North-Western Journal of Zoology
P-ISSN: 1584-9074, E-ISSN: 1843-5629

Vol. 5, No. 1, 2009, pp.16-25
Article No.: 051103

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

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Abstract. The alien invasive anuran *Eleutherodactylus coqui* is presently distributed in many Caribbean islands and Hawaiian Islands where it causes major ecological and socioeconomic problems, especially evident in the later. Here, I use a maximum entropy ecological niche modeling approach to model the native geographic distribution of this species and to project that model into other potentially threatened areas. The projection results under current climatic conditions suggested high probabilities of occurrence in tropical regions including the Caribbean, Florida, major parts of the Amazon basin and adjacent Andes, the Pantepui region, the Congo basin, and most Asian islands. Projections of potential distributions under future anthropogenic global warming scenarios within the Hawaiian Islands suggest an overall stable potential distribution, but fine scale patterns suggest a possible range allocation towards higher elevations which may affect natural reserves. 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.

Key words: Climate Envelope, Ecological Niche Modelling, Exotic species, Maxent, Worldclim

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 & Campbell 2002). This species is a small (33-57 mm), brown or gray-brown, arboreal frog, which has been accidently 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 & Woolbright 1995). *Eleutherodactylus coqui* utilize internal fertilization and fertilized eggs undergo direct development making them independent from stagnant water (Townsend & 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 & 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 & 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). The diet of *E. coqui* 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 & 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 & 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 non-indigenous feral populations, as reported for the Bahamas (Kairo et al. 2003), Culebra and Vieques (Joglar 1998, Joglar & Rios-López 1998), the Dominican Republic (Campbell 2000), Maui, the Island of Hawaii, Kauai, Oahu (Kraus et al. 1999), the Galapagos Islands (Snell & 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 & 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 & Campbell 2002, Kraus et al. 1999). Residents are encountering reduced property values and increased difficulty selling property (Kraus & 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 & 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 Mayor of Hilo declared a state of emergency as a result of the coqui situation due to '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 & 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 potential for coqui invasions and (ii) possible changes within its current range as an invasive species in Hawaii by 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 & Graham 2006, Peterson & Nyári 2007, Carnaval & Moritz 2008, Malcom et al. 2006). 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 & Graham 2005; but see also Pearman et al. 2007). Herein, Maxent 3.2.1 (Phillips et al. 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 a 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; Hutchinson 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 green-house 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 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. 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 & McNeil 1982, Phillips et al. 2006). This method is recommended for ecological applications because it is non-parametric (Pearce & 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 (Fig. 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 (Fig. 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 (Fig. 3). These areas are highly overlapping with urban areas, whereas the species finds proportionally less suitable areas within reserves (Fig. 4).

Projections of the CEM of *E. coqui* onto the future climate change scenarios revealed that, overall, the amount of suitable grid cells remain roughly stable (i.e. changes are less than 10 % relative to current conditions) 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

Table 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 %

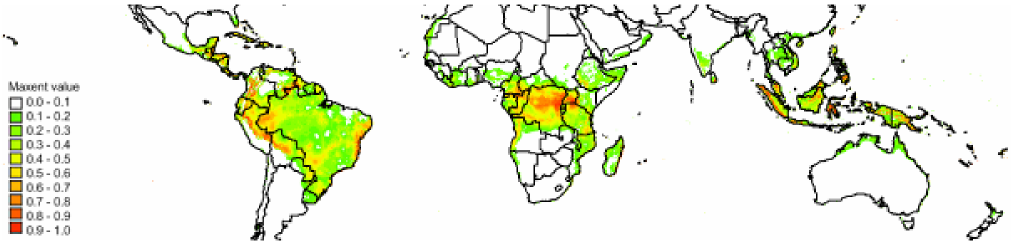

Figure 1. Potential distribution of *Eleutherodactylus coqui* under current climate conditions. Higher Maxent values suggest higher climatic suitability.

