed. Additional presence data were taken from scientific collections. As an altitudinal limit for pre-Andean/western Amazonia we chose 800 m above sea level, the approximate upper border of the tierra caliente lowlands. Latitude and longitude coordinates for presence data points were obtained from the sources listed in the Appendix. If not provided, they were obtained through the Alexandria Digital Library Gazetteer (HILL and ZHENG 1999; http://www.alexandria.ucsb.edu/gazetteer).

In addition, 42 data points of apparent absence of harlequin frogs, illustrated in Figure 4.2-2 (see Appendix 4.2-S1), were obtained from published references and expert interviews as described above. We only included data points at elevations $\leq$ 800 m above sea level and situated in an area defined through a Minimum Convex Polygon (MCP) for all presence data, created with DIVA-GIS 5.4 (Points to Convex Polygon function).

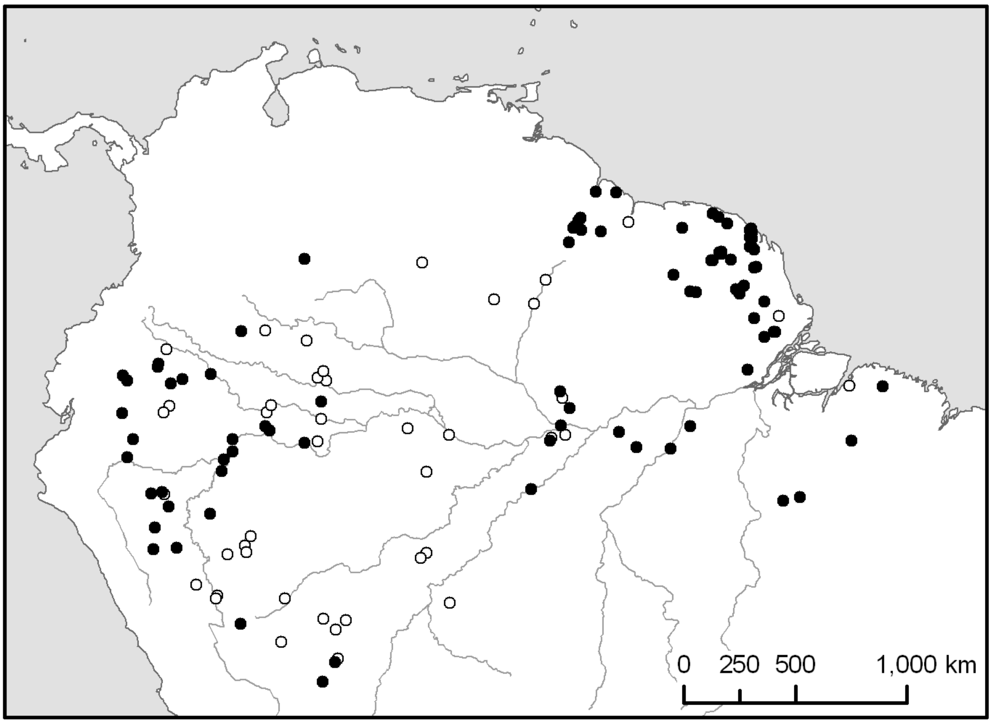

Figure 4.2-2 Northern South America showing data points of presence (filled circles) and apparent absence (open circles) of harlequin frogs in Amazonia (see Appendix).

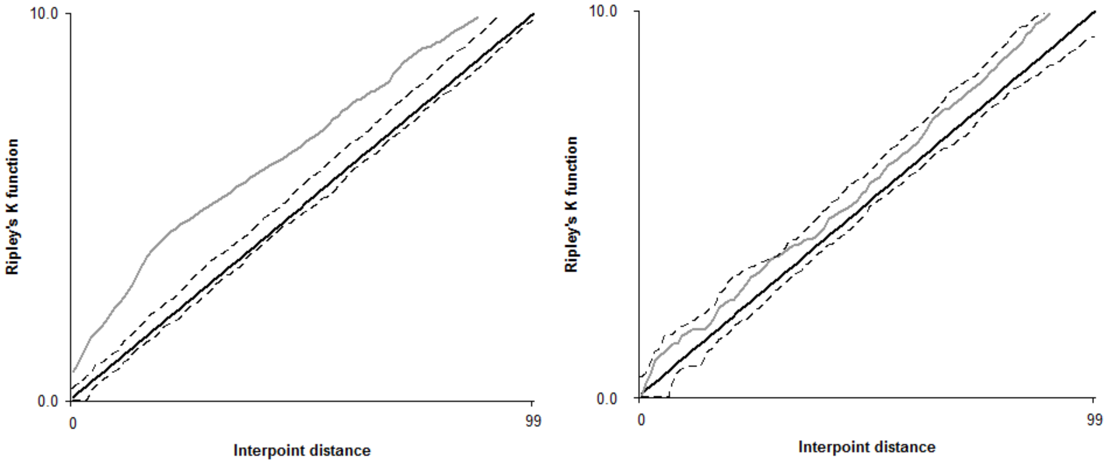

Figure 4.2-3 Ripley's K functions showing that presence data points (left) are significantly inhomogeneous (i.e. clustered) while apparent absence data points are homogeneously distributed (compare Fig. 2). Bold lack line: expected K function with lower and upper confidence envelopes (dashed), bold grey line: observed K function.

Ripley's K function, a multi-distance spatial cluster analysis, was used to study spatial dependence of both presence and apparent absence point patterns (Figure 4.2-2) by comparison to homogenous point patterns (RIPLEY 1977). If the K function varies significantly from a homogenous function, data points under study are clustered. Analysis was performed with the Spatial Statistics (confidence envelope: 99 permutations) tool box of ArcGIS Desktop 9.2 (ESRI; http://www.esri.com).

Nested monophyly of eastern Amazonian Atelopus

NOONAN and GAUCHER (2005) based their study on fragments of the mitochondrial genes cyt b and ND2. We here chose a fragment of the mitochondrial 16S rRNA gene for two reasons. First, this locus is a widely used marker in amphibian systematics, especially suitable because of strong constancy of priming sites and information content at the species level (VENCES et al. 2005). Second, the use of 16S allowed us to maximize the species sample size in order to study nested monophyly of eastern Amazonian harlequin frogs. As listed in Table 4.2-1, sequences of nine *Atelopus* (three outgroup species) were available via GenBank (http://www.ncbi.nlm.nih.gov; BENSON et al. 2004). We supplemented these data by sequencing 16S for 11 additional *Atelopus* plus four outgroup taxa (Table 1; Appendix 4.2-S2).

DNA was extracted from toe clips. Tissue samples (stored in 99 % ethanol) were digested using proteinase K (final concentration 1 mg/mL), homogenised and subsequently purified following a high-salt extraction protocol (BRUFORD et al. 1992). Polymerase chain reaction (PCR) primers for the fragment of the 16S rRNA gene were 16SA-L and 16SB-H of PALUMBI et al. (1991), used as in VAN DER MEIJDEN et al. (2007). PCR products were purified via spin columns (Qiagen). Sequencing was performed directly using the corresponding PCR primers. New sequences were combined with existing sequences taken from GenBank in the final dataset containing 27 taxa including bufonid and non-bufonid outgroups (Table 1). Sequences were aligned using ClustalW (THOMPSON et al. 1994) and subsequently edited by hand. The final alignment contained a total of 570 positions of which 219 were variable and 136 were parsimony-informative.

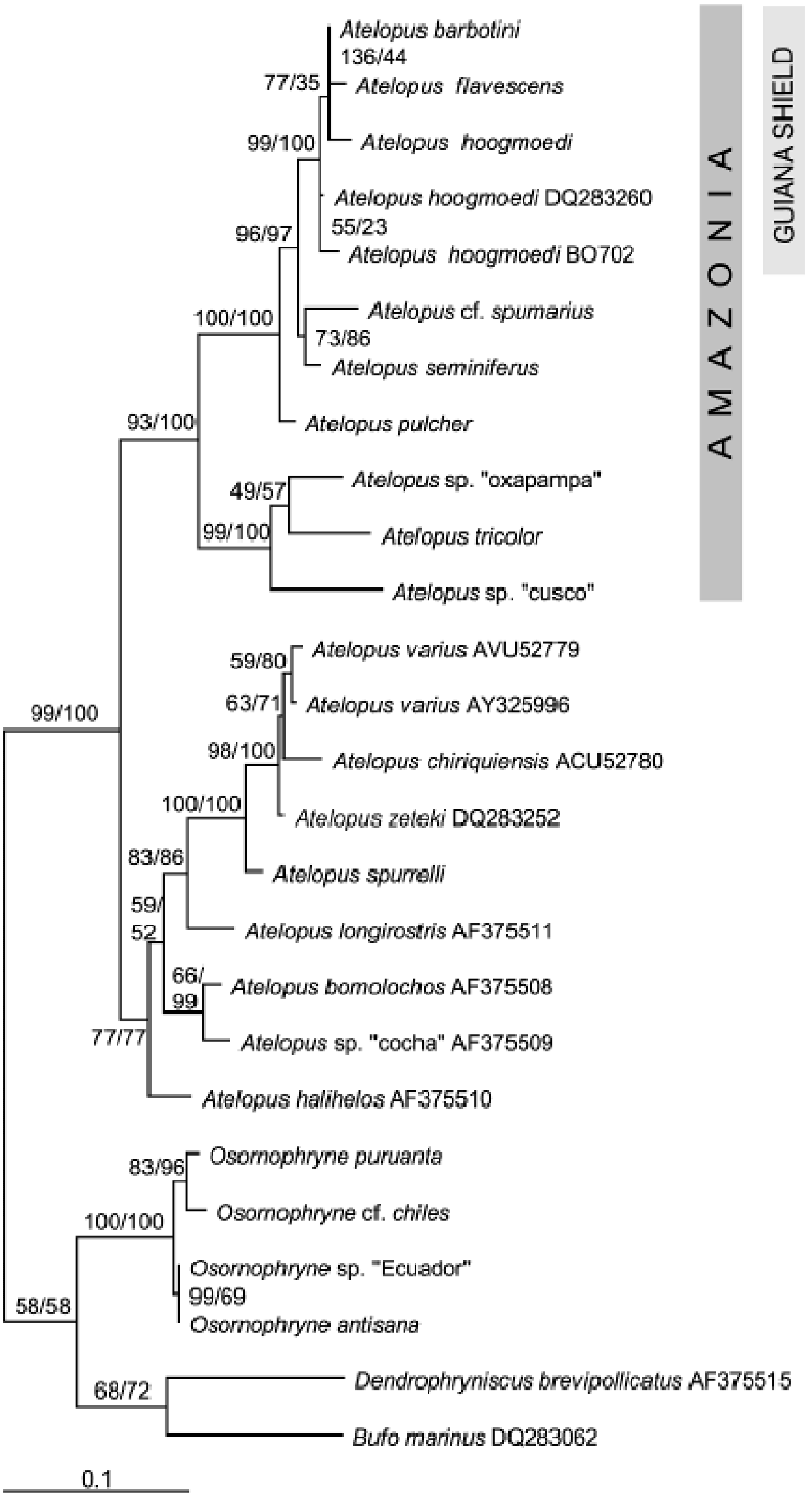

Figure 4.2-4 ML phylogram of different *Atelopus* species from all over the genus' range (Table 1) based on the mitochondrial 16S rRNA gene. Numbers above branches indicate Maximum Likelihood bootstrap support/Bayesian posterior probabilities values. Species names are accompanied by GenBank accession numbers. This tree was rooted with *Eleutherodactylus johnstonei* (not shown).

Phylogeny reconstruction was performed using Maximum Likelihood (ML) and Bayesian Inference (BI) methods. Gaps were treated as unknown characters. The best fitting models of sequence evolution were determined by the AIC criterion as implemented in Modeltest 3.06 (POSADA and CRANDALL 1998). ML tree searches were performed using PhyML, version 2.4.4 (GUINDON and GASCUEL 2003). Bootstrap branch support values were calculated with 200 replicates. The Bayesian analyses of the combined and separate datasets was conducted with MrBayes 2.0 (HUELSENBECK and RONQUIST 2001) with 2 million generations, sampling trees every 10th generation and calculating a consensus tree after omitting the first 200,000 trees as burn-in determined with the Tracer 1.4 (http://beast.bio.ed.ac.uk/Tracer). No well supported topological differences were found between the BI and ML trees; the ML tree was used in the subsequent analysis.

Divergence in climate envelopes and allopatry

Climate envelopes for western and eastern Amazonian *Atelopus* were modelled, compared and subsequently mapped into geographic space. For our approach we used the presence data points listed in the Appendix (30 for all western and 54 for all eastern Amazonian *Atelopus*; Figure 4.2-2) and seven macroscale bioclimatic parameters (Table 2) describing the availability of thermal energy and water, widely used in climate envelope models (e.g. CARNAVAL and MORITZ 2008). Using DIVA-GIS 5.4 (HIJMANS et al. 2001; http://www.diva-gis.org), bioclimatic parameters were extracted from the Worldclim 1.4 interpolation model with grid cell resolution 2.5 minutes for the period 1950-2000 (HIJMANS et al. 2005; http://www.worldclim.org). Climate envelope models were generated and mapped with MaxEnt 3.2.19 (PHILLIPS et al. 2006; http://www.cs.princeton.edu/~shapire/maxent) following the principle of maximum entropy (JAYNES 1957). This approach reveals more reliable results than comparable methods (ELITH et al. 2006; HEIKKINEN et al. 2006; WISZ et al. 2008), especially when data points for species number relatively few (e.g. HERNANDEZ et al. 2006). Using default settings, 25 % of the data points were randomly reserved for model testing (duplicate presence records in one grid cell were automatically removed). Prediction accuracy was evaluated through threshold-independent receiver operating characteristic (ROC) curves and the calculation of the area under the curve (AUC) method (e.g. HANLEY and MCNEIL 1982). We acknowledge that there is currently some discussion about the suitability of AUC (LOBO et al. 2008). However, for our application, AUC is the best possible choice, following ELITH and GRAHAM (in press) who pointed out that none of the frequently applied statistics is misleading and that appropriate statistics relevant to the application of the model need to be selected. The logistic MaxEnt output was chosen which is continuous and linear scaled (0-1, with 0.1 already suggesting suitability to the species under study; PHILLIPS et al. 2006).

We quantitatively compared climate envelopes of western and eastern Amazonian *Atelopus* with Schoener's index (D) and Hellinger distance (I) as modified by WARREN et al. (2008). Both indices allow for testing climate envelope similarity between two probability distributions of (e.g. climate envelope) distributions over geographic space, whereby D and I values range from 0 to 1 (i.e. models have no to entire overlap). We evaluated the significance of D and I values with null models regarding climate envelope similarity and equivalency representing two extremes within the spectrum of niche conservatism (WARREN et al. 2008). Tests were performed separately for each climatic parameter in the manner of RÖDDER and LÖTTERS (in press). Moreover, for climate envelope equivalency, we applied a randomization test as proposed by WARREN et al. (2008) which relies on the metrics D and I. For western and eastern Amazonian harlequin frog occurrences 100 pseudoreplicate datasets were created by randomly partitioning the pooled sets of $n_{western}$ + $n_{eastern}$ occurrences into sets of the same size of $n_{western}$ and $n_{eastern}$, respectively. Climate envelope models were built from each pseudoreplicate and compared to the percentiles of these null distributions in a one-tailed test to evaluate the hypothesis that climate envelope models for western and eastern records were not significantly different. This test allows for an assessment of climate envelope maintenance (i.e. niche conservancy) in a strictest sense, i.e. the effective equivalency of the climate envelope in the western and eastern geographic ranges. It is expected to be only met if western and eastern harlequin frogs tolerate exactly the same set of climatic conditions and have the same set of environmental conditions available to them.

In order to assess climate envelope similarity, we again used a randomization test of WARREN et al. (2008). It compares the actual similarity of climate envelopes in terms of D and I values to the distribution of similarities obtained by comparing them to a climate envelope model created through randomly choosing cells from among the cells in the study area. The same procedure was performed in both directions (western to eastern records vice versa) 100 times to construct an expected distribution of D and I values between a climate envelope model generated using actual occurrences and another one generated from random background data points extracted within a MCP enclosing one set of records.

These null distributions served as a two-tailed test to assess the null hypothesis that measured climate envelope overlap between western and eastern Amazonian *Atelopus* is explained by regional similarities or differences in available habitat. This hypothesis is rejected if the actual similarity falls outside the 95 % confidence limits of the null distribution. Significantly higher values suggest that climate envelopes are more similar than expected by chance and lower values indicate greater differences. Computations of D, I, climate envelope similarity and equivalency were performed with a Perl script developed by WARREN et al. (2008).

Results and Discussion

A central Amazonian distribution gap

Figure 4.2-2 suggests that indeed Amazonian harlequin frogs display a distribution gap in central Amazonia. Ripley’s K function for presence data points revealed significantly clustered results (i.e. inhomogeneous distributions), while those of apparent absence data points fall within the confidence intervals of a homogenous function (Figure 4.2-3). Clustered presence data points advocate that the distribution gap (Figure 4.2-2) is not random. Likewise, equally distributed absence data points (i.e. over the entire study area; Figure 4.2-2) suggest that not sampling bias can be made responsible for this distribution gap. These findings meet our expectation and hence support DV in Amazonian harlequin frogs. Taking into consideration other possible scenarios of Amazonian historical biogeography (summarized by NOONAN and WRAY 2006; HAFFER 2008), the paleogeographic hypothesis needs to be addressed here. It proposes marine incursions from the Pacific Ocean and the Caribbean Sea into western Amazonia in Late Miocene/Pliocene or an extensive Amazonian lake in Pliocene (see HAFFER 2008 and references therein). This may well explain a nowadays *Atelopus* distribution gap in this region. But also, the paleogeographic hypothesis does not contradict DV, as under both it is predicted that during Pliocene species were retracted to higher elevations, as shown in Figure 4.2-1B.

Table 4.2-1 List of species used for the molecular analysis, their GenBank accession numbers and origin. Note that some sequences provided in Appendix 4.2-S2 will only be uploaded to Gene Bank upon acceptance of the manuscript.

Species	Accession number	Locality
Atelopus bomolochos	AF375508	Ecuador: near Zhund
Atelopus chiriquiensis	U52780	Panama
Atelopus flavescens	flavescens 328	French Guiana: Lac des Americains
Atelopus barbotini	barbotini neu 336	French Guiana: near Saül
Atelopus halihelos	AF375510	Ecuador: near Plan de Milagro
Atelopus hoogmoedi	hoogmoedi 334	French Guiana: Monts Bakra
Atelopus longirostris	AF375511	Ecuador
Atelopus pulcher	pulcher s str Peru 298	Peru: Tarapoto region
Atelopus hoogmoedi	rafael BO702	Guiana: Mabura Hill region
Atelopus hoogmoedi	DQ283260	French Guiana: near Saül
Atelopus spurrelli	Spurrelli	Colombia: Bahía Solano
Atelopus seminiferus	*semiferus* Peru 308	Peru: Alto Mayo
Atelopus cf. *spumarius*	cf. Spumarius Peru 317	Peru: Iquitos region
Atelopus tricolor	tricolor Bolivi 319	Bolivia: Yungas de La Paz
Atelopus varius	U52779	Panama
Atelopus varius	AY325996	Costa Rica: near Las Alturas
Atelopus zeteki	DQ283252	Panama: Las Filipinas
Atelopus sp. ‘oxapampa’	sp Peru 299	Peru: Oxapampa region
Atelopus sp. ‘cusco	sp. Peru 320	Peru: near Puente Fortaleza
Atelopus sp. ‘cocha’	AF375509	Ecuador
Bufo marinus	DQ283062	Peru
Dendrophryniscus brevipollicatus	AF375515	Brazil
Osornophryne cf. *Chiles*	AGG532	Ecuador
Osornophryne puruanta	AGG572	Ecuador
Osornophryne antisana	antisana LaAngelin	Ecuador
Osornophryne sp. ‘Ecuador’	Osorno Equador 312	Ecuador
Eleutherodactylus cf. *johnstonei*	AF124123	unknown

Nested monophyly of eastern Amazonian Atelopus

Figure 4.2-4 illustrates a ML phylogram for 20 harlequin frogs and outgroups. All Amazonian *Atelopus* comprise a well supported monophyletic lineage, which is sister to all other members in the genus (i.e. a combination of Andean and trans-Andean species; Table 4.2-1). Within this Amazonian clade, two sub-clades are evident, supported by high bootstrap and Bayesian posterior probability values. One unites the species from central to southern Peru and Bolivia, i.e. an *Atelopus tricolor*-clade (compare Figure 4.2-4). The other is comprised of species from the region of the upper portion of the Amazon River plus the Guiana Shield and the adjacent Amazon basin. This clade provides strong support for the Guiana Shield *Atelopus* forming a monophyletic lineage. As already shown by NOONAN and GAUCHER (2005), *Atelopus* species within this clade are little differentiated, as reflected by the weak support of groupings among them.

In summary, evidently a single *Atelopus* ancestor has survived and recently speciated in eastern Amazonia, in particular on the Guiana Shield. This does not only well support findings by NOONAN and GAUCHER (2005) but also well meets our expectation under DV. The molecular phylogenetic data leave little space for other interpretations than DV (see discussion in NOONAN and GAUCHER 2005).

Divergence in climate envelopes and allopatry

Prediction accuracy of MaxEnt climate envelope models computed with all bioclimatic variables was high as suggested by ‘excellent’ AUC values (western Amazonian *Atelopus*: test 0.955, training 0.980; eastern Amazonian *Atelopus*: test 0.979, training 0.985) following the classification accuracy of SWETS (1988).

Comparing box plots (Figure 4.2-5), climate envelopes of western and eastern Amazonian *Atelopus* are similar as ranges of all bioclimatic parameters in our modelling approach overlap. Two of the temperature parameters, ‘annual mean temperature’ and ‘maximum temperature of the warmest month’, are rather alike (not significantly different; Table 4.2-2), while one temperature and two of the precipitation parameters, ‘mean monthly temperature range’, ‘precipitation of the wettest month’ and ‘precipitation of the driest month’, show significant divergence (Table 2). These observations are highly coincident with the D and I values characterizing the climate envelope overlap (Table 2). The niche identity tests revealed that the climate envelopes of eastern and western harlequin frogs were identical in terms of annual means of temperature and precipitation, slightly divergent in the 'maximum temperature of the warmest month' and the 'mean monthly temperature range' (significance level < 0.05). The null hypothesis that climate envelopes are equivalent in the western and eastern ranges was rejected for all other parameters. The climate envelope similarity test revealed that overlap in the 'annual mean temperature' and the 'maximum temperature of the warmest month' can be traced back to active habitat choice. These findings corroborate our expectation that climate envelopes of western and eastern Amazonian harlequin frogs show some divergence. However, background effects may at least partly explain the overlap patterns observed the other parameters, whereby eastern Atelpus actively chose their habitats according to some parameters but background effects have been involved in the habitat choice of western *Atelopus* vice versa. Such patterns are reasonable since different parameter may be widely available or limiting in eastern or western ranges influencing habitat choice.

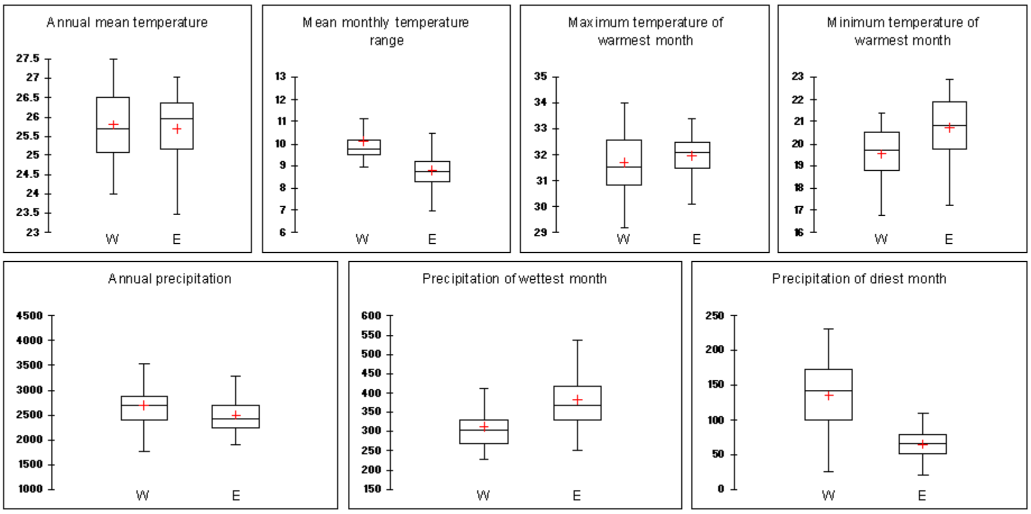

Figure 4.2-5 Box plots of seven bioclimatic parameters in climate envelope models of western and eastern Amazonian *Atelopus*. Values given in the upper row refer to temperature in °C and those in the lower row refer to precipitation in mm.

Table 4.2-2 AUC values per model, climate envelope overlap in terms of *I* and *D* values and assessment of their similarity and equivalency via randomization tests (see text). Significant values of climate envelope equivalency are indicated with asterisks; ns = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$. Values where observed overlap is greater than the null distribution are indicated in bold, values where overlap was smaller than the null distribution are italicized.

Bioclimatic variables	Model fit	*D*			*I*		
	$\text{AUC}_{\text{Western}}$, $\text{AUC}_{\text{Eastern}}$	Overlap	Identity	Similarity	Overlap	Identity	Similarity
				Western, Eastern			Western, Eastern
Annual mean temperature	0.798, 0.750	0.93	ns	**< 0.001**, **< 0.05**	0.94	ns	**< 0.001**, **< 0.05**
Mean monthly temperature range	0.796, 0.896	0.58	< 0.001	< *0.001*, ns	0.72	< 0.05	< *0.001*, ns
Maximum temperature of the warmest month	0.738, 0.806	0.81	< 0.05	**< 0.05**, < *0.001*	0.87	< 0.05	< 0.05, < *0.001*
Minimum temperature of the coldest month	0.871, 0.850	0.74	< 0.001	**< 0.05**, ns	0.82	< 0.001	**< 0.05**, ns
Annual precipitation	0.881, 0.839	0.90	ns	**< 0.001**, ns	0.94	ns	**< 0.001**, ns
Precipitation of the wettest month	0.743, 0.849	0.78	< 0.001	ns, **< 0.001**	0.86	< 0.001	ns, **< 0.05**
Precipitation of the driest month	0.914, 0.857	0.55	< 0.001	ns, < *0.001*	0.70	< 0.001	ns, < *0.001*

Due to 'excellent' AUC values suggesting high prediction accuracy (see above), we mapped climate envelope of western and eastern Amazonian *Atelopus* into geographic space on the full presence data point sets (i.e. this time no data points were set aside for testing), to take advantage of all available information and to provide best estimated prediction maps (see PHILLIPS et al. 2006). Results are shown in Figure 4.2-6. Fitting well with the comparison of the climate envelops of the two units studied (Figure 4.2-5; Table 4.2-2), their geographic distributions are largely allopatric with overlap corresponding to lower suitability (i.e. lower MaxEnt values). Areas of higher suitability of climate envelopes (i.e. warmer colours in Figure 4.2-6) of western and eastern Amazonian *Atelopus* show little or no overlap.

Application of a climate envelope modelling approach and using macroscale bioclimate supports the presence of a western and eastern group of Amazonian *Atelopus*. Taking into account the different historical biogeographic scenarios of Amazonian diversification (summarized by NOONAN and WRAY 2006; HAFFER 2008), none of these addresses climate envelope change. In contrast, climate envelope maintenance due to geographic distribution change is expectable in the disturbance-vicariance, paleogeographic, riverine barrier, refuge, river-refuge, canopy density, gradient and museum hypotheses. On the other hand, this does not per se rule out climate envelope change posterior to geographic range increase, decrease or shift. Such a scenario is most plausible in the case of cool-adapted taxa of Andean origin.

Conclusions

Different scenarios have been proposed attempting to explain plant and animal diversification and distributions in the Amazon basin and adjacent areas. There is an ongoing debate on them, as hypotheses in part contradict, while others can be 'harmonised' with each other (e.g. DV and the paleogeographic hypothesis as discussed above). We here address DV in harlequin frogs and found that four expectations formulated, combining different methods, were fulfilled reinforcing this hypothesis. We suggest that not only species change their geographic ranges but also their climate envelopes. This led us to include a climate envelope assessment, never addressed before in historical biogeography of Amazonia and its vicinities.

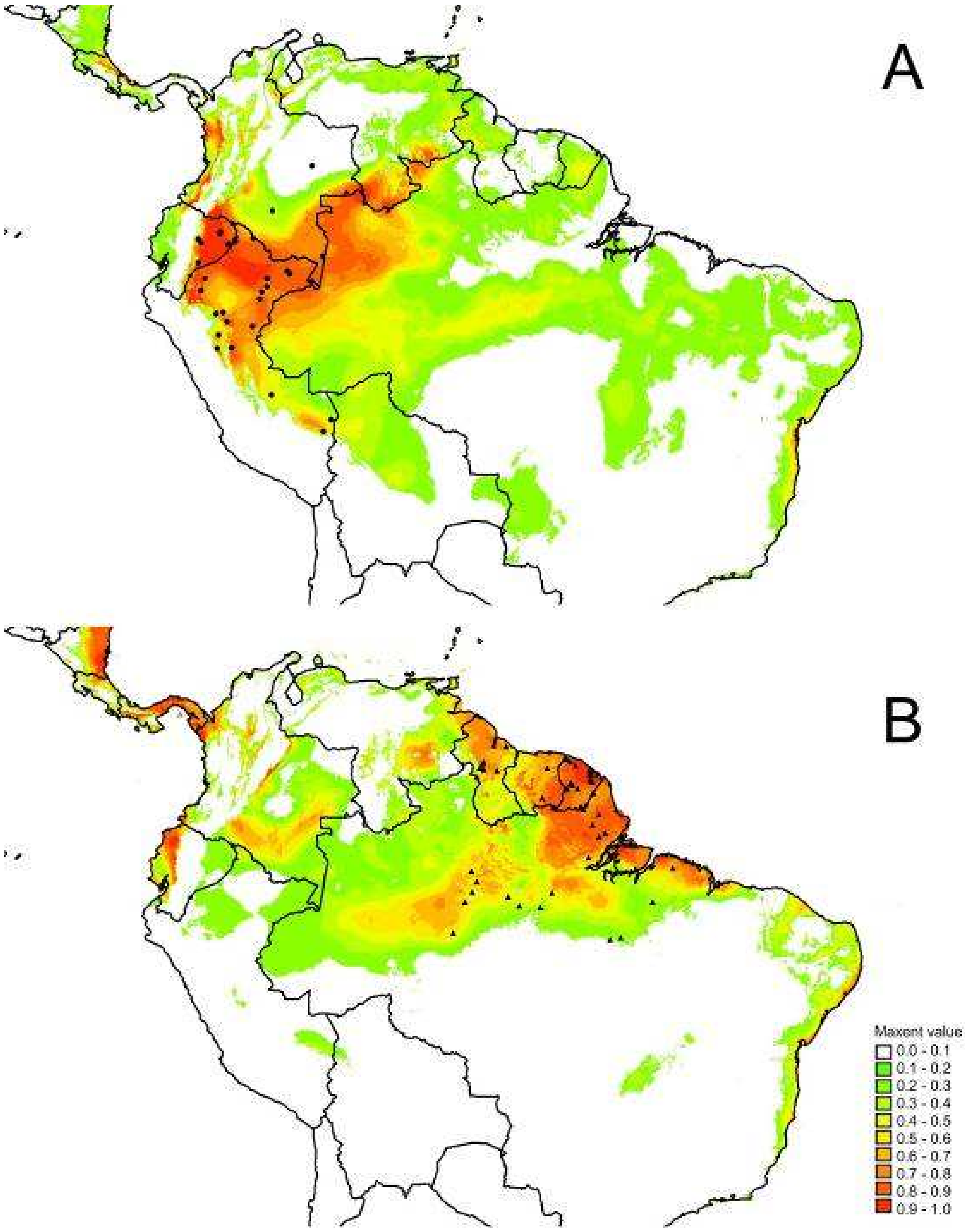

Figure 4.2-6 Potential distributions of western (A) and eastern (B) Amazonian *Atelopus*. Colours from green via yellow to red refer to MaxEnt values of probability with warmer colours standing for areas with better predicted conditions (range 0-1, logistic MaxEnt output). Illustrations were performed with DIVA-GIS 5.4.

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5. SUMMARY

The present thesis investigates relationships of variation in large scale climate, ecological niches of amphibians and reptiles and their corresponding geographic distribution patterns. As suggested by several authors, anthropogenic climate change may harm much of the world's biota. However, our knowledge on processes leading to these threats and our ability to make robust predictions of possible impacts is still limited but pivotal to develop successful management strategies. The goal of the thesis at hand is to narrow some of those knowledge gaps. The results are presented in four sections, each with several chapters focussing on different aspects of the link between macro-climate, species' ecological niches and their distribution patterns.

Section 1

A general overview is provided of the pertinent knowledge on the impact of climate change on biota, ecological niche concepts, availability of both climate and species occurrence data and the methods used herein. Additionally, potential methodical or conceptual 'pitfalls' when applying so called environmental niche models or climate envelope models are highlighted, illustrated and discussed using examples.

Section 2

The focus here lays on the structure of species' climate niches. Climatic variability within species ranges and habitat choice are analysed and discussed in the context of natural history properties of the respective species.

