

Article

Invasive house geckos (*hemidactylus* spp.): their current, potential and future distribution

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Received on 13 May 2017; accepted on 25 August 2017

Abstract

In this study, we identified the current distribution of five globally distributed invasive *Hemidactylus* species and predicted their potential and future distribution using species distribution models based on climate and elevation data. These species included *H. brookii*, *H. frenatus*, *H. garnotii*, *H. mabouia*, and *H. turcicus*. We show that many regions with tropical and Mediterranean climates are suitable for most of these species. However, their current and potential distributions suggest that climate is not the only limiting factor. We hypothesize that climatic conditions may affect competition and other interactions resulting in a segregated distribution of the studied *Hemidactylus* species. As an effect of global climate change it is likely that *H. brookii* will expand its range to areas that are currently colonized by *H. mabouia* and/or *H. frenatus*, while *H. turcicus* is likely to expand its range to areas that are not yet invaded by any *Hemidactylus* species. The role of species interactions in the range expansion of these five *Hemidactylus* species still remains poorly understood, but could be of major importance in understanding and managing these invasive species.

Key words: *Hemidactylus*, invasive species, species distribution modeling, climate change

Invasive species are a major cause of various environmental problems ranging from biodiversity loss to disrupted ecosystem services (Gurevitch and Padilla 2004; Butchart et al. 2010). In the United States alone invasive species are estimated to be responsible for an economic burden of \$120 billion annually related to, for example, pest control, crop damage, and loss of ecosystem services such as pollination (Pimentel et al. 2005; Cook et al. 2006). Invasive species are also considered to be a major threat to numerous threatened and endangered species (Gurevitch and Padilla 2004). Invasive herpetofauna are an important cause of the global decline in biodiversity. This becomes particularly evident when considering that species richness of these invasive species is much higher in biodiversity hotspots (Li et al. 2016). In addition, climate change may exacerbate these impacts because it affects both the establishment of new invasive species and the distribution of existing invasive species (Hellmann et al. 2008). However, these effects are species dependent; where some invasive species may thrive in a changing climate others may not. Species distribution models (SDM) are a useful tool to predict these effects by modeling the distribution of species under current and future climatic conditions (Jeschke and Strayer 2008).

Here, we investigate the distribution of five invasive gecko species from the genus *Hemidactylus*. Several species of house geckos from this genus belong to the world's most widely distributed and invasive lizards. The Asian house gecko *Hemidactylus frenatus*, for example, is not including central and south America, northern Australia as well as parts of Africa (Rödder et al. 2008). Other species such as the tropical house gecko *Hemidactylus mabouia* have also been introduced to many regions outside their native range (Rödder et al. 2008). The introduction of *Hemidactylus* species may lead to various problems to native lizard species through processes such as competition and the introduction of exotic parasites, ultimately leading to the decline of native species (Petren and Case 1996; Hoskin 2011). Another problem associated with *Hemidactylus* species is their fecal droppings, which can be a source of salmonella poisoning in people (Callaway et al. 2011).

Several *Hemidactylus* species are highly adapted to living in close proximity to people. They oftentimes feed on insects that are attracted to artificial light sources (Tkaczenco et al. 2014). Some *Hemidactylus* species are also known to forage in garbage bins and on tables where they feed on leftovers such as boiled rice (Weterings

2017). These highly opportunistic behaviors have contributed to their successful invasion of many regions. Due to living in close proximity to people, they get accidentally stowed away in boxes which are placed on boats, cars or trucks, allowing them to quickly disperse over large distances (Heinsohn 2003; Short and Petren 2011; Norval et al. 2012). Females of some species, such as, *H. frenatus* are able to store sperm for many months. Therefore, the species can reproduce easily in areas where it is newly introduced if environmental conditions are suitable (Murphy-Walker and Haley 1996). Individuals of *Hemidactylus* species arrive in many areas of the world, but not always manage to establish viable populations. For example, *Hemidactylus mabouia* has been found as stow-aways in several European countries such as the Netherlands¹ and Iceland². Climatic conditions at these locations are limiting the establishment of populations from these species. However, under a changing climate these conditions may become more favorable and certain species may be able to also establish in these regions.

The current study focused on the five most common and invasive *Hemidactylus* species; *H. brookii* Gray, 1845, *H. frenatus* Schlegel, 1836, *H. garnotii* Duméril and Bibron 1836, *H. mabouia* (Moreau de Jonnès, 1818), and *H. turcicus* (L., 1758). *Hemidactylus brookii*, *H. frenatus*, and *H. garnotii* are native to Asia and are genetically similar, belonging to the tropical Asian clade. *Hemidactylus mabouia* is native to Africa and belongs to the African Atlantic clade and *H. turcicus* is native to the Mediterranean and belongs to the Arid clade (Carranza and Arnold 2006; Bauer et al. 2010). *Hemidactylus brookii*, *H. frenatus* and *H. garnotii* are sympatric in their native range where *H. frenatus* is often the more dominant species of the three (Zug et al. 2007). *Hemidactylus mabouia* and *H. brookii* are sympatric in large parts of *H. mabouia*'s native range (Leaché 2005). *Hemidactylus frenatus*, and *H. mabouia* are sympatric in their invasive range in parts of the Americas (Krysko et al. 2003) as well as *H. garnotii* and *H. turcicus* (Meshaka Jr. 2000). Certain interactions between these different species may cause shifts in abundance. Interactions may include competition for food or space resulting in fighting or sexual interference (Frankenberg 1984; Dame and Petren 2006; Hoskin 2011). In certain parts of Florida, *H. turcicus* was one of the most common invasive *Hemidactylus* species (Meshaka Jr 1995). After introduction of the much larger *H. garnotii* [snout vent length: 49–66 mm versus 40–60 mm (Selcer 1986; Zug et al. 2007)] this species became slowly displaced, because *H. garnotii* has superior fighting abilities (Frankenberg 1984). In Florida and certain Pacific islands, however, *H. garnotii* on its turn is being displaced by the smaller *H. frenatus* [SVL: 42–59 mm (Zug et al. 2007)] and *H. mabouia* [(SVL: 40–61 mm, Meshaka Jr 1995; Dame and Petren 2006; Iturriaga and Marrero 2013]. Displacement by *H. frenatus* is thought to be caused by sexual interference, where the sexual *H. frenatus* appears to interfere with the asexual *H. garnotii* (Dame and Petren 2006). Interactions as such may have a strong effect on the distribution and population size of these highly invasive species and are important to take into consideration when evaluating possibilities to control spreading of invasive species and develop management strategies.

In this study, we aimed to 1) identify the current distribution of five globally distributed invasive *Hemidactylus* species and 2)

predict their potential and future distribution. We used historical occurrence data to map the current distribution and create species distribution models in order to predict their potential and future distribution. We discuss these results in the context of species interactions and how the distribution of one *Hemidactylus* species may affect the distribution of others.

Materials and Methods

Species occurrence

Species occurrence records for *H. brookii* ($n=4,150$), *H. frenatus* ($n=19,609$), *H. garnotii* ($n=1,659$), *H. mabouia* ($n=7,672$), and *H. turcicus* ($n=7,597$) were retrieved from the Global Biodiversity Information Facility (GBIF) database (2 January 2017; www.gbif.org). This database contains species records from museum collections and other published sources. These GBIF data were considered sufficient because of two reasons. First, the database contained a very large number of occurrences which very well approximates the known range of all five species. Second, the five focal species are often found in urban areas and residential situation and therefore easily observed. Thus, it is unlikely that areas where the species is common are not included in the data. In addition, *H. frenatus*, for example, is mostly found within the urban areas and less so in the natural habitat surrounding these urban areas (Newbery and Jones 2007). Therefore, we can safely assume that the occurrence records for *Hemidactylus* species in the GBIF database provide a sufficient base for distribution modelling. For the SDM, presence data were needed. Therefore, these records had to be cleaned and filtered in order to remove double records, records from the exact same location, and erroneous geo-referenced records.

First all records were geocoded using the described localities provided with each record. Records containing only country information were removed from the dataset. For all other records, the described localities were checked for inconsistencies and other features that might cause problems during the geocoding process. Inconsistent records were corrected where possible and otherwise deleted from the dataset. The localities were then geocoded using the Bing Maps API (Microsoft 2017). For all records that could not be correctly geocoded the localities were re-checked. At this stage, the most common problem was the usage of old colonial names in historical records such as “Batavia, Indonesia” instead of “Jakarta, Indonesia”. In these instances, the names were looked up using various internet resources and the current name was added to the record in order to re-geocode the given records.

After all records were geocoded the dataset was minimized to contain only one record per location for each species. These records were then overlaid with a map containing country boundaries using a geographical information system (ArcGIS 10.1; ESRI 2012). Based on this overlay, we removed records where the country code from the dataset did not correspond with those from the map. The final dataset contained a total of 6,404 records for *Hemidactylus brookii* ($n=720$), *H. frenatus* ($n=2,065$), *H. garnotii* ($n=359$), *H. mabouia* ($n=1,429$), and *H. turcicus* ($n=1,831$).

