

**Predicting the potential distributions
of two alien invasive Housegeckos (Gekkonidae:
Hemidactylus frenatus, *Hemidactylus mabouia*)**

Dennis RÖDDER^{1,2,*}, Mirco SOLÉ³ and Wolfgang BÖHME¹

1. Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn

2. Biogeography Department, University of Trier, D-54286 Trier, Germany

3. Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas,

Rodovia Ilhéus-Itabuna, km 16, Salobrinho, 45662-000 - Ilhéus, BA, Brazil

* Corresponding author: Zoologisches Forschungsmuseum Alexander Koenig Adenauerallee 160,
D-53113 Bonn, E-Mail: d.roedder.zfmk@uni-bonn.de

Abstract. Globalization has led to an increased spread of alien invasive species, which can alter mutualistic relationships, community dynamics, ecosystem function, and resource distributions. They can cause extinctions thereby affecting local and global diversity. Among reptiles two gecko species, *Hemidactylus frenatus* and *Hemidactylus mabouia*, have considerably increased their range during the last century. Both have already caused local decimations and extinctions of native species. Records of invasive populations of *H. frenatus* are known from tropical Asia through Central America and Florida, whilst invasive populations of *H. mabouia* can be found in Central and Southern Africa, as well as in large parts of Central and South America. Only a few sympatric populations are known. Herein, we identify areas potentially suitable for the geckos using a climate envelope approach, we predict their potential distribution under current conditions and a future climate change scenario, and try to assess why sympatric populations of both geckos are apparently rare. Our results suggest that areas of suitable climatic conditions for both species can be found in nearly all tropical regions. Future projections revealed that the amount of climatically suitable areas will increase for *H. frenatus* on a global scale, but decrease for *H. mabouia*. The greatest changes are suggested for South America where further spreading of *H. frenatus* will be enhanced due to better climatic conditions. In contrast, climatic conditions for *H. mabouia* will degrade in this region. We conclude that both competitive exclusion and a non equilibrium in the ranges of the species explain the virtual absence of sympatric populations, although the impact of climate on competitive success is pending further testing in the field.

Key words Bioclim, Climate Envelope Modelling, Climate change, Exotic species, Maxent

Introduction

Globalization has led to an increased 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 & Cleland 2001). They

can also cause extinctions, thereby affecting local and global diversity (Collins et al. 2002, Vitousek et al. 1996).

Within the Squamata, some *Hemidactylus* geckos (*Hemidactylus mabouia* (Moreau de Jonnés, 1818), *H. turcicus* Linnaeus, 1758, *H. brookii* Gray, 1845, *H. frenatus* Schlegel 1836, *H. garnotii* Duméril & Bibron, 1836, *H. persicus* Anderson, 1872, *H. flaviviridis* Rüpel, 1835 and *H.*

bowringii Gray, 1845) have appreciably extended their ranges during the last century (e.g. Carranza & Arnold 2006). They represent the most obvious cases of large range extensions of any 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 & 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, *Hemidactylus mabouia* is also abundant in natural environments of several biomes, e.g. within Brazil (Colli 2005, Vanzolini 1968a,b, Zamprogno & Teixeira 1997). Both species are very adaptable and are effective colonizers (e.g. Bonfiglio et al. 2006, Case et al. 1994, Fuenmayor et al. 2005). They are widely distributed in tropical regions and may have reached South America by both natural transmarine colonization (Kluge 1969) and human-mediated colonization (Carranza & Arnold 2006). The latter is suggested by the lack of significant genetic variation over their huge ranges and their presence in many coastal urban areas (Carranza & 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 & Vences 2007).

On occasion, the introduction of *H. frenatus* and *H. mabouia* has had devastating consequences for native species independent of ecotypes such as small and large species, diurnal and nocturnal taxa, as well as species with parthenogenetic and sexual reproduction. *Hemidactylus frenatus* is displacing *Lepidodactylus lugubris* Duméril & Bibron, 1836 and *H. garnotii* on a global scale (Case et al. 1994, Petren et al. 1993, Petren & Case 1995, Dame & 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 & 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 Islands 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 & 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 & Peterson 2003, Peterson & Vieglais 2001, Ficetola *et al.* 2007). Such approaches rely 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 evolutionarily relatively short time frames (e.g., some hundreds to thousands of years; Wiens & Graham 2005).

Herein, we aim 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). Data from published literature was added for complementation purposes (Böhme 1975, Gow 1981, Glaw & 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 were checked in the DIVA-GIS software (Hijmans *et al.* 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 a spatial resolution of approximately 1 × 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, Hutchinson 2004).