Chapter 2.1. Climate is suggested to be one major driver shaping species range patterns. Especially species with temperature-dependent sex determination may rely on particular climatic conditions, such as the Slider (*Trachemys scripta*) from North America. In this chapter, it is hypothesised that climatic requirements allowing successful egg incubation and balanced sex ratios in *T. scripta* are the major driver for the species' geographic distribution. It is tested if the observed variation in monthly mean temperatures at 377 records throughout the native distribution of the target species can be used as a predictor for its geographic range. This study shows that apparently climatic requirements during egg-incubation are the major driver for the species' distribution. Merely freezing events during winter may regionally limit its distribution. Adaptive strategies such as nest site choice by females, plasticity in nesting phenology or regional variation in embryonic temperature sensitivity exist. However, regional variation may account only for partial compensation of negative effects caused by regional differences in temperature related parameters or a changing climate.

Chapter 2.2. Recently, several authors have observed a climatic mismatch between native and invasive ranges predicted by Climate Envelope Models (CEMs). The present chapter address the issue of climate niche shift in alien invasive species versus variable choice by deriving CEMs based on multiple variable sets. The first selection of predictors aims at representing the physiological limits of the well studied alien invasive Slider. This model was compared to numerous other models based on various subsets of environmental variables or aiming at comprehensiveness. The CEMs aiming to represent the species physiology depicts its worldwide potential distribution better than any of the other approaches. The results indicate that a natural history driven understanding is crucial in developing statistical models of niches while ‘comprehensive’ or ‘standard’ sets of explanatory variables may be of limited use.

Chapter 2.3. The use of CEMs to predict potential distributions of species is steadily increasing. A necessary assumption is that climatic niches are rather conservative, but recent findings of (climate) niche shifts during biological invasion indicate that this assumption is not valid in every case. Selection of predictor variables may be one reason for observed shifts. This chapter addresses differences in climatic niches in the native and invaded ranges of the Mediterranean Housegecko (*Hemidactylus turcicus*) in terms of commonly applied climate variables in CEMs. It is analyzed which variables are more conserved versus relaxed (i.e. subject to niche shift). Furthermore, the predictive power of different sets of climate variables is studied. Models for the Mediterranean region and the conterminous United States (US) are created using various subsets of variables out of 19 environmental layers. Occurrence data from the native range in the Mediterranean region were used to predict the introduced range in the US and vice versa. Niche similarity and conservatism per predictor and per set of predictors are contrasted using Schoener’s index and modified Hellinger distance. Significance of results was tested using null models. The results indicate that the degree of niche similarity and conservatism vary greatly among predictors and variable sets applied. Shifts observed in some variables can be attributed to active habitat selection whereby others apparently reflect so called background effects. The study is based on comprehensive occurrence data from all regions where *H. turcicus* is present in Europe and the New World providing a robust fundament for the study. Further, the results suggest that the degree of niche similarity and conservatism considerably vary among predictors and variable sets applied. These results have important implications for studies of biological invasion, impacts of climate change and niche evolution.

Section 3

This part of the thesis at hand focus on the relative importance of dispersal abilities, accessibility and biotic interactions shaping a species' realized distribution.

Chapter 3.1. Globalization has led to a heightened spread of alien invasive species, which can alter mutualistic relationships, community dynamics, ecosystem function resource distributions etc. They can cause species extinctions affecting thereby local and global diversity. Among the reptiles two gecko species, *Hemidactylus frenatus* and *H. mabouia*, have considerably increased their geographic ranges during the last century. It has been shown that within their invasive ranges both have caused local decimations and extinctions of native taxa. Records of invasive populations of *H. frenatus* are known from tropical Asia, Central America and adjacent North America (Florida), while invasive *H. mabouia* populations occur in Central and Southern Africa as well as in large portions of Central and South America. Only few sympatric populations of these geckos are known. The aim here is to identify worldwide areas potentially suitable for these species using CEMs, to predict their potential distributions under current conditions and a future climate change scenario and to try to assess for what reason sympatric populations of both are apparently rare. The results demonstrate that climatically suitable areas of both species can be found in nearly all tropical regions. Future projections revealed that the amount of climatic suitable areas will increase for *H. frenatus* at the global scale, but decrease for *H. mabouia*. Most remarkable changes are suggested for South America where further spreading of *H. frenatus* will be enhanced due to changing climate. In contrast, climatic conditions for *H. mabouia* will be aggravated here. It is concluded that both competitive exclusion and a non equilibrium in the geographic ranges of these geckos explain the virtual absence of sympatry, although the impact of climate on competition success is pending further testing in the field.

Chapter 3.2. It is suggested that CEMs may only be of limited use if the target species' range is not predominately limited by unsuitable climate. The goal of this chapter is to test this assumption using the alien invasive anuran *Eleutherodactylus coqui* as a model species, originating from Puerto Rico. It is presently distributed on many Caribbean islands and Hawaiian Islands where it causes major ecological and socioeconomic problems. In the given approach the climate envelope of the native potential distribution of this species is projected into geographic space in order to identify further areas suitable for successful establishment. The results advocate that under current climate there exist high probabilities of occurrence in tropical regions including the Caribbean, Florida, major parts of the Amazon basin and the adjacent Andes, the Pantepui region, Africa's Congo basin and many Asian islands. Using native Puerto Rican occurrence data for CEM training, the results indicate that the invasive range on the Hawaiian Islands can be predicted with high accuracy. Projections of potential distributions under future anthropogenic global warming scenarios on the Hawaiian Islands suggest an overall stable potential distribution, but fine scale patterns suggest a possible range allocation towards higher elevations which may affect existing nature reserves of high species richness and endemism. If the predictive maps are interpreted as depicting invasiveness potential of *E. coqui,* strategies to prevent further invasion should focus on biosafety measurements within the areas highlighted.

Chapter 3.3. Here, the invasive alien treefrog *Osteopilus sepentrionalis,* native to Cuba, the Bahamas and some adjacent islands, was used as an example to study if climate is not the predominantly driver of the geographic range. This anuran was accidentally introduced to Florida, Puerto Rico and some Hawaiian islands, where it it predates to and competes with native wildlife. The potential spread derived from present climate conditions in its native geographic distribution is modeled and projected onto future climate change scenarios in order to detect new areas which are potentially threatened. The CEM, applying current climatic conditions, suggests high probabilities of occurrence in the Gulf of Mexico. As in chapter 3.2, the findings indicate that the invasive range in Florida can be predicted with high accuracy using native records only (Cuba and Bahamas) for model training if the predictor variables are carefully chosen in respect of natural history properties of the target species.

Chapter 3.4. Biotic interaction such as competitive exclusion or predation limits the realized distribution of species although climatic conditions are well suitable to them. Such a pattern is assessed here, as observed in the Brown tree snake (*Boiga irregularis*). This snake is native to South-East Asia and Australia and has been introduced to the island of Guam. Here, it has caused major ecological and socioeconomic problems and why it is considered as one of the 100 worldwide worst alien invasive species. A CEM is used to identify areas outside the species' known range which worldwide are potentially suitable under current climate. Projections revealed that this invasive alien species potentially occurs in tropical and in part subtropical regions. In the larger vicinity of the snake's known distribution, highest suitability was found for the Northern Mariana and Hawaiian Islands, Madagascar, New Caledonia and Fiji Islands, all areas of high species richness and/or local endemism. However, although most East Asian mainland and island areas are climatically suitable to *B. irregularis*, the invasive populations of this species do virtually not exist. The predicted potential distribution is highly coincident with the general distribution of the genus *Boiga*. Since *B. irregularis* does not coexist with other members of the genus or other potential competitors in its native range, competitive exclusion may be considered as a possible explanation for the observed pattern.

Chapter 3.5. Anthropogenic habitat alteration has a strong impact on native biota and can significantly shape distribution patterns. *Eleutherodactylus johnstonei*, native to the northern lesser Antilles, has established numerous invasive populations on Caribbean islands and the adjacent Central and South American mainland. The species is a highly successful colonizer, but is able to invade anthropogenic disturbed habitats only. A CEM is applied to model the geographic distribution of this species and to project it onto other potentially threatened areas. Results obtained from the model are compared with a measure of anthropogenic habitat disturbance (Human Footprint). Results suggest a high probability of occurrence in large parts of southern Central America, at the northern and north-eastern coast of South America and in the Andes of Colombia, Ecuador and Venezuela. The Andean region, harbouring a diverse amphibian fauna, which is considered to be highly threatened due to anthropogenic habitat alteration, appears to be at highest risk with regard to further spread of *E. johnstonei*. If the predictive maps are interpreted as depicting invasiveness potential of this species, strategies to prevent further invasion should focus on biosafety measurements within the areas identified here.

Section 4

The breadths of climate niches, their evolution and dynamics in space and time are the target here.

Chapter 4.1. If climate changes a species' range may shift as a respond. If dispersal limitation exists hampering range shifts, a species' range may (i) shrink, (ii) the species' niche breadth may be large enough to buffer changing environmental conditions or (iii) the species may adapt to them. The day-gecko *Phelsuma parkeri*, endemic to the island of Pemba (Tanzania, with elevational range 0 to < 100 m a.s.l. only), is used as a case study to focus on these aspects. Information on its distribution on the island and its conservation status is poor. Information on the potential distribution of *P. parkeri* and its adaptability to habitat modification and changing climates are provided here using a CEM. Findings suggest that *P. parkeri* is hitherto highly adaptable to anthropogenic habitat modification. A comparison with paleoclimatic conditions during the Last Glacial Maximum (ca. 21 k BP) on Pemba revealed that this reptile and likewise other endemic species of the island survived an entirely different climate compared to today due to the absence of possibilities to compensate these changes by altitudinal range shift. it is concluded that *P. parkeri* is currently unlikely to be threatened by climate change although projection of its current realized climate niche suggest a complete range loss. The main potential threat identified may include the introduction of invasive species such as *Phelsuma dubia*, which is already established on the nearest island Zanzibar. Based on the findings, it is propose that *P. parkeri* should be categorized as Near Threatened under the IUCN Red List of Threatened Species.

Chapter 4.2. The disturbance vicariance hypothesis (DV) has been proposed to explain speciation in Amazonia, especially its edge regions, e.g. in Guianan harlequin frogs (*Atelopus*). There is evidence that these have originated from a cool-adapted Andean ancestor. In this chapter, in concordance with DV predictions, it is expected that: (i) these amphibians display a natural distribution gap in central Amazonia; (ii) east of this gap they constitute a monophyletic lineage which is nested within in a pre-Andean/western clade; (iii) climate envelopes of *Atelopus* west and east of the distribution gap show some macroclimatic divergence due to regional climate envelope shift; (iv) geographic distributions of climate envelopes of western and eastern *Atelopus* (i.e. the species' potential distributions) range into central Amazonia but with limited spatial overlap. It is tested if presence and apparent absence data points of *Atelopus* are homogenously distributed applying Ripley’s K function. A molecular phylogeny (mitochondrial 16S rRNA gene), by application of Maximum Likelihood and Bayesian Inference, was reconstructed to study if Guianan *Atelopus* constitute a nested clade within a larger genus phylogeny. Climate envelope divergence and geographic distribution are focused by computing CEMs based on macroscale bioclimatic parameters and testing them with using Schoener’s index and modified Hellinger distance. All four expectations are corroborated leading to the conclusion that DV predictions are well applicable to Amazonian harlequin frogs.

Conclusions in brief

The results of this thesis update our status of knowledge on the link between climate change and corresponding responses of species in terms of changes in their phenology and/or their distribution patterns. They will hopefully enhance our ability to understand and probably manage some of the problems arising due to anthropogenic climate change. However, although our qualitative understanding of processes and mechanisms causing patterns of species phenology and distribution has been largely extended during the last decades, it is still far from being comprehensive and our ability to make robust quantitative predictions is still limited.

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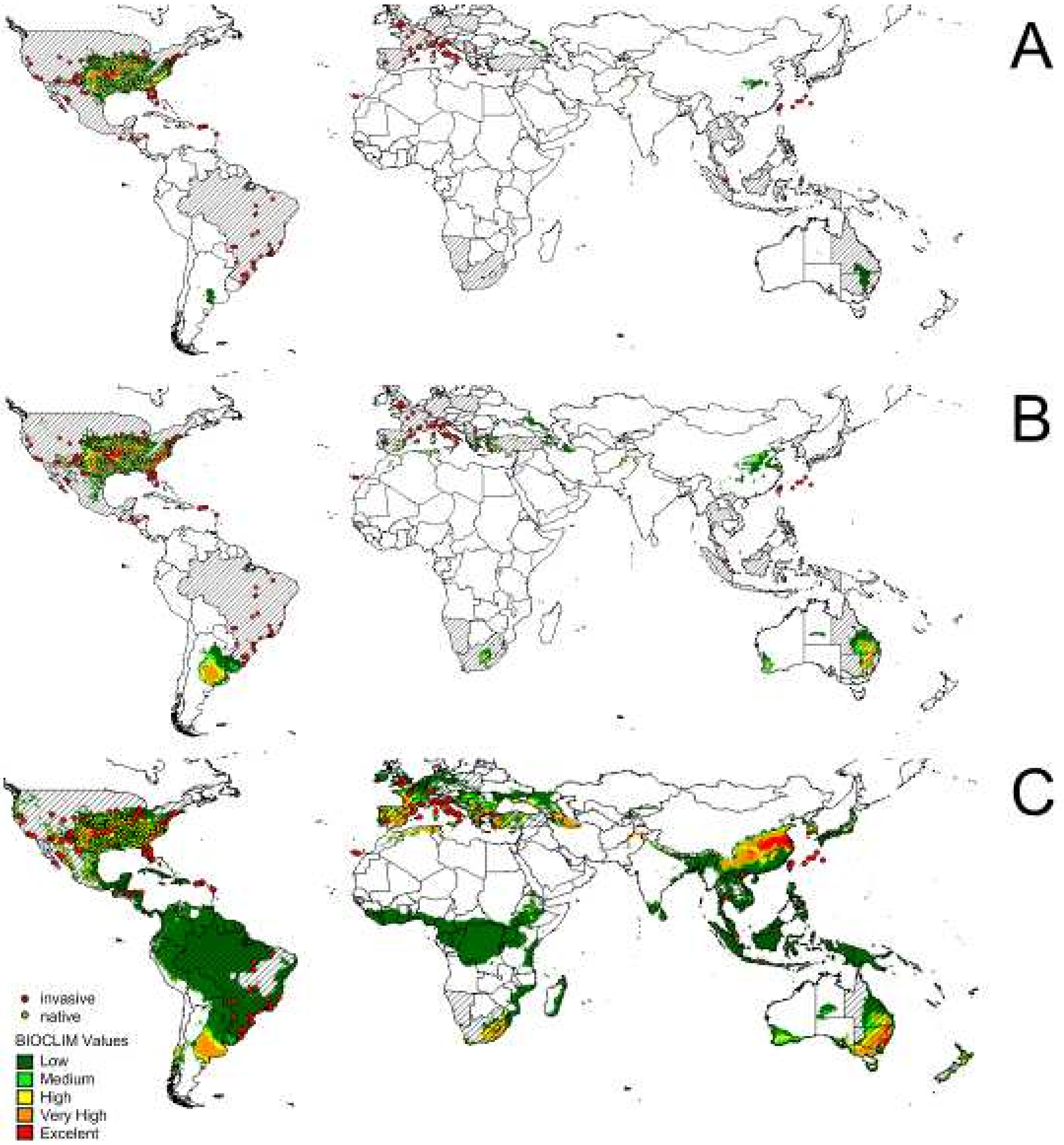
7. APPENDIX

Appendix 2.2-S1

Variation of 19 ‘bioclimate’ variables within the native and invasive ranges of the Slider.

	Native records				Invasive Records			
	min	mean	max	SD	min	mean	max	SD
annual mean temperature [°C]	8.3	15.6	23.3	2.9	6.4	16.8	28.0	5.4
mean monthly temperature [°C]	7.6	13.4	18.6	1.8	5.3	11.5	20.0	3.8
Isothermality	26.2	37.3	48.5	4.6	26.4	45.2	76.6	12.5
temperature seasonality	548.6	849.1	1095.4	130.0	41.0	564.5	1123.1	270.1
maximum temperature warmest month [°C]	28.9	33.3	37.4	1.6	19.2	30.5	41.4	4.0
minimum temperature coldest month [°C]	-12.6	-2.9	8.9	4.7	-12.6	3.7	21.8	8.7
temperature annual range [°C]	24.6	36.2	44.5	4.5	9.3	26.8	43.4	9.2
mean temperature wettest quarter [°C]	5.3	20.0	27.9	5.7	1.9	19.8	32.3	7.1
mean temperature driest quarter [°C]	-5.8	10.4	28.7	9.5	-5.6	14.5	28.0	8.8
mean temperature warmest quarter [°C]	21.2	25.8	30.1	1.5	13.3	23.7	32.5	3.5
mean temperature coldest quarter [°C]	-5.8	4.8	15.8	4.4	-5.6	9.9	26.9	8.2
annual precipitation [mm]	278.0	989.6	1652.0	372.1	142.0	942.6	2682.0	521.4
precipitation wettest month [mm]	55.0	121.9	203.0	32.9	25.0	135.2	460.0	80.9
precipitation driest month [mm]	6.0	47.3	102.0	28.7	0.0	34.6	114.0	26.8
precipitation seasonality	9.9	35.6	77.3	18.3	7.9	48.1	118.3	27.1
precipitation wettest quarter [mm]	138.0	327.6	524.0	89.8	59.0	369.1	1190.0	221.8
precipitation driest quarter [mm]	22.0	164.6	337.0	96.1	2.0	121.2	389.0	87.9
precipitation warmest quarter [mm]	123.0	277.8	524.0	82.1	6.0	281.6	967.0	207.1
precipitation coldest quarter [mm]	22.0	202.6	449.0	139.0	9.0	176.7	674.0	116.2



Appendix 2.2-S2
Presence of the Slider in its native range (green dots) and invasive range where it is known to reproduce (red dots), countries from which reproducing populations are known but no specific localities are available (hatched) and potential distribution derived from BIOCLIM climate envelope (colored): (A) using 19 'bioclimate' variables, approach 'comprehensive'; (B) using 7 'bioclimate' variables, approach 'minimalistic'; (C) using 5 'bioclimate' variables derived from physiological and natural history traits of the Slider, approach 'natural history'.

Appendix 2.3-S1

Additional records of *Hemidactylus turcicus* were obtained from the following references:

BEAMAN, K.R., D.M. GOODWARD, N.T. MOORHATCH & C.W. BROWN (2005) Geographic distribution: *Hemidactylus turcicus* (Mediterranean House Gecko). *Herpetological Review* 36: 79.

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CONANT, R. & J.T. COLLINS (1998) Reptiles and amphibians of eastern / central North America. 3rd edition, Houghton Mifflin Company, New York.

DANIEL, R.E., B.S. EDMOND & J.T. BRIGGLER (2004) New herpetological records from Missouri for 2004. *Newsletter of the Missouri Herpetological Association* 17: 9-12.

DOWLING, R.G. (1996) The Mediterranean gecko, *Hemidactylus trucicus*, in Prattville, Alabama. *Bulletin of the Chicago Herpetological Society* 21: 203.

EASON, G.W., & D.R. MCMILLAN (2000) Geographic distribution: *Hemidactylus turcicus*. *Herpetological Review* 31: 53.

GOMEZ-ZLATAR, P., M.P. MOULTON & R. FRANZ (2006) Microhabitat use by introduced *Hemidactylus turcicus* (Mediterranean Gecko) in North Central Florida. *Southeastern Naturalist* 5: 425-434.

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KNIGHT, C.M. (1993) A northern range extension of *Hemidactylus turcicus* in the United States. *Dactylus* 2: 49-50.

KRYSKO, K.L., K.M. ENGE, J.H. TOWNSEND, E.M. LANGAN, S.A. JOHNSON & T.S. CAMPBELL (2005) New country records of amphibians and reptiles from Florida. *Herpetological Review* 36: 85-87.

LEE, J.R. (2008) Geographic distribution of *Hemidactylus turcicus* (Reptilia: Squamata: Gekkonidae) in Mississippi. *Journal of the Mississippi Academy of Sciences* 53: 184-188.

LARDIE, R.L. (2001) Geographic distribution: *Hemidactylus turcicus*. *Herpetological Review* 32: 119.

MANNING, G.J., & J.T. BRIGGLER (2003) Geographic distribution: *Hemidactylus turcicus*. *Herpetological Review* 34: 384.

NORDEN, A.W., & B.B. NORDEN (1991) The Mediterranean gecko (*Hemidactylus turcicus*) in Baltimore, Maryland. *Maryland Naturalist* 33: 57-58.

PAINTER, C.W., P.W. HYDER & G. SWINFORD (1992) Three species new to the herpetofauna of New Mexico. *Herpetological Review* 23: 62.

PAULISSEN, M.A., & T.M. BUCHANAN (1990) Geographic distribution: *Hemidactylus turcicus*. *Herpetological Review* 21: 22.

SAETHRE, M.B., & P.A. MEDICA (1993) *Hemidactylus turcicus* (Mediterranean gecko). USA: Nevada. *Herpetological Review* 24: 154-155.

SATTLER, P., C. LANE & K. HARRIS (2007) Status and distribution of the Mediterranean gecko (*Hemidactylus turcicus*) in Virginia. *Catesbeiana*, **27**.

SIAS, D.S., & P.E. HUMPHREY (2002) Geographic distribution: *Hemidactylus turcicus*. *Herpetological Review* 33: 66.

SHEEHY, C.M.I. (2004) Geographic distribution: *Hemidactylus turcicus. Herpetological Review* 35: 287.

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UGURTAS, I.H., H.S. YILDIRIMHAN & M. SEVINC (2007) Distribution of the gekkonidae species in southeast Anatolia, Turkey, and new localities. *Turkish Journal of Zoology* 31: 137-141.

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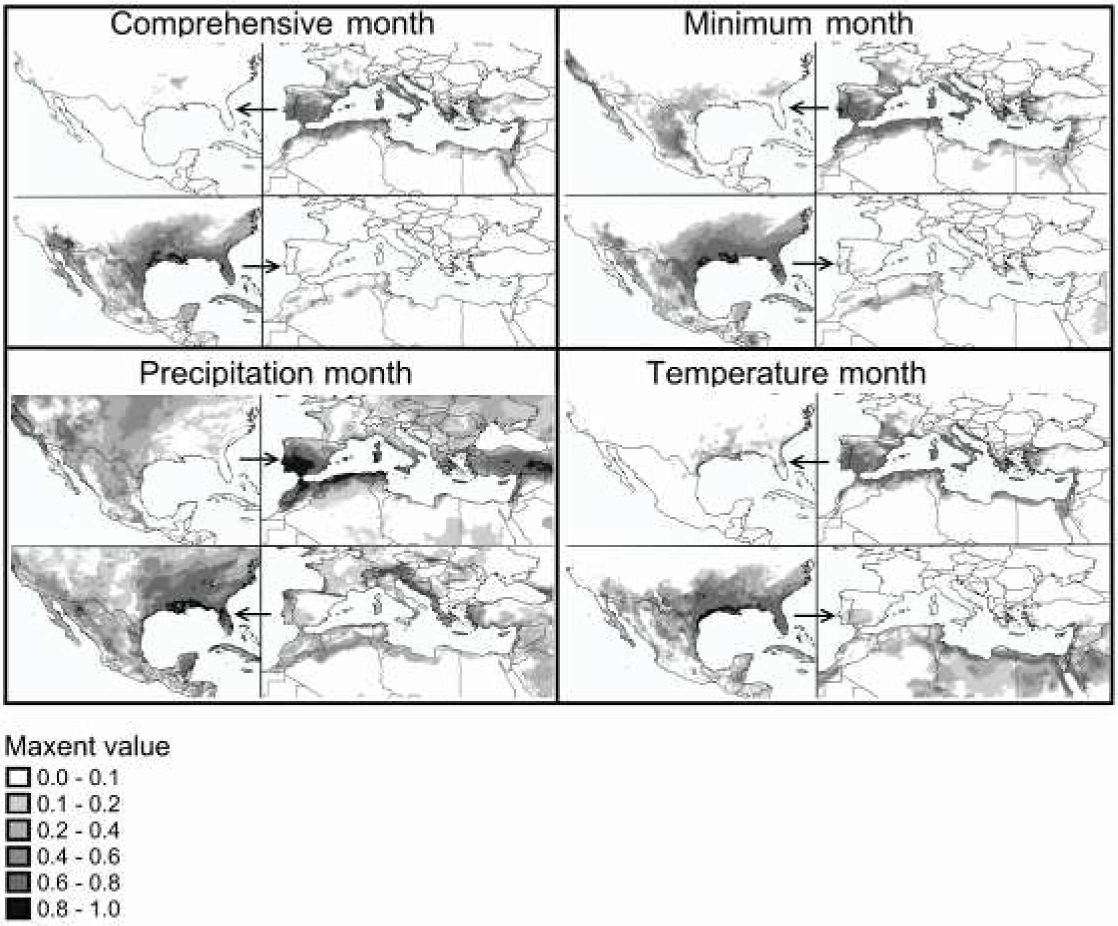
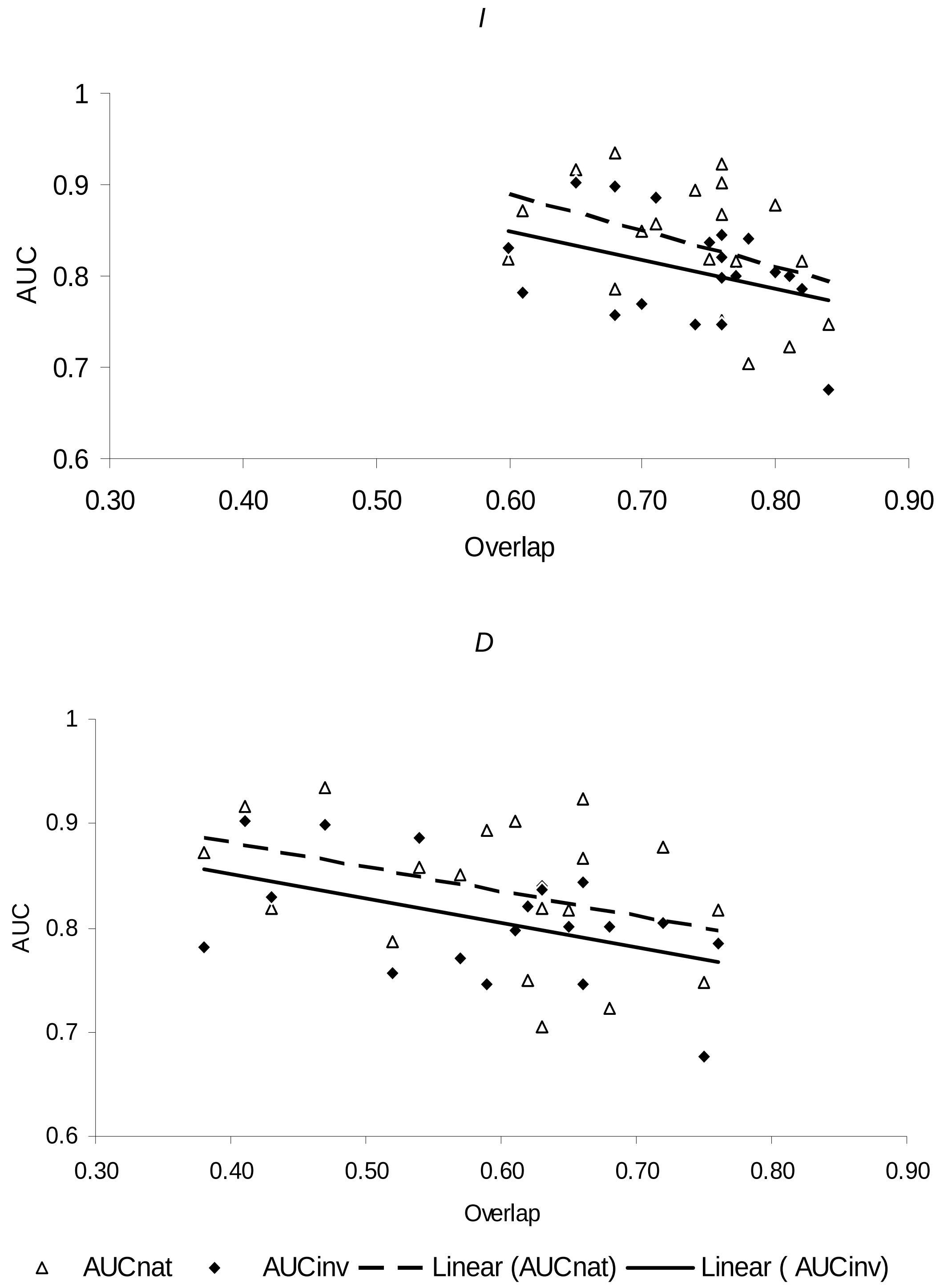
Appendix 2.3-S2

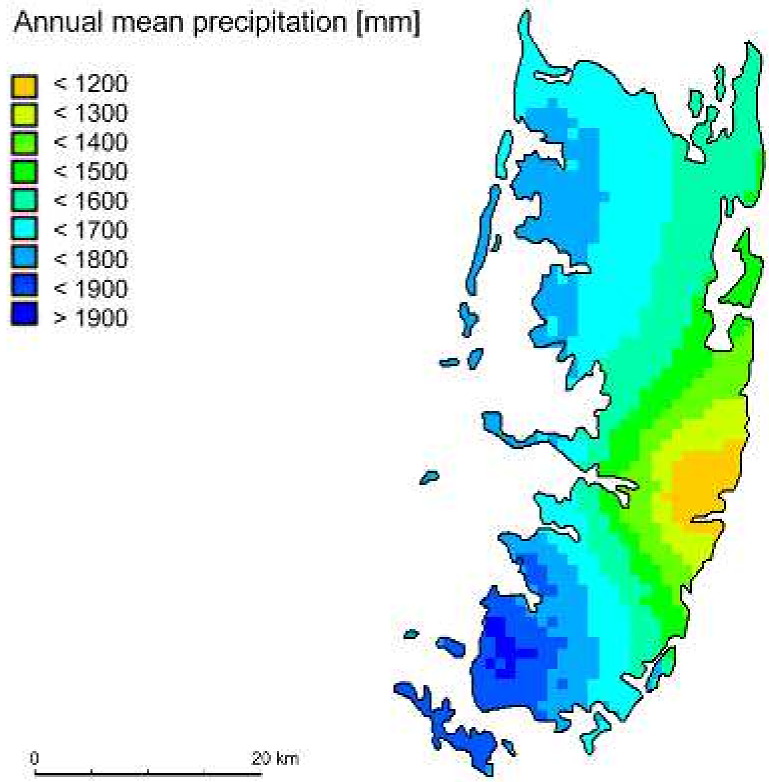
Crosswise projections of climate envelopes developed with variable sets ‘Comprehensive’, ‘Minimum’, ‘Precipitation’, and ‘Temperature’. Arrows indicate direction of projections, i.e. climate envelopes were developed based on records within one area and projected into the other.





Appendix 2.3-S3

Relationship between niche overlap in terms of *D* and *I* values and performance of model trained with native or invasive records in terms of AUC values of the 19 bioclimatic parameters analyzed (for details see Table 2.3-1). $R^2_{D\ nat} = 0.140$, $P_{D\ nat} = 0.020$; $R^2_{D\ inv} = 0.207$, $P_{D\ inv} = 0.004$; $R^2_{I\ nat} = 0.160$, $P_{I\ nat} = 0.013$; $R^2_{I\ inv} = 0.147$, $P_{I\ inv} = 0.017$.



Appendix 4.1-S1

Variation in annual mean precipitation throughout Pemba Island based on the sources described in the chapter "climate data".

Appendix 4.2-S1

List of localities in Amazonia and on the Guiana Shield of presence and apparent absence of harlequin frogs (*Atelopus*).

Abbreviations: Depto. = Departamento; Edo. = Estado; Prov. = Provincia; PN = Parque Nacional/Nacionão; + = present; — = apparently absent; pc = personal communication; AMNH = American Museum of Natural History, New York; BM = British Museum (Natural History), London; ICN = Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santafé de Bogotá; KU = Natural History Museum, The University of Kansas, Lawrence; MUSM = Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MZUSP = Museu de Zoologia, Universidade de São Paulo; NRM = Naturhistoriska Rijkmuseet, Stockholm; QCAZ = Pontificia Universidad Católica del Ecuador, Quito; ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn; ZUEC = Museu de História Natural, Universidade Estadual de Campinas, São Paulo.