Species distribution modelling

We developed SDMs using both MaxEnt and ensemble models. MaxEnt stands for maximum entropy and is a modeling software specifically designed for SDMs (Phillips et al. 2006). MaxEnt allows the usage of presence-only data to model the probability of occurrence based on a species' environmental constraints. MaxEnt is a

- 1 Preserved specimen in the Natural History Museum Rotterdam. Specimen collected in 2001 in the Merwede Harbor, Rotterdam, Netherlands.
- 2 Preserved specimen in the Yale Peabody Museum of Natural History. Specimens collected in 2009 in Iceland.

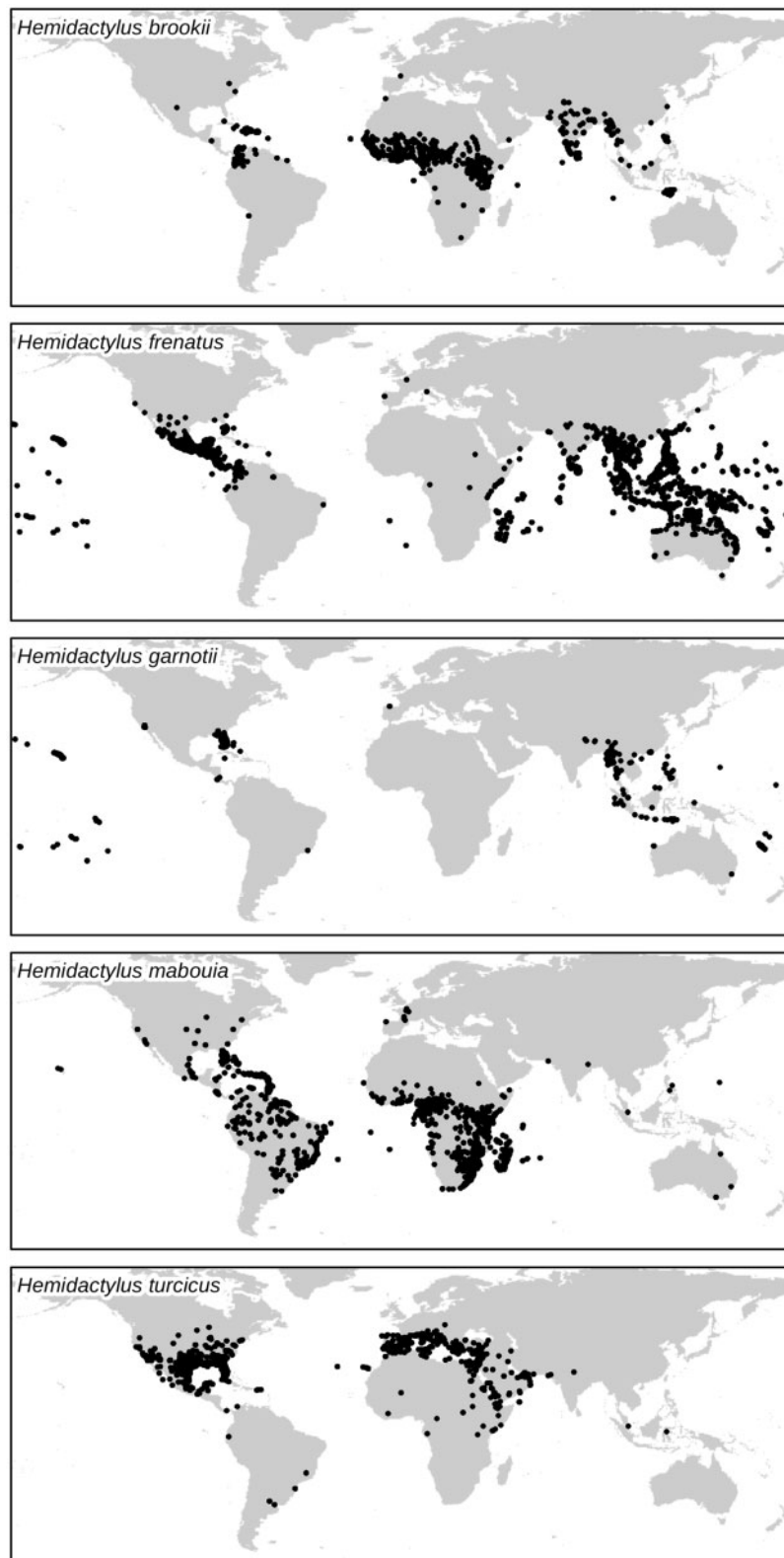


Figure 1. Current distribution of five *Hemidactylus* species. Each dot displays a location where one or more specimen was recorded. Some solitary dots in northern regions, show specimen that were discovered during transportation in, for example, freight containers and boxes. These records were not excluded because they display the potential of the species to spread to other regions.

Table 1. Co-occurrence of historical records for five *hemidactylus* species. Each row gives the percentage of occurrence records for a given species that co-occur with the species in each column. Where rows intersect with the column of the same species the percentage of occurrence records that do not co-occur with other species is given. When a species occurrence record was found in 0.5 degree (~55.5 km) grid cell with any of the other species it was considered to co-occur.

	<i>H. brookii</i> (%)	<i>H. frenatus</i> (%)	<i>H. garnotii</i> (%)	<i>H. mabouia</i> (%)	<i>H. turcicus</i> (%)
<i>H. brookii</i>	47.1	19.1	4.5	25.7	3.6
<i>H. frenatus</i>	9.5	66.4	11.1	7.8	5.1
<i>H. garnotii</i>	10.4	52.2	11.4	14.4	11.4
<i>H. mabouia</i>	17.5	10.7	4.2	61.7	5.8
<i>H. turcicus</i>	3.2	9.1	4.4	7.6	75.8

Table 2. Results from the distribution models for all five species. The upper part of the table gives the test statistics in which AUC stands for the Area Under the Curve. The lower part of the table gives the importance (%) of each model parameter for each species.

Species	<i>H. brookii</i>		<i>H. frenatus</i>		<i>H. garnotii</i>		<i>H. mabouia</i>		<i>H. turcicus</i>	
	MaxEnt	Ensemble	MaxEnt	Ensemble	MaxEnt	Ensemble	MaxEnt	Ensemble	MaxEnt	Ensemble
AUC test samples	0.902	0.954	0.885	0.964	0.966	0.990	0.902	0.965	0.904	0.974
Kappa		0.615		0.786		0.835		0.761		0.827
TSS		0.786		0.822		0.914		0.810		0.846
Number of training samples	612		1,756		306		1,215		1,557	
Number of test samples	108		309		53		214		274	
Permutation importance										
Mean temp.	9.4	11.5	7.4	29.3	8.1	19.9	12.2	38.1	53.2	32.1
Max temp. of hottest month	0.4	6.6	3.8	6.9	1.7	8.5	13.3	20.2	7.9	10.9
Min temp. of coldest month	76.3	57.4	57.5	33.2	29.5	18.9	47.8	24.2	16.0	14.9
Annual precipitation	5.2	8.7	10.1	2.4	19.7	8.7	9.1	4.9	8.5	15.3
Precipitation of driest month	2.9	5.2	0.5	1.1	4.8	6.3	3.3	2.9	1.6	6.6
Precipitation of hottest quarter	2.9	6.0	11.8	18.8	14.9	11.8	10.5	5.0	4.5	12.0
Elevation	2.9	4.6	8.9	8.2	21.3	26.0	3.6	4.6	8.2	8.2

very popular method for modeling presence-only data and has previously been used for modelling the distribution of *Hemidactylus* species (Rödder et al. 2008; Rödder and Lötters 2009; Kurita 2013).

For the ensemble models, we used the biomod2 library (Thuiller et al. 2009) for R 3.4.0 (R Development Core Team 2017). Ensemble models combine various algorithms to calculate an averaged model (Thuiller et al. 2009). We used only algorithms that allowed the usage of weights in order to incorporate sampling bias. These algorithms included: Generalized Linear Models (GLM), General Additive Models (GAM), Multiple Adaptive Regression Splines (MARS), Generalized Boosting Model (GBM), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), and Artificial Neural Networks (ANN). Individual models were only included in the ensemble model when the AUC score was higher than 0.8 and the TSS score higher than 0.7.