Projected climate data we used are derived from 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 × 50 km² spatial resolution to simulate conditions at doubled atmospheric levels of CO₂ 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 × 1 km² by Hijmans & 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 Climate Envelope Models (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 yields better results than comparable methods (Elith *et al.* 2006, Heikkinen *et al.* 2006), especially when the number of data points is relatively small (Hernandez *et al.* 2006).

Maxent allows for model testing by calculation of the Area Under the 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) ran 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, to identify 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

CEM Models

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, also resulted in '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 1 and 2.

Our CEMs suggest that *H. frenatus* can find climatically optimal habitats under current conditions in tropical Asia, on the Australian east coast, Central America, within the Amazon basin, the Guiana

Region, and the West African coast (Fig. 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 on the eastern Coast of Brazil in Bahia (Fig. 2). In most regions it is already invasive. Risk of further invasion is highest in Central America and tropical Asia.

Under CCM3 conditions, there will be more regions with suitable climate for *H. frenatus* and less for *H. mabouia* (Figure 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, in our scenario, would be situated on 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.

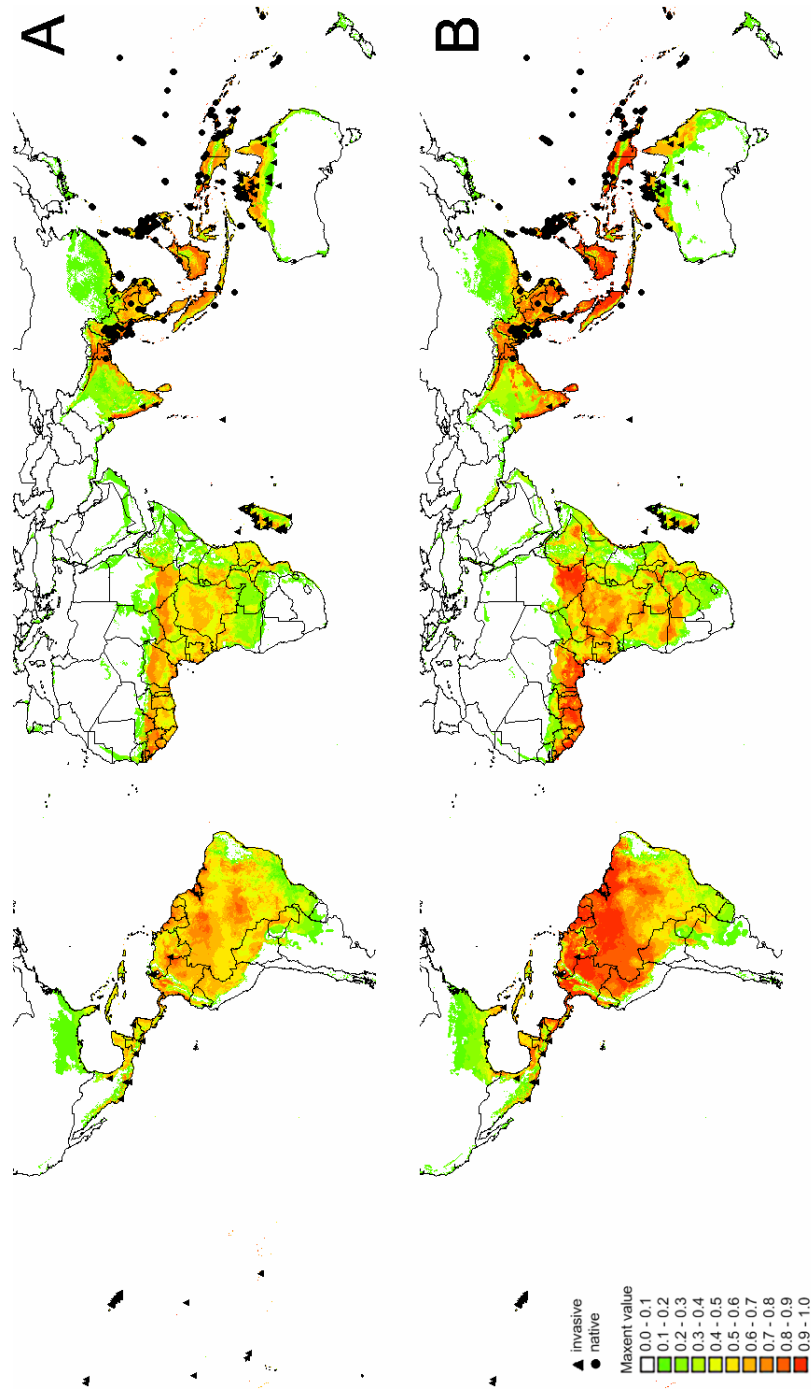


Figure 1. Predicted potential distribution for *Hemidactylus frenatus* under current (A) and future (B; CCM3) conditions. Higher Maxent values reflect a higher climatic suitability for the species.