Locality	Approximate Location	Presence or Apparent Absence	Source(s)
Bolivia (3 localities, 0 presence)			
Cobija, Depto. Pando	11.01S, 68.45W	—	Köhler and Lötters, 1999
Río Ortón, Depto. Pando	10.58S, 69.40W	—	I. De la Riva, pc; S. Reichle, pc
Tahuamanu, Depto. Pando	11.24S, 69.10W	—	I. De la Riva, pc; S. Reichle, pc
Brazil (39 localities, 21 presence)			
Ajarani region, Edo. Roraima	02.0N, 62.45W	—	C. Azevedo-Ramos, pc
Alto Rio Juruá region, Edo. Amazonas	08.0S, 72.50W	—	C. Azevedo-Ramos, pc
Baixo Rio Juruá region, Edo. Amazonas	03.15S, 66.15W	—	C. Azevedo-Ramos, pc
Belém region, Edo. Pará	01.29S, 48.24W	—	C. Azevedo-Ramos, pc
Boa Vista region, Edo. Roraima	02.49N, 60.40W	—	J.P. Caldwell, pc
Caiman region, Edo. Amapá	03.18N, 52.15W	+	Lescure, 1981a

Chanpiom region, Edo. Pará	01.20N, 51.16W	—	C. Azevedo-Ramos, pc
Carajás region, Edo. Pará	06.02S, 50.25W	+	C. Azevedo-Ramos, pc
CEMEX, SE of Santarém, Edo. Pará	03.09S, 54.51W	+	J.P. Caldwell, pc
Cruzeiro do Sul, Edo. Acre	07.37S, 72.35W	—	authors’ pers. observ.
Igarapé de Piranha, Edo. Amazonas	05.43S, 61.16W	+	MZUSP
Ituxi region, Edo. Amazonas	08.17S, 65.30W	—	C. Azevedo-Ramos, pc
Jacareacanga, Edo. Pará	01.32S, 47.03W	+	ZUEC
Lago do Castanho, Edo. Amazonas	03.45S, 60.30W	+	ZUEC
Mamirauá region, Edo. Amazonas	03.30S, 64.35W	—	C. Azevedo-Ramos, pc
Maués, Edo. Amazonas	03.24S, 57.42W	+	AMNH
Monte Cristo, Edo. Pará	04.40S, 55.38W	+	MZUSP
Municipio de Castanho, Edo. Amazonas	03.30S, 59.54W	—	J.P. Caldwell, pc
Paragominas region, Edo. Pará	03.45S, 48.20W	+	C. Azevedo-Ramos, pc
PN da Serra do Divisor, Edo. Acre	08.20S, 73.32W	—	authors’ pers. observ.
Pojuca, Serra do Carajás, Edo. Pará	06.10S, 51.05W	+	ZUEC
Porto Platon, Edo. Amapá	00.42N, 51.27W	+	MZUSP
Porto Grande, Edo. Amapá	00.42N, 51.24W	+	ZUEC
Porto Walter, Edo. Acre	08.15S, 72.47W	—	J.P. Caldwell, pc
Presidente Figuereido, Edo. Amazonas	02.00S, 60.00W	—	authors’ pers. observ.
Reserva Campina, Edo. Amazonas	03.07S, 60.03W	+	ZUEC
Reserva INPA-WWF, Edo. Amazonas	02.25S, 59.43W	+	MZUSP
Reserva Pacanari, Edo. Pará	00.52S, 52.31W	+	ZUEC

Río Amaparí, Edo. Amapá	01.15N, 52.15W	+	MZUSP
Rio Formoso, Edo. Rondônia	10.19S, 64.34W	—	J.P. Caldwell, pc
Rio Ituxi, Edo. Amazonas	08.29S, 65.43W	—	J.P. Caldwell, pc
Rio Manjuru, Edo. Amazonas	04.00S, 57.00W	+	AMNH
Río Maú, Edo. Roraima	04.20N, 59.45W	+	MZUSP
Serra do Navio, Edo. Amapá	01.55N, 51.50W	+	MZUSP; McDiarmid, 1973
Terra Verde Lodge, Edo. Amazonas	03.37S, 59.86W	—	J.P. Caldwell, pc
Urucú region, Edo. Amazonas	05.00S, 65.30W	—	C. Azevedo-Ramos, pc
Circa 90 km N of Manaus, Edo. Amazonas	01.45S, 60.05W	+	Gascon, 1989
1.0 km NW of Caracaraí, Edo. Roraima	01.50N, 61.08W	—	J.P. Caldwell, pc

Colombia (11 localities, 3 presence)

Calderón, Depto. Amazonas	03.46S, 69.53W	—	Ardila-R. and Ruiz-C, 1997
Caño Cabina, Léticia, Depto. Amazonas	03.40N, 70.25W	+	J.M. Renjifo, pc
Igara Parana, Depto. Amazonas	00.44N, 72.58W	+	BM; Lescure, 1981a
La Pedrera, Depto. Amazonas	01.18S, 69.22W	—	Ardila-R. and Ruiz-C, 1997
Río Apaporis, Depto. Vaupes	00.45N, 72.00W	—	J.M. Renjifo, pc
Río Mirití, Depto. Amazonas	01.12S, 69.53 W	—	Ardila-R. and Ruiz-C, 1997
Río Puré, Depto. Putumayo	02.10S, 69.42W	+	ICN
Río Tiquie, Depto. Vaupes	00.20N, 70.20W	—	J.M. Renjifo, pc
Tarapacá, Depto. Amazonas	02.52S, 69.44W	—	Ardila-R. and Ruiz-C, 1997
Tomachipan, Depto. Guaviare	02.18S, 71.46W	—	J.M. Renjifo, pc

Serrania de Taraira, Depto. Vaupes	00.55S, 69.40W	—	J.M. Renjifo, pc
Ecuador (8 localities, 7 presence)			
Cuyabeno Reserve, Prov. Sucumbíos	00.00, 76.00W	—	L.A. Coloma, pc; J.P. Caldwell, pc
Jatun Sacha Reserve, Prov. Napo	01.05S, 77.45W	+	L.A. Coloma, pc
Miazal, Prov. Morona-Santiago	02.37S, 77.47W	+	Rivero, 1968
PN Yasuní, Prov. Orellana	00.36S, 76.20 W	+	QCAZ
Río Cononaco, Prov. Orellana	01.25S, 75.50W	+	Patzelt, 1989
Río Oglán, Prov. Pastaza	01.19S, 77.35W	+	Rivero, 1968
Río Villano, Prov. Pastaza	01.29S, 77.38W	+	BM
Circa 66 km E of Pompeya, PN Yasuní, Prov. Orellana	00.45S, 76.21W	+	QCAZ
French Guiana (24 localities, 24 presence)			
Between Dorlin and Sophie	03.51N, 53.34W	+	McDiarmid, 1973
Between La Greve and Sophie	03.57N, 53.35W	+	McDiarmid, 1973
Boulanger	04.32N, 52.25W	+	ZFMK
Cayenne region	04.50N, 52.22W	+	Lescure, 1976
Chaumière	04.53N, 52.22W	+	Lescure, 1973
Crique Grégoire (Kerenroch)	05.05N, 53.20W	+	Lescure, 1973
Crique Ipoucin	04.09N, 52.25W	+	Lescure, 1976
Kaw region	04.29N, 52.20W	+	Lescure, 1976, 1981b

Koulimapopane	02.19N, 54.36W	+	Lescure, 1976
Maripasoula	03.37N, 53.12W	+	NRM
Matoury	04.50N, 52.25W	+	Lescure, 1976
Montagne Belvédère	03.37N, 53.12W	+	Kok, 2000
Montagne Saint-Marcel	02.25N, 53.00W	+	Lescure, 1981a
Monts Atachi-Bacca	03.35N, 54.00W	+	Lescure, 1976
Petit Saut	05.21N, 53.41W	+	Hoogmoed and Avila-Pires, 1991
Rivière Matarony	04.02N, 52.15W	+	McDiarmid, 1973
Rivière Yaroupi	02.35N, 52.40W	+	Lescure, 1976
Roura region	04.45N, 52.20W	+	Lescure, 1976
Saint Laurent region	05.30N, 53.55W	+	Lescure, 1981a
Saül region	03.35N, 53.55W	+	Lescure, 1981a
Sophie region	03.55N, 53.40W	+	Lescure, 1981a
Tortue region	04.11N, 52.23W	+	Lescure, 1976
Trois-Sauts	02.15N, 52.50W	+	Lescure, 1981a; Lescure and Gasc, 1986
Circa 30 km S of Saül	03.20N, 52.10W	+	Lescure, 1981a
Guiana (9 localities, 9 presence)			
Between Chenapowu and Saveritih	04.55N, 59.34W	+	AMNH
Demerara River	04.47N, 58.26W	+	AMNH
Iwokrama	04.50N, 59.15W	+	M.L. Donnelly, pc

Kalacoon	06.24N, 58.39W	+	AMNH; McDiarmid, 1973
Kangaruma	05.18N, 59.17W	+	AMNH; McDiarmid, 1973
Karisparu	04.58N, 59.30W	+	BM
Kartabo	06.21N, 57.50W	+	AMNH; McDiarmid, 1973
Potaro River	05.20N, 59.17W	+	BM
25 mi WSW of Mabura Hill	05.13N, 59.21W	+	AMNH
Peru (31 localities, 21 presence)			
Achinamisa, Depto. San Martín	06.25S, 75.54W	+	AMNH
Balta, Depto. Ucayali	10.08S, 71.13W	—	Duellman and Thomas, 1996
Barranca, Depto. San Martín	07.16S, 76.28W	+	AMNH
Bolognesi region, Depto. Ucayali	10.02S, 73.57W	—	Lehr, 2002
Cachiyacu, Depto. San Martín	05.44S, 77.29W	+	Rivero, 1968
Chayahuitas, Depto. Loreto	05.50S, 76.10W	+	Rivero, 1968; Lötters et al. 2002
Cocha Cashu/PN Manu, Depto. Madre de Dios	11.54S, 71.22W	—	Rodríguez, 1992
Cuzco Amazónico, Madre de Dios	12.35S, 69.05W	—	Duellman and Salas, 1991
Explorama, Depto. Loreto	02.35S, 71.57W	—	Duellman and Thomas, 1996
Genaro Herrera, Depto. Loreto	04.59S, 73.46W	+	MUSM
Iquitos region, Depto. Loreto	03.40S, 73.20W	+	AMNH; Rodríguez and Duellman, 1994
Manseriche, Depto. Loreto	04.25S, 77.35W	+	Rivero, 1968
Milagros, Depto. Ucayali	10.08S, 74.01W	—	Lehr, 2002

Monte Alegre, Depto. Loreto	06.42S, 74.15W	+	AMNH
Nauta region, Depto. Loreto	04.30S, 73.40W	+	Asquith and Altig, 1987
Panguana, Depto. Huánuco	09.35S, 74.48W	—	Schlüter, 2005
Pebas region, Depto. Loreto	03.20S, 71.50W	+	AMNH; Lescure, 1981a
Roabaya, Depto. Loreto	04.10S, 73.20W	+	Rivero, 1968
Río Ampiyacu, Depto. Loreto	03.10S, 72.00W	+	Lötters et al. 2002
Río Cachiyacu, Depto. Loreto	08.09S, 76.32W	+	Lötters et al. 2002
Río Loretoyacu, Depto. Loreto	03.49S, 70.26W	+	AMNH
Río Pisqui, Depto. Loreto	08.05S, 75.35W	+	Lötters et al. 2002
Río Sepahua, Depto. Ucayali	11.10S, 73.01W	+	Rivero, 1968
Río Távara, Depto. Puno	13.31S, 69.41W	+	Bärtschi and MacQuarrie, 2001
Río Tambo, Depto. Loreto	01.15S, 75.21W	+	Rivero, 1968
Río Yubineto, Depto. Loreto	01.02S, 74.13W	+	Lescure and Gasc, 1986, Lescure, 1981a
San Jacinto, Depto. Loreto	02.19S, 75.52W	—	Duellman and Mendelson, 1995
Tacsha, Depto. Loreto	03.40S, 77.21W	+	Rivero, 1968
Tambopata, Depto. Madre de Dios	12.44S, 69.11W	+	MUSN
Teniente López, Depto. Loreto	02.36S, 76.07W	—	Duellman and Mendelson, 1995
Yurimaguas, Depto. Loreto	05.54S, 76.05W	—	authors’ pers. observ
Suriname (4 localities, 3 presence)			
Brownsberg	04.55N, 55.10W	+	AMNH, KU

Corentijne River	05.10N, 57.20W	—	S. Reichle, pc
Monts Tumuc-Humac	02.20N, 54.40W	+	Lescure, 1976, 1981a
Mt. Kasikasima	03.00N, 55.30W	+	MZUSP
Venezuela (1 locality, 0 presence)			
Cerro Duida, Edo. Amazonas	03.30N, 65.40W		

Appendix 4.2-S2

Atelopus flavescens 328

???????????TGC-CCAGTGATTCCTGTTAACGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGNAATCACT
TGTTCTTTAAATGAGGACTAGTATGAATGGCACCACGAAGGTTTTACTGTCTCCTTTTCCTAATCAGTGAAA
CT-AATCTTCCCGTGAAGAAGCGGGAATAAACGAATAAGACGAGAAGACCCTATGGAGCTTTAAACACAAT
AACAAATACTACTTTA-AACAAAAAT-TTCTTAATGAC---TTACTTACTGGTATTATGATTATTAGTTTTAGGTT
GGGGTGACCGCGGAGAAAAACACAACCTCCACATTGAATGATAAAA-TTCTAAGCAAAGAATTACATTTCC
ACGCATCAATACATTGACATCAATTGACCCAA-TTATTTT-GATCAACGAACCAAGTTACCCTAGGGATAACA
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Atelopus spumarius barbotini neu 336

??????????????-?????????????TTAACGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGGAATCACTTG
TTCTTTAAATGAGGACTAGTATGAATGGCACCACGAAGGTTTTACTGTCTCCTTTTCCTAATCAGTGAAACT-
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GGTGCAGCCGCTACTAAAGGTTCGTTTGTTCAACGATTAAAACCCTACGTGATCTGAGT

Atelopus hoogmoedi 334

??????????????-???-???????????????????????????
???????????????????????????GTTTTACTGTCTCCTTTTCCTAATCAGTGAAACT-AATCTTCCCGTGAAG
AAGCGGGAATAAACGAATAAGACGAGAAGACCCTATGGAGCTTTAAACACAATAACAAATACTACTTTAA
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CATCAATTGACCCAA-TTATTTT-GATCAACGAACCAAGTTACCCTAGGGATAACAGCGCAATCTACTTCAAG
AGCCCATATCGACAAGTGGGTTTACGACCTCGATGTT-GGATCAGGGTACCCCAGTGGTGCAGCCGCTACT
AAAGGTTCGTTTGGTCAACGATTAAAACCCTACGTGATCTGAGT

Atelopus pulcher s. str. Peru 298

GAGGTCCCGCCTGC-CCAGTGATTTAATTTAACGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGTAATCA
CTTGTTCTTTAAATGAGGACTAGTATGAATGGCATCACGAGGGTTTTACTGTCTCCTTTTCTTAATCAGTGAA
ACT-AATCTTCCCGTGAAGAAGCGGGAATAAACGAATAAGACGAGAAGACCCTATGGAGCTTTAAACACAA
TAACAAGTACTACTTTA-AACAAAA-T-TTCTTAATAAC---TTACTACCTGGTACTATGATTATTAGTTTTAGGT
TGGGGTGACCGCGGAGAAAAACATAACCTCCACAT-GAATGATAAAA-TTCTAAGCAAAGAATTACATCTCT
AAGCATCAATATATTGACATCAATTGACCCAA-TTATTTT-GATCAACGAACCAAGTTACCCTAGGGATAACA
GCGCAATCTACTTCAAGAGCCCATATCGACAAGTGGGTTTACGACCTCGATGTT-GGATCAGGGTACCCCA
GTGGTGCAGCCGCTACTAAAGGTTCGT?????????????????????????????????

Atelopus rafael BO702

?AGGTCCAGCCTGC-CCAGTGATTAAATTTAACGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGTAATCA
CTTGTTCTTTAAATGAGGACTAGTATGAATGGCACCACGAAGGTTTTACTGTCTCCTTTTCCTAATCAGTGA
AACT-AATCTTCCCGTGAAGAAGCGGGAATAAGCGAATAAGACGAGAAGACCCTATGGAGCTTTAAACACA
ATAACAAATACTACTTTA-AACAAAAAT-TTCTTAATGAC---TTACTCCCCGGTATTATGATTATTAGTTTTAG
GTTGGGGTGACCGCGGAGAAAAACACAACCTCCACATTGAATGATAAAA-TTCTAAGCAAAGAATCACATT
TCCACGCATCAATACATTGACATCAATTGACCCAA-TTATTTT-GATCAACGAACCAAGTTACCCTAGGGATA
ACAGCGCAATCTACTTCAAGAGCCCATATCGACAAGTGGGTTTACGACCTCGATGTT-GGATCAGGGTACC
CCAGCGGTGCAGACGCTACTAAAGGTTCGTTTGTTCAACGATTAAAACCC??????????????

Atelopus spurrelli

GAGGTCCCGCCTGC-CCAGTGATTAAATTTAACGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGTAATCA
CTTGTTCTTTAAATGAGGACTAGTATGAACGGCATCACGAAGGTTACACTGTCTCCTTTTTCTAATCAGTGA
AACT-AATTTCCCCGTGAAGAAGCGGGGATACTTTAATAAGACGAGAAGACCCTATGGAACTTTAAACAAA
GTAACAAGTACTATCATTTATTAATAAATTTCCGAAT-CA-AACATGACCTAGTATTATGATTACTAGTTTTAG
GTTGGGGTGACCGCGGAGAAAAACATAACCTCCACATTGAAAGAAAAAC-TCTAAGCCCAAAGCTACAACT
TAAAGCATCAACATATTGACATTAATTGACCCAA-TTAAATT-GAGCAACGAACCAAGCTACCCTAGGGATA
ACAGCGCAATCCACTTTAAGAGCCCCTATCGACAAGTGGGTTTACGACCTCGATGTT-GGATCAGGGTTTCC
CAGTGGTGCAGCCGCTACTAAAGGTTCGTTTGTTCAACGATTAATACCCT?????????????

Atelopus semiferus Peru 308

?????????????-????AGATTAAATTTAACGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGTAATCACTT
GTTCTTTAAATGAGGACTAGTATGAATGGCACCACGAAGGTTTTACTGTCTCCTTTTCCTAATCAGTGAAAC
T-AATCTTCCCGTGAAGAAGCGGGAATAAACGAATAAGACGAGAAGACCCTATGGAGCTTTAAACACAATA
ACAAGTACTACTTTA-AACAAAA-T-TTCTTAATGAC-TTACTACCTGGTATCATGATTATTAGTTTTAGGTTGG
GGTGACCGCGGAGAAAAACATAACCTCCACATTGAATGATAAAG-TTCTAAGCAAAGAACTACATTTCTAT
GCATCAATATATTGACATCAATTGACCCAA-TTATTTT-GATCAACGAACCAAGTTACCCTAGGGATAACAGC
GCAATCTACTTCAAGAGTCCATATCGACAAGTGGGTTTACGACCTCGATGTT-GGATCAGGGTACCCnAGTG
GTGCAGCCGCTACTAAAGGTTCGTTTGTTCAACGATTA????????????????????

Atelopus cf. *spumarius* Peru 317

????????????TC-CATAAGCTTAAATTTAACGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGTAATCACT
TGTTCTTTAAATGAGGACTAGTATGAATGGCACCACGAAGGTTTTACTGTCTCCTTTTCCTAATCAGTGAAA
CT-AATCTTCCCGTGAAGAAGCGGGAATAAACGAATAAGACGAGAAGACCCTATGGAGCTTTAAACACAAT
AACAAGTACTACTTTA-AACAAAAAT-TTCTTAATCAC---TCTTCACCTGGTATTATGATTATTAGTTTTAGGTT
GGGGTGACCGCGGAGAAAAACATAACCTCCACATTGAATGATAAAA-TTCTAAGCAAAGAATTACATTTCT
ATGCATCAACACATTGACATCAATTGACCCAA-TTATTTT-GAGCAACGAACCAAGTTACCCTAGGGATAACA
GCGCAATCTACTTCAAGAGCCCATATCGACAAGTGGGTTTACGACCTCGATGTT-GGATCAGGGTACCCCA
GTGGTGCAGCCTCTACTAAAGGTTCGTTTGTTCAACGATTAA???????????????????

Osornophryne cf. *chiles* AGG532

??????????CTGC-CCAGTGACTCAATTCAACGGCCGCGGTATCCTAACCGTGCAAA-GGTAGCGTAATCACT
TGTTCTTTAAATCAGGACTAGTATGAACGGCATCACGAAGGTTATACTGTCTCCTTTTTCCAATCAGTGAAA
CT-AATCTCCCCGTGAAGAAGCGGGGATAGAACTATAAGACGAGAAGACCCTATGGAGCTTCAAACGACAC

AACAAATGCTAAACT-ACTTAAAAAT-TTCAGAACCAC-AACTC-TATAGCACTATGATTGTTAATTTTAGGTTGGGGTGACCGCGGAGCAAAACACAACCTCCACATTGAAAGAATTTTATTCTAAGCCAAGAACCACAACTCAAAGCATCAATACACTGACATA-ATTGACCCAATAAACTT---GAACAACGAACCAAGTTACCCTAGGGATAACAGCGCAATCTACTTCAAGAGCCCCTATCGACAAGTAGGTTTACGACCTCGATGTT-GGATCAGGGTCTCCCAGTGGTGCAGCCACTACTAAAGGTTCGTTTGTTCAACGATTAATAC????????????????

Osornophryne puruanta AGG572

???AGCCAGCCTGC-CCAGTGACTCAATTCAACGGCCGCGGTATCCTAACCGTGCAAA-GGTAGCGTAATCACTTGTTCTTTAAATCAGGACTAGTATGAACGGCATCACGAAGGTTATACTGTCTCCTTTTTCCAATCAGTGAAACT-AATTTCCCCGTGAAGAAGCGGGGATATAACTATAAGACGAGAAGACCCTATGGAGCTTCAAACGACACAACAAATGCTAAACT-CCTTAAAAAT-TTCAGAACCCCCCAACTCACTATAGCACCATGATTGTTAGTTTTAGGTTGGGGTGACCGCGGAGCAAAACACAACCTCCACATTGAAAGAATTTTATTCTAAGCCAAGAACCACAACTCAAAGCATCAATACACTGACATA-ATTGACCCAATAAACTT---GAACAACGAACCAAGTTACCCTAGGGATAACAGCGCAATCTACTTCAAGAGCCCCTATCGACAAGTAGGTTTACGACCTCGATGTT-GGATCAGGGTCTCCCGGTGGTGCAGCCGCTACTAAAGGTTCGTTTGTTCAACGATTAATACCCTACGTGATCTGAGT

Osornophryne antisana La Angelin

???????AGCCTGC-CCAGTGACTCAATTCAACGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGTAATCACTTGTTCTTTAAATCAGGACTAGTATGAACGGCATCACGAAGGTTATACTGTCTCCTTTTTCCAATCAGTGAAACT-AATTTCCCCGTGAAGAAGCGGGGATAGAACTATAAGACGAGAAGACCCTATGGAGCTTCAAACGACACAACAAATGCTAAACT-CCTTAAAAAT-TTCAGAACCCC-AACTCACTATAGCACTATGATTGTCAGTTTTAGGTTGGGGTGACCGCGGAGCAAAACACAACCTCCACATTGAAAGAATTCCATTCTAAGCCAAGAACCACAACTCAAAGCATCAATACACTGACATA-ATTGACCCAATACACTT---GAACAACGAACCAAGTTACCCTAGGGATAACAGCGCAATCTACTTCAAGAGCCCCTATCGACAAGTAGGTTTACGACCTCGATGTT-GGATCAGGGTCTCCCAGTGGTGCAGCCGCTACTAAAGGTTCGTTTGTTCAACGATTAATACCCTACGTGATCTGAGT

Osornophryne Equador 312

??????????CTGCTCCAGTGACTCAATTCA-CGGCCGCGGTATCCTAACCGTGCGAA-GGTAGCGTAATCACTTGTTCTTTAAATCAGGACTAGTATGAACGGCATCACGAAGGTTATACTGTCTCCTTTTTCCAATCAGTGAAACT-AATTTCCCCGTGAAGAAGCGGGGATAGAACTATAAGACGAGAAGACCCTATGGAGCTTCAAACGACACAACAAATGCTAAACT-CCTTAAAAAT-TTCAGAACCCC-AACTCACTATAGCACTATGATTGTCAGTTTTAGGTTGGGGTGACCGCGGAGCAAAACACAACCTCCACATTGAAAGAATTCCATTCTAAGCCAAGAACCACAACTCAAAGCATCAATACACTGACATA-ATTGACCCAATACACTT---GAACAACGAACCAAGTTACCCTAGGGATAACAGCGCAATCTACTTCAAGAGCCCCTATCGACAAGTAGGTTTACGACCTCGATGTT-GGATCAGGGTCTCCCAGTGGTGCAGCCGCTACTAAAGGTTCGTTTGTTCAACGATTAATACCCTACGTGATCTGAGT

Appendix 7.1. Species records used in this thesis

(given as: Longitude, Latitude, Loclity)

Atelopus, eastern

-59.3500, 5.2167, Guyana, Potaro-Siparuni; -59.5667, 4.9167, Guyana, Potaro-Siparuni; -53.5667, 3.8500, Guyane, Saint-Laurent-du-Maroni, Maripasoula; -53.5833, 3.9500, Guyane, Saint-Laurent-du-Maroni, Saül; -52.4167, 4.5333, Guyane, Cayenne, Roura; -55.1667, 4.9167, Suriname, Brokopondo, Sarakreek; -52.2500, 3.3000, Guyane, Cayenne, Camopi; -50.4167, -6.0333, Brazil, Pará, Parauapebas, Parauapebas; -52.3667, 4.8333, Guyane, Cayenne, Matoury; -54.8500, -3.1500, Brazil, Pará, Belterra, Belterra; -52.3667, 4.8833, Guyane, Cayenne, Matoury; -52.1667, 3.3333, Brazil, Amapá, Oiapoque, Clevelandia do Norte; -60.0833, -1.7500, Brazil, Amazonas, Presidente Figueiredo, Balbina; -53.3333, 5.0833, Guyane, Cayenne, Iracoubo; -52.4167, 4.1500, Guyane, Cayenne, Régina (-Kaw); -58.4333, 4.7833, Guyana, Upper Takutu-Upper Essequibo; -61.2667, -5.7167, Brazil, Amazonas, Manicore, Manicore; -59.2500, 4.8333, Guyana, Potaro-Siparuni; -47.0500, -1.5333, Brazil, Pará, Ourém, Ourém; -58.6500, 6.4000, ; -59.2833, 5.3000, Guyana, Potaro-Siparuni; -59.5000, 4.9667, Guyana, Potaro-Siparuni; -57.8333, 6.3500, Guyana, Essequibo Islands-West Demerara, Rising Sun / Profit; -52.3333, 4.4833, Guyane, Cayenne, Roura; -54.6000, 2.3167, Brazil, Amapá, Laranjal do Jari, Laranjal do Jari; -60.5000, -3.7500, Brazil, Amazonas, Manaquiri, Manaquiri; -53.2000, 3.6167, Guyane, Saint-Laurent-du-Maroni, Saül; -52.4167, 4.8333, Guyane, Cayenne, Montsinéry-Tonnégrande; -57.7000, -3.4000, Brazil, Amazonas, Maués, Maués; -53.2000, 3.6167, Guyane, Saint-Laurent-du-Maroni, Saül; -53.0000, 2.4167, Guyane, Cayenne, Camopi; -55.6333, -4.0667, Brazil, Pará, Aveiro, Brazilia Legal; -54.0000, 3.5833, Suriname, Sipaliwini, Tapanahony; -54.8333, 2.3333, Brazil, Pará, Almerim, Monte dourado; -55.5000, 3.0000, Suriname, Sipaliwini, Tapanahony; -48.3333, -3.7500, Brazil, Pará, Paragominas, Paragominas; -53.6833, 5.3500, Guyane, Saint-Laurent-du-Maroni, Mana; -51.0833, -6.1667, Brazil, Pará, Parauapebas, Parauapebas; -51.4000, 0.7000, Brazil, Amapá, Porto Grande, Porto Grande; -51.4500, 0.7000, Brazil, Amapá, Porto Grande, Porto Grande; -59.2833, 5.3333, Guyana, Potaro-Siparuni; -60.0500, -3.1167, Brazil, Amazonas, Maués, Segunda R.A.; -59.7167, -2.4167, Brazil, Amazonas, Rio Preto da Eva, Rio Preto da Eva; -52.5167, -0.8667, Brazil, Pará, Almerim, Monte dourado; -52.2500, 1.2500, Brazil, Amapá, Serra do Navio, Serra do Navio; -57.0000, -4.0000, Brazil, Pará, Itaituba, Itaituba; -59.7500, 4.3333, Brazil, Roraima, Uiramutã, Uiramutã; -52.2500, 4.0333, Guyane, Cayenne, Régina (-Kaw); -52.6667, 2.5833, Guyane, Cayenne, Camopi; -52.3333, 4.7500, Guyane, Cayenne, Matoury; -53.9167, 5.5000, Guyane, Saint-Laurent-du-Maroni, Mana; -53.9167, 3.5833, Guyane, Saint-Laurent-du-Maroni, Maripasoula; -51.8333, 1.9167, Brazil, Amapá, Calçoene, Lourenco; -53.6667, 3.9167, Guyane, Saint-Laurent-du-Maroni, Maripasoula; -52.3833, 4.1833, Guyane, Cayenne, Régina (-Kaw); -52.8333, 2.2500, Brazil, Amapá, Oiapoque, Clevelandia do Norte; -51.8333, 0.5000, Brazil, Amapá, Porto Grande, Porto Grande.

Atelopus, western

-75.9000, -6.4167, Perú, San Martín, San Martín, Chipurana; -76.4667, -7.2667, Perú, San Martín, Bellavista, Alto Biavo; -76.6167, -5.8833, Perú, Loreto, Alto Amazonas, Balsapuerto; -70.4167, 3.6667, Colombia, Vichada, San Jose de Ocune; -76.1667, -5.8333, Perú, Loreto, Alto Amazonas, Yurimaguas; -76.3500, -0.7500, Ecuador, Orellana, Aguarico, Cononaco; -73.7667, -4.9833, Perú, Loreto, Requena, Jenaro Herrera; -72.9667, 0.7333, Colombia, Caquetá, Solano; -73.3333, -3.6667, Perú, Loreto, Maynas, Punchana; -77.7500, -1.0833, Ecuador, Orellana, Tena, Puerto Napo; -77.5833, -4.4167, Perú, Amazonas, Condorcanqui, Rio Santiago; -77.7833, -2.6167, Ecuador, Morona Santiago, Morona, Sevilla Don Bosco; -74.2500, -6.7000, Perú, Loreto, Requena, Alto Tapiche; -73.6667, -4.5000, Perú, Loreto, Loreto, Nauta; -71.8333, -3.3333, Perú, Loreto, Mariscal Ramón Castilla, Pebas; -76.3333, -0.6000, Ecuador, Orellana, Orellana, Taracoa; -72.0000, -3.1667, Perú, Loreto, Mariscal Ramón Castilla, Pebas; -76.5333, -8.1500, Perú, San Martín, Tocache, Tocache; -75.8333, -1.4167, Ecuador, Pastaza, Pastaza, Curaray; -70.4333, -3.8167, Colombia, Amazonas, Puerto Nariño; -77.5833, -1.3167, Ecuador, Pastaza, Pastaza, Curaray; -75.5833, -8.0833, Perú, Loreto, Ucayali, Contamana; -69.7333, -2.1667, Colombia, Amazonas, Tarapacá; -73.0167, -11.1667, Perú, Ucayali, Atalaya, Sepahua; -75.3500, -1.2500, Perú, Loreto, Maynas, Napo; -69.6833, -13.5167, Perú, Puno, Sandia, Limbani; -74.2167, -1.0333, Perú, Loreto, Maynas, Putumayo; -73.3333, -4.1667, Perú, Loreto, Maynas, Fernando Lores; -77.3500, -3.6667, Perú, Loreto, Alto Amazonas, Morona; -69.1833, -12.7333, Perú, Madre de Dios, Tambopata, Tambopata.