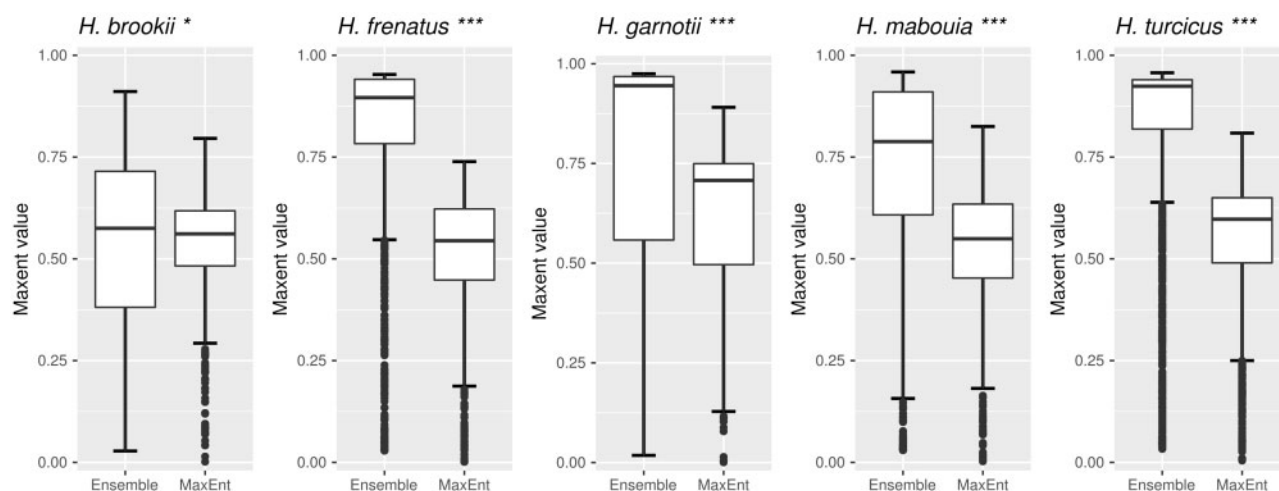
Both MaxEnt and ensemble models in this study used the previously described presence-only records and 10,000 random background points to develop models for the current and future probability of occurrence of the five invasive *Hemidactylus* species. The background points were used in the model to sample the density of covariates from the landscape (world) and compare these to those from the points where the species is known to be present (Elith et al. 2011). For both model types, we used 15% of randomly selected samples as test samples. Climatic niche shifts have been observed for non-native herpetofauna, therefore using only a species' native range for model fitting will result in a poor model (Li et al. 2014). Hence, we did not differentiate between a species native and non-native range within the models and thus included a species' complete

climatic range for both training and testing the models. The output of the models was maps showing the probability of occurrence for each species. Model fit was evaluated using the area under the curve (AUC) for both model types. The MaxEnt models were also assessed by comparing the omission rate with the predicted omission. While for the ensemble models we also assessed the TSS and Kappa statistics. An AUC value higher than 0.8 generally indicates a good model fit (Swets 1988), for the TSS and Kappa statistics values higher than 0.5 are generally considered good (Allouche et al. 2006).

An important and often overlooked issue with SDMs is sampling bias (Fourcade et al. 2014). Species occurrence data may be clustered around certain areas, which may over-represent and/or under-represent the species in a given locality and its environmental characteristics. For example, in the vicinity of a long-term ecological research station many samples may be collected over time while an adjacent area may not be sampled at all. These data might suggest that the species is more common around the research station while in fact the species could be equally distributed in both areas. A sampling bias as such may be particularly evident in species that are abundant in urban areas, which are readily accessible and highly populated. Such urban species may very well occur in natural habitats, but are simply sampled more often in urban areas. This sampling bias can be accounted for in MaxEnt using data that approximates the sampling bias. Within MaxEnt a bias file can be included, in which higher values indicate a higher bias. For ensemble models the sampling bias can be accounted for by using model weights in which records with higher weights are given more importance in the model. We calculated two different sets of values

Table 3. Total potential area per species for which Maxent values are 50% or higher. Area is given in million km².

Species	<i>H. brookii</i>	<i>H. frenatus</i>	<i>H. garnotii</i>	<i>H. mabouia</i>	<i>H. turcicus</i>
Current					
MaxEnt	15.4	7.5	1.7	7.3	6.3
Ensemble	9.6	26.1	1.6	17.5	14.6
RCP 2.6					
MaxEnt	22.5 (46%)	9.1 (22%)	1.4 (-17%)	4.3 (-41%)	6.8 (8%)
Ensemble	15.2 (58%)	25.3 (-3)	1.1 (-30%)	9.8 (-44%)	16.0 (10%)
RCP 4.5					
MaxEnt	24.1 (56%)	9.0 (21%)	1.4 (-19%)	3.6 (-51%)	6.8 (8%)
Ensemble	17.0 (76%)	26.0 (0%)	1.1 (-32%)	8.3 (-52%)	16.4 (12%)
RCP 6.0					
MaxEnt	23.8 (55%)	9.0 (20%)	1.4 (-19%)	3.7 (-49%)	6.8 (9%)
Ensemble	16.3 (69%)	25.9 (-1%)	1.1 (-32%)	9.1 (-48%)	16.1 (10%)
RCP 8.5					
MaxEnt	28.5 (85%)	8.6 (14%)	1.2 (-27%)	3.3 (-55%)	8.0 (27%)
Ensemble	18.8 (95%)	25.5 (-2%)	1.0 (-36%)	7.1 (-60%)	17.1 (17%)

**Figure 2.** Comparison of probabilities of occurrence for the MaxEnt models versus the ensemble models for all five *Hemidactylus* species. Differences between models were analysed using the Mann-whitney U-test. *P*-values < 0.05 are indicated with * and *P*-values < 0.001 are indicated with ***

that approximated the sampling bias. First, we calculated the density of sampling points using a density kernel (Fourcade et al. 2014) and second, we calculated the distance to urban areas and used this as our sampling bias. Urban areas were derived from global land cover data (~1 km spatial resolution) that were retrieved from the United States Geological Survey (http://landcover.usgs.gov/documents/GlobalLandCover_tif.zip), after which we calculated the distance to urban areas for each grid cell using the Euclidean Distance function in ArcGIS 10.1. These distance values were then inverted, giving urban areas the highest values and remote areas the lowest values. Using the bias correction based on the distance to urban areas resulted consistently in better models in comparison to the density kernel. Therefore, all MaxEnt models were fitted using the inverted distance to urban areas for correcting the sampling bias. In the ensemble models, the sampling bias can be accounted for by including weights. Lower weights give an occurrence records less importance in the model. Therefore, we did not use the inverted distance to urban areas but the actual distance.

Finally, we sampled the predicted probability of occurrence of one species on the location of all other species (Rodder et al. 2006),

for both the MaxEnt and ensemble model. This allowed us to assess how suitable these location are for the specific species, whether species are likely to co-occur and to quantify overlap in certain environmental conditions. Resulting values were compared using a Mann-Whitney U-test and plotted in a series of boxplots using RStudio (RStudio 2013) built on R 3.4.0 (Development Core Team 2017). We also sampled the probability of occurrence in order to compare predicted values for both model types. All plots were created using the ggplot2 package for R (Wickman 2009), while all maps were created using ArcGIS 10.1.

Environmental data

Environmental data that were used in the SDMs consisted of mapped so-called bioclim variables, which are available from <http://www.worldclim.org/>. Bioclim variables consist of a set of 19 variables that represent climatic variables that may be relevant to the biological and ecological characteristics of certain species; these data are based on the climate data developed by Hijmans et al. (2005). Six variables were selected based on 1) their ability to