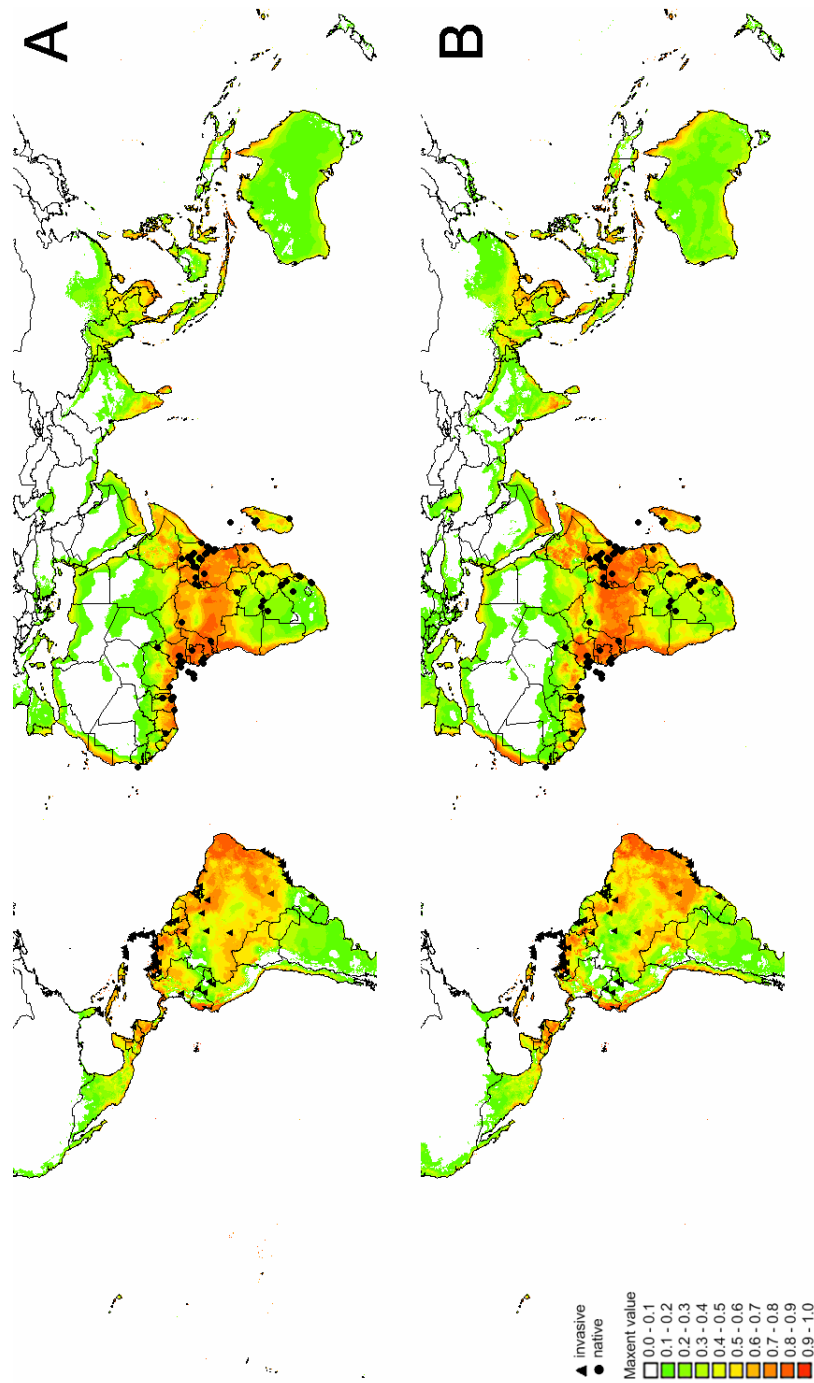


Figure 2. Predicted potential distribution for *Hemidactylus mabouia* under current (A) and future (B; CCM3) conditions. Higher Maxent values reflect a higher climatic suitability for the species.