Boiga irregularis, native

129.6330, -15.6000, Australia, Northern Territory; 130.8330, -12.4500, Australia, Northern Territory, Darwin; 131.1170, -12.9830, Australia, Northern Territory, Coomalie; 131.2000, -13.0500, Australia, Northern Territory, Coomalie; 131.2500, -12.6330, Australia, Northern Territory, Litchfield; 131.3830, -13.4500, Australia, Northern Territory; 132.1330, -11.3670, Australia, Northern Territory; 132.2670, -14.4670, Australia, Northern Territory, Katherine; 132.2670, -14.1500, Australia, Northern Territory; 132.3000, -14.5000, Australia, Northern Territory, Katherine; 132.6500, -12.7500, Australia, Northern Territory; 132.8330, -12.8830, Australia, Northern Territory; 132.9000, -12.5330, Australia, Northern Territory; 132.9170, -12.5500, Australia, Northern Territory; 132.9500, -12.5170, Australia, Northern Territory; 133.0670, -14.9330, Australia, Northern Territory; 133.0670, -14.7830, Australia, Northern Territory; 134.7000, -14.7000, Australia, Northern Territory; 134.7330, -14.7330, Australia, Northern Territory; 134.8000, -12.4000, Australia, Northern Territory; 134.9000, -12.1000, Australia, Northern Territory; 135.0000, -12.4000, Australia, Northern Territory; 135.7000, -14.3000, Australia, Northern Territory; 135.7330, -14.2830, Australia, Northern Territory; 136.4670, -13.9830, Australia, Northern Territory; 136.6000, -13.8000, Australia, Northern Territory; 141.8670, -12.5670, Australia, Queensland, Cook; 141.9000, -12.6330, Australia, Queensland, Cook; 142.0500, -12.2500, Australia, Queensland, Cook; 142.1330, -11.2170, Australia, Queensland, Cook; 142.2830, -10.6170, Australia, Queensland, Torres; 142.6670, -9.3830, Australia, Queensland, Torres; 143.4670, -13.8170, Australia, Queensland, Cook; 143.7000, -16.0000, Australia, Queensland, Cook; 144.2500, -16.9170, Australia, Queensland, Mareeba; 144.6830, -17.3500, Australia, Queensland, Mareeba; 144.8500, -17.9670, Australia, Queensland, Mareeba; 145.0000, -17.7500, Australia, Queensland, Herberton; 145.0830, -17.0170, Australia, Queensland, Mareeba;

145.1330, -16.5330, Australia, Queensland, Mareeba; 145.2400, -15.4600, Australia, Queensland, Cook; 145.2400, -15.4600, Australia, Queensland, Cook; 145.2500, -15.4670, Australia, Queensland, Cook; 145.2670, -17.7330, Australia, Queensland, Herberton; 145.3170, -15.9670, Australia, Queensland, Douglas; 145.3330, -15.9500, Australia, Queensland, Cook; 145.3830, -17.3830, Australia, Queensland, Herberton; 145.5700, -17.0000, Australia, Queensland, Mareeba; 145.5700, -17.0000, Australia, Queensland, Mareeba; 145.7670, -16.9170, Australia, Queensland, Cairns; 145.7700, -16.9200, Australia, Queensland, Cairns; 145.7700, -16.9200, Australia, Queensland, Cairns; 145.8900, -17.5800, Australia, Queensland, Johnstone; 145.9670, -17.5330, Australia, Queensland, Johnstone; 146.0170, -17.7500, Australia, Queensland, Johnstone; 146.0330, -17.5330, Australia, Queensland, Johnstone; 146.0330, -17.5330, Australia, Queensland, Johnstone; 146.1500, -17.9500, Australia, Queensland, Cardwell; 146.8170, -19.2670, Australia, Queensland, Townsville; 147.7170, -20.7330, Australia, Queensland, Bowen; 148.0500, -19.9660, Australia, Queensland, Bowen; 148.0500, -19.9660, Australia, Queensland, Bowen; 149.0330, -20.4500, Australia, Queensland, Mackay; 149.1830, -21.1500, Australia, Queensland, Mackay; 150.6670, -32.9670, Australia, New South Wales, Singleton; 150.7330, -33.4330, Australia, New South Wales, Hawkesbury; 150.7330, -23.2670, Australia, Queensland, Livingstone; 150.8170, -34.0670, Australia, New South Wales, Campbelltown; 150.9670, -34.1830, Australia, New South Wales, Wollongong; 151.0110, -32.6690, Australia, New South Wales, Singleton; 151.0330, -33.6830, Australia, New South Wales, Hornsby; 151.0330, -23.6670, Australia, Queensland, Calliope; 151.0500, -33.6500, Australia, New South Wales, Hornsby; 151.0670, -34.1170, Australia, New South Wales, Sutherland; 151.0670, -34.0330, Australia, New South Wales, Sutherland; 151.0670, -33.9830, Australia, New South Wales, Hurstville; 151.1170, -33.9500, Australia, New South Wales, Rockdale; 151.1170, -33.8830, Australia, New South Wales, Ashfield; 151.1170, -33.7170, Australia, New South Wales, Ku-ring-gai; 151.1500, -33.7500, Australia, New South Wales, Ku-ring-gai; 151.1670, -33.7670, Australia, New South Wales, Ku-ring-gai; 151.1830, -33.7170, Australia, New South Wales, Ku-ring-gai; 151.2000, -33.9000, Australia, New South Wales, South Sydney; 151.2000, -24.0000, Australia, Queensland, Calliope; 151.2170, -33.8000, Australia, New South Wales, Willoughby; 151.2170, -33.7670, Australia, New South Wales, Warringah; 151.2170, -33.7330, Australia, New South Wales, Warringah; 151.2170, -33.6500, Australia, New South Wales, Warringah; 151.2340, -33.4350, Australia, New South Wales, Gosford; 151.2500, -33.8330, Australia, New South Wales, Mosman; 151.2500, -33.7670, Australia, New South Wales, Warringah; 151.2500, -33.6670, Australia, New South Wales, Warringah; 151.2670, -33.8000, Australia, New South Wales, Manly; 151.2830, -33.7830, Australia, New South Wales, Warringah; 151.2830, -33.6500, Australia, New South Wales, Pittwater; 151.3000, -33.7170, Australia, New South Wales, Warringah; 151.3000, -33.6830, Australia, New South Wales, Pittwater; 151.3000, -33.5500, Australia, New South Wales, Gosford; 151.3330, -33.4830, Australia, New South Wales, Gosford; 151.3500, -33.4330, Australia, New South Wales, Gosford; 151.4830, -24.5170, Australia, Queensland, Miriam Vale; 151.6170, -25.6170, Australia, Queensland, Gayndah; 151.7500, -30.5330, Australia, New South Wales, Dumaresq; 151.9500, -25.0000, Australia, Queensland, Kolan; 152.3330, -29.5330, Australia, New South Wales, Severn; 152.4000, -24.9000, Australia, Queensland, Burnett; 152.4670, -27.1330, Australia, Queensland, Esk; 152.4830, -31.9000, Australia, New South Wales, Greater Taree; 152.6000, -29.2170, Australia, New South Wales, Copmanhurst; 152.6030, -29.9550, Australia, New South Wales, Nymboida; 152.6170, -29.5500, Australia, New South Wales, Nymboida; 152.6330, -30.7170, Australia, New South Wales, Nambucca; 152.7000, -29.5000, Australia, New South

Wales, Copmanhurst; 152.7170, -31.5170, Australia, New South Wales, Hastings; 152.7500, -29.7500, Australia, New South Wales, Nymboida; 152.7670, -29.5830, Australia, New South Wales, Copmanhurst; 152.8330, -31.0830, Australia, New South Wales, Kempsey; 152.8330, -30.3670, Australia, New South Wales, Bellingen; 152.8570, -27.5670, Australia, Queensland, Brisbane; 152.8570, -27.5670, Australia, Queensland, Brisbane; 152.8830, -30.7670, Australia, New South Wales, Nambucca; 152.9000, -30.4500, Australia, New South Wales, Bellingen; 152.9830, -30.7330, Australia, New South Wales, Nambucca; 152.9830, -30.0500, Australia, New South Wales, Ulmarra; 153.0500, -28.8670, Australia, New South Wales, Casino; 153.1000, -30.3000, Australia, New South Wales, Coffs Harbour; 153.1160, -30.2600, Australia, New South Wales, Coffs Harbour; 153.1330, -30.3000, Australia, New South Wales, Coffs Harbour; 153.1500, -30.2330, Australia, New South Wales, Coffs Harbour; 153.1670, -30.1170, Australia, New South Wales, Coffs Harbour; 153.2000, -29.7670, Australia, New South Wales, Ulmarra; 153.2000, -29.4670, Australia, New South Wales, Maclean; 153.2670, -28.8170, Australia, New South Wales, Lismore; 153.2670, -28.3500, Australia, New South Wales, Tweed; 153.3500, -29.1000, Australia, New South Wales, Richmond Valley; 153.3500, -28.5330, Australia, New South Wales, Byron; 153.4330, -29.0170, Australia, New South Wales, Richmond Valley; 153.4330, -28.9830, Australia, New South Wales, Ballina; 153.4330, -28.8330, Australia, New South Wales, Ballina; 153.4670, -28.8500, Australia, New South Wales, Ballina; 153.4670, -28.2830, Australia, New South Wales, Tweed; 153.5670, -28.3330, Australia, New South Wales, Tweed; 153.6170, -28.6500, Australia, New South Wales, Byron; 120.0000, 0.0000, Indonesia, Sulawesi Tengah, Parigi Moutong; 120.4170, -3.7330, Indonesia, Sulawesi Selatan, Wajo; 128.2000, 1.1000, Indonesia, Maluku Utara, Halmahera Tengah; 129.0000, -3.0000, Indonesia, Maluku, Maluku Tengah; 129.3500, -3.3330, Indonesia, Maluku, Maluku Tengah; 133.0500, -5.6000, Indonesia, Maluku, Maluku Tenggara; 133.0830, -0.8670, Indonesia, Irian Jaya Barat, Manokwari; 134.0830, -0.8670, Indonesia, Irian Jaya Barat, Manokwari; 134.0830, -0.8670, Indonesia, Irian Jaya Barat, Manokwari; 136.0500, -4.0830, Indonesia, Papua, Nabire; 136.6700, -1.7500, Indonesia, Papua, Yapen Waropen; 138.6000, -3.6300, Indonesia, Papua, Tolikara; 126.5170, -3.7670, Indonesia, Maluku, Buru; 128.2000, -3.7170, Indonesia, Maluku, Maluku Tengah; 128.2170, -3.6660, Indonesia, Maluku, Maluku Tengah; 126.5170, -3.6330, Indonesia, Maluku, Buru; 126.5330, -3.4330, Indonesia, Maluku, Buru; 129.0000, -3.0000, Indonesia, Maluku, Maluku Tengah; 128.0000, 1.0000, Indonesia, Maluku Utara, Halmahera Tengah; 128.4100, 2.3330, Indonesia, Maluku Utara, Halmahera Utara; 140.9000, -6.6000, Papua New Guinea, Western, North Fly; 141.1830, -3.2330, Papua New Guinea, Sandaun, Vanimo-Green River; 141.2000, -4.5830, Papua New Guinea, Sandaun, Telefomin; 141.4330, -6.7830, Papua New Guinea, Western, Bamu Rural; 141.4330, -5.1170, Papua New Guinea, Sandaun, Telefomin; 141.6330, -5.1370, Papua New Guinea, Sandaun, Telefomin; 142.1000, -3.4170, Papua New Guinea, Sandaun, Aitape-Lumi; 142.3500, -3.1330, Papua New Guinea, Sandaun, Aitape-Lumi; 142.5230, -3.3990, Papua New Guinea, Sandaun, Nuku; 142.6750, -4.5230, Papua New Guinea, East Sepik, Ambunti-Drekikir; 142.7110, -4.4660, Papua New Guinea, East Sepik, Ambunti-Drekikir; 142.7330, -9.2670, Papua New Guinea, Western, Morehead Rural; 142.7670, -6.2000, Papua New Guinea, Southern Highlands, Komo-Margarima; 142.7830, -6.2500, Papua New Guinea, Southern Highlands, Nipa-Kutubu; 142.8330, -3.8000, Papua New Guinea, East Sepik, Wosera Gawi; 142.9000, -8.8500, Papua New Guinea, Western, Morehead Rural; 142.9000, -8.7000, Papua New Guinea, Western, Morehead Rural; 142.9500, -3.8500, Papua New Guinea, East Sepik, Wosera Gawi; 142.9570, -8.0470, Papua New Guinea, Western, Bamu Rural; 143.0000, -3.9670, Papua New Guinea, East Sepik, Wosera Gawi; 143.0830, -6.5170, Papua New Guinea, Southern Highlands, Nipa-Kutubu; 143.1830, -9.0330, Papua New Guinea, Western, Morehead Rural; 143.2000, -9.0830, Papua New Guinea, Western, Morehead Rural; 143.6330, -3.7000, Papua New Guinea, East Sepik, Boikin-Dagua Rural; 143.6330, -3.5500, Papua New Guinea, East Sepik, Boikin-Dagua Rural; 143.9170, -5.6170, Papua New Guinea, Enga, Wapenamanda; 144.0000, -5.5500, Papua New Guinea, Western Highlands, Mul-Baiyer; 144.2330, -5.9000, Papua New Guinea, Western Highlands, Mount Hagen; 144.8330, -6.5500, Papua New Guinea, Chimbu, Karimui-Nomane; 144.8500, -6.5330, Papua New Guinea, Chimbu, Karimui-Nomane; 145.0370, -6.7890, Papua New Guinea, Chimbu, Karimui-Nomane; 145.0370, -6.7890, Papua New Guinea, Chimbu, Karimui-Nomane; 145.0670, -4.0670, Papua New Guinea, Madang, Bogia; 145.3560, -5.5640, Papua New Guinea, Madang, Usino Bundi; 145.6000, -6.2170, Papua New Guinea, Eastern Highlands, Henganofi; 145.7830, -5.2000, Papua New Guinea, Madang, Madang; 145.7830, -5.1000, Papua New Guinea, Madang, Madang; 145.9000, -4.6170, Papua New Guinea, Madang, Sumgilbar Rural; 145.9000, -4.6000, Papua New Guinea, Madang, Sumgilbar Rural; 145.9100, -5.9970, Papua New Guinea, Morobe, Markham; 145.9100, -4.7000, Papua New Guinea, Madang, Sumgilbar Rural; 145.9110, -5.9970, Papua New Guinea, Morobe, Markham; 145.9160, -6.0060, Papua New Guinea, Morobe, Markham; 145.9200, -4.6900, Papua New Guinea, Madang, Sumgilbar Rural; 145.9510, -6.0490, Papua New Guinea, Morobe, Markham; 145.9670, -4.6170, Papua New Guinea, Madang, Sumgilbar Rural; 146.0000, -4.5670, Papua New Guinea, Madang, Sumgilbar Rural; 146.0460, -6.0110, Papua New Guinea, Morobe, Markham; 146.4960, -7.7350, Papua New Guinea, Gulf, Kerema; 146.4960, -7.7350, Papua New Guinea, Gulf, Kerema; 146.5580, -7.1830, Papua New Guinea, Morobe, Bulolo; 146.6000, -7.9000, Papua New Guinea, Central, Goilala; 146.6000, -5.9330, Papua New Guinea, Madang, Rai Coast; 146.6330, -7.1830, Papua New Guinea, Morobe, Bulolo; 146.6390, -7.2030, Papua New Guinea, Morobe, Bulolo; 146.6810, -7.2740, Papua New Guinea, Morobe, Bulolo; 146.7010, -7.3420, Papua New Guinea, Morobe, Bulolo; 146.7040, -7.3400, Papua New Guinea, Morobe, Bulolo; 146.7060, -7.3500, Papua New Guinea, Morobe, Bulolo; 146.7070, -7.3440, Papua New Guinea, Morobe, Bulolo; 146.7130, -7.3430, Papua New Guinea, Morobe, Bulolo; 146.7170, -7.3330, Papua New Guinea, Morobe, Bulolo; 146.7420, -7.3720, Papua New Guinea, Morobe, Bulolo; 146.7430, -7.3750, Papua New Guinea, Morobe, Bulolo; 146.7650, -7.2890, Papua New Guinea, Morobe, Bulolo; 146.7690, -7.2830, Papua New Guinea, Morobe, Bulolo; 146.7700, -7.2830, Papua New Guinea, Morobe, Bulolo; 146.7740, -7.2780, Papua New Guinea, Morobe, Bulolo; 147.0830, -2.1170, Papua New Guinea, Manus, Manus; 147.0930, -7.2960, Papua New Guinea, Morobe, Huon; 147.1500, -6.6670, Papua New Guinea, Morobe, Nabak Rural; 147.3500, -2.3830, Papua New Guinea, Manus, Manus; 147.3690, -2.0570, Papua New Guinea, Manus, Manus; 147.3690, -2.0570, Papua New Guinea, Manus, Manus; 147.4000, -2.0670, Papua New Guinea, Manus, Manus; 147.4170, -2.0170, Papua New Guinea, Manus, Manus; 147.8670, -6.6330, Papua New Guinea, Morobe, Finschafen; 147.9220, -9.4630, Papua New Guinea, Central, Rigo; 147.9840, -9.4440, Papua New Guinea, Central, Rigo; 148.1670, -8.9330, Papua New Guinea, Northern, Ijivitari; 148.2250, -8.7750, Papua New Guinea, Northern, Ijivitari; 148.2350, -8.7640, Papua New Guinea, Northern, Ijivitari; 148.2830, -8.7080, Papua New Guinea, Northern, Ijivitari; 148.2850, -8.7070, Papua New Guinea, Northern, Ijivitari; 148.3170, -8.7080, Papua New Guinea, Northern, Ijivitari; 149.5950, -10.0210, Papua New Guinea, Milne Bay, Alotau; 150.4000, -10.3000, Papua New Guinea, Milne Bay, Alotau; 150.5470, -9.4690, Papua New Guinea, Milne Bay, Esa'ala; 150.6170, -6.1000, Papua New Guinea, West New Britain, Kandrian-Gloucester; 150.7830, -2.5670, Papua New Guinea, New Ireland, Kavieng; 150.7890, -9.4580, Papua New Guinea, Milne

Bay, Esa'ala; 150.8250, -9.4520, Papua New Guinea, Milne Bay, Esa'ala; 150.8330, -2.6000, Papua New Guinea, New Ireland, Kavieng; 150.9720, -10.0520, Papua New Guinea, Milne Bay, Esa'ala; 150.9810, -10.0330, Papua New Guinea, Milne Bay, Esa'ala; 150.9820, -10.0390, Papua New Guinea, Milne Bay, Esa'ala; 151.0670, -8.5330, Papua New Guinea, Milne Bay, Kiriwina-Goodenough; 151.4630, -5.4470, Papua New Guinea, East New Britain, Pomio; 151.4630, -5.4450, Papua New Guinea, East New Britain, Pomio; 151.4890, -5.5000, Papua New Guinea, East New Britain, Pomio; 151.5020, -5.5190, Papua New Guinea, East New Britain, Pomio; 152.0000, -4.5830, Papua New Guinea, East New Britain, Gazelle; 152.0000, -3.3170, Papua New Guinea, New Ireland, Namanatai; 152.1830, -4.2000, Papua New Guinea, East New Britain, Rabaul; 152.2000, -4.2000, Papua New Guinea, East New Britain, Rabaul; 152.4670, -4.1670, Papua New Guinea, East New Britain, Kokopo; 152.8330, -10.6670, Papua New Guinea, Milne Bay, Samarai-Murua; 152.9370, -4.5040, Papua New Guinea, New Ireland, Namanatai; 152.9370, -4.5030, Papua New Guinea, New Ireland, Namanatai; 152.9430, -9.2230, Papua New Guinea, Milne Bay, Samarai-Murua; 153.0200, -4.6310, Papua New Guinea, New Ireland, Namanatai; 153.4200, -11.4900, Papua New Guinea, Milne Bay, Samarai-Murua; 154.6830, -5.4000, Papua New Guinea, North Solomons, North Bougainville; 154.9000, -5.7000, Papua New Guinea, North Solomons, North Bougainville; 155.0000, -6.2000, Papua New Guinea, North Solomons, South Bougainville; 155.0940, -5.6450, Papua New Guinea, North Solomons, North Bougainville; 155.1000, -6.2000, Papua New Guinea, North Solomons, South Bougainville; 155.3000, -6.4000, Papua New Guinea, North Solomons, South Bougainville; 155.6830, -6.7670, Papua New Guinea, North Solomons, South Bougainville; 155.7000, -6.8000, Papua New Guinea, North Solomons, South Bougainville; 155.7330, -6.8330, Papua New Guinea, North Solomons, South Bougainville; 155.5500, -7.3500, Solomon Islands, Western, 155.5670, -7.3500, Solomon Islands, Western, 155.7500, -7.0500, Solomon Islands, Western; 156.5330, -6.7670, Solomon Islands, Choiseul; 156.7000, -7.9330, Solomon Islands, Western; 156.7770, -7.0490, Solomon Islands, Choiseul; 156.9640, -8.0420, Solomon Islands, Western; 157.6170, -8.2930, Solomon Islands, Western; 157.6170, -8.2930, Solomon Islands, Western; 157.8170, -8.3170, Solomon Islands, Western; 159.0000, -8.0000, Solomon Islands, Isabel; 159.1000, -9.0500, Solomon Islands, Guadalcanal; 159.5330, -8.1170, Solomon Islands, Isabel; 159.8070, -8.3850, Solomon Islands, Isabel; 159.9400, -9.4300, Solomon Islands, Guadalcanal; 159.9670, -9.4670, Solomon Islands, Guadalcanal; 159.9800, -9.4800, Solomon Islands, Guadalcanal; 160.0170, -9.8000, Solomon Islands, Guadalcanal; 160.1980, -9.5860, Solomon Islands, Guadalcanal; 160.1980, -9.5860, Solomon Islands, Guadalcanal; 160.2000, -9.5330, Solomon Islands, Guadalcanal; 160.2670, -9.4170, Solomon Islands, Guadalcanal; 160.4830, -9.5330, Solomon Islands, Guadalcanal; 160.6000, -8.4000, Solomon Islands, Malaita; 160.6760, -8.5950, Solomon Islands, Malaita; 160.7600, -8.8900, Solomon Islands, Malaita; 160.7700, -8.8800, Solomon Islands, Malaita; 160.7900, -8.8900, Solomon Islands, Malaita; 161.0000, -9.0000, Solomon Islands, Malaita; 127.7000, 0.9000, 127.9000, 1.0000, Australia; 130.8000, -12.5000, Australia; 130.8000, -12.4500, Australia; 132.1330, -11.2000, Australia; 132.1330, -11.1170, Australia; 132.1500, -11.2670, Australia; 132.1500, -11.1670, Australia; 134.2170, -12.0500, Australia; 136.4330, -13.9000, Australia; 136.5000, -1.2500, Australia; 141.8000, -12.7000, Australia; 141.8670, -12.6170, Australia; 143.6000, -12.9000, Australia;143.7670, -14.2330, Australia; 145.7920, -5.1500, Papua New Guinea; 145.8000, -16.9000, Australia; 145.8000, -16.7000, Australia; 145.8000, -5.1330, Papua New Guinea; 145.8830, -4.6330, Papua New Guinea; 145.9330, -4.5500, Papua New Guinea; 147.0000, -6.8000, Papua New Guinea; 147.0000, -6.7500, Papua New Guinea; 147.1500, -9.4670, Papua New Guinea;

147.2000, -9.5000, Papua New Guinea; 147.3100, -2.0600, Papua New Guinea; 147.3600, -1.9800, Papua New Guinea; 147.3670, -2.0330, Papua New Guinea; 147.8420, -6.6640, Papua New Guinea; 147.8420, -6.6640, Papua New Guinea; 149.1000, -20.5000, Australia; 149.2830, -20.8170, Australia; 150.0170, -10.6000, Australia; 150.6500, -10.6000, Australia; 151.2170, -33.7830, Australia; 151.2830, -33.8000, Australia; 151.3330, -33.4330, Australia; 151.6830, -10.0670, Australia; 152.9330, -9.2500, Australia; 153.1500, -30.2830, Australia; 153.6670, -4.0830, Australia; 155.6000, -6.2000, Australia; 155.8670, -7.0500, Australia; 156.5960, -7.8500, Australia; 156.8500, -8.1000, Australia; 157.3950, -8.4400, Australia; 159.5820, -8.1320, Australia; 159.5830, -8.1330, Australia; 159.9430, -9.4250, Australia; 160.0000, -10.0000, Australia; 160.4170, -9.4330, Australia; 132.6600, -5.7500, Australia; 128.3000, -2.0330, Australia; 127.4000, 0.8000, Australia.

Boiga irregularis, invasive

144.6210, 13.4430, Guam, Santa Rita; 144.6210, 13.4490, Guam, Santa Rita; 144.6210, 13.4430, Guam, Santa Rita; 144.6210, 13.4490, Guam, Santa Rita; 144.6240, 13.4430, Guam, Santa Rita; 144.6240, 13.4430, Guam, Santa Rita; 144.6740, 13.3540, Guam, Agat; 144.6740, 13.3540, Guam, Agat; 144.6800, 13.3500, Guam, Agat; 144.6990, 13.3640, Guam, Santa Rita; 144.6990, 13.3640, Guam, Santa Rita; 144.7020, 13.3780, Guam, Santa Rita; 144.7020, 13.3780, Guam, Santa Rita; 144.7350, 13.4750, Guam, Agana Heights; 144.7670, 13.4780, Guam, Mongmong-Toto-Maite; 144.7670, 13.4780, Guam, Mongmong-Toto-Maite; 144.7700, 13.4100, Guam, Yona; 144.7820, 13.4830, Guam, Tamuning; 144.7820, 13.4830, Guam, Tamuning; 144.7950, 13.4900, Guam, Tamuning; 144.8000, 13.5000, Guam, Tamuning; 144.8600, 13.5900, Guam, Dededo; 144.8600, 13.6500, Guam, Dededo; 144.8640, 13.6510, Guam, Yigo; 144.8640, 13.6510, Guam, Yigo; 144.9200, 13.5700, Guam, Yigo, -157.9190, 21.3290, United States, Hawaii, Honolulu; -157.9700, 21.3300, United States, Hawaii; 144.6240, 13.4490, United States, Hawaii; 144.6240, 13.4490, United States, Hawaii; 144.9620, 13.6390, United States, Hawaii; 144.9620, 13.6390, United States, Hawaii; 145.2000, 14.2000, United States, Hawaii; 145.8000, 15.2000, United States, Hawaii.

Eleutherodactylus coqui, native

-67.1400, 18.2031, Puerto Rico, Mayagüez; -66.8775, 18.2967, Puerto Rico, Lares; -66.7922, 18.2922, Puerto Rico, Utuado; -66.7225, 18.1647, Puerto Rico, Adjuntas; -66.5110, 18.1607, Puerto Rico, Orocovis; -66.5000, 18.3333, Puerto Rico, Ciales; -66.4614, 18.0788, Puerto Rico, Juana Díaz; -66.4143, 18.2947, Puerto Rico, Morovis; -66.2664, 18.1419, Puerto Rico, Aibonito; -66.2520, 18.1941, Puerto Rico, Comerío; -66.2196, 18.3119, Puerto Rico, Naranjito; -66.1703, 17.9553, Puerto Rico, Guayama; -66.1664, 18.1139, Puerto Rico, Cayey; -66.1166, 18.2306, Puerto Rico, Aguas Buenas; -66.1033, 18.2589, Puerto Rico, Aguas Buenas; -66.0489, 18.2361, Puerto Rico, Caguas; -65.9317, 18.1224, Puerto Rico, San Lorenzo; -65.8623, 18.2520, Puerto Rico, Juncos; -65.8324, 18.3168, Puerto Rico, Río Grande; -65.8261, 18.3408, Puerto Rico, Río Grande; -65.8261, 18.3408, Puerto Rico, Río Grande; -65.8200, 18.3217, Puerto Rico, Río Grande; -65.7931, 18.2997, Puerto Rico, Río Grande; -65.7917, 18.3133, Puerto Rico, Río Grande; -65.7917, 18.3125, Puerto Rico, Río Grande; -65.7892, 18.3003, Puerto Rico, Río Grande; -65.7858, 18.2969, Puerto Rico, Río Grande; -65.7833, 18.3347, Puerto Rico, Río Grande; -65.7594, 18.3692, Puerto Rico, Luquillo; -65.4528, 18.1407, Puerto Rico, Vieques.

Eleutherodactylus coqui, invasive

-78.0170, 24.7300, Bahamas, North Andros; -91.1310, -0.4060, Ecuador, Galápagos, Isabela; -65.3300, 18.3300, Puerto Rico, Culebra; -69.9750, 18.6060, República Dominicana, Santo Domingo; -154.9020, 19.4830, United States, Hawaii, Hawaii; -154.9120, 19.4610, United States, Hawaii, Hawaii; -154.9360, 19.4600, United States, Hawaii, Hawaii; -154.9510, 19.4980, United States, Hawaii, Hawaii; -155.0730, 19.6020, United States, Hawaii, Hawaii; -155.0760, 19.5120, United States, Hawaii, Hawaii; -155.0790, 19.5910, United States, Hawaii, Hawaii; -155.0800, 19.5910, United States, Hawaii, Hawaii; -155.1000, 19.7300, United States, Hawaii, Hawaii; -155.1010, 19.6010, United States, Hawaii, Hawaii; -155.1520, 19.5150, United States, Hawaii, Hawaii; -155.2130, 19.4340, United States, Hawaii, Hawaii; -155.8260, 19.1100, United States, Hawaii, Hawaii; -155.9450, 19.6190, United States, Hawaii, Hawaii; -156.2600, 20.9200, United States, Hawaii, Maui; -156.3200, 20.9200, United States, Hawaii, Maui; -156.3260, 20.9180, United States, Hawaii, Maui; -156.3390, 20.8300, United States, Hawaii, Maui; -156.3400, 20.7800, United States, Hawaii, Maui; -156.6540, 21.0000, United States, Hawaii, Maui; -156.6650, 21.0030, United States, Hawaii, Maui; -157.0120, 21.1740, United States, Hawaii, Kalawao; -157.7250, 21.3400, United States, Hawaii, Honolulu; -157.8300, 21.2970, United States, Hawaii, Honolulu; -157.8480, 21.4700, United States, Hawaii, Honolulu; -158.0020, 21.5020, United States, Hawaii, Honolulu; -158.0330, 21.3320, United States, Hawaii, Honolulu; -158.0850, 21.6140, United States, Hawaii, Honolulu; -158.0850, 21.6180, United States, Hawaii, Honolulu; -80.1340, 26.0590, United States, Florida, Broward; -80.3000, 25.8420, United States, Florida, Miami-Dade; -80.4540, 25.5020, United States, Florida, Miami-Dade; -64.7480, 17.7660, U.S. Virgin Islands, Saint Croix, -64.8820, 17.7140, U.S. Virgin Islands, Saint Croix, -156.1570, 20.8630, United States; -157.8370, 21.4630, United States; -64.8200, 18.3220, United States; -65.4450, 18.1490, United States.

Eleutherodactylus johnstonei, native

-61.8833, 17.0333, Antigua and Barbuda, Saint Mary; -61.8000, 17.0500, Antigua and Barbuda, Saint Paul; -61.7000, 17.0667, Antigua and Barbuda, Saint Philip; -61.8500, 17.1167, Antigua and Barbuda, Saint John; -61.8333, 17.6333, Antigua and Barbuda, Barbuda; -61.6333, 15.9667, Guadeloupe, Basse-Terre; -61.6833, 15.9833, Guadeloupe, Basse-Terre; -61.5167, 16.2333, Guadeloupe, Pointe-à-Pitre; -61.7167, 16.2833, Guadeloupe, Basse-Terre; -60.8833, 14.4333, Martinique, Le Marin, Sainte-Anne; -61.1667, 14.7333, Martinique, Saint-Pierre, Saint-Pierre; -61.1333, 14.7333, Martinique, Saint-Pierre, Saint-Pierre; -61.1333, 14.7667, Martinique, Saint-Pierre, Le Morne-Rouge; -61.2167, 14.8000, Martinique, Saint-Pierre, Le Prêcheur; -61.1167, 14.8667, Martinique, Le Trinité, Basse-Pointe; -62.2167, 16.7167, Montserrat; -62.2000, 16.7333, Montserrat; -62.2167, 16.7500, Montserrat; -62.2000, 16.7667, Montserrat; -62.1833, 16.7667, Montserrat; -62.5500, 17.1167, Saint Kitts and Nevis, Saint George Gingerland; -62.6167, 17.1333, Saint Kitts and Nevis, Saint John Figtree; -62.5667, 17.1333, Saint Kitts and Nevis, Saint George Gingerland; -62.6167, 17.1667, Saint Kitts and Nevis, Saint Thomas Lowland; -62.7167, 17.3333, Saint Kitts and Nevis, Saint Peter Basseterre; -60.9500, 13.7167, Santa Lucia, Vieux Fort; -61.0500, 13.8500, Santa Lucia, Soufrière; -61.0000, 13.9667, Santa Lucia, Castries; -60.9833, 13.9833, Santa Lucia, Castries; -61.0000, 14.0000, Santa Lucia, Castries; -60.9833, 13.7333, Santa Lucia, Castries; -61.0333, 14.4667, Santa Lucia, Castries; -60.9167, 14.4667, Martinique; -61.5833, 16.0000, Martinique; -62.2167, 16.7000, Martinique; -62.2333, 16.7167, Martinique; -62.2194, 16.7819, Martinique; -62.5500, 17.2000, Martinique; -62.8333, 17.8833, Martinique.

Eleutherodactylus johnstonei, invasive

-66.9167, 10.5000, Venezuela, Distrito Capital, Caracas, Isla de Aves; -66.9167, 10.5000, Venezuela, Distrito Capital, Caracas, Isla de Aves; -79.5333, 8.9667, Panamá, Panamá, Panamá, La Exposición o Calidonia; -70.0019, 12.5199, Aruba, -59.5500, 13.1333, Barbados, Saint George, -59.6333, 13.2000, Barbados, Saint James, -64.7839, 32.2942, Bermuda, Hamilton Municipality, -64.6781, 32.3817, Bermuda, Saint George municipality, -74.7958, 10.9727, Colombia, Atlántico, Barranquilla; -73.1258, 7.1297, Colombia, Santander, Bucaramanga; -76.5225, 3.4372, Colombia, Valle del Cauca, Santiago de Cali; -75.5144, 10.3997, Colombia, Bolívar, Cartagena de Indias; -83.9975, 10.0000, Costa Rica, San José, Vásquez de Coronado; -61.7500, 12.0167, Grenada, Saint George, -61.6830, 12.0330, Grenada, Saint David, -61.7167, 12.0333, Grenada, Saint George, -61.6667, 12.0333, Grenada, Saint David, -61.7500, 12.0500, Grenada, Saint George, -61.6833, 12.0500, Grenada, Saint David, -61.7330, 12.0670, Grenada, Saint George, -61.7167, 12.0833, Grenada, Saint George, -61.6167, 12.1333, Grenada, Saint Andrew, -61.6170, 12.1500, Grenada, Saint Andrew, -61.6333, 12.2167, Grenada, Saint Patrick, -58.1667, 6.8000, Guyana, East Berbice-Corentyne, City of Georgetown; -52.7667, 4.7500, Guyane, Cayenne, Kourou; -52.3333, 4.9333, Guyane, Cayenne, Rémire-Montjoly; -76.8000, 18.0000, Jamaica, Saint Andrew, -77.5000, 18.0333, Jamaica, Manchester, -76.7167, 18.0833, Jamaica, Portland, -77.2333, 18.1500, Jamaica, Clarendon, -77.4833, 18.1667, Jamaica, Manchester, -77.0833, 18.1833, Jamaica, Saint Catherine, -76.4667, 18.1833, Jamaica, Portland; -77.6167, 18.2500, Jamaica, Trelawny; -78.3500, 18.2667, Jamaica, Westmoreland; -77.3500, 18.3167, Jamaica, Saint Ann; -76.9000, 18.3667, Jamaica, Saint Mary; -77.4833, 18.4167, Jamaica, Trelawny; -77.4000, 18.4500, Jamaica, Saint Ann; -77.5333, 18.4667, Jamaica, Trelawny; -68.8784, 12.1491, Nederlandse Antillen, Curaçao; -68.2585, 12.1767, Nederlandse Antillen, Bonaire; -61.4446, 12.6049, Saint Vincent and the Grenadines, Grenadines; -61.3282, 12.7254, Saint Vincent and the Grenadines, Grenadines; -61.1796, 12.8799, Saint Vincent and the Grenadines, Grenadines; -61.2333, 13.0167, Saint Vincent and the Grenadines, Grenadines; -61.2000, 13.1333, Saint Vincent and the Grenadines, Saint George; -61.2330, 13.2000, Saint Vincent and the Grenadines, Saint Andrew; -61.2167, 13.2000, Saint Vincent and the Grenadines, Saint Andrew; -61.2170, 13.2330, Saint Vincent and the Grenadines, Saint Patrick, -61.2170, 13.2500, Saint Vincent and the Grenadines, Saint Patrick; -61.2500, 13.2667, Saint Vincent and the Grenadines, Saint Patrick; -61.2167, 13.3167, Saint Vincent and the Grenadines, Saint David; -61.1670, 13.3330, Saint Vincent and the Grenadines, Charlotte; -61.5167, 10.6500, Trinidad and Tobago, Port of Spain; -62.8333, 7.6500, Venezuela, Bolívar, Piar; -62.3989, 8.0861, Venezuela, Bolívar, Piar; -63.5497, 8.1222, Venezuela, Anzoátegui, Independencia; -71.1450, 8.5983, Venezuela, Mérida, Libertador; -71.0922, 9.1544, Venezuela, Mérida, Tulio Febres Cordero; -69.3228, 10.0739, Venezuela, Lara, Iribarren; -66.2117, 10.2053, Venezuela, Miranda, Acevedo; -64.1833, 10.4667, Venezuela, Sucre, Sucre; -66.9333, 10.6000, Venezuela, Distrito Capital, Vargas; -66.9833, 10.6000, Venezuela, Distrito Capital, Vargas; -64.6167, 10.2167, Venezuela, Anzoátegui, Sotillo; -67.5958, 10.2469, Venezuela, Aragua, Girardot; -62.6528, 8.3533, Venezuela, Monagas, Sotillo; -62.7186, 8.2981, Venezuela, Bolívar, Caroní; -68.0186, 10.2600, Venezuela, Carabobo, Montalbán; -71.2000, 8.5667, Venezuela, Mérida, Campo Elías; -66.9278, 10.3467, Venezuela, Miranda, Guaicaipuro; -63.4989, 10.1744, Venezuela, Monagas, Caripe; -63.1767, 9.7500, Venezuela, Monagas, Maturín; -64.1667, 10.4667, Venezuela, Sucre, Sucre; -62.5842, 10.5675, Venezuela, Sucre, Mariño; -61.6170, 12.1170, -61.6330, 12.2330, Grenada, -61.2333, 12.9833, St. Vincent and the Grenadines; -59.5833, 13.0667, St. Vincent and the Grenadines; -61.2167, 13.1333, St. Vincent and the Grenadines; -59.5167, 13.2167, St. Vincent and the Grenadines; -77.1167, 18.4167, St. Vincent and the Grenadines; -64.7000, 32.3667, St. Vincent and the Grenadines.