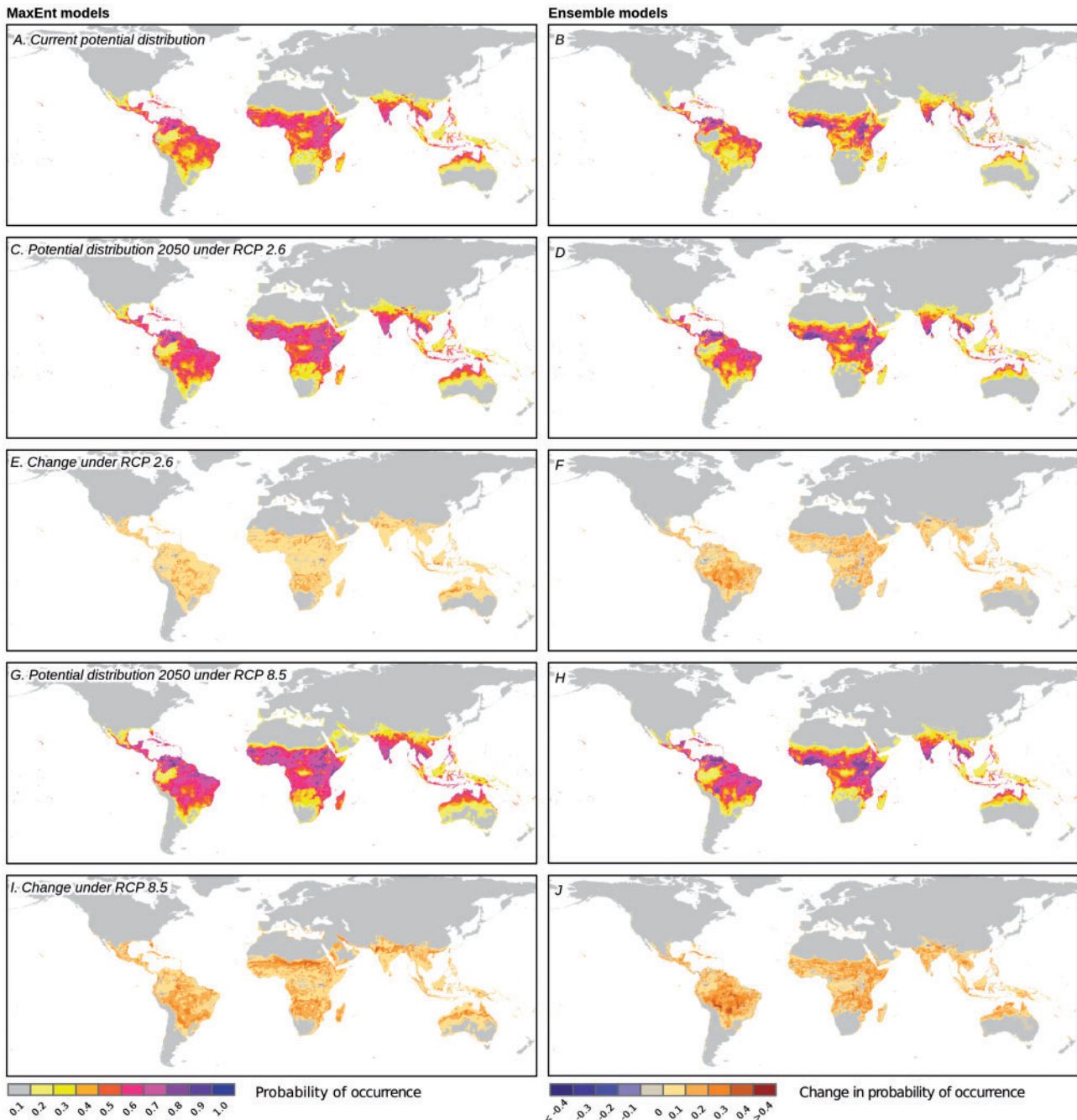


Figure 3. Results from the MaxEnt and ensemble models for *H. brookii* based on current climate conditions and projected for 2,050 using two representative concentrations pathways (RCP). (A) Current potential distribution for the MaxEnt and (B) the ensemble model. (C) Predicted potential distribution under RCP 2.6 for the MaxEnt model and (D) the ensemble model. (E) Change in probability of occurrence between the current and future potential distribution under RCP 2.6 for the MaxEnt model and (F) the ensemble model. (G) Predicted potential distribution under RCP 8.5 for the MaxEnt model and (H) the ensemble model. (I) Change in probability of occurrence between the current and future potential distribution under RCP 8.5 for the MaxEnt model and (J) the ensemble model. Potential distributions are given as the probability of occurrence.

represent the environmental limitations of *Hemidactylus* species and 2) their ability to conserve the climatic niche of a species. These variables included: annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of driest month, and precipitation of the warmest quarter (Rödger et al. 2008; Liu et al. 2017). Data with a spatial resolution of 5 arc minutes (~10 km) was used. In addition to climatic data, we also used elevation data as an

environmental predictor in our models. A world digital elevation model was downloaded from www.ngdc.noaa.gov/mgg/topo/globe.html. These data had a spatial resolution of 30 arc second (~1 km) and were resampled to the same resolution as the bioclim data using bilinear interpolation.

In order to predict changes in potential species distribution under a changing climate, we used bioclim variables predicted for the year 2050. These data were based on 11 CMIP5 climate

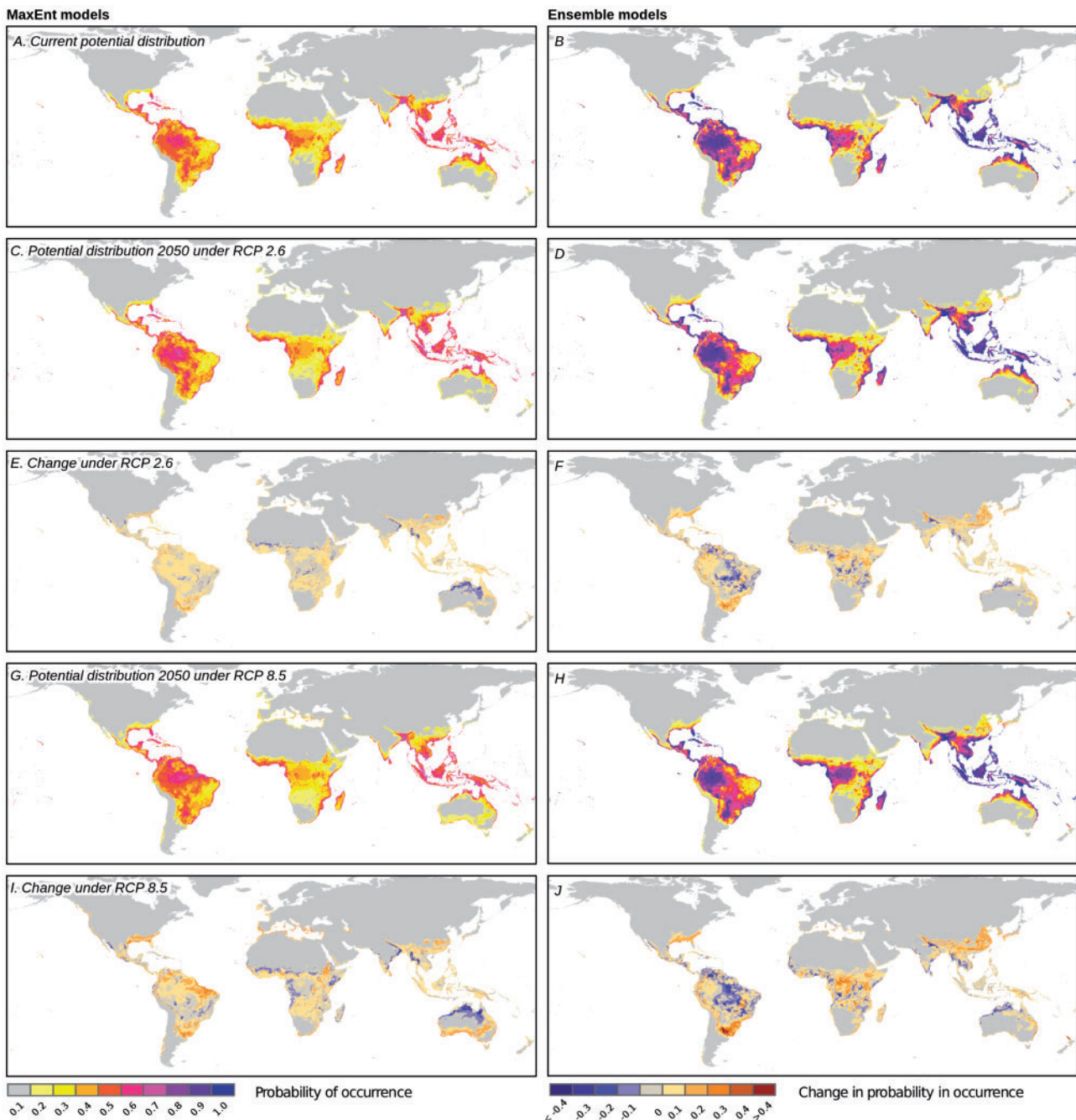


Figure 4. Results from the MaxEnt and ensemble models for *H. frenatus* based on current climate conditions and projected for 2050 using two representative concentrations pathways (RCP). (A) Current potential distribution for the MaxEnt and (B) the ensemble model. (C) Predicted potential distribution under RCP 2.6 for the MaxEnt model and (D) the ensemble model. (E) Change in probability of occurrence between the current and future potential distribution under RCP 2.6 for the MaxEnt model and (F) the ensemble model. (G) Predicted potential distribution under RCP 8.5 for the MaxEnt model and (H) the ensemble model. (I) Change in probability of occurrence between the current and future potential distribution under RCP 8.5 for the MaxEnt model and (J) the ensemble model. Potential distributions are given as the probability of occurrence.

models (BCC-CSM1-1, CCSM4, GISS-E2-R, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MRI-CGCM3, and NorESM1-M) for four representative concentration pathways (RCP 2.6, RCP 4.5, RCP 6, and RCP 8.5). Data from these models were resampled following Hijmans et al. (2005). We calculated the potential future distribution for each species based on all four RCPs for all 11 climate models. We then calculated the mean probability of occurrence for the

MaxEnt and ensemble models based on all climate models for each RCP.