On a global scale, a crosswise comparison between the Maxent probabilities at the localities 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*' localities under current conditions (Fig. 3). This difference was significant (Mann-Whitney-U test: $P = 0.046$). However, the climatic suitability for both of the species within their invasive ranges is much lower in crosswise comparisons than within the known ranges of each species (Fig. 3).

Discussion

Although there are differences in the 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 are obvious and it is surprising that they apparently only occasionally co-occur. *Hemidactylus frenatus* seems to be absent in Africa and large 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.

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

As a result of 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 shortly after World War II (Case et al. 1994). Its colonization success is very high; in 1971 it was absent in Vanuatu (Medway & 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 records from Australia, but from where it was reported by Gow (1981) and where it is common today (Fig. 1). The summary given by the authors supports the hypothesis that *H. frenatus* could be still spreading eastward from its native range. When it reached Central and South America remains unclear, but it has been suggested that the species was established in Venezuela more than 10 years ago (Fuenmayor et al. 2005). Recent dispersal is supported by genetic studies, since specimens of *H. frenatus* from Hawaii and Colombia are genetically identical (Carranza & Arnold 2006).

Time series illustrating the dispersal of *H. mabouia* in the Americas remain widely unknown. *Hemidactylus mabouia* was recorded in Curaçao in the late 1980's, in Bonaire around 2000, and 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 & Arnold 2006). In tropical America, recent records indicate that it is still spreading (e.g. Van Buurt 2006, Carranza & Arnold 2006, Fuenmayor et al. 2005).

We believe that, the hypothesis that these geckos are still spreading and simply not have reached their maximal distribution can only partly explain the apparent absence of *H. mabouia* in tropical Asia and the rarity of *H. frenatus* in South America. Both *H. frenatus* and *H. mabouia* were introduced to nearly all tropical regions including even the 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 of detecting them

and therefore enhance their chance of representation 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 & Petren 2006). Habitat features such as structure have an effect on successful competition (e.g. Petren & Case 1996), but ability for successful competition may be related to climatic suitability of a region too. Rather negative climatic conditions may cause environmental stress, which can reduce a species' fitness and its ability for successful competition.

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

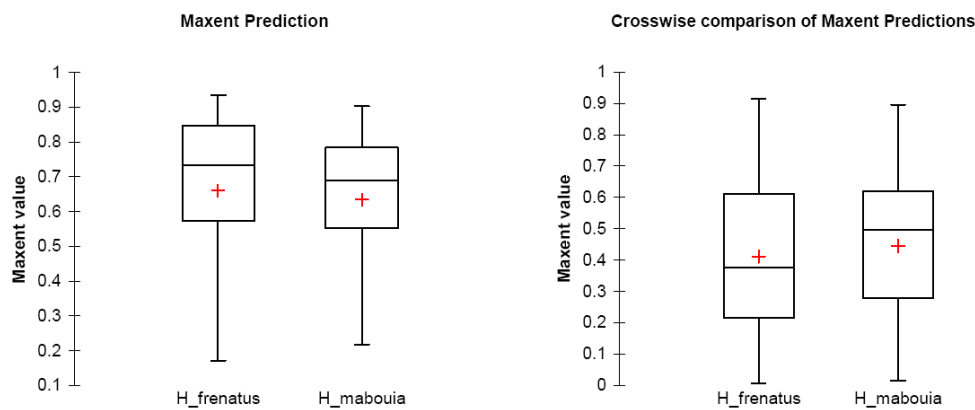


Figure 3. Maxent values at the records for each species (left) and crosswise comparison between the Maxent values per species record (right). For the crosswise comparison, Maxent values of one species were extracted at records where the other was found.

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 unconfirmed and requires further study. On a global scale, the crosswise comparison between the Maxent probabilities at the localities revealed that the climatic suitability for *H. frenatus* at *H. mabouia*'s localities is significantly higher than the climatic suitability for *H. mabouia* at *H. frenatus*' recorded localities (Fig. 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 (Fig. 3). The greater 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* in these regions.

Conclusions

We conclude that both competitive exclusion and non-equilibrium in the ranges of the species explain the virtual lack of sympatric populations, although the impact of climate on competitive success is uncertain pending further testing in the field. The increased climatic suitability for *H. frenatus* combined with the reduced suitability for *H. mabouia* within the Amazon basin and the Guiana Highlands in our future climatic scenario may alter the abundances of the species

here, which might provide an interesting possibility for field studies. Further research is needed to start understanding the dynamics of competitive exclusion, climate and competitive success.

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