Hemidactylus frenatus, native

121.0500, 14.4167, Pilipinas, Metropolitan Manila, Muntinlupa, Alabang; 122.1069, 11.4158, Pilipinas, Antique, Culasi, Alojipan; 99.9394, 9.5539, Thailand, Surat Thani, Ko Samui, Ang Thong; 102.8000, 16.5000, Thailand, Khon Kaen, Muang Khon Kaen, Ban Kho; 125.0256, 12.0549, Pilipinas, Samar, San Jose de Buan, Barangay 4; 123.5706, 9.8555, Pilipinas, Cebu, Argao, Bogo; 124.0490, 12.9660, Pilipinas, Sorsogon, Sorsogon, Buhatan; 108.0500, 12.6667, Vietnam, Tây Nguyên, Buon Ma Thuot City; 108.0500, 12.6667, Vietnam, Tây Nguyên, Buon Ma Thuot City; 121.5000, 19.3000, Pilipinas, Cagayan, Calayan, Cabudadan; 122.6644, 12.4612, Pilipinas, Romblon, Cajidiocan, Cambalo; 123.9010, 10.3182, Pilipinas, Cebu, Cebu City, Camputhaw; 121.9682, 14.7526, Pilipinas, Quezon, Polillo, Canicanian; 119.2500, 10.1500, Pilipinas, Palawan, Roxas, Caramay; 125.5737, 10.3619, Pilipinas, Surigao Del Norte, Loreto, Carmen; 109.5500, 19.5000, China, Hainan, Hainan, Danzhou; 109.6595, 19.2658, China, Hainan, Hainan, Danzhou; 109.6600, 19.2658, China, Hainan, Hainan, Danzhou; 123.3077, 9.3155, Pilipinas, Negros Oriental, Dumaguete City, Daro; 125.6109, 10.3864, Pilipinas, Surigao Del Norte, Loreto, Esperanza; 125.6138, 10.3850, Pilipinas, Surigao Del Norte, Loreto, Esperanza; 124.8836, 11.7664, Pilipinas, Samar, Catbalogan, Guinsorongan; 105.8500, 21.0333, Vietnam; 105.8500, 21.0333, Vietnam; 88.4600, 22.9500, India, West Bengal, Nadia, Kalyani; 96.2472, 23.0879, Myanmar, Shan, Shan, Kyaukme, Mong Mit; 96.3421, 23.0711, Myanmar, Shan, Shan, Kyaukme, Mong Mit; 96.3572, 23.0704, Myanmar, Shan, Shan, Kyaukme, Mong Mit; 96.0080, 21.6434, Myanmar, Mandalay, Mandalay, Kyaukse, Kyaukse; 96.1487, 21.6006, Myanmar, Mandalay, Mandalay, Kyaukse, Kyaukse; 96.2568, 21.3760, Myanmar, Mandalay, Mandalay, Kyaukse, Myitha; 121.4125, 18.3491, Pilipinas, Cagayan, Abulug, Libertad, 122.7826, 14.0899, Pilipinas, Camarines Norte, Labo, Lugui, 123.6667, 13.7197, Pilipinas, Camarines Sur, Presentacion, Maangas; 121.1726, 17.3471, Pilipinas, Kalinga, Lubuagan, Mabilong; 121.4141, 12.7354, Pilipinas, Oriental Mindoro, Bongabong, Malitbog; 96.1141, 22.0056, Myanmar, Mandalay, Mandalay, Mandalay, Mandalay; 97.7173, 16.3409, Myanmar, Mon, Mon, Mawlamyine, Mudon; 122.6556, 10.6925, Pilipinas, Guimaras, Buenavista, Mclain; 95.9600, 20.9600, Myanmar, Mandalay, Mandalay, Meiktila, Wudwin; 95.9652, 20.9686, Myanmar, Mandalay, Mandalay, Meiktila, Wudwin; 95.9700, 20.9700, Myanmar, Mandalay, Mandalay, Meiktila, Wudwin; 96.0731, 21.3299, Myanmar, Mandalay, Mandalay, Meiktila, Wudwin; 96.3108, 20.7542, Myanmar, Mandalay, Mandalay, Meiktila, Thazi; 94.4564, 20.1924, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.4587, 20.1931, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.4632, 20.1915, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.4637, 20.1908, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.4825, 20.1862, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5254, 20.2634, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5314, 20.2373, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5369, 20.2186, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5371, 20.2236, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5418, 20.3259, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5509, 20.2899, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5531, 20.2322, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5547, 20.3143, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5558, 20.2312, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5577, 20.3013, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5681, 20.3197, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.5938, 20.0567, Myanmar, Magway, Magway, Minbu, Minbu (Sagu); 94.5975, 20.0579, Myanmar, Magway, Magway, Minbu, Minbu (Sagu); 94.6107, 20.1156, Myanmar, Magway, Magway, Minbu, Minbu (Sagu); 94.6211, 20.1233, Myanmar, Magway, Magway, Minbu, Minbu (Sagu); 94.6365, 20.1265, Myanmar, Magway, Magway, Minbu, Minbu (Sagu); 94.6429, 20.1459, Myanmar, Magway, Magway, Minbu, Minbu (Sagu); 94.6812, 20.3370, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.7465, 20.3243, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.7690, 20.3200, Myanmar, Magway, Magway, Minbu, Pwinbyu; 94.4139, 21.8820, Myanmar, Sagaing, Sagaing, Monywa, Pale; 94.4334, 21.8730, Myanmar, Sagaing, Sagaing, Monywa, Pale; 94.4756, 22.3185, Myanmar, Sagaing, Sagaing, Monywa, Kani; 94.4757, 22.3182, Myanmar, Sagaing, Sagaing, Monywa, Kani; 94.4865, 22.3223, Myanmar, Sagaing, Sagaing, Monywa, Kani; 94.4874, 22.3207, Myanmar, Sagaing, Sagaing, Monywa, Kani; 94.6177, 22.2176, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.6305, 22.2444, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.6495, 22.2444, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.6497, 22.2434, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.6517, 22.2569, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.6737, 22.1608, Myanmar, Sagaing, Sagaing, Monywa, Pale; 94.6781, 22.2109, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.6782, 22.1995, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.6833, 22.1863, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.7689, 22.0796, Myanmar, Sagaing, Sagaing, Monywa, Pale; 94.8602, 22.0884, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.8620, 22.0893, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 94.9016, 22.0726, Myanmar, Sagaing, Sagaing, Monywa, Yinmabin; 95.3400, 22.2100, Myanmar, Sagaing, Sagaing, Monywa, Ayadaw; 95.3413, 22.2182, Myanmar, Sagaing, Sagaing, Monywa, Ayadaw; 94.8587, 21.1287, Myanmar, Mandalay, Mandalay, Myingyan, Nyaungu; 95.2421, 20.8998, Myanmar, Mandalay, Mandalay, Myingyan, Kyaukpadaung; 95.2559, 20.9732, Myanmar, Mandalay, Mandalay, Myingyan, Kyaukpadaung; 95.2583, 20.9185, Myanmar, Mandalay, Mandalay, Myingyan, Kyaukpadaung; 95.7738, 21.3777, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.7773, 21.4081, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.7836, 21.4533, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.7856, 21.3996, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.7865, 21.3963, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.7977, 21.3992, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.8017, 21.4027, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.8064, 21.3907, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.8106, 21.3839, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 95.8317, 21.4121, Myanmar, Mandalay, Mandalay, Myingyan, Natogyi; 94.7332, 16.2770, Myanmar, Ayeyarwady, Ayeyarwady, Myoungmya, Myaungmya;

94.7541, 16.2778, Myanmar, Ayeyarwady, Ayeyarwady, Myoungmya, Myaungmya; 94.7687, 16.2806, Myanmar, Ayeyarwady, Ayeyarwady, Myoungmya, Myaungmya; 94.7706, 16.2910, Myanmar, Ayeyarwady, Ayeyarwady, Myoungmya, Myaungmya; 94.7707, 16.2791, Myanmar, Ayeyarwady, Ayeyarwady, Myoungmya, Myaungmya; 94.7732, 16.2781, Myanmar, Ayeyarwady, Ayeyarwady, Myoungmya, Myaungmya; 98.3000, 7.9000, Thailand, Phuket, Kathu, Pa Tong; 94.1597, 21.0079, Myanmar, Magway, Magway, Pakokku, Saw; 94.1649, 21.2460, Myanmar, Magway, Magway, Pakokku, Saw; 95.0656, 21.5930, Myanmar, Magway, Magway, Pakokku, Myaing; 95.1010, 21.5896, Myanmar, Magway, Magway, Pakokku, Yesagyo; 95.2278, 21.5346, Myanmar, Magway, Magway, Pakokku, Yesagyo; 123.2477, 13.6151, Pilipinas, Camarines Sur, Pili, Palestina; 124.2717, 7.3697, Pilipinas, Maguindanao, Parang, Poblacion II; 122.1341, 12.5670, Pilipinas, Romblon, San Agustin, Poblacion; 124.0014, 12.9695, Pilipinas, Sorsogon, Sorsogon, Polvorista; 95.9872, 22.8898, Myanmar, Mandalay, Mandalay, Pyin-Oo-Lwin, Thabeikkyin; 96.0493, 23.0120, Myanmar, Mandalay, Mandalay, Pyin-Oo-Lwin, Thabeikkyin; 96.0508, 23.0140, Myanmar, Mandalay, Mandalay, Pyin-Oo-Lwin, Thabeikkyin; 96.1041, 22.9129, Myanmar, Mandalay, Mandalay, Pyin-Oo-Lwin, Thabeikkyin; 96.1071, 22.9783, Myanmar, Mandalay, Mandalay, Pyin-Oo-Lwin, Thabeikkyin; 96.1469, 23.0844, Myanmar, Mandalay, Mandalay, Pyin-Oo-Lwin, Thabeikkyin; 96.1519, 23.1012, Myanmar, Mandalay, Mandalay, Pyin-Oo-Lwin, Thabeikkyin; 96.2407, 22.9547, Myanmar, Mandalay, Mandalay, Pyin-Oo-Lwin, Mogok; 110.4167, 19.2500, China, Hainan, Hainan, Qionghai; 110.4170, 19.2500, China, Hainan, Hainan, Qionghai; 109.6640, 19.0563, China, Hainan, Hainan, Qiongzhong Li and Miao; 109.6643, 19.0563, China, Hainan, Hainan, Qiongzhong Li and Miao; 109.7400, 19.2196, China, Hainan, Hainan, Qiongzhong Li and Miao; 109.9550, 19.1622, China, Hainan, Hainan, Qiongzhong Li and Miao; 106.6700, 10.7500, Vietnam, Đông Nam B?, H? Chí Minh city; 122.0617, 12.6179, Pilipinas, Romblon, Calatrava, San Roque; 121.7249, 12.9156, Pilipinas, Romblon, Concepcion, San Vicente; 125.0231, 11.9396, Pilipinas, Samar, Motiong, Sarao; 95.7380, 23.5740, Myanmar, Sagaing, Sagaing, Shwebo, Kanbalu; 122.5909, 12.4916, Pilipinas, Romblon, Magdiwang, Silum; 124.3000, 13.8000, Pilipinas, Catanduanes, Gigmoto, Sioron; 92.8782, 21.0174, Myanmar, Rakhine, Rakhine, Sittwe, Kyauktaw; 92.9807, 21.0065, Myanmar, Rakhine, Rakhine, Sittwe, Kyauktaw; 92.9987, 21.0066, Myanmar, Rakhine, Rakhine, Sittwe, Kyauktaw; 122.6928, 10.9217, Pilipinas, Iloilo, Barotac Nuevo, Sohoton; 108.4830, 15.5667, Vietnam, Nam Trung B, Qung Nam, Tam K; 108.4833, 15.5667, Vietnam, Nam Trung B, Qung Nam, Tam K; 96.8910, 20.0788, Myanmar, Shan, Shan, Taunggye, Pinlaung; 96.1700, 18.8600, Myanmar, Bago, Bago, Taungoo, Thoungoo; 96.1726, 18.8560, Myanmar, Bago, Bago, Taungoo, Thoungoo; 96.1732, 18.8545, Myanmar, Bago, Bago, Taungoo, Thoungoo; 94.5429, 17.7248, Myanmar, Rakhine, Rakhine, Thandwe, Gwa; 94.5888, 17.6160, Myanmar, Rakhine, Rakhine, Thandwe, Gwa; 94.6086, 17.5164, Myanmar, Rakhine, Rakhine, Thandwe, Gwa; 123.4024, 9.9291, Pilipinas, Cebu, Moalboal, Tomonoy; 120.1597, 13.7955, Pilipinas, Occidental Mindoro, Lubang, Vigo; 96.0926, 17.0462, Myanmar, Yangon, Yangon, Yangon-N, Hmawbi; 96.0934, 17.0455, Myanmar, Yangon, Yangon, Yangon-N, Hmawbi; 96.0950, 17.0475, Myanmar, Yangon, Yangon, Yangon-N, Hmawbi; 96.0971, 17.0456, Myanmar, Yangon, Yangon, Yangon-N, Hmawbi; 96.0984, 17.0406, Myanmar, Yangon, Yangon, Yangon-N, Hmawbi; 96.0997, 17.0427, Myanmar, Yangon, Yangon, Yangon-N, Hmawbi; 96.1161, 17.0432, Myanmar, Yangon, Yangon, Yangon-N, Hlegu; 96.1174, 17.0434, Myanmar, Yangon, Yangon, Yangon-N, Hlegu; 96.1186, 17.0425, Myanmar, Yangon, Yangon, Yangon-N, Hlegu; 96.1193, 17.0439, Myanmar, Yangon, Yangon, Yangon-N, Hlegu; 96.2519, 17.0630, Myanmar, Yangon, Yangon, Yangon-N, Hlegu; 96.1379, 16.8596, Myanmar, Yangon,

Yangon, Yangon-W, Yangon (Rangoon); 96.1386, 16.8596, Myanmar, Yangon, Yangon, Yangon-W, Yangon (Rangoon); 96.1400, 16.8600, Myanmar, Yangon, Yangon, Yangon-W, Yangon (Rangoon); 96.1413, 16.8580, Myanmar, Yangon, Yangon, Yangon-W, Yangon (Rangoon); 105.5800, -10.5000, Christmas Island; 105.5830, -10.5000, Christmas Island; 177.4198, -17.7700, Fiji, Western, Ba; 144.6236, 13.4431, Guam, Santa Rita; 144.6622, 13.3831, Guam, Agat; 144.6710, 13.4600, Guam, Piti; 144.6889, 13.3789, Guam, Santa Rita; 144.6942, 13.4592, Guam, Piti; 144.7067, 13.4689, Guam, Piti; 144.7669, 13.4778, Guam, Mongmong-Toto-Maite; 144.8000, 13.5000, Guam, Tamuning; 144.8489, 13.6331, Guam, Dededo; 144.8600, 13.5900, Guam, Dededo; 144.8600, 13.6500, Guam, Dededo; 144.8639, 13.6511, Guam, Yigo; 102.2708, -5.3474, Indonesia, Bengkulu, Bengkulu Utara; 102.2710, -5.3474, Indonesia, Bengkulu, Bengkulu Utara; 102.2740, -5.3484, Indonesia, Bengkulu, Bengkulu Utara; 102.2743, -5.3484, Indonesia, Bengkulu, Bengkulu Utara; 102.2766, -5.3483, Indonesia, Bengkulu, Bengkulu Utara; 102.2770, -5.3483, Indonesia, Bengkulu, Bengkulu Utara; 102.2810, -5.3628, Indonesia, Bengkulu, Bengkulu Utara; 102.2812, -5.3628, Indonesia, Bengkulu, Bengkulu Utara; 102.2825, -5.3573, Indonesia, Bengkulu, Bengkulu Utara; 102.2830, -5.3573, Indonesia, Bengkulu, Bengkulu Utara; 102.2830, -5.3584, Indonesia, Bengkulu, Bengkulu Utara; 102.2834, -5.3584, Indonesia, Bengkulu, Bengkulu Utara; 106.8000, -6.1700, Indonesia, Jakarta Raya, Jakarta Barat; 135.4830, -3.3670, Indonesia, Papua, Nabire; 136.1000, -1.1700, Indonesia, Papua, Biak Numfor; 136.2300, -1.8800, Indonesia, Papua, Yapen Waropen; 140.6200, -2.6000, Indonesia, Papua, Jayapura; 113.8000, 3.8000, Malaysia, Sarawak, Niah Suai; 151.8440, 7.4292, Micronesia, Chuuk, 158.2030, 6.9667, Micronesia, Pohnpei, 158.2080, 6.9611, Micronesia, Pohnpei, 158.2080, 6.9667, Micronesia, Pohnpei, 162.9810, 5.2866, Micronesia, Kosrae, 162.9815, 5.2866, Micronesia, Kosrae, 164.9330, -20.6833, New Caledonia, Nord, Hienghène; 164.9333, -20.6833, New Caledonia, Nord, Hienghène; 166.8330, -22.3000, New Caledonia, Sud, Mont-Dore; 127.7747, 26.3478, Nippon, Saga; 127.7750, 26.3478, Nippon, Saga; 128.0240, 26.5781, Nippon, Saga; 128.0244, 26.5781, Nippon, Saga; 135.7756, 34.9481, Nippon, Kyoto; 135.7760, 34.9481, Nippon, Kyoto; 145.1294, 14.1311, Northern Mariana Islands, Rota; 145.1417, 14.1419, Northern Mariana Islands, Rota; 145.2406, 14.1775, Northern Mariana Islands, Rota; 145.2414, 14.1783, Northern Mariana Islands, Rota; 145.7461, 15.0961, Northern Mariana Islands, Saipan; 145.7480, 15.1925, Northern Mariana Islands, Saipan; 145.7481, 15.1925, Northern Mariana Islands, Saipan; 134.4539, 7.3331, Palau, Koror; 134.4739, 7.3350, Palau, Koror; 134.4780, 7.3403, Palau, Koror; 134.4790, 7.3417, Palau, Koror; 134.4800, 7.3353, Palau, Koror; 134.4950, 7.3339, Palau, Koror; 134.4950, 7.3381, Palau, Koror; 134.5011, 7.4561, Palau, Aimeliik; 134.5170, 7.3600, Palau, Airai; 134.6000, 7.5000, Palau, Melekeok; 134.6290, 7.4880, Palau, Melekeok; 134.6340, 7.5520, Palau, Ngiwal; 141.5850, -3.3890, Papua New Guinea, Sandaun, Vanimo-Green River; 145.8000, -5.1600, Papua New Guinea, Madang, Madang; 145.8820, -5.9538, Papua New Guinea, Madang, Usino Bundi; 145.9100, -5.9968, Papua New Guinea, Morobe, Markham; 146.5480, -7.6840, Papua New Guinea, Morobe, Bulolo; 146.6387, -7.2029, Papua New Guinea, Morobe, Bulolo; 146.6390, -7.2028, Papua New Guinea, Morobe, Bulolo; 146.6650, -6.7906, Papua New Guinea, Morobe, Bulolo; 146.7010, -7.3420, Papua New Guinea, Morobe, Bulolo; 146.7050, -7.3410, Papua New Guinea, Morobe, Bulolo; 146.7270, -6.5680, Papua New Guinea, Morobe, Huon; 147.0010, -6.7342, Papua New Guinea, Morobe, Lae; 147.1410, -7.8760, Papua New Guinea, Morobe, Bulolo; 147.5980, -9.4380, Papua New Guinea, Central, Kairuku-Hiri; 150.3070, -10.4184, Papua New Guinea, Milne Bay, Alotau; 151.5020, -5.5190, Papua New Guinea, East New Britain, Pomio; 152.0000, -4.3333, Papua New Guinea, East New Britain, Gazelle; 152.6870, -10.6588, Papua New

Guinea, Milne Bay, Samarai-Murua; 152.6940, -10.6594, Papua New Guinea, Milne Bay, Samarai-Murua; 152.8420, -10.6899, Papua New Guinea, Milne Bay, Samarai-Murua; 152.9430, -9.2233, Papua New Guinea, Milne Bay, Samarai-Murua; 153.0130, -4.6410, Papua New Guinea, New Ireland, Namanatai; 153.2340, -11.3161, Papua New Guinea, Milne Bay, Samarai-Murua; 155.0940, -5.6449, Papua New Guinea, North Solomons, North Bougainville; 121.4141, 12.0228, Pilipinas, Antique, Caluya; 120.6330, 23.0000, Taiwan, Taiwan, Kaohsiung; 120.6333, 23.0000, Taiwan, Taiwan, Kaohsiung; 120.9500, 23.9667, Taiwan, Taiwan, Nantou; 120.9500, 23.9667, Taiwan, Taiwan, Nantou; 100.9330, 13.3333, Thailand, Chon Buri, Muang Chon Buri; 100.9333, 13.3333, Thailand, Chon Buri, Muang Chon Buri; 101.2887, 14.2703, Thailand, Nakhon Nayok, Muang Nakhon Nayok; 101.2890, 14.2703, Thailand, Nakhon Nayok, Muang Nakhon Nayok; 101.3786, 14.4097, Thailand, Nakhon Nayok, Muang Nakhon Nayok; 101.3790, 14.4097, Thailand, Nakhon Nayok, Muang Nakhon Nayok; 120.2044, 14.4144; 120.2167, 14.7500; 120.2170, 14.7500; 121.8403, 20.2903; 122.9700, -12.1700; 123.0300, -12.5000; 124.3814, 10.6730; 127.7000, 0.9000; 127.9000, 1.0000; 128.0000, 1.1000; 134.2670, -1.3500; 134.4470, 7.3250; 134.4470, -7.3250; 134.4489, 7.3261; 134.4720, 7.3333; 144.6169, 13.4461; 144.6439, 13.4131, Northern Mariana Islands; 144.6481, 13.3761, Northern Mariana Islands; 144.6489, 13.3781, Northern Mariana Islands; 144.6500, 13.2400; 144.7039, 13.2431, Northern Mariana Islands; 144.7669, 13.4911, Northern Mariana Islands; 144.9619, 13.6389; 145.6000, 14.8000; 147.2920, -2.0180; 149.5330, -6.2333; 153.0600, -4.5350; 158.2639, 6.9819; 158.2640, 6.9819; 163.0090, 5.3785; 165.8090, -21.8453, New Caledonia; 166.4390, -22.3056; 166.4394, -22.3056; 166.6300, 19.3000; 94.5321, 17.7177; 98.2833, 7.8955, Thailand.

Hemidactylus frenatus, invasive

48.3600, -13.6600, Madagascar, Antsiranana, Diana, Ambanja, Ankatafa; 44.3300, -22.4500, Madagascar, Toliary, Atsimo-Andrefana, Ankazoabo-Sud, Ankazoabo; 50.2100, -14.7500, Madagascar, Antsiranana, Sava, Antalaha, Ampahana; 44.6100, -18.7000, Madagascar, Mahajanga, Melaky, Antsalova, Antsalova; 49.2000, -12.4800, Madagascar, Antsiranana, Diana, Antsiranana Rural, Joffreville; 49.3600, -12.3600, Madagascar, Antsiranana, Diana, Antsiranana Rural, Ramena; 44.5000, -16.4600, Madagascar, Mahajanga, Melaky, Besalampy, Soananga; 44.7600, -16.4000, Madagascar, Mahajanga, Melaky, Besalampy, Ankasakasa Tsibiray; -170.7000, -14.3000, American Samoa, Eastern, Ituau, Faganeanea, 46.5600, -18.5000, Madagascar, Antananarivo, Bongolava, Fenoarivo-Centre, Fenoarivobe; 76.0000, 13.5000, India, Karnataka, Chikmagalur, Kadur; 46.3100, -15.7100, Madagascar, Mahajanga, Boeny, Mahajanga Urban, Mahajanga I; 43.8600, -21.7600, Madagascar, Toliary, Menabe, Manja, Ankiliabo; 47.0300, -16.1500, Madagascar, Mahajanga, Boeny, Marovoay, Ankazomborona; 45.4600, -19.5100, Madagascar, Toliary, Menabe, Miandrivazo, Miandrivazo; 43.6100, -21.9500, Madagascar, Toliary, Atsimo-Andrefana, Morombe, Basibasy; 76.5000, 10.0000, India, Kerala, Ernakulam, Perumbavur, 47.6100, -15.5600, Madagascar, Mahajanga, Sofia, Port Berg, Boriziny CR; 44.5330, -22.9000, Madagascar, Toliary, Atsimo-Andrefana, Sakaraha, Sakaraha; 49.5000, -14.0000, Madagascar, Antsiranana, Sava, Sambava, Bevohotra; 47.2100, -24.7600, Madagascar, Toliary, Anosy, Taolagnaro, Mahatalaky; 43.7600, -23.5500, Madagascar, Toliary, Atsimo-Andrefana, Toliary, Saint Augustin; 43.6600, -23.3500, Madagascar, Toliary, Atsimo-Andrefana, Toliary Urban, Toliara I; 130.3000, -13.6300, Australia, Northern Territory; 130.6300, -11.4000, Australia, Northern Territory; 130.6700, -11.4200, Australia, Northern Territory; 130.8300, -

12.4500, Australia, Northern Territory, Darwin; 130.8330, -12.4500, Australia, Northern Territory, Darwin; 130.8330, -12.4583, Australia, Northern Territory, Darwin; 130.8500, -11.8500, Australia, Northern Territory; 130.8500, -12.3833, Australia, Northern Territory, Darwin; 130.8500, -12.4167, Australia, Northern Territory, Darwin; 130.8500, -12.4500, Australia, Northern Territory, Darwin; 130.8500, -12.4600, Australia, Northern Territory, Darwin; 130.8500, -12.4700, Australia, Northern Territory, Darwin; 130.8670, -12.3833, Australia, Northern Territory, Darwin; 130.8700, -12.4200, Australia, Northern Territory, Darwin; 130.8800, -12.4200, Australia, Northern Territory, Darwin; 130.8800, -12.4300, Australia, Northern Territory, Darwin; 130.8900, -11.7700, Australia, Northern Territory; 130.9000, -12.3833, Australia, Northern Territory, Darwin; 130.9200, -12.4200, Australia, Northern Territory, Darwin; 130.9200, -12.4700, Australia, Northern Territory; 130.9700, -12.7000, Australia, Northern Territory, Litchfield; 131.0170, -12.5167, Australia, Northern Territory, Litchfield; 131.0330, -12.0500, Australia, Northern Territory; 131.0500, -12.4500, Australia, Northern Territory, Litchfield; 131.1170, -13.2500, Australia, Northern Territory, Coomalie; 131.1200, -15.6200, Australia, Northern Territory; 131.3200, -12.6500, Australia, Northern Territory, Litchfield; 131.7200, -12.6700, Australia, Northern Territory; 132.1500, -11.1500, Australia, Northern Territory; 132.2700, -14.4700, Australia, Northern Territory, Katherine; 132.5700, -11.1500, Australia, Northern Territory; 132.8830, -12.6500, Australia, Northern Territory; 133.0700, -14.9300, Australia, Northern Territory; 133.3830, -16.3000, Australia, Northern Territory; 133.4200, -22.0800, Australia, Northern Territory; 133.4200, -22.1300, Australia, Northern Territory; 134.1830, -19.6500, Australia, Northern Territory, Tennant Creek; 134.3700, -14.6700, Australia, Northern Territory; 134.8830, -12.0833, Australia, Northern Territory; 134.9200, -12.1100, Australia, Northern Territory; 135.4000, -19.4300, Australia, Northern Territory; 135.5670, -12.0333, Australia, Northern Territory; 135.8280, -19.7114, Australia, Northern Territory; 136.3000, -16.0700, Australia, Northern Territory; 136.7300, -11.0300, Australia, Northern Territory; 139.4830, -20.7333, Australia, Queensland, Mount Isa; 144.1920, -20.8500, Australia, Queensland, Flinders; 144.3190, -18.1483, Australia, Queensland, Etheridge; 145.7670, -16.9333, Australia, Queensland, Cairns; 146.8170, -19.2667, Australia, Queensland, Townsville; 146.8170, -19.2670, Australia, Queensland, Townsville; -67.4800, 6.1800, Colombia, Vichada, Puerto Carreño; 43.3278, -11.3812, Comoros, Njazídja, 43.3278, -11.3812, Comoros, Njazídja, -149.8263, -17.4906, French Polynesia, -100.0106, 17.9325, México, Guerrero, General Heliodoro Castillo; -100.0110, 17.9325, México, Guerrero, General Heliodoro Castillo; -104.3156, 19.0517, México, Colima, Manzanillo; -104.3160, 19.0517, México, Colima, Manzanillo; -92.6903, 15.2814, México, Chiapas, Acapetahua; -92.6903, 15.2814, México, Chiapas, Acapetahua; -99.0097, 21.9819, México, San Luis Potosí, Ciudad Valles; -99.0097, 21.9819, México, San Luis Potosí, Ciudad Valles; -99.9536, 16.8969, México, Guerrero, Acapulco de Juárez; -99.9536, 16.8969, México, Guerrero, Acapulco de Juárez; 49.1788, 11.2855, Somalia, Bari, Bosaaso; -155.0874, 19.7004, United States, Hawaii, Hawaii; -155.0930, 19.2969, United States, Hawaii, Hawaii; -155.0980, 19.2951, United States, Hawaii, Hawaii; -155.1470, 19.2915, United States, Hawaii, Hawaii; -155.8180, 20.0243, United States, Hawaii, Hawaii; -155.9050, 19.4143, United States, Hawaii, Hawaii; -155.9080, 19.4187, United States, Hawaii, Hawaii; -155.9743, 19.6037, United States, Hawaii, Hawaii; -156.0210, 19.6815, United States, Hawaii, Hawaii; -156.0210, 19.6843, United States, Hawaii, Hawaii; -156.0220, 19.6827, United States, Hawaii, Hawaii; -156.4440, 20.8935, United States, Hawaii, Maui; -156.4560, 20.8964, United States, Hawaii, Maui; -156.6160, 20.5417, United States, Hawaii, Maui; -156.9200, 20.8255, United States, Hawaii, Maui; -157.0120, 21.1401, United States, Hawaii, Maui; -

157.7888, 21.4324, United States, Hawaii, Honolulu; -157.7890, 21.4324, United States, Hawaii, Honolulu; -157.8000, 21.4113, United States, Hawaii, Honolulu; -157.8690, 21.3370, United States, Hawaii, Honolulu; -157.8710, 21.3332, United States, Hawaii, Honolulu; -158.0350, 21.6795, United States, Hawaii, Honolulu; -158.1000, 21.4313, United States, Hawaii, Honolulu; -158.1290, 21.4758, United States, Hawaii, Honolulu; -158.1300, 21.4389, United States, Hawaii, Honolulu; -158.1320, 21.4700, United States, Hawaii, Honolulu; -158.1340, 21.4714, United States, Hawaii, Honolulu; -158.1390, 21.4340, United States, Hawaii, Honolulu; -158.1410, 21.4270, United States, Hawaii, Honolulu; -158.1440, 21.4520, United States, Hawaii, Honolulu; -158.2740, 21.5737, United States, Hawaii, Honolulu; -80.4872, 25.4836, United States, Florida, Miami-Dade; -176.4794, 0.1947, United States Minor Outlying Island, Baker, -177.3900, 28.2000, United States Minor Outlying Island, Midway, -71.8881, 10.5531, Venezuela, Zulia, Jesús Enrique Lossada; -72.0778, 11.1220, Venezuela, Zulia, Páez; -156.4320, 20.9057, United States; -156.4350, 20.9067, United States; -156.4360, 20.9053, United States; -156.4410, 20.9031, United States; -156.8200, 20.0284; -157.4140, 1.9860, Kiribati; -157.7210, 21.4000, United States; -171.8000, -13.8000, -177.3700; 28.2000, -178.3000; 28.4000, -178.3130 28.3875; 43.6100, -23.1500, Madagascar; 72.4167, -7.3333; 72.4631, -7.3494; -85.2000, 15.9000, Honduras; -89.3167, 13.4833, El Salvador; 130.0300, -13.0200, 130.2000, -11.6500, Australia; 130.8200, -12.4000, Australia; 132.1700, -11.2300, Australia; 132.5700, -11.3500, Australia; 133.0200, -10.9000, Australia; 133.0300, -10.9200, Australia, 122.2000, -17.9500, Australia.