Results

Historical records showed that our studied species are widely distributed with some species overlapping in certain areas while other areas are mainly occupied by single species (Figure 1). *Hemidactylus*

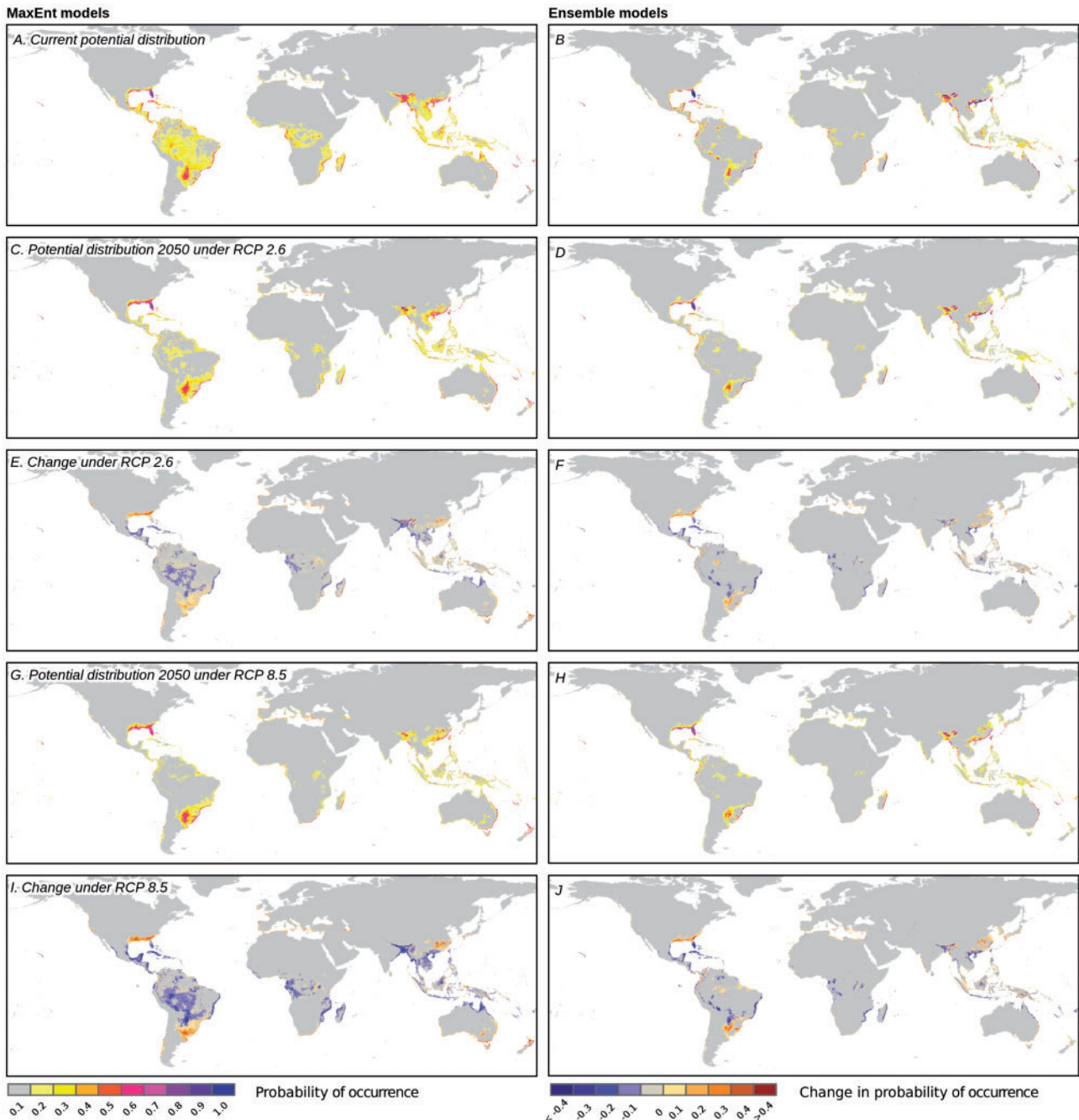


Figure 5. Results from the MaxEnt and ensemble models for *H. garnotii* based on current climate conditions and projected for 2,050 using two representative concentrations pathways (RCP). (A) Current potential distribution for the MaxEnt and (B) the ensemble model. (C) Predicted potential distribution under RCP 2.6 for the MaxEnt model and (D) the ensemble model. (E) Change in probability of occurrence between the current and future potential distribution under RCP 2.6 for the MaxEnt model and (F) the ensemble model. (G) Predicted potential distribution under RCP 8.5 for the MaxEnt model and (H) the ensemble model. (I) Change in probability of occurrence between the current and future potential distribution under RCP 8.5 for the MaxEnt model and (J) the ensemble model. Potential distributions are given as the probability of occurrence.

brookii is mostly found in south Asia, central Africa and northern parts of South America. *Hemidactylus frenatus* is mainly found in South East Asia, northern Australia, Madagascar, Central America, and many Pacific islands. *Hemidactylus garnotii* is mostly found in Southeast Asia, Florida, and various Pacific islands, *Hemidactylus mabouia* in central and southern Africa and in most parts of the

neotropics and *H. turcicus* is currently found in most of the Mediterranean region, Mexico, and the southern states of the United States. Most species showed little overlap in their actual distribution with the other species, with *H. garnotii* as an exception. In total, 74.9% of all occurrence records did not co-occur with any other species within a 0.5 degree (~55.5 km) sampling grid

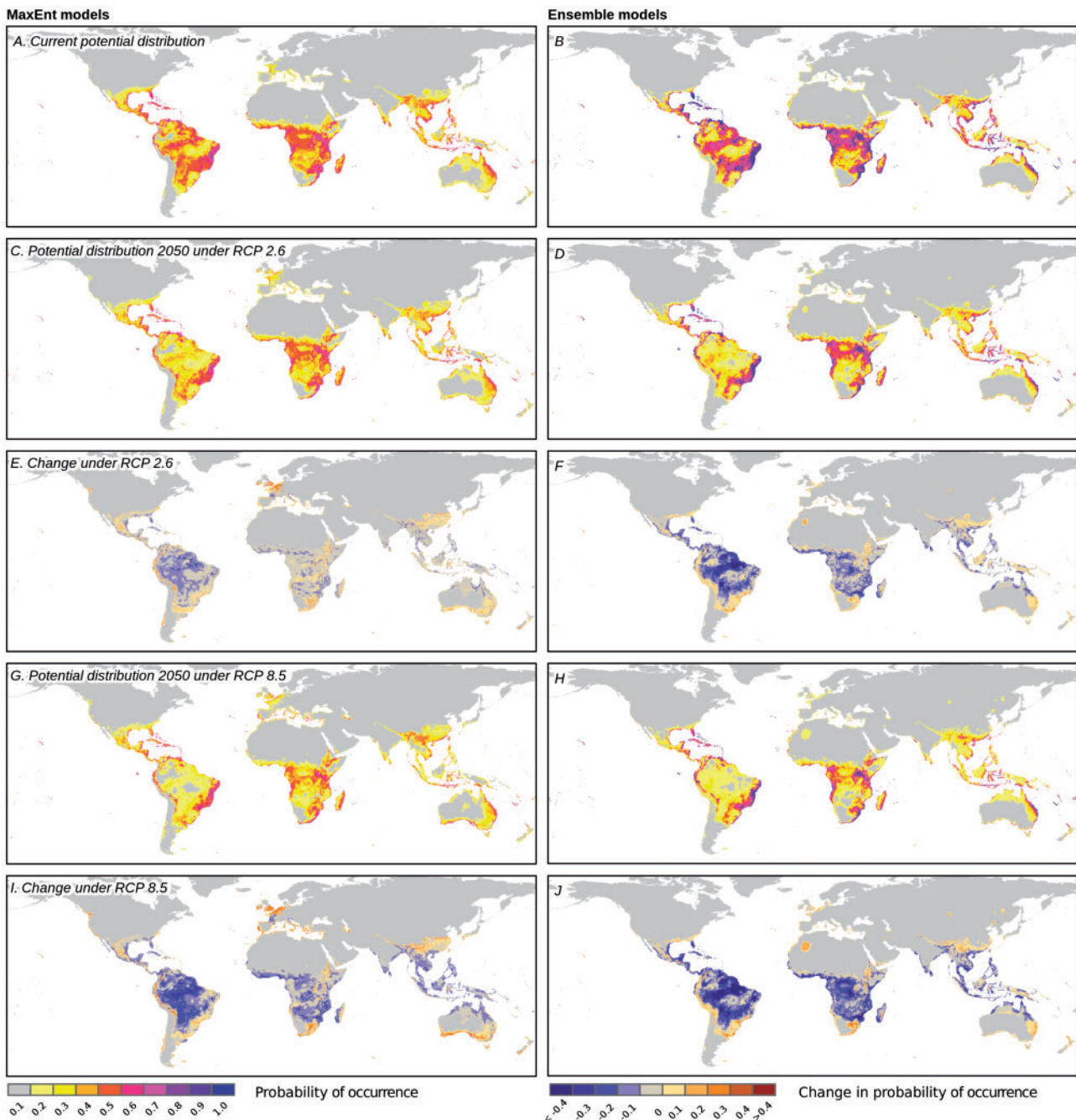


Figure 6. Results from the MaxEnt and ensemble models for *H. mabouia* based on current climate conditions and projected for 2050 using two representative concentrations pathways (RCP). (A) Current potential distribution for the MaxEnt and (B) the ensemble model. (C) Predicted potential distribution under RCP 2.6 for the MaxEnt model and (D) the ensemble model. (E) Change in probability of occurrence between the current and future potential distribution under RCP 2.6 for the MaxEnt model and (F) the ensemble model. (G) Predicted potential distribution under RCP 8.5 for the MaxEnt model and (H) the ensemble model. (I) Change in probability of occurrence between the current and future potential distribution under RCP 8.5 for the MaxEnt model and (J) the ensemble model. Potential distributions are given as the probability of occurrence.

(Table 1). *Hemidactylus turcicus* showed the least overlap in its known historical distribution with other species (24.2%), while *H. garnotii* was often recorded in grid cells where other species were recorded as well (88.6%). *Hemidactylus frenatus*, *H. mabouia*, and *H. brookii* co-occurred with other species in respectively, 33.7%, 38.3%, and 52.9% of the cases. The largest overlap was between *H. brookii* and *H. mabouia*, where the southern and northern edge of their historical distribution meet in Central

Africa and the Caribbean. Florida and Myanmar had the highest number of species being recorded within single grid cells. In Myanmar, these were three native species (*H. brookii*, *H. frenatus*, and *H. garnotii*), while in Florida these were four invasive species (*H. frenatus*, *H. garnotii*, *H. mabouia*, and *H. turcicus*).