Hemidactylus mabouia, native

3.3800, 6.4400, Nigeria, Lagos, Apapa, Apapa; 39.8750, -3.5360, Kenya, Coast, Kilifi, Bahari, Tezo, Mtondia Majaoni; 39.8750, -3.5360, Kenya, Coast, Kilifi, Bahari, Tezo, Mtondia Majaoni; 39.8750, -3.5360, Kenya, Coast, Kilifi, Bahari, Tezo, Mtondia Majaoni; 37.1120, 1.5800, Kenya, Rift Valley, Samburu, Baragoi, Ndoto, Latakweny; 37.1120, 1.5800, Kenya, Rift Valley, Samburu, Baragoi, Ndoto, Latakweny; 31.8770, -0.3560, Uganda, Masaka, Bukoto, Bukakata/Mpugwe; 31.8770, -0.3560, Uganda, Masaka, Bukoto, Bukakata/Mpugwe; 31.8770, -0.3560, Uganda, Masaka, Bukoto, Bukakata/Mpugwe; 31.8780, -0.3530, Uganda, Masaka, Bukoto, Bukakata/Mpugwe; 31.8780, -0.3530, Uganda, Masaka, Bukoto, Bukakata/Mpugwe; 31.8780, -0.3530, Uganda, Masaka, Bukoto, Bukakata/Mpugwe; 20.3000, 3.3000, The Democratic Republic of the Congo, Équateur, Nord-Ubangi, Businga; 20.3000, 3.3000, The Democratic Republic of the Congo, Équateur, Nord-Ubangi, Businga; 36.6230, -1.9270, Kenya, Rift Valley, Nakuru, Central, Loodokilani, Elangata-Wuas; 36.6230, -1.9270, Kenya, Rift Valley, Nakuru, Central, Loodokilani, Elangata-Wuas; 36.6230, -1.9270, Kenya, Rift Valley, Nakuru, Central, Loodokilani, Elangata-Wuas; 36.8160, -1.2750, Kenya, Nairobi, Nairobi, Central, Ngara, Ngara West; 36.8160, -1.2750, Kenya, Nairobi, Nairobi, Central, Ngara, Ngara West; 36.8160, -1.2750, Kenya, Nairobi, Nairobi, Central, Ngara, Ngara West; 36.9100, -1.2800, Kenya, Nairobi, Nairobi, Embakasi, Njiru, Umoja; 38.3300, 0.0830, Kenya, Eastern, Isiolo, Garba Tulla, Kinna, Rapsu; 32.9000, -2.5100, Tanzania, Mwanza, Nyamagana, Isamilo; 39.5500, -3.9000, Kenya, Coast, Kilifi, Kalolenli, Rabai, Kaliang'ombe/Jimba; 39.5500, -3.9000, Kenya, Coast, Kilifi, Kalolenli, Rabai, Kaliang'ombe/Jimba; 27.9100, -11.1800, The Democratic Republic of the Congo, Katanga, Haut-Shaba, Kasenga; 29.6160, -0.9890, Uganda, Kanungu, Kinkizi, Kayonza; 29.6160, -0.9890, Uganda, Kanungu, Kinkizi, Kayonza; 29.6160, -0.9890, Uganda, Kanungu, Kinkizi, Kayonza; 15.3150, -4.3300, The Democratic Republic of the Congo, Kinshasa City, Kinshasa, Kinshasa Urban; 15.3150, -4.3300, The

Democratic Republic of the Congo, Kinshasa City, Kinshasa, Kinshasa Urban; 38.6330, -5.1000, Tanzania, Tanga, Muheza, Kisiwani; 38.6330, -5.1000, Tanzania, Tanga, Muheza, Kisiwani; 38.6330, -5.1000, Tanzania, Tanga, Muheza, Kisiwani; 40.8380, -1.7760, Kenya, Coast, Lamu, Kiunga, Kiunga, Milimani; 40.8380, -1.7760, Kenya, Coast, Lamu, Kiunga, Kiunga, Milimani; 30.1420, -0.0250, Uganda, Kasese, Busongora, Lake Katwe; 30.1420, -0.0250, Uganda, Kasese, Busongora, Lake Katwe; 46.3100, -15.7100, Madagascar, Mahajanga, Boeny, Mahajanga Urban, Mahajanga I; 46.3200, -15.7200, Madagascar, Mahajanga, Boeny, Mahajanga Urban, Mahajanga I; 39.8740, -3.1770, Kenya, Coast, Kilifi, Malindi, Jilore, Makobeni; 39.8740, -3.1770, Kenya, Coast, Kilifi, Malindi, Jilore, Makobeni; 39.8740, -3.1780, Kenya, Coast, Kilifi, Malindi, Jilore, Makobeni; 36.0000, 0.5000, Kenya, Rift Valley, Baringo, Marigat, Marigat, Perkerra; 46.6300, -16.1000, Madagascar, Mahajanga, Boeny, Marovoay, Marovoay; 39.1000, -13.3830, Mozambique, Cabo Delgado, Namuno, Meloco; 39.1000, -13.3830, Mozambique, Cabo Delgado, Namuno, Meloco; 36.7850, 3.2400, Kenya, Eastern, Marsabit, North Horr, North Horr, Galas; 36.7850, 3.2400, Kenya, Eastern, Marsabit, North Horr, North Horr, Galas; 34.5000, -0.5000, Kenya, Nyanza, Homa Bay, Rangwe, East Kanyada, Kothidha; 34.7500, 0.0700, Kenya, Western, Vihiga, Sabatia, North Maragoli, Kivagala; 34.7500, 0.0700, Kenya, Western, Vihiga, Sabatia, North Maragoli, Kivagala; -8.7000, 7.3620, Liberia, Nimba, Sanniquelleh-Mahn, Sehyi; 47.2100, -24.7600, Madagascar, Toliary, Anosy, Taolagnaro, Mahatalaky; 37.9100, -2.9100, Kenya, Coast, Taita Taveta, Tsavo National Park (E&W); 38.5670, -3.3830, Kenya, Coast, Taita Taveta, Voi, Voi, Mwangea; 38.5670, -3.3830, Kenya, Coast, Taita Taveta, Voi, Voi, Mwangea; 38.5670, -3.3830, Kenya, Coast, Taita Taveta, Voi, Voi, Mwangea; 37.3170, 1.5670, Kenya, Rift Valley, Samburu, Wamba, Ngilai, Ngare Narok; 37.3170, 1.5670, Kenya, Rift Valley, Samburu, Wamba, Ngilai, Ngare Narok; 37.5570, 0.8540, Kenya, Rift Valley, Samburu, Wamba, Wamba, Koiting; 37.5570, 0.8540, Kenya, Rift Valley, Samburu, Wamba, Wamba, Koiting; 37.5570, 0.8540, Kenya, Rift Valley, Samburu, Wamba, Wamba, Koiting; 23.1000, -19.1000, Botswana, North-West, Ngamiland West; 23.1000, -19.1000, Botswana, North-West, Ngamiland West; 11.5100, 3.8000, Cameroun, Centre, Méfou; 11.5100, 3.9000, Cameroun, Centre, Mfoundi; 11.5100, 3.9000, Cameroun, Centre, Mfoundi; 13.7110, 9.5160, Cameroun, Nord, Bénoué; 9.7000, 4.0500, Cameroun, Littoral, Moungo; 9.7000, 4.0500, Cameroun, Littoral, Moungo; 9.7500, 3.7500, Cameroun, Littoral, Wouri; 9.9100, 2.9500, Cameroun, Sud, Océan; 8.5520, 3.4610, Equatorial Guinea, Bioko Sur; 8.5520, 3.4610, Equatorial Guinea, Bioko Sur; 8.5520, 3.4610, Equatorial Guinea, Bioko Sur; 8.7810, 3.7570, Equatorial Guinea, Bioko Norte; 8.7810, 3.7570, Equatorial Guinea, Bioko Norte; 8.7810, 3.7570, Equatorial Guinea, Bioko Norte; 8.7830, 3.7520, Equatorial Guinea, Bioko Norte; 8.7830, 3.7520, Equatorial Guinea, Bioko Norte; 8.7830, 3.7520, Equatorial Guinea, Bioko Norte; 10.5920, -2.3370, Gabon, Nyanga, Mougoutsi; 10.5920, -2.3370, Gabon, Nyanga, Mougoutsi; 10.7340, -2.5580, Gabon, Nyanga, Douigny; 10.7340, -2.5580, Gabon, Nyanga, Douigny; 12.8600, 0.5600, Gabon, Ogooué-Ivindo, Ivindo; 9.6000, -2.3000, Gabon, Ogooué-Maritime, Ndougou; 9.6000, -2.3000, Gabon, Ogooué-Maritime, Ndougou; 9.8810, -1.9370, Gabon, Ogooué-Maritime, Étimboué; 9.8810, -1.9370, Gabon, Ogooué-Maritime, Étimboué; 0.0380, 5.8800, Ghana, Greater Accra, Dangbe East; 0.0380, 5.8800, Ghana, Greater Accra, Dangbe East; 0.5090, 8.2580, Ghana, Volta, Nkwanta; 0.5090, 8.2580, Ghana, Volta, Nkwanta; 0.5550, 8.3250, Ghana, Volta, Nkwanta; 0.5550, 8.3250, Ghana, Volta, Nkwanta; 0.5560, 8.3230, Ghana, Volta, Nkwanta; 0.5560, 8.3230, Ghana, Volta, Nkwanta; -2.6490, 5.2840, Ghana, Western, Jomoro; -2.6490, 5.2840, Ghana, Western, Jomoro; 6.6510, 0.2610, São Tomé and Príncipe, São Tomé; 6.6510, 0.2610, São Tomé and Príncipe, São Tomé; 6.6510, 0.2610, São Tomé and Príncipe, São Tomé; 6.6770, 0.1710, São Tomé and Príncipe, São Tomé; 6.6770, 0.1710, São Tomé and Príncipe, São Tomé; 6.6770, 0.1710, São Tomé and Príncipe, São Tomé; 6.7170, 0.3740, São Tomé and Príncipe, São Tomé; 6.7170, 0.3740, São Tomé and Príncipe, São Tomé; 6.7170, 0.3740, São Tomé and Príncipe, São Tomé; 6.7290, 0.3300, São Tomé and Príncipe, São Tomé; 6.7290, 0.3300, São Tomé and Príncipe, São Tomé; 6.7290, 0.3300, São Tomé and Príncipe, São Tomé; 7.4200, 1.6410, São Tomé and Príncipe, Príncipe; 7.4200, 1.6410, São Tomé and Príncipe, Príncipe; 7.4200, 1.6410, São Tomé and Príncipe, Príncipe; 28.1660, -25.7500, South Africa, Gauteng, Pretoria; 29.8300, -22.7100, South Africa, Limpopo, Messina; 29.8300, -22.7100, South Africa, Limpopo, Messina; 30.0000, -22.4100, South Africa, Limpopo, Messina; 30.0000, -22.4100, South Africa, Limpopo, Messina; 30.5100, -30.6600, South Africa, KwaZulu-Natal, Port Shepstone; 30.6080, -30.2730, South Africa, KwaZulu-Natal, Umzinto; 30.6080, -30.2730, South Africa, KwaZulu-Natal, Umzinto; 30.8300, -24.0700, South Africa, Limpopo, Phalaborwa; 30.8300, -24.0700, South Africa, Limpopo, Phalaborwa; 32.2190, -27.5990, South Africa, KwaZulu-Natal, Ubombo; 32.2190, -27.5990, South Africa, KwaZulu-Natal, Ubombo; 32.4230, -27.0430, South Africa, KwaZulu-Natal, Ingwavuma; 32.4230, -27.0430, South Africa, KwaZulu-Natal, Ingwavuma; 24.2810, -17.4850, Zambia, Western; 24.2810, -17.4850, Zambia, Western; 24.2810, -17.4850, Zambia, Western; 25.8600, -17.8500, Zambia, Southern; 32.7760, -17.6040, Zimbabwe, Manicaland, Nyanga; 32.7760, -17.6040, Zimbabwe, Manicaland, Nyanga.

Hemidactylus mabouia, invasive

-52.2000, -3.2000, Brazil, Pará, Altamira, Altamira; -52.2000, -3.2000, Brazil, Pará, Altamira, Altamira; -50.0000, -0.5000, Brazil, Pará, Anajas, Anajas; -50.0000, -0.5000, Brazil, Pará, Anajas, Anajas; -48.4800, -1.4500, Brazil, Pará, Belém, Belém; -48.4833, -1.4500, Brazil, Pará, Belém, Belém; -48.4833, -1.4500, Brazil, Pará, Belém, Belém; -60.7000, 2.8000, Brazil, Roraima, Boa Vista, Boa Vista; -60.7000, 2.8000, Brazil, Roraima, Boa Vista, Boa Vista; -45.4100, -23.6100, Brazil, São Paulo, Caraguatatuba, Caraguatatuba; -42.2000, -22.4800, Brazil, Rio de Janeiro, Casimiro de Abreu, Casimiro de Abreu; -60.6300, -9.1600, Brazil, Mato Grosso, Aripuanã, Colniza; -47.5617, -24.6956, Brazil, São Paulo, Iguape, Iguape; -47.5617, -24.6956, Brazil, São Paulo, Iguape, Iguape; -45.3000, -23.8000, Brazil, São Paulo, Ilhabela, Ilhabela; -45.3000, -23.8000, Brazil, São Paulo, Ilhabela, Ilhabela; -73.2500, -3.7600, Perú, Loreto, Maynas, Iquitos; -66.9100, 10.5000, Venezuela, Distrito Capital, Caracas, Isla de Aves; -66.9100, 10.5000, Venezuela, Distrito Capital, Caracas, Isla de Aves; -43.1000, -22.4000, Brazil, Rio de Janeiro, Petrópolis, Itaipava; -43.1000, -22.4000, Brazil, Rio de Janeiro, Petrópolis, Itaipava; -46.7800, -24.1800, Brazil, São Paulo, Itanhaém, Itanhaém; -42.8100, -22.9100, Brazil, Rio de Janeiro, Maricá, Maricá; -73.9500, -4.6330, Perú, Loreto, Loreto, Nauta; -55.5100, -1.9000, Brazil, Pará, Óbidos, Óbidos; -50.4000, -19.9000, Brazil, São Paulo, Ouroeste, Ouroeste; -50.4000, -19.9000, Brazil, São Paulo, Ouroeste, Ouroeste; -45.5337, -23.5067, Brazil, São Paulo, Paraibuna, Paraibuna; -45.5337, -23.5067, Brazil, São Paulo, Paraibuna, Paraibuna; -51.1800, -30.0600, Brazil, Rio Grande do Sul, Porto Alegre, Porto Alegre; -40.6000, -19.9100, Brazil, Espírito Santo, Santa Teresa, Santa Teresa; -39.8500, -18.7300, Brazil, Espírito Santo, São Mateus, São Mateus; -60.0200, -3.1133, Brazil, Amazonas, Maués, Sexta R.A.; -60.0253, -3.1133, Brazil, Amazonas, Maués, Sexta R.A.; -60.0253, -3.1133, Brazil, Amazonas, Maués, Sexta R.A.; -75.1781, -0.9706, Perú, Loreto, Maynas, Torres Causana; -75.1781, -0.9706, Perú, Loreto, Maynas, Torres Causana; -76.1600, -

2.5100, Perú, Loreto, Loreto, Trompeteros; -70.0300, 12.5100, Aruba; -64.6000, 18.4500, British Virgin Islands; -76.5500, 3.4167, Colombia, Valle del Cauca, Santiago de Cali; -76.5500, 3.4167, Colombia, Valle del Cauca, Santiago de Cali; -76.5500, 3.4167, Colombia, Valle del Cauca, Santiago de Cali; -75.2000, 20.1450, Cuba, Guantánamo; -61.4600, 12.4600, Grenada, Carriacou; -61.5800, 16.2500, Guadeloupe, Basse-Terre; -61.6000, 15.8600, Guadeloupe, Basse-Terre; -57.8589, 5.6819, Guyana, Upper Takutu-Upper Essequibo, Berbice River settlements; -57.8589, 5.6819, Guyana, Upper Takutu-Upper Essequibo, Berbice River settlements; -58.0000, 6.7000, Guyana, East Berbice-Corentyne, Grove / Haslington; -58.0000, 6.7000, Guyana, East Berbice-Corentyne, Grove / Haslington; -58.2000, 6.8000, Guyana, Demerara-Mahaica, Meer Zorgen / Malgre Tout; -58.2000, 6.8000, Guyana, Demerara-Mahaica, Meer Zorgen / Malgre Tout; -65.4100, 18.1250, Puerto Rico, Vieques, -65.4664, 18.1415, Puerto Rico, Vieques; -65.4664, 18.1415, Puerto Rico, Vieques; -66.8594, 17.9556, Puerto Rico, Yauco; -66.8594, 17.9557, Puerto Rico, Yauco; -66.8594, 17.9556, Puerto Rico, Yauco; -61.2333, 13.1667, Saint Vincent and the Grenadines, Saint Andrew; -61.2333, 13.1667, Saint Vincent and the Grenadines, Saint Andrew; -60.9500, 14.0660, Santa Lucia, Gros Islet; -61.0000, 14.0160, Santa Lucia, Castries; -57.3000, 4.8000, Suriname, Sipaliwini, Kabalebo; -57.3000, 4.8000, Suriname, Sipaliwini, Kabalebo; -60.5000, 11.3000, Trinidad and Tobago, Tobago; -60.5000, 11.3000, Trinidad and Tobago, Tobago; -60.8300, 11.1500, Trinidad and Tobago, Tobago; -80.4711, 25.4472, United States, Florida, Miami-Dade; -80.4711, 25.4472, United States, Florida, Miami-Dade; -80.5844, 25.3944, United States, Florida, Miami-Dade; -80.5844, 25.3944, United States, Florida, Miami-Dade; -80.6567, 25.4017, United States, Florida, Miami-Dade; -80.6567, 25.4017, United States, Florida, Miami-Dade; -80.9228, 25.1425, United States, Florida, Monroe; -80.9228, 25.1425, United States, Florida, Monroe; -81.7408, 24.5722, United States, Florida, Monroe; -81.7828, 24.5553, United States, Florida, Monroe; -63.1400, 10.6100, Venezuela, Sucre, Benítez; -63.1400, 10.6100, Venezuela, Sucre, Benítez; -63.1800, 10.2500, Venezuela, Sucre, Andrés Eloy Blanco; -63.1800, 10.2500, Venezuela, Sucre, Andrés Eloy Blanco; -63.9400, 11.0300, Venezuela, Nueva Esparta, Díaz; -63.9400, 11.0300, Venezuela, Nueva Esparta, Díaz; -64.5000, 9.0000, Venezuela, Anzoátegui, Aragua; -64.5000, 9.0000, Venezuela, Anzoátegui, Aragua; -64.7200, 10.0260, Venezuela, Anzoátegui, Bolívar; -64.7200, 10.0260, Venezuela, Anzoátegui, Bolívar; -66.4500, 10.5300, Venezuela, Miranda, Zamora; -66.4500, 10.5300, Venezuela, Miranda, Zamora; -66.8500, 10.5500, Venezuela, Distrito Capital, Vargas; -66.8500, 10.5500, Venezuela, Distrito Capital, Vargas; -67.1800, 10.3600, Venezuela, Aragua, José Félix Ribas; -67.1800, 10.3600, Venezuela, Aragua, José Félix Ribas; -67.4800, 10.4400, Venezuela, Aragua, Santiago Mariño; -67.4800, 10.4400, Venezuela, Aragua, Santiago Mariño; -67.8600, 10.3800, Venezuela, Carabobo, Guacara; -67.8600, 10.3800, Venezuela, Carabobo, Guacara; -68.3200, 10.2100, Venezuela, Carabobo, Miranda; -68.3200, 10.2100, Venezuela, Carabobo, Miranda; -68.4100, 9.4700, Venezuela, Cojedes, San Carlos; -68.4100, 9.4700, Venezuela, Cojedes, San Carlos; -68.4700, 10.3400, Venezuela, Yaracuy, Autonomo San Felipe; -68.4700, 10.3400, Venezuela, Yaracuy, Autonomo San Felipe; -68.8900, 10.7000, Venezuela, Lara, Urdaneta; -68.8900, 10.7000, Venezuela, Lara, Urdaneta; -69.5200, 10.1900, Venezuela, Lara, Iribarren; -69.5200, 10.1900, Venezuela, Lara, Iribarren; -69.5900, 11.4100, Venezuela, Falcón, Colina; -69.5900, 11.4100, Venezuela, Falcón, Colina; -70.8900, 9.3700, Venezuela, Trujillo, Rafael Rangel; -70.8900, 9.3700, Venezuela, Trujillo, Rafael Rangel; -71.8200, 10.8000, Venezuela, Zulia, Mara; -71.8200, 10.8000, Venezuela, Zulia, Mara; -61.1160, 16.1600; -61.1300, 14.6300; -61.1600, 16.2500, Guadeloupe; -61.2500, 13.0000; -61.2500, 13.0000; -61.3800, 12.5100; -61.4800, 16.2000; -62.2167, 16.7000; -62.2167, 16.7000; -62.2167, 16.7000; -

66.2064, 17.9476, Puerto Rico; -66.2064, 17.9476, Puerto Rico; -69.7890, 18.0830; -85.2000, 15.9000, Honduras; -85.2000, 15.9000, Honduras; -39.2500, -17.7500, Brazil.

Hemidactylus turcicus, native

-0.4150, 38.5970, España, Comunidad Valenciana, Alicante, Alacanti, Torremanzanas; -0.4200, 38.4200, España, Comunidad Valenciana, Alicante, Alacanti, Sant Joan d'Alacant; -0.4200, 38.5100, España, Comunidad Valenciana, Alicante, Alacanti, Busot; -0.5300, 38.5100, España, Comunidad Valenciana, Alicante, Alacanti, Jijona; -0.5400, 38.3300, España, Comunidad Valenciana, Alicante, Alacanti, Alicante; -0.5400, 38.4200, España, Comunidad Valenciana, Alicante, Alacanti, San Vicente del Raspeig; -0.6500, 38.4200, España, Comunidad Valenciana, Alicante, Alacanti, Agost; -0.6500, 38.5100, España, Comunidad Valenciana, Alicante, Alcoia, Tibi; -0.4800, 39.9500, España, Comunidad Valenciana, Castellón, Alt Palancia, Matet; -0.4900, 39.7700, España, Comunidad Valenciana, Castellón, Alt Palancia, Segorbe; -0.6100, 39.7700, España, Comunidad Valenciana, Castellón, Alt Palancia, Altura; -0.9890, 38.6080, España, Comunidad Valenciana, Alicante, Alt Vinalopo, Villena; -0.9900, 38.6100, España, Comunidad Valenciana, Alicante, Alt Vinalopo, Villena; -0.9900, 38.6060, España, Comunidad Valenciana, Alicante, Alt Vinalopo, Villena; -1.1000, 38.6100, España, Región de Murcia, Murcia, Altiplano, Yecla; -1.1100, 38.3400, España, Región de Murcia, Murcia, Altiplano, Jumilla; -1.2200, 38.4300, España, Región de Murcia, Murcia, Altiplano, Jumilla; -1.2300, 38.3400, España, Región de Murcia, Murcia, Altiplano, Jumilla; -1.3400, 38.5200, España, Región de Murcia, Murcia, Altiplano, Jumilla; -1.5810, 37.7150, España, Región de Murcia, Murcia, Alto Guadalentin, Lorca; -1.5820, 37.7140, España, Región de Murcia, Murcia, Alto Guadalentin, Lorca; -1.5900, 37.4400, España, Región de Murcia, Murcia, Alto Guadalentin, Águilas; -1.7000, 37.4400, España, Región de Murcia, Murcia, Alto Guadalentin, Lorca; -1.8100, 37.5400, España, Región de Murcia, Murcia, Alto Guadalentin, Puerto Lumbreras; -1.8100, 37.7200, España, Región de Murcia, Murcia, Alto Guadalentin, Lorca; -3.1700, 37.9000, España, Andalucía, Jaén, Alto Guadalquivir, Peal de Becerro; -3.6200, 37.8100, España, Andalucía, Jaén, Área metropolitana de Jaén, Mancha Real; 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Córdoba; -4.8800, 38.0700, España, Andalucía, Córdoba, Villaviciosa de Córdoba; -4.8800, 38.1600, España, Andalucía, Córdoba, Pozoblanco; -4.9000, 38.6100, España, Andalucía, Córdoba, Santa Eufemia; -4.9000, 38.7000, España, Castilla-La Mancha, Ciudad Real, Guadalmez; -4.9500, 36.5300, España, Andalucía, Málaga, Marbella; -4.9600, 36.6200, España, Andalucía, Málaga, Istán; -4.9600, 36.8000, España, Andalucía, Málaga, El Burgo; -4.9600, 36.8900, España, Andalucía, Málaga, Cañete la Real; -4.9850, 37.7070, España, Andalucía, Córdoba, La Carlota; -4.9850, 37.7060, España, Andalucía, Córdoba, La Carlota; -4.9970, 38.1560, España, Andalucía, Córdoba, Espiel; -4.9980, 38.1570, España, Andalucía, Córdoba, Espiel; -5.0000, 38.1600, España, Andalucía, Córdoba, Espiel; -5.0000, 38.3400, España, Andalucía, Córdoba, Villanueva del Duque; -5.1100, 38.1500, España, Andalucía, Córdoba, Espiel; -5.1100, 38.2400, España, Andalucía, Córdoba, Villanueva del Rey; -5.1200, 38.4200, España, Andalucía, Córdoba, Hinojosa del Duque; -5.1200, 38.6000, España, Andalucía, Córdoba, Belalcázar; -5.1300, 38.6900, España, Andalucía, Córdoba, El Viso; -5.1400, 39.2300, España, Extremadura, Badajoz, Valdecaballeros; -5.1800, 36.4400, España, Andalucía, Málaga, Estepona; -5.1800, 36.7100, España, Andalucía, Málaga, Ronda; -5.1900, 36.8000, España, Andalucía, Málaga, Ronda; -5.2300, 38.1500, España, Andalucía, Córdoba, Villanueva del Rey; -5.2300, 38.2400, España, Andalucía, Córdoba, Belmez; -5.2400, 38.6900, España, Extremadura, Badajoz, Cabeza del Buey; -5.2800, 36.3500, España, Andalucía, Málaga, Manilva; -5.2900, 36.4400, España, Andalucía, Málaga, Casares; -5.2900, 36.6200, España, Andalucía, Málaga, Benadalid; -5.3000, 36.7100, España, Andalucía, Málaga, Montejaque; -5.3000, 36.8000, España, Andalucía, Málaga, Ronda; -5.3100, 37.0700, España, Andalucía, Sevilla, Morón de la Frontera; -5.4000, 36.5300, España, Andalucía, Málaga, Gaucín; -5.4000, 36.6200, España, Andalucía, Málaga, Cortes de la Frontera; -5.4200, 36.9800, España, Andalucía, Sevilla, Coripe; -5.4200, 37.1600, España, Andalucía, Sevilla, Morón de la Frontera; -5.4200, 37.2500, España, Andalucía, Sevilla, Marchena; -5.4400, 37.7900, España, Andalucía, Sevilla, La Puebla de los Infantes; -5.4500, 38.1500, España, Andalucía, Córdoba, Fuente Obejuna; -5.5100, 36.5200, España, Andalucía, Málaga, Cortes de la Frontera; 2.6950, 42.6790, France, Languedoc-Roussillon, Pyrénées-Orientales, 2.6950, 42.6770, France, Languedoc-Roussillon, Pyrénées-Orientales, 3.7770, 43.4700, France, Languedoc-Roussillon, Hérault, 3.9280, 43.5760, France, Languedoc-Roussillon, Hérault, 3.9290, 43.5740, France, Languedoc-Roussillon, Hérault, 4.5590, 44.0200, France, Languedoc-Roussillon, Gard, 4.5600, 44.0180, France, Languedoc-Roussillon, Gard, 5.1670, 43.5570, France, Provence-Alpes-Côte-d'Azur, Bouches-Du-Rhône, 5.1670, 43.5590, France, Provence-Alpes-Côte-d'Azur, Bouches-Du-Rhône, 5.5770, 43.2900, France, Provence-Alpes-Côte-d'Azur, Bouches-Du-Rhône, 5.7370, 43.5470, France, Provence-Alpes-Côte-d'Azur, Var; 5.7380, 43.5450, France, Provence-Alpes-Côte-d'Azur, Var; 6.2970, 43.1100, France, Provence-Alpes-Côte-d'Azur, Var; 6.3930, 43.0050, France, Provence-Alpes-Côte-d'Azur, Var; 19.8500, 39.5480, Hellas, Ionioi Nisoi, Corfu; 20.6070, 38.6500, Hellas, Ionioi Nisoi, Levkas; 21.2850, 38.5620, Hellas, Dytiki Ellada, Aitolia and Akarnania; 21.6460, 37.0750, Hellas, Peloponnisos, Messinia; 22.2790, 36.8990, Hellas, Peloponnisos, Messinia; 22.4110, 36.8280, Hellas, Peloponnisos, Laconia; 22.5170, 36.7490, Hellas, Peloponnisos, Laconia; 22.6930, 37.6380, Hellas, Peloponnisos, Argolis; 22.8430, 39.3630, Hellas, Thessalia, Magnesia; 22.9830, 36.2740, Hellas, Attiki, Attica; 23.1240, 37.9900, Hellas, Peloponnisos, Corinth; 23.1510, 37.3740, Hellas, Peloponnisos, Argolis; 23.3000, 35.8870, Hellas, Attiki, Attica; 23.4150, 37.4880, Hellas, Attiki, Attica; 23.5950, 35.2750, Hellas, Kriti, Khania; 23.6000, 38.4000, Hellas, Stereá Elláda, Euboea; 23.6790, 39.1430, Hellas, Thessalia, Magnesia; 23.8110, 38.5790, Hellas, Stereá Elláda, Euboea; 24.0350, 35.2530, Hellas, Kriti, Khania; 24.0920, 35.5920, Hellas, Kriti, Khania;