Our models that predicted the potential distribution performed well, with both the MaxEnt and ensemble models having AUC values higher than 0.88 (Table 2). The ensemble model for *H. brookii*

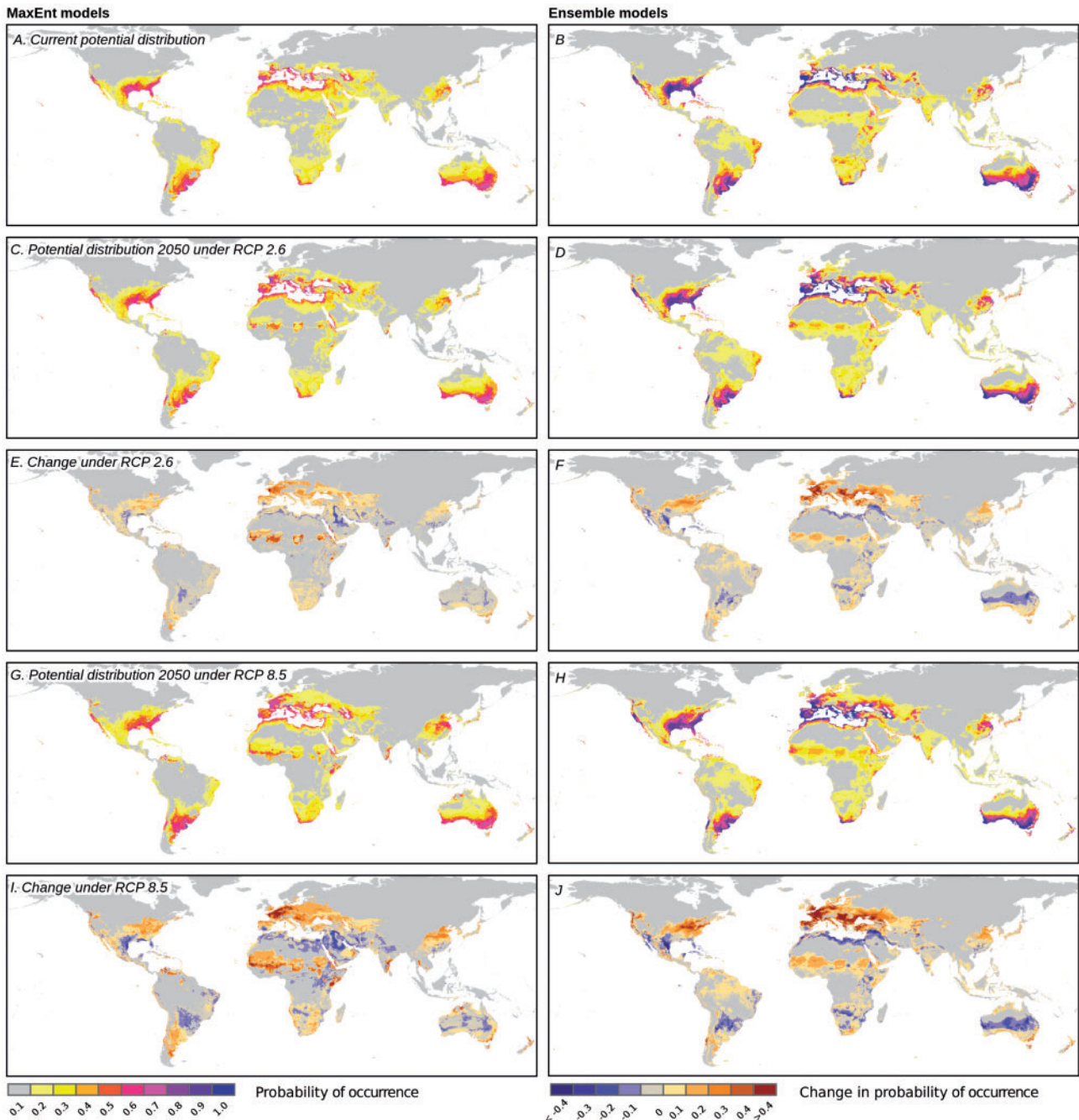


Figure 7. Results from the MaxEnt and ensemble models for *H. turcicus* based on current climate conditions and projected for 2050 using two representative concentrations pathways (RCP). (A) Current potential distribution for the MaxEnt and (B) the ensemble model. (C) Predicted potential distribution under RCP 2.6 for the MaxEnt model and (D) the ensemble model. (E) Change in probability of occurrence between the current and future potential distribution under RCP 2.6 for the MaxEnt model and (F) the ensemble model. (G) Predicted potential distribution under RCP 8.5 for the MaxEnt model and (H) the ensemble model. (I) Change in probability of occurrence between the current and future potential distribution under RCP 8.5 for the MaxEnt model and (J) the ensemble model. Potential distributions are given as the probability of occurrence.

had a lower kappa statistic (0.615) than all other ensemble models but this was still within the acceptable range. In general, ensemble models resulted in larger areas that are considered suitable in comparison to MaxEnt models (Table 3). Probabilities sampled at the location of the occurrence records also showed significant higher probabilities given by ensemble models in comparison to MaxEnt models (Figure 2). Although probabilities were generally higher for

ensemble models, the general extent of the predicted potential distribution and predicted changes as an effect of climate change were similar for both model types except for *H. frenatus* models (Figures 3–7, Table 3). MaxEnt models predicted an increase in *H. frenatus*' potential distribution, while the ensemble models predicted a very small decrease. Nevertheless, the increase predicted by the MaxEnt model was mostly within regions also considered

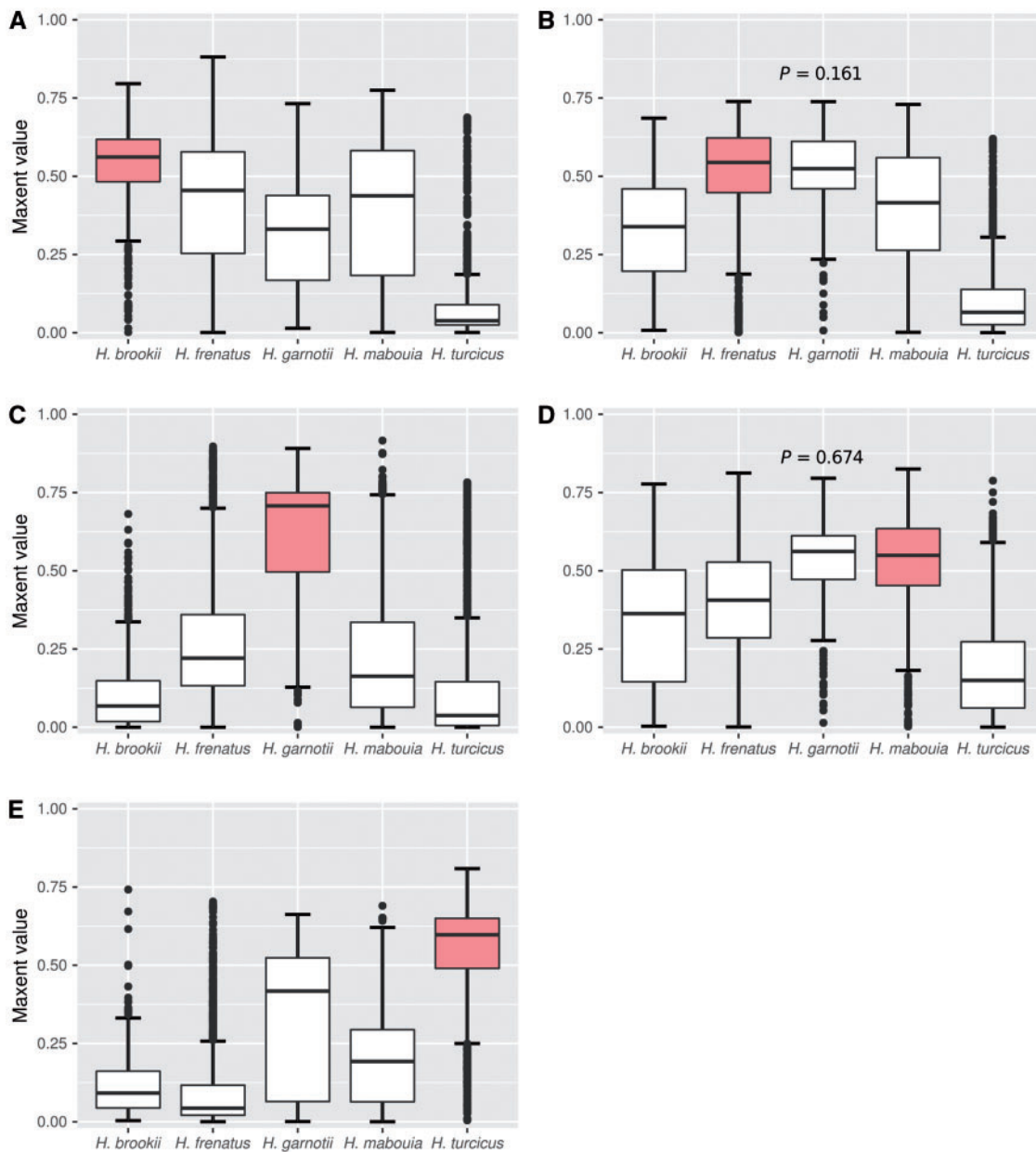


Figure 8. Comparison of probability of occurrence from MaxEnt models for each *Hemidactylus* species on locations of occurrence records for (A) *H. brookii*, (B) *H. frenatus*, (C) *H. garnotii*, (D) *H. mabouia*, and (E) *H. turcicus*. *P*-values are given for each species when compared to the focal species (red box). If differences are non-significant a given species' probability of occurrence is similar on locations where the focal species (red box) occurred.

suitable by the ensemble model. The minimum temperature of the coldest month proved to be the most important variable for all species except for *H. turcicus* (Table 2). *Hemidactylus turcicus*' distribution was better explained by annual temperature. Annual precipitation was more important in the *H. garnotii* model in comparison with other species. Elevation was also more important for *H. garnotii*.