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14.9000, 37.0000, Italia, Sicily, Syracuse; 14.9000, 37.4000, Italia, Sicily, Syracuse; 15.1000, 37.6000, Italia, Sicily, Catania; 15.3000, 40.7000, Italia, Campania, Salerno; 15.3000, 41.5000, Italia, Apulia, Foggia; 15.3000, 41.6000, Italia, Apulia, Foggia; 15.4000, 40.0000, Italia, Campania, Salerno; 15.5000, 40.1000, Italia, Campania, Salerno; 15.5000, 41.5000, Italia, Apulia, Foggia; 15.5000, 41.9000, Italia, Apulia, Foggia; 15.6000, 40.1000, Italia, Campania, Salerno; 15.7000, 38.1000, Italia, Calabria, Reggio di Calabria; 15.7000, 40.0000, Italia, Basilicata, Potenza; 16.0000, 38.0000, Italia, Calabria, Reggio di Calabria; 16.0000, 38.6000, Italia, Calabria, Vibo Valentia; 16.0000, 41.3000, Italia, Apulia, Barletta-Andria-Trani; 16.0000, 41.7000, Italia, Apulia, Foggia; 16.1000, 38.1000, Italia, Calabria, Reggio di Calabria; 16.1000, 38.2000, Italia, Calabria, Reggio di Calabria; 16.1000, 38.3000, Italia, Calabria, Reggio di Calabria; 16.1000, 38.4000, Italia, Calabria, Reggio di Calabria; 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-5.8440, 34.9150, Morocco, Gharb - Chrarda - Béni Hssen, Sidi Kacem; -6.0620, 35.1550, Morocco, Tanger - Tétouan, Larache; -7.3950, 33.5600, Morocco, Grand Casablanca, Sidi Bern./Moham.-Znata; -7.6160, 33.5930, Morocco, Grand Casablanca, Casa-Anfa; -6.9760, 39.0580, Portugal, Portalegre; -6.9780, 39.0570, Portugal, Portalegre; -7.0000, 38.1600, Portugal, Beja; -7.0100, 38.0700, Portugal, Beja; -7.1200, 38.0700, Portugal, Beja; -7.4700, 37.4400, Portugal, Faro; -7.4700, 37.7100, Portugal, Beja; -7.4700, 37.8000, Portugal, Beja; -7.4800, 37.2600, Portugal, Faro; -7.4800, 37.3500, Portugal, Faro; -7.5630, 38.6160, Portugal, Évora; -7.5640, 38.6150, Portugal, Évora; -7.5810, 37.7150, Portugal, Beja; -7.5820, 37.7140, Portugal, Beja; -7.5890, 37.2650, Portugal, Faro; -7.5900, 37.2630, Portugal, Faro; -8.1370, 38.6220, Portugal, Évora; -8.1380, 38.6200, Portugal, Évora; -8.1530, 37.2700, Portugal, Faro; -8.1540, 37.2690, Portugal, Faro; -8.7170, 37.2730, Portugal, Faro; -8.7180, 37.2710, Portugal, Faro; 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Maras; 36.9500, 36.8800, Turkey, Gaziantep; 37.0580, 37.7860, Turkey, K. Maras; 37.0800, 36.7300, Turkey, Gaziantep; 37.1500, 38.7900, Turkey, Sivas; 37.1500, 38.8000, Turkey, Sivas; 37.2300, 38.4500, Turkey, K. Maras; 37.6600, 36.7500, Turkey, Gaziantep; 37.8600, 38.4500, Turkey, Malatya; -0.1700, 39.1300, Spain; -0.1900, 38.5000, Spain; -0.2700, 39.3100, Spain; -0.3590, 38.1430, Spain; -0.4300, 38.1500, Spain; -0.4300, 38.3300, Spain; -0.4310, 38.1470, Spain; -0.5500, 38.1500, Spain; -0.6170, 35.7170, Algeria; -0.6700, 37.9700; -0.7900, 37.7000; -0.7900, 37.7900; -1.2500, 37.5300; -1.5890, 37.2650; -1.5900, 37.2630; -1.7000, 37.2600; -1.8200, 37.0900; -1.8200, 37.1800, Spain; -2.0500, 36.7300, Spain; -2.3800, 36.8200, Spain; -2.5000, 36.8200, Spain; -2.9400, 36.7300, Spain; -3.0600, 36.7300, Spain; -3.1700, 36.7300, Spain; -3.2800, 36.7300, Spain; -3.8400, 36.7300, Spain; -4.0600, 36.7300, Spain; -4.2600, 35.1900, Spain; -4.3930, 36.3640, Spain; -4.3930, 36.3620, Spain; -4.4000, 36.7200, Spain; -4.5100, 36.5400, Spain; -4.9500, 36.4400, Spain; -4.9500, 36.3560, Spain; -4.9500, 36.3540, Spain; -5.0600, 36.4400, Spain; -5.2700, 35.9000, Spain; -5.2800, 36.2600, Spain; -5.3900, 36.0800, Spain; -5.3900, 36.1700, Spain; -5.4930, 35.8960, Spain; -5.4930, 35.8930, Spain; -5.6100, 35.9800, Spain; -5.8300, 36.0700, Spain; -6.2700, 36.4300, Spain; -6.3700, 36.6100, Spain; -6.3700, 36.7900, Spain; -6.4760, 36.7960, Spain; -6.4780, 36.7940, Spain; -6.5800, 36.9800, Spain; -6.6900, 37.0700, Spain; 0.0000, 38.5910, Spain; -7.0300, 37.1700, Spain; -8.1580, 36.8200, Spain; -8.1590, 36.8180, Spain; 0.0200, 39.9400, Spain; 0.0700, 38.5900, Spain; 0.1300, 40.0300, Spain; 0.1800, 38.6800, Spain; 0.1800, 38.8600, Spain; 0.3290, 39.9440, Spain; 0.3290, 39.9460, Spain; 0.3440, 39.0460, Spain; 0.3440, 39.0440, Spain; 0.3520, 38.5940, Spain; 0.4160, 38.5970, Spain; 0.5800, 40.5800, Spain; 0.9230, 40.8590, Spain; 0.9240, 40.8570, Spain; 0.9760, 39.0580, Spain; 0.9780, 39.0570, Spain; 1.2100, 38.9700, Spain; 1.3200, 39.0600, Spain; 1.3300, 38.6100, Spain; 1.4400, 38.8800, Spain; 1.4500, 38.7900, Spain; 1.5500, 39.1600, Spain; 1.5600, 38.7000, Spain; 1.5600, 38.9800, Spain; 1.5630, 38.6160, Spain; 1.5640, 38.6150, Spain; 1.8700, 41.2300, Spain; 1.9900, 41.2300, Spain; 10.0000, 42.6000, Spain; 10.1000, 42.9000, Spain; 10.2000, 42.3000, Spain; 10.5000, 42.9000, Spain; 11.1000, 42.3000, Spain; 11.7000, 42.2000, Italy; 12.1000, 41.9000, Italy; 12.2000, 37.9000, Italy; 12.4000, 37.9000, Italy; 12.5000, 41.5000, Italy; 12.9000, 35.9000, Italy; 12.9000, 40.9000, Italy; 13.0000, 38.1000, Italy; 13.0000, 41.3000, Italy; 13.2000, 43.8000, Italy; 13.3000, 43.7000, Italy; 13.5000, 43.7000, Italy; 13.6000, 43.6000, Italy; 13.7000, 43.4000, Italy; 13.7000, 45.7000, Italy; 13.8000, 40.7000, Italy; 13.8000, 40.8000, Italy; 14.0000, 40.8000, Italy; 14.1000, 40.8000, Italy; 14.2000, 40.5000, Italy; 14.4000, 38.5000, Italy; 14.4000, 40.7000, Italy; 14.5000, 40.6000, Italy; 14.7000, 36.7000, Italy; 14.8000, 38.6000, Italy; 14.9000, 40.3000, Italy; 14.9000, 40.4000, Italy; 15.1000, 37.4000, Italy; 15.3000, 37.2000, Italy; 15.3000, 37.3000, Italy; 15.3000, 37.7000, Italy; 15.6000, 38.0000, Italy; 15.6000, 38.2000, Italy; 15.7000, 38.3000, Italy; 15.7000, 42.3000, Italy; 16.0000, 37.9000, Italy; 16.0000, 39.4000, Italy; 16.1000, 37.9000, Italy; 16.1000, 41.7000, Italy; 16.3000, 38.1000, Italy; 16.3000, 38.2000, Italy; 16.4000, 38.3000, Italy; 16.5000, 41.3000, Italy; 16.6000, 38.4000, Italy; 16.6000, 38.6000, Italy; 16.6000, 38.7000, Italy; 16.7000, 41.2000, Italy; 16.7000, 41.4000, Italy; 16.8000, 41.2000, Italy; 16.9000, 41.2000, Italy; 17.0000, 43.0000, Italy; 17.1000, 41.1000, Italy; 17.3000, 41.1000, Italy; 18.1000, 39.8000, Italy; 18.2000, 39.8000, Italy; 2.2200, 41.3200; 2.4600, 41.5100; 2.5900, 39.5200; 2.7060, 39.9770; 2.7070, 39.9750; 2.7080, 39.5260; 2.7090, 39.5240; 2.7110, 39.0750; 2.7110, 39.0740; 2.8200, 39.8900; 2.9400, 39.1600; 20.7040, 39.0110; 20.9500, 32.7170, Libya; 23.5290, 35.3230; 23.6170, 35.5210, Greece; 24.0170, 35.5210, Greece; 24.0970, 39.3540; 24.4000, 36.7500; 25.1000, 31.7660; 25.1090, 35.3450; 25.9000, 36.7300; 26.9600, 37.7600; 3.0600, 41.7800; 3.1800, 42.1400; 3.1800, 42.2300; 3.1800, 42.4100, Spain; 3.2900, 39.4300, Spain; 3.3000, 41.7790, Spain; 3.3010, 41.7770, Spain; 3.3020, 42.2290, Spain; 3.3030, 42.2270, Spain; 3.3050, 42.6790, Spain; 3.3050, 42.6770, Spain; 3.3070, 43.1300, Spain; 3.3070, 43.1270, Spain; 3.8800, 40.0600, Spain; 30.3500, 32.1800, Spain; 30.7000, 36.8800, Spain; 33.6170, 28.2330, Egypt; 35.0830, 33.0170; 35.1200, 33.2100; 4.0000, 40.0600, Spain; 4.1100, 40.0600, Spain; 4.2300, 40.0600, Spain; 4.3400, 39.8800, Spain; 4.4630, 39.9680, Spain; 4.4640, 39.9660, Spain; 5.1510, 43.1090, Spain; 5.1510, 43.1080, Spain; 5.7280, 43.0970, Spain; 5.7290, 43.0950, Spain; 6.2700, 43.0970, Spain; 6.2710, 43.0950, Spain; 7.7000, 43.7000, Italy; 7.8000, 43.7000, Italy; 8.1000, 43.9000, Italy; 8.2000, 39.2000, Italy; 8.2000, 39.3000, Italy; 8.2000, 41.1000, Italy; 8.3000, 38.8000, Italy; 8.3000, 39.2000, Italy; 8.3000, 39.3000, Italy; 8.3000, 41.2000, Italy; 8.4000, 39.3000, Italy; 8.4000, 39.6000, Italy; 8.4000, 40.3000, Italy; 8.9000, 44.4000, Italy; 9.1000, 44.3000, Italy; 9.4000, 41.2000, Italy; 9.6000, 39.2000, Italy; 9.7000, 43.0000, Italy; 9.7000, 44.0000, Italy; 9.9000, 43.4000, Italy.

Hemidactylus turcicus, invasive

-48.9330, -27.1000, Brazil, Santa Catarina, Brusque, Brusque; -15.4600, 28.0700, España, Islas Canarias, Las Palmas, Las Palmas de Gran Canaria; -43.8500, -19.9830, Brazil, Minas Gerais, Nova Lima, Nova Lima; -81.5780, 23.0410, Cuba, Matanzas, -82.4300, 23.0770, Cuba, Ciudad de la Habana, -100.1830, 26.5000, México, Nuevo León, Sabinas Hidalgo; -102.0400, 26.0900, México, Coahuila, Parras; -102.0670, 26.9830, México, Coahuila, Cuatrociénegas; -102.0800, 26.9500, México, Coahuila, Cuatrociénegas; -103.4300, 26.0300, México, Coahuila, Francisco I. Madero; -103.9200, 24.0100, México, Durango, Poanas; -104.0300, 24.8400, México, Durango, Peñón Blanco; -104.0700, 24.4800, México, Durango, Guadalupe Victoria; -105.9100, 27.0800, México, Chihuahua, Hidalgo del Parral; -108.9800, 27.4000, México, Sonora, Álamos; -110.7600, 29.2100, México, Sonora, Hermosillo; -111.3500, 26.0170, México, Baja California Sur, Comondú; -89.4100, 20.3000, México, Yucatán, Maní; -90.0300, 21.1600, México, Yucatán, Hunucmá; -90.4000, 20.8500, México, Yucatán, Celestún; -90.4000, 20.8600, México, Yucatán, Celestún; -93.3500, 16.3300, México, Chiapas, Villaflores; -96.1600, 19.1300, México, Veracruz, Medellín; -97.0600, 16.4100, México, Oaxaca, Dist. Ejutla; -97.1830, 18.2500, México, Puebla, San José Miahuatlán; -97.7340, 25.3790, México, Tamaulipas, Matamoros; -97.7900, 22.9800, México, Tamaulipas, Aldama; -97.8130, 22.2840, México, Tamaulipas, Ciudad Madero; -98.7800, 21.2600, México, San Luis Potosí, Tamazunchale; -98.9500, 20.6800, México, Hidalgo, Cardonal; -99.1400, 19.4400, México, Distrito Federal, Azcapotzalco; -99.7100, 27.5500, México, Tamaulipas, Nuevo Laredo; -99.7500, 25.1800, México, Nuevo León, Montemorelos; -100.3100, 28.7900, United States, Texas, Maverick; -101.1600, 29.9400, United States, Texas, Val Verde; -103.2500, 29.8300, United States, Texas, Brewster; -105.9200, 32.9000, United States, New Mexico, Otero; -106.2300, 31.7900, United States, Texas, El Paso; -107.2600, 33.1200, United States, New Mexico, Sierra; -107.2600, 33.1300, United States, New Mexico, Sierra; -109.5400, 31.3400, United States, Arizona, Cochise; -110.9330, 32.2670, United States, Arizona, Pima; -110.9670, 32.2670, United States, Arizona, Pima; -110.9760, 32.2760, United States, Arizona, Pima; -111.3330, 32.0000, United States, Arizona, Pima; -111.7900, 31.9100, United States, Arizona, Pima; -111.8400, 33.3000, United States, Arizona, Maricopa; -111.9090, 33.4150, United States, Arizona, Maricopa; -112.1300, 33.4400, United States, Arizona, Maricopa; -112.7120, 32.9480, United States, Arizona, Maricopa; -114.2400, 33.5700, United States, Arizona, La Paz; -114.2960, 34.1660, United States, California, San Bernardino; -114.3010, 34.1650, United States, California, San Bernardino; -114.6300, 32.7200, United States, Arizona, Yuma; -114.6600, 34.6600, United States, California, San Bernardino; -114.6700, 33.7000, United States, California, Riverside; -115.1020, 36.1570, United States, Nevada, Clark; -115.5520, 32.7780, United States, California, Imperial; -115.5940, 32.7860, United States, California, Imperial; -115.7200, 33.0600, United States, California, Imperial; -115.9930, 32.7390, United States, California, Imperial; -116.2200, 33.8000, United States, California, Riverside; -116.9100, 32.7600, United States, California, San Diego; -76.7100, 39.2500, United States, Maryland, Baltimore; -76.9300, 39.1100, United States, Maryland, Montgomery; -77.1800, 38.8700, United States, Virginia, Fairfax; -79.2500, 37.3700, United States, Virginia, Bedford; -80.1700, 26.0500, United States, Florida, Broward; -80.3400, 27.4800, United States, Florida, Saint Lucie; -80.4200, 37.2200, United States, Virginia, Montgomery; -80.9500, 27.4500, United States, Florida, Okeechobee; -81.5700, 29.2200, United States, Florida, Volusia; -81.6200, 30.4800, United States, Florida, Duval; -81.7100, 26.0500, United States, Florida, Collier; -81.7600, 28.5300, United States, Florida, Lake; -82.0000, 28.2900, United States, Florida, Polk; -82.0300, 29.7800, United States, Florida, Clay; -82.0500, 29.7000, United States, Florida, Putnam; -82.0700, 29.7000, United States, Florida, Alachua; -82.0800, 27.3100, United States, Florida, Manatee; -82.0800, 29.3000, United States, Florida, Marion; -82.3300, 28.8380, United States, Florida, Citrus; -82.3700, 28.8900, United States, Florida, Citrus; -82.4300, 29.7000, United States, Florida, Alachua; -82.4900, 30.1100, United States, Florida, Columbia; -82.5000, 27.5800, United States, Florida, Manatee; -82.5700, 28.5100, United States, Florida, Hernando; -82.5800, 28.9100, United States, Florida, Citrus; -82.6000, 29.9900, United States, Florida, Columbia; -82.6900, 29.3900, United States, Florida, Levy; -82.7200, 28.1100, United States, Florida, Pinellas; -82.8300, 29.7900, United States, Florida, Gilchrist; -82.9400, 30.4400, United States, Florida, Hamilton; -83.0300, 29.3000, United States, Florida, Levy; -83.5000, 30.6000, United States, Florida, Madison; -84.7500, 30.2400, United States, Florida, Liberty; -84.7600, 30.0000, United States, Florida, Franklin; -84.9830, 29.7260, United States, Florida, Franklin; -85.0200, 29.7400, United States, Florida, Franklin; -85.5500, 30.6500, United States, Florida, Washington; -87.3500, 31.4600, United States, Alabama, Monroe; -88.6500, 31.6800, United States, Mississippi, Wayne; -88.8300, 30.4800, United States, Mississippi, Jackson; -88.9500, 30.4900, United States, Mississippi, Harrison; -89.0100, 31.1700, United States, Mississippi, Perry; -89.1400, 30.8200, United States, Mississippi, Stone; -89.1800, 31.1100, United States, Mississippi, Forrest; -89.2500, 31.1800, United States, Mississippi, Forrest; -89.2900, 31.3100, United States, Mississippi, Forrest; -89.3100, 31.2900, United States, Mississippi, Forrest; -89.3800, 31.2900, United States, Mississippi, Lamar; -89.4700, 30.8900, United States, Mississippi, Pearl River; -89.5800, 30.2600, United States, Mississippi, Hancock; -89.5800, 34.3600, United States, Mississippi, Lafayette; -89.6300, 30.3500, United States, Mississippi, Hancock; -89.6700, 30.4900, United States, Mississippi, Pearl River; -89.7200, 30.2700, United States, Louisiana, Saint Tammany; -89.7900, 33.4800, United States, Mississippi, Carroll; -89.8300, 30.3300, United States, Louisiana, Saint Tammany; -89.9700, 32.5400, United States, Mississippi, Madison; -90.0200, 29.9200, United States, Louisiana, Orleans; -90.0400, 30.5100, United States, Louisiana, Saint Tammany; -90.1300, 29.7200, United States, Louisiana, Jefferson; -90.1600, 29.8600, United States, Louisiana, Jefferson; -90.1700, 29.9200, United States, Louisiana, Jefferson; -90.2900, 32.1900, United States, Mississippi, Hinds; -90.3500, 29.8700, United States, Louisiana, Saint Charles; -90.4200, 38.7100, United States, Missouri, Saint Louis; -90.4400, 30.5200, United States, Louisiana, Tangipahoa; -90.6900, 29.3800, United States, Louisiana, Terrebonne; -90.7700, 35.7700, United States, Arkansas, Craighead; -90.8700, 32.3800, United States, Mississippi, Warren; -90.9500, 30.2500, United States, Louisiana, Ascension; -91.1300, 30.8200, United States, Louisiana, East Feliciana; -91.1700, 30.5500, United States, Louisiana, East Baton Rouge; -91.1800, 30.4000, United States, Louisiana, East Baton Rouge; -91.3500, 30.4700, United States, Louisiana, West Baton Rouge; -91.3600, 30.7900, United States, Louisiana, West Feliciana; -91.3600, 31.5600, United States, Mississippi, Adams; -91.3700, 30.5990, United States, Louisiana, Pointe Coupee; -91.8200, 30.0100, United States, Louisiana, Iberia; -91.8500, 35.2200, United States, Arkansas, White; -92.0700, 30.5400, United States, Louisiana, Saint Landry; -92.1400, 32.4400, United States, Louisiana, Ouachita; -92.1500, 32.4900, United States, Louisiana, Ouachita; -92.2300, 30.9300, United States, Louisiana, Avoyelles; -92.3000, 34.6600, United States, Arkansas, Pulaski; -92.3200, 30.6100, United States, Louisiana, Evangeline; -92.3600, 30.2300, United States, Louisiana, Acadia; -92.4300, 30.4900, United States, Louisiana, Saint Landry; -92.4300, 30.6000, United States, Louisiana, Evangeline; -92.5400, 30.0300, United States, Louisiana, Vermilion; -92.7100, 29.7000, United States, Louisiana, Cameron; -93.0800, 31.7200, United States, Louisiana, Natchitoches; -93.1800, 31.0900, United States, Louisiana, Vernon; -93.1900, 34.0200, United States, Arkansas, Clark; -93.2000, 34.5400, United States, Arkansas, Garland; -93.2600, 32.6400, United States, Louisiana, Webster; -93.3100, 30.2000, United States, Louisiana, Calcasieu; -93.5300, 34.4800, United States, Arkansas, Montgomery; -93.7400, 32.4600, United States, Louisiana, Caddo; -93.9200, 33.2600, United States, Arkansas, Miller; -94.0500, 30.4200, United States, Texas, Jasper; -94.2000, 35.8200, United States, Arkansas, Washington; -94.2400, 35.1900, United States, Arkansas, Sebastian; -94.2500, 31.9400, United States, Texas, Shelby; -94.2600, 29.8800, United States, Texas, Jefferson; -94.3100, 32.6100, United States, Texas, Harrison; -94.6300, 32.9900, United States, Texas, Cass; -94.7600, 31.8900, United States, Texas, Rusk; -94.9400, 32.5300, United States, Texas, Gregg; -94.9400, 33.2400, United States, Texas, Titus; -95.0500, 29.3800, United States, Texas, Galveston; -95.1400, 32.2700, United States, Texas, Smith; -95.2700, 29.7900, United States, Texas, Harris; -95.2700, 31.9500, United States, Texas, Cherokee; -95.3700, 30.2500, United States, Texas, Montgomery; -95.4700, 32.3000, United States, Texas, Henderson; -95.5000, 32.6600, United States, Texas, Wood; -95.5400, 29.1100, United States, Texas, Brazoria; -95.7000, 32.6700, United States, Texas, Van Zandt; -95.7300, 29.4300, United States, Texas, Fort Bend; -95.9700, 31.9500, United States, Texas, Anderson; -96.1000, 29.1800, United States, Texas, Wharton; -96.2200, 32.1200, United States, Texas, Navarro; -96.2600, 30.5900, United States, Texas, Brazos; -96.2800, 32.7300, United States, Texas, Kaufman; -96.4100, 33.6100, United States, Texas, Grayson; -96.4900, 29.6600, United States, Texas, Colorado; -96.8700, 29.3500, United States, Texas, Lavaca; -96.9400, 28.8100, United States, Texas, Victoria; -96.9400, 28.9400, United States, Texas, Victoria; -96.9400, 30.2800, United States, Texas, Lee; -97.0000, 29.8100, United States, Texas, Fayette; -97.0900, 31.5700, United States, Texas, McLennan; -97.1600, 29.1300, United States, Texas, Dewitt; -97.2400, 28.2600, United States, Texas, Refugio; -97.3300, 32.6600, United States, Texas, Tarrant; -97.3400, 32.4700, United States, Texas, Johnson; -97.4770, 35.6520, United States, Oklahoma, Oklahoma; -97.5100, 27.9800, United States, Texas, San Patricio; -97.5500, 26.0800, United States, Texas, Cameron; -97.5700, 32.5300, United States, Texas, Johnson; -97.5800, 29.3000, United States, Texas, Gonzales; -97.6000, 30.2800, United States, Texas, Travis; -97.6500, 26.4500, United States, Texas, Willacy; -97.7000, 34.9100, United States, Oklahoma, Grady; -97.7100, 27.7400, United States, Texas, Nueces; -97.8700, 28.9100, United States, Texas, Karnes; -97.8900, 30.0600, United States, Texas, Hays; -97.9400, 27.4300, United States, Texas, Kleberg; -98.1200, 27.7400, United States, Texas, Jim Wells; -98.2100, 27.0800, United States, Texas, Brooks; -98.3600, 29.4700, United States, Texas, Bexar; -98.4100, 26.2330, United States, Texas, Hidalgo; -98.7000, 26.5300, United States, Texas, Starr; -98.7000, 27.0400, United States, Texas, Jim Hogg; -99.0400, 28.2800, United States, Texas, La Salle; -99.0800, 28.3700, United States, Texas, La Salle; -99.1600, 27.0300, United States, Texas, Zapata; -99.2800, 27.7400, United States, Texas, Webb; -99.8400, 28.8100, United States, Texas, Zavala.

Osteopilus septentrionalis, native

-75.1136, 23.2211, Bahamas, Long Island; -77.9382, 24.7259, Bahamas, North Andros; -76.2372, 24.7547, Bahamas, South Eleuthera; -78.0536, 24.9565, Bahamas, North Andros; -76.7057, 25.4849, Bahamas, North Eleuthera; -77.1021, 26.3981, Bahamas, Central Abaco; -78.5437, 26.7153, Bahamas, West Grand Bahama; -77.6303, 26.8926, Bahamas, North Abaco; -81.3000, 19.2667, Cayman Islands, Bodden Town; -81.2000, 19.3000, Cayman Islands, North Side; -80.0000, 19.7000, Cayman Islands, Little Cayman; -77.7333, 19.8832, Cuba, Granma; -77.7002, 19.9062, Cuba, Granma; -75.1065, 19.9121, Cuba, Guantánamo; -75.1148, 19.9189, Cuba, Guantánamo; -75.1217, 19.9189, Cuba, Guantánamo; -75.1262, 19.9268, Cuba, Guantánamo; -77.6499, 19.9615, Cuba, Granma; -76.8300, 19.9800, Cuba, Santiago de Cuba; -76.8333, 19.9833, Cuba, Santiago de Cuba; -75.8219, 20.0247, Cuba, Santiago de Cuba; -77.4350, 20.1419, Cuba, Granma; -74.2754, 20.1445, Cuba, Guantánamo; -75.2061, 20.1453, Cuba, Guantánamo; -74.6833, 20.1500, Cuba, Guantánamo; -75.1492, 20.1505, Cuba, Guantánamo; -74.2967, 20.3008, Cuba, Guantánamo; -75.0000, 20.3167, Cuba, Guantánamo; -74.5000, 20.3500, Cuba, Guantánamo; -74.8200, 20.5639, Cuba, Holguín; -77.1676, 20.7623, Cuba, Las Tunas; -75.7186, 20.9625, Cuba, Holguín; -78.0190, 21.2875, Cuba, Camagüey; -77.9167, 21.3833, Cuba, Camagüey; -78.0034, 21.3833, Cuba, Camagüey; -77.9848, 21.4472, Cuba, Camagüey; -82.8333, 21.6667, Cuba, Isla de la Juventud; -84.9508, 21.8631, Cuba, Pinar del Río; -82.8000, 21.8833, Cuba, Isla de la Juventud; -80.0219, 21.9136, Cuba, Villa Clara; -80.0000, 21.9333, Cuba, Villa Clara; -80.1558, 21.9333, Cuba, Cienfuegos; -80.1667, 22.0667, Cuba, Cienfuegos; -81.0317, 22.0669, Cuba, Matanzas; -80.4403, 22.1444, Cuba, Cienfuegos; -84.0800, 22.2000, Cuba, Pinar del Río; -83.4000, 22.3000, Cuba, Pinar del Río; -83.7500, 22.3167, Cuba, Pinar del Río; -80.5500, 22.3333, Cuba, Cienfuegos; -83.6981, 22.4175, Cuba, Pinar del Río; -80.4667, 22.4667, Cuba, Cienfuegos; -79.5500, 22.5000, Cuba, Villa Clara; -83.4158, 22.5183, Cuba, Pinar del Río; -79.4669, 22.5206, Cuba, Villa Clara; -79.8220, 22.5526, Cuba, Villa Clara; -83.7078, 22.6164, Cuba, Pinar del Río; -83.3500, 22.6167, Cuba, Pinar del Río; -83.3697, 22.6467, Cuba, Pinar del Río; -83.7167, 22.6667, Cuba, Pinar del Río; -83.1833, 22.7500, Cuba, Pinar del Río; -83.0167, 22.8000, Cuba, Pinar del Río; -80.6833, 22.8167, Cuba, Villa Clara; -80.4667, 22.9000, Cuba, Villa Clara; -81.2047, 23.0375, Cuba, Matanzas; -82.4300, 23.0767, Cuba, Ciudad de la Habana; -82.1667, 23.1319, Cuba, Ciudad de la Habana; -82.3667, 23.1333, Cuba, Ciudad de la Habana; -81.2000, 19.4000; -76.8000, 19.9333, Cuba; -84.6000, 21.8500; -84.2850, 22.4906; -75.4299, 24.2069, Bahamas; -75.5452, 24.4664, Bahamas.

Osteopilus septentrionalis, invasive

-72.0830, 18.3000, Haiti, Sud-Est, Belle-Anse, Belle-Anse; 80.4524, 25.4238, India, Uttar Pradesh, Banda, Naraini; -63.0410, 18.2333, Anguilla Island; -61.8164, 17.0981, Antigua and Barbuda, Saint John; -64.5700, 18.3500, British Virgin Islands; -62.8333, 17.9000, Guadeloupe, Saint-Martin et Saint-Barthélémy; -63.0667, 18.0667, Guadeloupe, Saint-Martin et Saint-Barthélémy; -63.0668, 18.0667, Guadeloupe, Saint-Martin et Saint-Barthélémy; -63.0669, 18.0667, Guadeloupe, Saint-Martin et Saint-Barthélémy; -68.9589, 12.1503, Nederlandse Antillen, Curaçao; -68.9611, 12.1519, Nederlandse Antillen, Curaçao; -67.1146, 18.4557, Puerto Rico, Aguadilla; -156.4470, 20.7250, United States, Hawaii, Maui; -160.0800, 21.9867, United States, Hawaii, Kauai; -81.7920, 24.5540, United States, Florida, Monroe; -81.7840, 24.5561, United States, Florida, Monroe; -81.7794, 24.5562, United States, Florida, Monroe; -81.7408, 24.5722, United States, Florida, Monroe; -81.7499, 24.5728, United States, Florida, Monroe; -81.3876, 24.6742, United States, Florida, Monroe; -81.4074, 24.6831, United States, Florida, Monroe; -81.3689, 24.6868, United States, Florida, Monroe; -81.3689, 24.6868, United States, Florida, Monroe; -81.0903, 24.7138, United States, Florida, Monroe; -80.6380, 24.9140, United States, Florida, Monroe; -80.4180, 25.1185, United States, Florida, Monroe; -80.9375, 25.1383, United States, Florida, Monroe; -80.9228, 25.1425, United States, Florida, Monroe; -80.9056, 25.1750, United States, Florida, Monroe; -80.8503, 25.2153, United States, Florida, Miami-Dade; -80.7833, 25.3206, United States, Florida, Miami-Dade; -80.8339, 25.3206, United States, Florida, Miami-Dade; -80.5844, 25.3944, United States, Florida, Miami-Dade; -80.6567, 25.4017, United States, Florida, Miami-Dade; -80.6792, 25.4400, United States, Florida, Miami-Dade; -80.2500, 25.8170, United States, Florida, Miami-Dade; -80.4288, 25.9309, United States, Florida, Miami-Dade; -81.7008, 26.0532, United States, Florida, Collier; -80.4433, 26.1462, United States, Florida, Broward; -81.6713, 26.1551, United States, Florida, Collier; -81.8044, 26.1900, United States, Florida, Collier; -81.7330, 26.6830, United States, Florida, Lee; -81.1916, 26.6964, United States, Florida, Hendry; -80.0540, 26.7150, United States, Florida, Palm Beach; -81.1684, 26.8920, United States, Florida, Glades; -82.1312, 26.9529, United States, Florida, Charlotte; -82.1312, 26.9529, United States, Florida, Charlotte; -80.1286, 27.0061, United States, Florida, Martin; -80.2559, 27.1324, United States, Florida, Martin; -82.3989, 27.1649, United States, Florida, Sarasota; -81.8720, 27.2010, United States, Florida, Desoto; -81.8720, 27.2010, United States, Florida, Desoto; -80.3151, 27.2574, United States, Florida, Saint Lucie; -80.8709, 27.3252, United States, Florida, Okeechobee; -81.4285, 27.4397, United States, Florida, Highlands; -82.5491, 27.4878, United States, Florida, Manatee; -82.5491, 27.4878, United States, Florida, Manatee; -

81.8091, 27.5382, United States, Florida, Hardee; -82.4590, 27.9470, United States, Florida, Hillsborough; -82.2542, 28.0792, United States, Florida, Hillsborough; -81.3197, 28.2319, United States, Florida, Osceola; -81.3908, 28.4711, United States, Florida, Orange; -81.3108, 28.7099, United States, Florida, Seminole; -82.4692, 28.8946, United States, Florida, Citrus; -82.1275, 29.1808, United States, Florida, Marion; -82.3720, 29.6133, United States, Florida, Alachua; -81.6223, 30.1807, United States, Florida, Duval; -84.2609, 30.4629, United States, Florida, Leon; -84.2609, 30.4629, United States, Florida, Leon; -64.8292, 18.3099, U.S. Virgin Islands, Saint Thomas, -64.9459, 18.3230, U.S. Virgin Islands, Saint Thomas; -64.8842, 18.3238, U.S. Virgin Islands, Saint Thomas; -64.8359, 18.3255, U.S. Virgin Islands, Saint Thomas; -64.7836, 18.3306, U.S. Virgin Islands, Saint John; -64.7820, 18.3377, U.S. Virgin Islands, Saint John; -64.9922, 18.3543, U.S. Virgin Islands, Saint Thomas; -64.8983, 18.3551, U.S. Virgin Islands, Saint Thomas; -65.0203, 18.3583, U.S. Virgin Islands, Saint Thomas.

Phelsuma parkeri

39.6530, -5.4340, Tanzania, Kusini-Pemba, Mkoani, Chokocho; 39.7530, -5.3030, Tanzania, Kusini-Pemba, Chakechake, Chonga; 39.6940, -5.3760, Tanzania, Kusini-Pemba, Mkoani, Kangani; 39.7170, -5.3960, Tanzania, Kusini-Pemba, Mkoani, Kengeja; 39.7300, -5.4220, Tanzania, Kusini-Pemba, Mkoani, Kengeja; 39.7300, -5.4330, Tanzania, Kusini-Pemba, Mkoani, Kengeja; 39.7140, -5.4080, Tanzania, Kusini-Pemba, Mkoani, Kengeja; 39.7100, -5.3870, Tanzania, Kusini-Pemba, Mkoani, Kengeja; 39.7220, -5.0600, Tanzania, Kaskazini-Pemba, Wete, Kipangani; 39.8060, -5.1510, Tanzania, Kaskazini-Pemba, Wete, Kiuyu; 39.7060, -4.9640, Tanzania, Kaskazini-Pemba, Micheweni, Konde; 39.7060, -4.9640, Tanzania, Kaskazini-Pemba, Micheweni, Konde; 39.7060, -4.9640, Tanzania, Kaskazini-Pemba, Micheweni, Konde; 39.7210, -4.9450, Tanzania, Kaskazini-Pemba, Micheweni, Konde; 39.7150, -4.9420, Tanzania, Kaskazini-Pemba, Micheweni, Konde; 39.7390, -4.9670, Tanzania, Kaskazini-Pemba, Micheweni, Konde; 39.6830, -4.9230, Tanzania, Kaskazini-Pemba, Micheweni, Makangale; 39.6660, -5.3750, Tanzania, Kusini-Pemba, Mkoani, Mbuguani; 39.7370, -4.9990, Tanzania, Kaskazini-Pemba, Micheweni, Mgogoni; 39.7370, -4.9990, Tanzania, Kaskazini-Pemba, Micheweni, Mgogoni; 39.7360, -5.0410, Tanzania, Kaskazini-Pemba, Micheweni, Mgogoni; 39.6680, -5.3990, Tanzania, Kusini-Pemba, Mkoani, Mkanyageni; 39.7560, -4.9220, Tanzania, Kaskazini-Pemba, Micheweni, Msuka; 39.7850, -5.3740, Tanzania, Kusini-Pemba, Mkoani, Mtangani; 39.7770, -5.3670, Tanzania, Kusini-Pemba, Mkoani, Mtangani; 39.7310, -5.4350, Tanzania, Kusini-Pemba, Mkoani, Muambe; 39.8000, -5.2620, Tanzania, Kusini-Pemba, Chakechake, Mvumoni; 39.6460, -5.3690, Tanzania, Kusini-Pemba, Mkoani, Ngombeni; 39.8000, -5.1840, Tanzania, Kaskazini-Pemba, Wete, Ole; 39.8010, -5.1870, Tanzania, Kaskazini-Pemba, Wete, Ole; 39.8070, -5.1880, Tanzania, Kaskazini-Pemba, Wete, Ole; 39.8120, -5.1840, Tanzania, Kaskazini-Pemba, Wete, Ole; 39.8220, -5.1700, Tanzania, Kaskazini-Pemba, Wete, Ole; 39.8220, -5.1700, Tanzania, Kaskazini-Pemba, Wete, Ole; 39.7760, -5.0970, Tanzania, Kaskazini-Pemba, Wete, Piki; 39.7690, -5.0870, Tanzania, Kaskazini-Pemba, Wete, Piki; 39.8160, -5.0430, Tanzania, Kaskazini-Pemba, Wete, Shengejuu; 39.7620, -5.2270, Tanzania, Kusini-Pemba, Chakechake, Tibirinzi; 39.8020, -4.9650, Tanzania, Kaskazini-Pemba, Micheweni, Tumbe; 39.7610, -5.3450, Tanzania, Kusini-Pemba, Mkoani, Ukutini; 39.7560, -5.0720, Tanzania, Kaskazini-Pemba, Wete, Utaani; 39.6740, -5.3050, Tanzania, Kusini-Pemba, Mkoani, Wambaa; 39.8060, -5.0180, Tanzania, Kaskazini-Pemba, Micheweni, Wingwi Mapofu; 39.8180, -5.0350, Tanzania, Kaskazini-Pemba, Micheweni, Wingwi

Njuguni; 39.8180, -5.0350, Tanzania, Kaskazini-Pemba, Micheweni, Wingwi Njuguni; 39.7780, -5.1920, Tanzania, Kusini-Pemba, Chakechake, Ziwani.