For *H. brookii* the total area, with a probability of occurrence higher than 0.5, was 1.6 times higher for the MaxEnt model in comparison to the ensemble model. This species had the largest potential distribution following the MaxEnt model but not for the ensemble model. In both models, the minimum temperature of the coldest month was the most important predictor followed by the mean

temperature. Both models predicted a strong increase in suitable area under all four climate change scenarios. The area increase ranged from 46% to 58% under RCP 2.6 and 85% to 95% under RCP 8.5 in large parts of South and Central America as well as Central Africa. The historical distribution of *H. brookii* was mostly concentrated in Sub-Saharan Africa, India, Myanmar, Colombia, and various islands of the Caribbean. The potential distribution, however, also covered large parts of tropical South and Central America.

Hemidactylus frenatus had the largest potential distribution (probability of occurrence > 0.50) for the ensemble model, which was 3.5 times higher than for the MaxEnt model. In both the MaxEnt and ensemble models, the minimum temperature of the

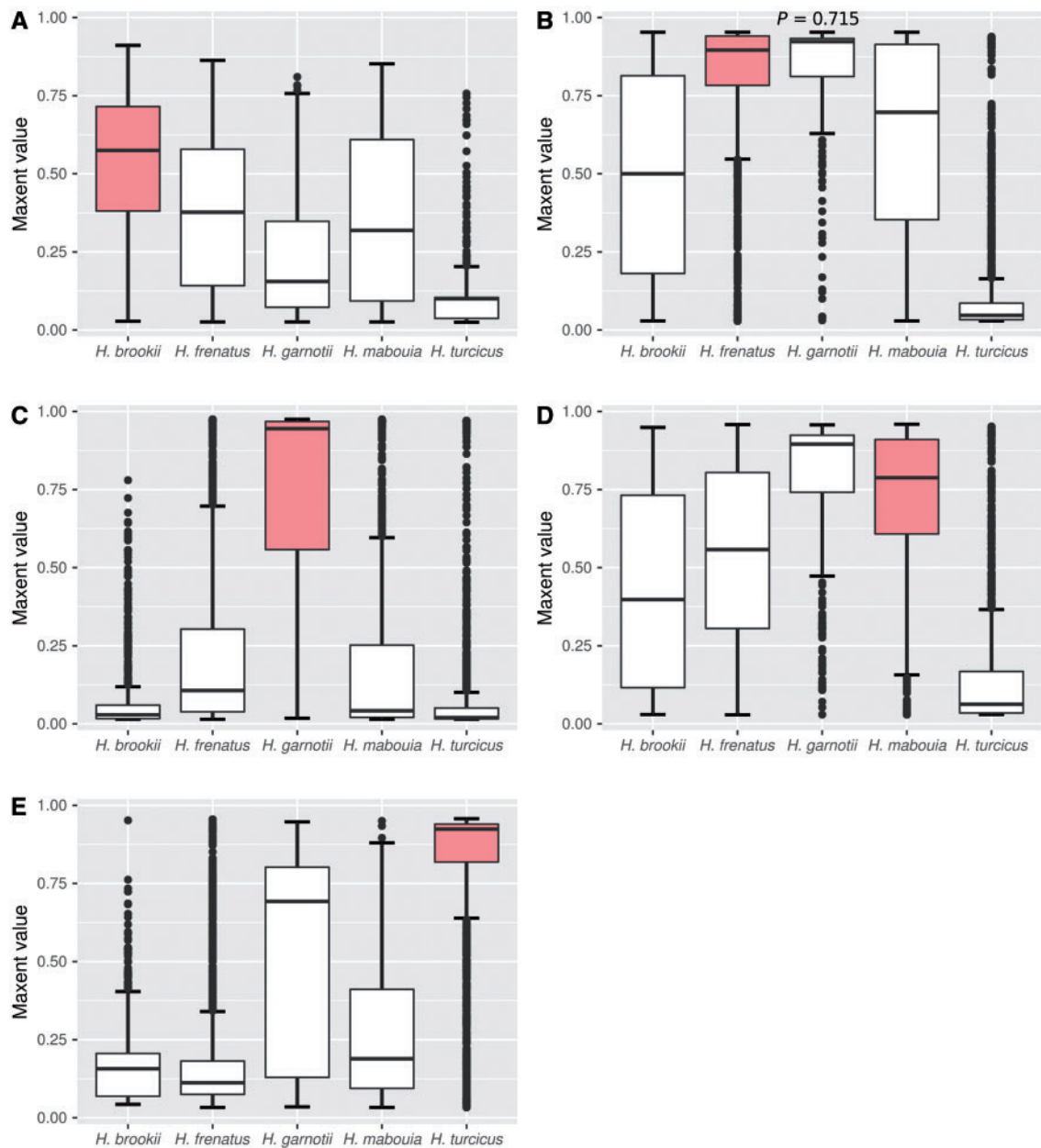


Figure 9. Comparison of probability of occurrence from ensemble models for each *Hemidactylus* species on locations of occurrence records for (A) *H. brookii*, (B) *H. frenatus*, (C) *H. garnotii*, (D) *H. mabouia*, and (E) *H. turcicus*. *P*-values are given for each species when compared to the focal species (red box). If differences are non-significant a given species' probability of occurrence is similar on locations where the focal species (red box) occurred.

coldest month was the most important variable. The mean temperature was also important in the ensemble model but not in the MaxEnt model. Precipitation of the hottest quarter was important in both models, although higher in the ensemble model. The historical distribution showed that *H. frenatus* was mostly concentrated in South East Asia, Northern Australia, Madagascar, Central America, Pacific islands, and Columbia. The potential distribution also covered parts of Central Africa, East Coast of Africa, and the Amazon. Under a changing climate, the probability of occurrence was predicted to decline in much of its current invasive range, but will expand outwards from the equator into new territories such as South Australia and the Gulf Coast of the United States.

Hemidactylus garnotii showed the smallest potential distribution for both models. In both models, elevation was an important variable as well as the minimum temperature of the coldest month. In the MaxEnt model, precipitation played a major role as well (annual precipitation and precipitation of hottest quarter), while in the ensemble model the mean temperature was important. The historical distribution showed that *H. garnotii* is mostly restricted to South East Asia, Florida, and Pacific islands. The potential distribution did not deviate much from the historical distribution except for the Pampas (lowland Argentina and Uruguay). Both models predicted a decline ranging between 17% to 30% for RCP 2.6 and 27% to 36% for RCP 8.5. Under these climate-change scenarios, *H. garnotii*'s

Table 4. Area covered by individual species and species groups relative to the total global area for which the probability was higher than 50% for at least one species. Species groups which covered less than 1% of the total area are excluded from the table. Results are given for all five focal *hemidactylus* species.

Species (groups)	Current		RCP 2.6		RCP 8.5	
	MaxEnt (%)	Ensemble (%)	MaxEnt (%)	Ensemble (%)	MaxEnt (%)	Ensemble (%)
<i>H. brookii</i>	35.3	9.4	46.7	13.6	53.6	17.5
<i>H. turcicus</i>	20.2	39.2	17.2	29.6	16.8	29.7
<i>H. frenatus</i>	11.5	31.8	11.5	26.0	6.5	25.5
<i>H. brookii</i> and <i>H. frenatus</i>	4.7	5.0	9.3	9.6	11.7	12.1
<i>H. frenatus</i> and <i>H. mabouia</i>	1.3	24.8	0.4	7.5	0.1	4.2
<i>H. mabouia</i>	8.7	8.9	3.4	3.0	2.1	2.0
<i>H. brookii</i> , <i>H. frenatus</i> and <i>H. mabouia</i>	4.7	8.9	2.8	4.2	1.3	3.2
<i>H. brookii</i> and <i>H. mabouia</i>	7.5	3.9	4.3	2.5	3.1	2.1

native range was predicted to become less suitable, but parts of the Gulf Coast of the United States, the Pampas, and New Zealand's North Island are predicted to become more suitable.