Trachemys scripta, native

-104.6700, 34.9100, United States, New Mexico, Guadalupe; -104.5700, 32.0000, United States, Texas, Culberson; -104.5300, 32.9400, United States, New Mexico, Eddy; -104.5000, 32.0700, United States, New Mexico, Eddy; -104.4200, 32.4800, United States, New Mexico, Eddy; -104.4100, 34.0700, United States, New Mexico, Debaca; -104.4100, 35.7000, United States, New Mexico, San Miguel; -104.4000, 33.4500, United States, New Mexico, Chaves; -104.3900, 33.4000, United States, New Mexico, Chaves; -104.3800, 32.0700, United States, New Mexico, Eddy; -104.3600, 33.2000, United States, New Mexico, Chaves; -104.3400, 32.0500, United States, New Mexico, Eddy; -104.3400, 33.3400, United States, New Mexico, Chaves; -104.3300, 33.3600, United States, New Mexico, Chaves; -104.3100, 32.1000, United States, New Mexico, Eddy; -104.2900, 32.0000, United States, Texas, Culberson; -104.2700, 32.5000, United States, New Mexico, Eddy; -104.2500, 32.0000, United States, Texas, Culberson; -104.2500, 32.4900, United States, New Mexico, Eddy; -104.2300, 32.1500, United States, New Mexico, Eddy; -104.2300, 32.4900, United States, New Mexico, Eddy; -104.2300, 35.4600, United States, New Mexico, San Miguel; -104.2200, 32.4100, United States, New Mexico, Eddy; -104.2200, 32.4200, United States, New Mexico, Eddy; -104.1900, 32.2200, United States, New Mexico, Eddy; -104.1900, 35.4000, United States, New Mexico, San Miguel; -104.1800, 35.4100, United States, New Mexico, San Miguel; -104.1700, 35.4200, United States, New Mexico, San Miguel; -104.1600, 32.3900, United States, New Mexico, Eddy; -104.1500, 32.3900, United States, New Mexico, Eddy; -104.0800, 32.1900, United States, New Mexico, Eddy; -104.0600, 32.0200, United States, New Mexico, Eddy; -104.0200, 32.0400, United States, New Mexico, Eddy; -104.0000, 31.0000, United States, Texas, Jeff Davis; -103.9900, 32.0300, United States, New Mexico, Eddy; -103.7200, 35.9600, United States, New Mexico, Harding; -103.3100, 36.0500, United States, New Mexico, Union; -101.9500, 33.7600, United States, Texas, Lubbock; -101.7300, 32.4200, United States, Texas, Martin; -101.3240, 37.5910, United States, Kansas, Grant; -101.3240, 37.5910, United States, Kansas, Grant; -100.9910, 37.9740, United States, Kansas, Finney; -100.9910, 37.9740, United States, Kansas, Finney; -100.8940, 37.0690, United States, Kansas, Seward; -100.8940, 37.0690, United States, Kansas, Seward; -100.7790, 37.1410, United States, Kansas, Seward; -100.7790, 37.1410, United States, Kansas, Seward; -100.5600, 38.0680, United States, Kansas, Finney; -100.5600, 38.0680, United States, Kansas, Finney; -100.3540, 37.7990, United States, Kansas, Gray; -100.3540, 37.7990, United States, Kansas, Gray; -100.3000, 37.2000, United States, Kansas, Meade; -100.1860, 37.7800, United States, Kansas, Ford; -100.1860, 37.7800, United States, Kansas, Ford; -100.1500, 38.3700, United States, Kansas, Ness; -100.1500, 38.3700, United States, Kansas, Ness; -100.0820, 38.0490, United States, Kansas, Hodgeman; -100.0820, 38.0490, United States, Kansas, Hodgeman; -100.0010, 38.0690, United States, Kansas, Hodgeman; -100.0010, 38.0690, United States, Kansas, Hodgeman; -100.0010, 38.0690, United States, Kansas, Hodgeman; -100.0000, 38.0690, United States, Kansas, Hodgeman; -99.9920, 38.5420, United States, Kansas, Ness; -99.8100, 31.5300, United States, Texas, Concho; -99.7800, 30.9100, United States, Texas, Menard; -99.7770, 37.0460, United States, Kansas, Clark; -99.7300, 33.1500, United States, Texas, Haskell; -99.7140, 38.7940, United States, Kansas, Trego; -99.7120, 29.5530, United States, Texas, Uvalde; 99.6850, 37.3100, United States, Kansas, Clark; -99.5700, 38.5800, United States, Kansas, Rush; -99.5700, 39.6600, United States, Kansas, Phillips; -99.4200, 27.7900, United States, Texas, Webb; -99.4200, 31.8200, United States, Texas, Coleman; -99.2700, 26.9000, United States, Texas, Zapata; -99.2240, 38.1820, United States, Kansas, Pawnee; -99.1710, 37.1210, United States, Kansas, Comanche; -99.1700, 33.1700, United States, Texas, Throckmorton; -99.1520, 38.7140, United States, Kansas, Ellis; -99.1510, 38.7140, United States, Kansas, Ellis; -99.1470, 37.2180, United States, Kansas, Comanche; -99.1470, 37.2180, United States, Kansas, Comanche; -99.0600, 32.3400, United States, Texas, Eastland; -98.9630, 37.1310, United States, Kansas, Barber; -98.9220, 37.2620, United States, Kansas, Barber; -98.7870, 39.5260, United States, Kansas, Osborne; -98.7870, 39.5260, United States, Kansas, Osborne; -98.7300, 29.2600, United States, Texas, Bexar; -98.7240, 37.2750, United States, Kansas, Barber; -98.7100, 31.1900, United States, Texas, San Saba; -98.6700, 30.7400, United States, Texas, Llano; -98.6500, 37.0640, United States, Kansas, Barber; -98.6280, 37.1230, United States, Kansas, Barber; -98.5830, 37.3010, United States, Kansas, Barber; -98.5100, 37.3000, United States, Kansas, Barber; -98.4900, 39.4260, United States, Kansas, Osborne; -98.4200, 30.0900, United States, Texas, Blanco; -98.3230, 39.5100, United States, Kansas, Mitchell; -98.2900, 32.7600, United States, Texas, Palo Pinto; -98.2600, 26.1000, United States, Texas, Hidalgo; -98.1450, 27.2250, United States, Texas, Brooks; -98.1200, 32.6600, United States, Texas, Palo Pinto; -98.1120, 37.1920, United States, Kansas, Harper; -98.0800, 26.1700, United States, Texas, Hidalgo; -97.9600, 32.6100, United States, Texas, Parker; -97.9290, 38.0900, United States, Kansas, Reno; -97.8400, 28.8100, United States, Texas, Karnes; -97.8220, 38.6680, United States, Kansas, Saline; -97.7700, 27.9500, United States, Texas, San Patricio; -97.7430, 30.2670, United States, Texas, Travis; -97.6100, 31.5400, United States, Texas, Coryell; -97.5570, 30.2680, United States, Texas, Travis; -97.5200, 34.9000, United States, Oklahoma, McClain; -97.4000, 30.5700, United States, Texas, Williamson; -97.3500, 35.0140, United States, Oklahoma, McClain; -97.3100, 30.1100, United States, Texas, Bastrop; -97.2700, 28.3000, United States, Texas, Refugio; -97.0830, 37.0780, United States, Kansas, Cowley; -97.0000, 28.8000, United States, Texas, Victoria; -96.9700, 30.8500, United States, Texas, Milam; -96.8800, 32.7100, United States, Texas, Dallas; -96.8680, 37.0490, United States, Kansas, Cowley; -96.8600, 29.6910, United States, Texas, Fayette; -96.8010, 33.7210, United States, Texas, Grayson; -96.7740, 33.6920, United States, Texas, Grayson; -96.7700, 32.2900, United States, Texas, Ellis; -96.6720, 33.7740, United States, Texas, Grayson; -96.6200, 33.0500, United States, Texas, Collin; -96.6090, 33.6200, United States, Texas, Grayson; -96.5300, 33.8000, United States, Texas, Grayson; -96.4820, 36.0030, United States, Oklahoma, Creek; -96.4500, 32.9300, United States, Texas, Rockwall; -96.4290, 30.5460, United States, Texas, Burleson; -96.4130, 33.6220, United States, Texas, Grayson; -96.3800, 32.5100, United States, Texas, Kaufman; -96.3340, 30.6280, United States, Texas, Brazos; -96.1600, 38.6500, United States, Kansas, Lyon; -96.1500, 30.3200, United States, Texas, Washington; -96.1000, 29.3100, United States, Texas, Wharton; -96.0700, 31.8400, United States, Texas, Freestone; -95.9550, 37.0260, United States, Kansas, Montgomery; -95.9280, 37.3980, United States, Kansas, Wilson; -95.8720, 36.0920, United States, Oklahoma, Tulsa; -95.8500, 36.9700, United States, Oklahoma, Washington; -95.6700, 32.6000, United States, Texas, Van Zandt; -95.4300, 32.9200, United States, Texas, Wood; -95.3390, 37.4170, United States, Kansas, Neosho; -95.3230, 37.6010, United States, Kansas, Neosho; -95.2790, 38.5710, United States, Kansas, Franklin; -95.2320, 37.0620, United States, Kansas, Labette; -95.1950, 39.8800, United States, Kansas, Doniphan; -95.1950, 39.8800, United States, Kansas, Doniphan; -95.1800, 37.5340, United States, Kansas, Neosho; -95.1680, 37.1630, United

States, Kansas, Labette; -95.1650, 37.1630, United States, Kansas, Labette; -95.1520, 37.4780, United States, Kansas, Neosho; -95.1520, 37.1280, United States, Kansas, Labette; -95.0820, 37.1660, United States, Kansas, Labette; -95.0700, 37.1800, United States, Kansas, Cherokee; -94.8910, 29.8480, United States, Texas, Chambers; -94.8700, 29.2700, United States, Texas, Galveston; -94.8370, 38.5690, United States, Kansas, Miami; -94.8080, 37.3300, United States, Kansas, Cherokee; -94.7800, 36.8500, United States, Oklahoma, Ottawa; -94.7610, 38.3500, United States, Kansas, Linn; -94.7580, 33.9510, United States, Oklahoma, McCurtain; -94.7030, 37.8370, United States, Kansas, Bourbon; -94.6950, 37.0750, United States, Kansas, Cherokee; -94.6900, 38.0640, United States, Kansas, Linn; -94.6400, 37.8560, United States, Kansas, Bourbon; -94.6360, 37.0410, United States, Kansas, Cherokee; -94.4400, 32.8800, United States, Texas, Marion; -94.3400, 32.7400, United States, Texas, Marion; -94.3200, 32.5400, United States, Texas, Harrison; -94.2500, 39.7600, United States, Missouri, De Kalb; -94.1100, 40.5800, United States, Iowa, Ringgold; -94.0600, 33.1900, United States, Texas, Cass; -94.0000, 31.0000, United States, Texas, Jasper; -93.9600, 36.6300, United States, Missouri, Barry; -93.8400, 31.3400, United States, Texas, Sabine; -93.8400, 31.5900, United States, Texas, Shelby; -93.8100, 38.4000, United States, Missouri, Henry; -93.8000, 36.6500, United States, Missouri, Barry; -93.7600, 31.2400, United States, Texas, Sabine; -93.7500, 30.8400, United States, Texas, Newton; -93.4570, 30.2360, United States, Louisiana, Calcasieu; -93.3200, 30.1000, United States, Louisiana, Calcasieu; -93.1600, 39.7800, United States, Missouri, Linn; -93.0800, 31.7400, United States, Louisiana, Natchitoches; -92.7800, 40.5700, United States, Missouri, Putnam; -92.5700, 30.2600, United States, Louisiana, Acadia; -92.4300, 31.3220, United States, Louisiana, Rapides; -92.0700, 32.7500, United States, Louisiana, Union; -92.0200, 30.2240, United States, Louisiana, Lafayette; -91.9700, 37.5500, United States, Missouri, Texas; -91.8900, 34.7800, United States, Arkansas, Lonoke; -91.8200, 29.9900, United States, Louisiana, Iberia; -91.7600, 39.1300, United States, Missouri, Audrain; -91.7360, 35.2510, United States, Arkansas, White; -91.7300, 39.6500, United States, Missouri, Monroe; -91.7000, 30.2100, United States, Louisiana, Saint Martin; -91.6800, 40.4200, United States, Missouri, Clark; -91.6700, 35.7300, United States, Arkansas, Independence; -91.4300, 30.7300, United States, Louisiana, Pointe Coupee; -91.4200, 31.5600, United States, Mississippi, Adams; -91.3400, 34.0200, United States, Arkansas, Arkansas; -91.2500, 32.0500, United States, Louisiana, Tensas; -91.2300, 31.2220, United States, Mississippi, Wilkinson; -91.1800, 30.4450, United States, Louisiana, East Baton Rouge; -91.1600, 30.3300, United States, Louisiana, West Baton Rouge; -91.1300, 33.7300, United States, Mississippi, Bolivar; -91.1300, 41.3700, United States, Iowa, Muscatine; -91.1100, 40.8000, United States, Iowa, Des Moines; -91.1100, 30.2900, United States, Louisiana, Iberville; -91.1000, 34.7300, United States, Arkansas, Monroe; -91.0700, 33.5900, United States, Mississippi, Bolivar; -90.9400, 40.2000, United States, Illinois, Hancock; -90.8000, 29.7600, United States, Louisiana, Lafourche; -90.7400, 36.6100, United States, Missouri, Ripley; -90.7200, 29.7500, United States, Louisiana, Lafourche; -90.7000, 32.8500, United States, Mississippi, Yazoo; -90.6200, 39.1500, United States, Illinois, Calhoun; -90.5800, 35.8100, United States, Arkansas, Craighead; -90.4290, 30.3970, United States, Louisiana, Tangipahoa; -90.3800, 34.6800, United States, Mississippi, Tunica; -90.2600, 39.9600, United States, Illinois, Cass; -90.2420, 30.4370, United States, Louisiana, Saint Tammany; -90.1900, 37.2100, United States, Missouri, Bollinger; -90.1670, 35.8800, United States, Arkansas, Mississippi; -90.1500, 29.9600, United States, Louisiana, Jefferson; -90.1400, 36.4500, United States, Arkansas, Clay; -90.1200, 29.9100, United States, Louisiana, Orleans; -90.1200, 32.4600, United States, Mississippi, Madison; -90.0300, 39.7200, United States, Illinois, Morgan; -89.9900, 35.2400, United States, Tennessee, Shelby; -89.8650, 30.5920, United States, Louisiana, Saint Tammany; -89.8500, 29.8600, United States, Louisiana, Saint Bernard; -89.8500, 35.1500, United States, Tennessee, Shelby; -89.8500, 39.8400, United States, Illinois, Sangamon; -89.8100, 35.4100, United States, Tennessee, Tipton; -89.7600, 38.9800, United States, Illinois, Madison; -89.7500, 40.7400, United States, Illinois, Peoria; -89.5800, 40.7100, United States, Illinois, Peoria; -89.4400, 35.2300, United States, Tennessee, Fayette; -89.3300, 40.4800, United States, Illinois, Tazewell; -89.3100, 33.8500, United States, Mississippi, Calhoun; -89.2000, 35.3600, United States, Tennessee, Fayette; -89.1900, 36.2400, United States, Tennessee, Obion; -89.1800, 36.5700, United States, Kentucky, Fulton; -89.0900, 41.3300, United States, Illinois, La Salle; -88.9800, 40.3700, United States, Illinois, McLean; 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-87.7800, 39.3600, United States, Illinois, Clark; -87.7200, 41.8400, United States, Illinois, Cook; -87.6800, 33.1030, United States, Alabama, Tuscaloosa; -87.6800, 33.1940, United States, Alabama, Tuscaloosa; -87.6410, 33.1190, United States, Alabama, Tuscaloosa; -87.6080, 33.1660, United States, Alabama, Tuscaloosa; -87.6050, 39.7300, United States, Illinois, Edgar; -87.5950, 32.7050, United States, Alabama, Hale; -87.5800, 39.5800, United States, Illinois, Edgar; -87.5700, 33.2110, United States, Alabama, Tuscaloosa; -87.5440, 32.6050, United States, Alabama, Hale; -87.5330, 32.5940, United States, Alabama, Hale; -87.5230, 33.1940, United States, Alabama, Tuscaloosa; -87.3170, 32.6340, United States, Alabama, Perry; -87.2500, 34.1400, United States, Alabama, Winston; -87.0000, 35.0000, United States, Tennessee, Giles; -87.0000, 36.0000, United States, Tennessee, Williamson; -86.9470, 34.6790, United States, Alabama, Limestone; -86.9100, 33.3300, United States, Alabama, Jefferson; -86.7900, 33.9300, United States, Alabama, Blount; -86.5800, 33.1100, United States, Alabama, Shelby; -86.5700, 34.7400, United States, Alabama, Madison; -86.5700, 35.3300, United States, Tennessee, Lincoln; -86.5120, 34.7450, United States, Alabama, Madison; -86.4570, 31.4320, United States, Alabama, Covington; -86.3100, 32.5300, United States, Alabama, Elmore; -86.2980, 34.3620, United States, Alabama, Marshall; -86.1400, 34.2400, United States, Alabama, Marshall; -86.0890, 33.9730, United States, Alabama, Etowah; -86.0700, 31.4800, United States, Alabama, Coffee; -86.0200, 33.6070, United States, Alabama, Calhoun; -86.0200, 36.5200, United States, Tennessee, Macon; -85.8280, 33.6640, United States, Alabama, Calhoun; -85.5970, 33.6590, United States, Alabama, Cleburne; -85.4400, 34.2400, United States, Georgia, Floyd; -85.3000, 37.3000, United States, Kentucky, Taylor; -85.1300, 33.1500, United States, Georgia, Troup; -85.0700, 33.1000, United States, Georgia, Troup; -85.0200, 38.0000, United States, Kentucky, Anderson; -84.9900, 37.9300, United States, Kentucky, Anderson; -84.9300, 32.4200, United States, Georgia, Muscogee; -84.7800, 33.6800, United States, Georgia, Douglas; -84.7100, 35.6800, United States, Tennessee, Meigs; -84.5100, 33.6900, United States, Georgia, Fulton; -84.4800, 33.8000, United States, Georgia, Fulton; -84.4600, 33.4100, United States, Georgia, Fayette; -84.4080, 30.3990, United States, Florida, Leon; -84.3550, 34.0280, United States, Georgia, Fulton; -84.3470, 30.4050, United States, Florida, Leon; -84.3330, 30.4670, United States, Florida, Leon; -84.2900, 33.7700, United States, Georgia, DeKalb; -84.2700, 38.0400, United States, Kentucky, Clark; -84.2400, 35.8000, United States, Tennessee, Loudon; -84.2100, 37.2900, United States, Kentucky, Laurel; -84.0700, 32.0100, United States, Georgia, Sumter; -84.0600, 34.3800, United States, Georgia, Dawson; -83.3800, 32.9000, United States, Georgia, Wilkinson; -82.8390, 34.6780, United States, South Carolina, Pickens; -82.6700, 38.6400, United States, Ohio, Lawrence; -82.5400, 37.3700, United States, Kentucky, Pike; -82.4700, 32.8700, United States, Georgia, Jefferson; -82.3500, 31.7900, United States, Georgia, Appling; -82.2430, 32.8070, United States, Georgia, Emanuel; -82.0000, 34.0000, United States, South Carolina, Greenwood; -81.9500, 32.3900, United States, Georgia, Candler; -81.1200, 31.9300, United States, Georgia, Chatham; -81.1000, 32.0000, United States, Georgia, Chatham; -80.3300, 35.6200, United States, North Carolina, Rowan; -80.0000, 35.0000, United States, North Carolina, Anson; -80.0000, 36.0000, United States, North Carolina, Guilford; -78.6420, 35.8210, United States, North Carolina, Wake; -78.6100, 36.5900, United States, Virginia, Mecklenburg; -78.5100, 35.8800, United States, North Carolina, Wake; -78.3060, 36.5860, United States, Virginia, Mecklenburg; -78.0440, 34.0420, United States, North Carolina, Brunswick; -77.4310, 34.7540, United States, North Carolina, Onslow; -77.1260, 36.9070, United States, Virginia, Sussex; -76.2900, 36.8400, United States, Virginia, Norfolk; -76.1500, 36.8200, United States, Virginia, Virginia Beach; -75.8870, 36.5810, United States, Virginia, Virginia Beach.

Trachemys scripta, invasive

-0.4000, 40.2100, España, Comunidad Valenciana, Castellón, Alt Millars, Villahermosa del Río; -55.9690, -20.5110, Brazil, Mato Grosso do Sul, Anastácio, Anastcio; -49.3330, -16.8280, Brazil, Goiás, Aparecida de Goiânia, Aparecida de Goiânia; -48.2670, -7.3170, Brazil, Tocantins, Araguaína, Araguaína; -43.4080, -22.7890, Brazil, Rio de Janeiro, Nova Iguaçu, Banco de Areia; -43.4690, -22.8780, Brazil, Rio de Janeiro, Rio de Janeiro, Bangu; -49.0890, -27.0190, Brazil, Santa Catarina, Blumenau, Blumenau; -47.9030, -15.8250, Brazil, Distrito Federal, Brasília, Brazilia; -42.8890, -22.8360, Brazil, Rio de Janeiro, Itaboraí, Cabucu; -43.5670, -22.7810, Brazil, Rio de Janeiro, Nova Iguaçu, CabuçU; -54.7470, -20.5280, Brazil, Mato Grosso do Sul, Campo Grande, Campo Grande; -52.5970, -29.7830, Brazil, Rio Grande do Sul, Candelária, Candelária; -52.4190, -31.8110, Brazil, Rio Grande do Sul, Capitão, Capão do Leão; -51.2560, -29.2690, Brazil, Rio Grande do Sul, Caxias do Sul, Caxias do Sul; -43.2000, -21.5330, Brazil, Minas Gerais, Goianá, Goianá; 105.8500, 21.0330, Vietnam; -43.7860, -22.7690, Brazil, Rio de Janeiro, Itaguaí, Ibituporanga; -43.7670, -22.7030, Brazil, Rio de Janeiro, Itaguaí, Ibituporanga; -43.9250, -22.9060, Brazil, Rio de Janeiro, Mangaratiba, Itacurussa; -43.4170, -22.9440, Brazil, Rio de Janeiro, Rio de Janeiro, Jagarepagua; -40.1690, -19.3530, Brazil, Espírito Santo, Linhares, Linhares; -44.1390, -22.9750, Brazil, Rio de Janeiro, Mangaratiba, Mangaratiba; -48.9250, -25.5810, Brazil, Paraná, Morretes, Morretes; -16.6400, 28.2700, España, Islas Canarias, Las Palmas, La Orotava; -15.5800, 28.0000, España, Islas Canarias, Las Palmas, Vega de San Mateo; 1.8000, 41.5000, España, Cataluña, Barcelona, Masquefa; -6.1830, 38.9830, España, Extremadura, Badajoz, Mérida; 4.0000, 40.0000, España, Islas Baleares, Baleares, Ferreries; -43.9860, -19.9780, Brazil, Minas Gerais, Belo Horizonte, Oeste; 7.8170, 48.5670, Deutschland, Baden-Württemberg, Freiburg, Ortenaukreis; -48.3890, -10.2190, Brazil, Tocantins, Palmas, Palmas; -48.3500, -9.9580, Brazil, Tocantins, Palmas, Palmas; -43.7860, -22.6810, Brazil, Rio de Janeiro, Paracambi, Paracambi; -43.4530, -22.8470, Brazil, Rio de Janeiro, Rio de Janeiro, Realengo; -52.2610, -32.2720, Brazil, Rio Grande do Sul, Rio Grande, Rio Grande; -49.3830, -25.4830, Brazil, Paraná, Curitiba, Santa Felicidade; -43.0560, -22.5810, Brazil, Rio de Janeiro, Magé, Santo Aleixo; -43.3670, -22.8030, Brazil, Rio de Janeiro, São João de Meriti, São João de Meriti; -42.7420, -22.7830, Brazil, Rio de Janeiro, Tanguá, Tanguá; -42.8860, -5.1420, Brazil, Goiás, Timon, Timon; -46.7310, -23.6250, Brazil, São Paulo, São Paulo, Vila Andrade; -54.5780, -25.5970, Argentina, Misiones, Iguazú; 151.2000, -33.8830, Australia, New South Wales, Sydney; -64.6230, 18.4270, British Virgin Islands; -64.4400, 18.4450, British Virgin Islands; 0.6830, 47.3830, France, Centre, Indre-Et-Loire; 1.4330, 43.6000, France, Midi-Pyrénées, Haute-Garonne; 2.3830, 48.9170, France, Île-de-France, Seine-Saint-Denis; 2.5000, 48.9500, France, Île-de-France, Seine-Saint-Denis; 4.0670, 44.1170, France, Languedoc-Roussillon, Gard; 4.7500, 44.5500, France, Rhône-Alpes, Drôme; 9.0000, 42.0000, France, Corse, Corse-Du-Sud; -61.5830, 16.2500, Guadeloupe, Basse-Terre, -92.1830, 14.5170, Guatemala, San Marcos, Ocos; -88.2400, 14.8460, Honduras, Santa Bárbara, Santa Bárbara; -86.6330, 14.0000, Honduras, El Paraíso, Jacaleapa; 112.1500, -7.5670, Indonesia, Jawa Timur, Jombang; 8.0000, 45.0000, Italia, Piemonte, Asti; 8.8330, 44.5000, Italia, Liguria, Genoa; 9.5000, 45.6600, Italia, Lombardia, Bergamo; 11.0000, 44.7500, Italia, Emilia-Romagna, Modena; 12.0330, 44.5000, Italia, Emilia-Romagna, Ravenna; 12.4830, 41.9000, Italia, Lazio, Rome; 12.5000, 42.0000, Italia, Lazio, Rome; 12.9000, 41.4830, Italia, Lazio, Latina; 13.4330, 46.0830, Italia, Friuli-Venezia Giulia, Udine; 13.7500, 42.2500, Italia, Abruzzo, L'Aquila; 14.4800, 41.6300, Italia, Molise, Campobasso; 16.2500, 41.2500, Italia, Apulia, Barletta-Andria-Trani; 16.5000, 40.5000, Italia, Basilicata, Matera; 16.5000, 39.0000, Italia, Calabria, Catanzaro; -111.0610, 24.8750, México, Baja California Sur, Comondú; -109.8910, 27.8130, México, Sonora, Cajeme; -108.8870, 26.9490, México, Sonora, Álamos; -108.6940, 26.9030, México, Sonora, Álamos; -103.0000, 29.0000, México, Coahuila, Ocampo; 128.1830, 26.7000, Nippon, Saga; 129.3330, 28.2500, Nippon, Saga; 126.7830, 26.3330, Nippon, Saga; 131.2500, 25.8330, Nippon, Saga; 125.3330, 24.7830, Nippon, Saga; -66.5040, 18.0660, Puerto Rico, Juana Díaz; -66.5410, 17.9860, Puerto Rico, Ponce; -65.3010, 18.3050, Puerto Rico, Culebra; -65.8280, 18.1520, Puerto Rico, Humacao; 13.6100, 45.5300, Republika Slovenija, Obalno-kraška, Izola; 22.7100, 42.9300, Serbia, Pirotski, Dimitrovgrad; 103.8560, 1.2930, Singapore, 120.6170, 24.0670, Taiwan, Taiwan, Changhwa; 121.0000, 24.0000, Taiwan, Taiwan, Nantou; 121.1170, 24.9000, Taiwan, Taiwan, Taoyuan; 121.2830, 25.0500, Taiwan, Taiwan, Taipei; 121.4500, 25.0000, Taiwan, Taipei, Taipei City; 100.5170, 13.7500, Thailand, Bangkok Metropolis, Pathum Wan; 27.3010, 37.0380, Turkey, Mugla; -2.1430, 50.7100, United Kingdom, England, Dorset; -2.0010, 50.6200, United Kingdom, England, Dorset; -1.8570, 51.6090, United Kingdom, England, Wiltshire; -1.5610, 52.3270, United Kingdom, England, Warwickshire; -0.7100, 51.3320, United Kingdom, England, Surrey; -157.9340, 21.3360, United States, Hawaii, Honolulu; -157.8070, 21.3120, United States, Hawaii, Honolulu; -157.7380, 21.3730, United States, Hawaii, Honolulu; -157.7170, 21.3830, United States, Hawaii, Honolulu; -122.2140, 40.4170, United States, California, Shasta; -121.1500, 38.6500, United States, California, Sacramento; -119.6630, 34.4190, United States, California, Santa Barbara; -118.8660, 34.1370, United States, California, Ventura; -117.8870, 33.8870, United States, California, Orange; -113.0000, 33.0000, United States, Arizona, Maricopa; -112.0000, 33.0000, United States, Arizona, Pinal; -111.9330, 33.4500, United States, Arizona, Maricopa; -111.8900, 40.7300, United States, Utah, Salt Lake; -108.7100, 32.7100, United States, New Mexico, Grant; -108.5800, 39.0850, United

States, Colorado, Mesa; -107.1900, 33.2500, United States, New Mexico, Sierra; -107.1700, 33.2000, United States, New Mexico, Sierra; -107.0600, 33.4900, United States, New Mexico, Socorro; -107.0000, 33.0000, United States, New Mexico, Sierra; -107.0000, 34.0000, United States, New Mexico, Socorro; -106.9100, 33.7600, United States, New Mexico, Socorro; -106.9070, 33.8050, United States, New Mexico, Socorro; -106.9000, 33.8300, United States, New Mexico, Socorro; -106.9000, 34.1200, United States, New Mexico, Socorro; -106.8900, 33.8100, United States, New Mexico, Socorro; -106.8800, 33.8200, United States, New Mexico, Socorro; -106.6000, 35.0800, United States, New Mexico, Bernalillo; -106.0000, 32.0000, United States, Texas, El Paso; -106.0000, 34.0000, United States, New Mexico, Socorro; -106.0000, 35.0000, United States, New Mexico, Torrance; -105.0350, 39.6960, United States, Colorado, Denver; -104.3700, 29.5600, United States, Texas, Presidio; -102.0180, 38.9680, United States, Kansas, Wallace; -99.8300, 40.9800, United States, Nebraska, Dawson; -93.6600, 41.6000, United States, Iowa, Polk; -91.6600, 42.0300, United States, Iowa, Linn; -86.0000, 39.0000, United States, Indiana, Jackson; -85.7920, 40.4540, United States, Indiana, Grant; -84.5000, 42.7000, United States, Michigan, Ingham; -84.3200, 42.2300, United States, Michigan, Jackson; -83.3670, 40.2330, United States, Ohio, Union; -83.0010, 29.2730, United States, Florida, Levy; -82.8000, 27.8000, United States, Florida, Pinellas; -82.7650, 29.9820, United States, Florida, Suwannee; -82.7000, 33.2100, United States, Georgia, Glascock; -82.6880, 27.7150, United States, Florida, Pinellas; -82.5000, 27.7000, United States, Florida, Hillsborough; -82.3320, 30.3860, United States, Florida, Baker; -81.3500, 28.4680, United States, Florida, Orange; -81.0000, 29.1500, United States, Florida, Volusia; -80.8110, 27.8300, United States, Florida, Brevard; -80.2530, 25.8440, United States, Florida, Miami-Dade; -80.2000, 26.0700, United States, Florida, Broward; -77.0000, 38.0000, United States, Virginia, Essex; -77.0000, 39.0000, United States, Maryland, Montgomery; -75.0000, 40.5000, United States, New Jersey, Hunterdon; -74.4800, 40.8200, United States, New Jersey, Morris; -74.1400, 41.1910, United States, New York, Rockland; -73.1820, 41.2090, United States, Connecticut, Fairfield; -73.0090, 41.3520, United States, Connecticut, New Haven.