The ensemble model for *H. mabouia* showed a 2.4 times larger potential area (probability of occurrence > 0.5) than the MaxEnt model. The minimum temperature of the coldest month was most important in the MaxEnt model, for the ensemble model this was the mean temperature followed by the minimum temperature of the coldest month. The historical distribution showed that the species is mostly concentrated in East and West Africa, tropical South America, and the Caribbean. The potential distribution also shows suitable areas in South East Asia and East Coast Australia. Under a changing climate the potential distribution was predicted to reduce with 41% to 44% under RCP 2.6 and by 55% to 60% under RCP 8.5. This decrease will cover most of its current potential range.

The ensemble model for *H. turcicus* also returned a larger suitable area than the MaxEnt model. The ensemble model resulted in a 2.3 times larger area (probability of occurrence > 0.5) than the MaxEnt model. In both models, the mean temperature was the most important variable followed by the minimum temperature of the coldest month for the MaxEnt model and annual precipitation and minimum temperature of the coldest month respectively for the ensemble model. Along the coastal areas of its current potential distribution, climatic conditions appear to become slightly more suitable. The historical distribution showed that the species is mostly found not only in arid and generally colder regions such as its native range surrounding the Mediterranean Sea and in its invasive range in the American Mid-West and California but also in Florida. The models also showed that its potential range extends to other areas such as the arid regions of Argentina, South Africa, and South Australia. Both models showed that the area of its potential distribution will increase from 8% to 10% under RCP 2.6 and from 17% to 27% under RCP 8.5. The distribution will mostly increase along the northern border of its current distribution within the northern hemisphere and along the southern border within in the southern hemisphere, while the suitability decreases in large parts of central Australia, the African Mediterranean coast, and along the Gulf Coast of the United States.

Conditions for *H. brookii* on locations where *H. frenatus* and *H. mabouia* were recorded were generally slightly less suitable, but for *H. garnotii* and *H. turcicus* locations the conditions were unsuitable (Figures 8 and 9). Conditions for *H. frenatus* and *H. mabouia* were equally suitable at locations where *H. garnotii* was recorded. Conditions for *H. garnotii* were highly unsuitable on most locations

were all other species were recorded. For *H. turcicus*, the conditions were also unsuitable where other species were sampled but were slightly better on *H. garnotii* sites. The MaxEnt models showed that from all species the potential area for *H. brookii* covered the largest area that was not suitable (probability < 0.5) for any other species followed by *H. turcicus* (Table 4). For the ensemble models, the largest area that was only suitable for one species was for *H. turcicus* followed by *H. frenatus*. Both models also showed that the potential distribution of *H. brookii* and *H. frenatus* covered large areas that were suitable for both species. The ensemble models also showed that large areas were suitable for both *H. frenatus* and *H. mabouia*.

Discussion

Our study showed that most of the focal species have already invaded large parts of their potential distribution, but do not cover all areas that are potentially suitable. Large areas suitable for *H. brookii* and *H. frenatus* in South America are not colonized by these species yet. In Continental Africa, *H. frenatus* is mostly absent, while climatic conditions are favourable. Most of these areas that are highly suitable for one or more species but have not yet been colonized by these species often contain other well established species. Areas where *H. brookii* or *H. frenatus* is absent are often colonized by *H. mabouia* and vice versa. For example, in Suriname (South America) *H. mabouia* is the most commonly distributed species (Nielsen et al. 2013), even though this area is also highly suitable for *H. brookii* and *H. frenatus*. In Ghana on the other hand, areas that are highly suitable for *H. mabouia* and *H. frenatus* are dominated by *H. brookii* (Leaché 2005). This segregated distribution of these species may have several causes. First, certain species have not yet been introduced to these areas. However, this is unlikely considering the wide scale of anthropogenic introduction of these species over the last few centuries. Second, certain species are better competitors under certain environmental conditions than other species (Rödger et al. 2008). When environmental conditions are more favorable for a given species their fitness increases, giving the species a competitive advantage over the other species. While under slightly different environmental conditions the competitive advantage may shift towards the other species. For example, in the native range of *H. brookii* and *H. frenatus* the tokay gecko (*Gekko gecko*) is an important predator of house geckos (personal observations). Behavioral differences may affect the rate on which house geckos are preyed upon and this may strongly affect community structure

(Abrams and Matsuda 1993; Schmitz 2005). In the absence of this predator other species specific traits may favor *H. brookii* instead.

As an effect of climate change, regions that are suitable for *H. brookii*, *H. frenatus*, and *H. turcicus* will increase. The SDMs showed that *H. brookii* and *H. turcicus* have the highest tolerance to extreme temperatures. *Hemidactylus turcicus* can tolerate colder temperatures than the other *Hemidactylus* species (Huey et al. 1989). *Hemidactylus brookii* seems to tolerate higher temperatures than the other species. This gives these two species the advantage that allows them to expand their range into regions that are less suitable to other species. An increase in suitable area does not necessarily mean that these species will occupy these areas in the near future. *Hemidactylus* species do not easily disperse over large distances by themselves, therefore, dispersal is very much restricted to human mediation. In Florida, *H. mabouia* has been shown to be genetically homogeneous across the state, indicating that human-mediated dispersal is frequent (Short and Petren 2011). However, on a global scale, Short and Petren (2011) showed that human-mediated dispersal is less common. *Hemidactylus* species are often found in and on cars by which they easily disperse long distances by road (Norval et al. 2012). Hence, regions in which humans move easily over large distances by road are therefore likely to become more quickly invaded by *Hemidactylus* species than regions that are more isolated. For example, *H. brookii* is now widely spread in Sub-Saharan Africa and is likely to extend its range further south into areas currently dominated by *H. mabouia* for which the environmental suitability will strongly decrease. However, in South America *H. brookii* is less widely established and the decrease in suitable area for *H. mabouia* does not necessarily mean *H. brookii* can easily occupy these regions. Currently, *H. brookii* is only present north of the Amazons, where the Amazons form a barrier and hinder easy dispersal mediated by anthropogenic activities. However, vast deforestation of the Amazons will increase trans-Amazon human movement and eventually this will mediate the dispersal of *H. brookii* into larger parts of South America as well.

Under a changing climate, *H. turcicus* is likely to expand its distribution vastly throughout North America and Europe. In these regions, human mobility is high (Hawelka et al. 2014) and a lack of natural barriers will easily facilitate the dispersal of this species. In Australia, where the species is absent but the environment is highly suitable, the species is likely to remain absent due to very strict biosecurity regulations (Nelson et al. 2014). However, if the species does establish in Australia it will likely become more widespread than the already present invasive *H. frenatus*.

The distribution of *H. garnotii* shows a tendency to decline in much of its native range. However, along the Gulf Coast of the United States, the climate will become more suitable, here the species is likely to replace *H. turcicus*. *H. garnotii*, is stronger in fights and currently already replaces *H. turcicus* in Florida due to this competitive advantage (Frankenberg 1984; Meshaka Jr 1995). However, this same region will also become more suitable for *H. frenatus*. This species is already well established in the south of Florida and is likely to spread along the coast facilitated by the high mobility of people. In areas where *H. garnotii* and *H. frenatus* co-occur, the smaller *H. frenatus* manages to suppress *H. garnotii* through sexual interference (Dame and Petren 2006). Hence, it is likely that in due time, populations of *H. garnotii* will also become smaller in this region. In addition our models showed that *Hemidactylus garnotii* is mostly restricted to lowland areas, which pose a barrier to further increase its distribution (Zug et al. 2007).

Similar to other studies in which both MaxEnt and ensemble models were used, our ensemble models generally tended to have higher probabilities of occurrence on the locations of the historical occurrence records in comparison to the MaxEnt models (Simpson et al. 2011; Baier et al. 2014; Ihlow et al. 2016; Ashraf et al. 2017). This often results in larger areas that are suitable for a given species (Simpson et al. 2011; Ihlow et al. 2016; Ashraf et al. 2017). Ensemble models tend to be more accurate for modeling the current distribution but perform less outside the range where occurrence data are sampled (Ashraf et al. 2017). While on the other hand, MaxEnt models have a higher predictive performance (Elith and Leathwick 2009).

In conclusion, as an effect of global climate change it is likely that *H. brookii* will expand its range to areas that are currently colonized by *H. mabouia* and/or *H. frenatus*. As these areas are already invaded by other *Hemidactylus* species it is likely that the expansion of *H. brookii* will only have minimal ecological impact on these areas. Of greater concern is the species *H. turcicus*, which is likely to expand its range to areas that are not yet invaded by any *Hemidactylus* species. More research is needed to elucidate the effects of climate change on interspecies interactions. Especially interactions between *H. brookii* and *H. frenatus* are important because the overlap in suitable area of these two species will double. The effects of interspecies interactions may severely affect the distribution of *Hemidactylus* species. Knowledge about these mechanisms may also provide further insight in the impacts of climate change on ecological systems in context of species distributions and territory expansion.

Funding

This study was funded by the Cat Drop Foundation.

Acknowledgments

We would like to thank the anonymous reviewers for their constructive comments that have helped to substantially improve the article.

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