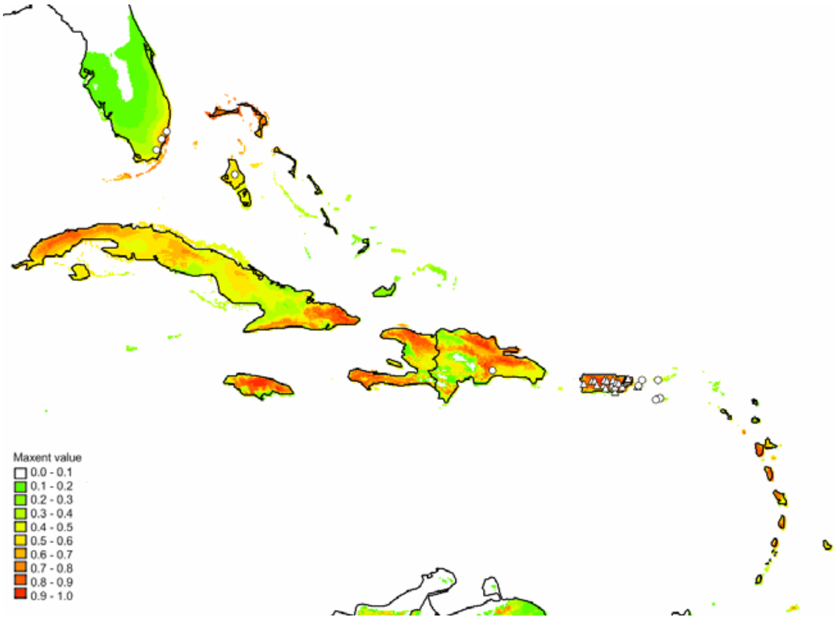

Figure 2. Potential distribution of *Eleutherodactylus coqui* under current climate conditions within the Caribbean. Higher Maxent values suggest higher climatic suitability. Native records are indicated as triangles and invasive as points.

(Figs 5-6). 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 patterns on the smaller islands Oahu and Kauai remain roughly stable.

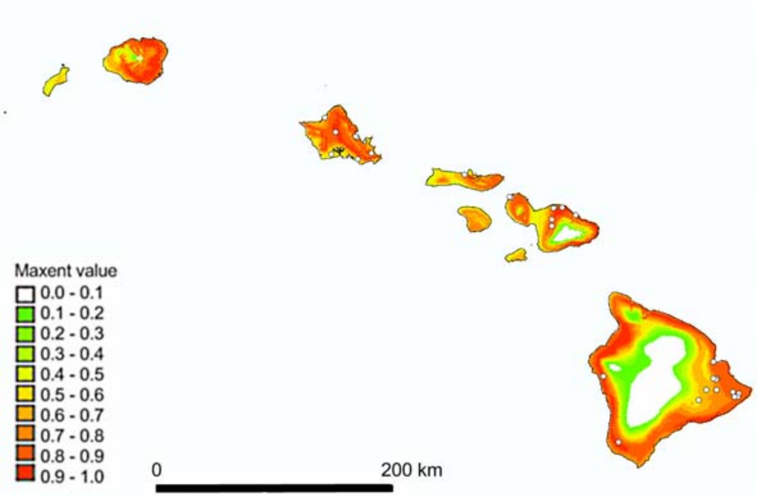

Figure 3. Potential distribution of *Eleutherodactylus coqui* under current climate conditions within Hawaii. Higher Maxent values suggest higher climatic suitability. Invasive records are indicated as points.

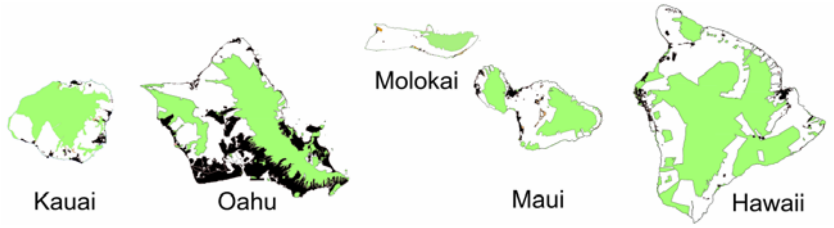

Figure 4. Land use patterns on the major Hawaiian Islands in 2007. Urban areas are indicated in black and reserves in green. Source: Land Use Commission of the State of Hawaii.

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, many of which are also ecologically similar (Hedges et al. 2008). This would most likely make a successful establishment *E. coqui* difficult. However, care needs 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 & Pitt 2006, Woolbright

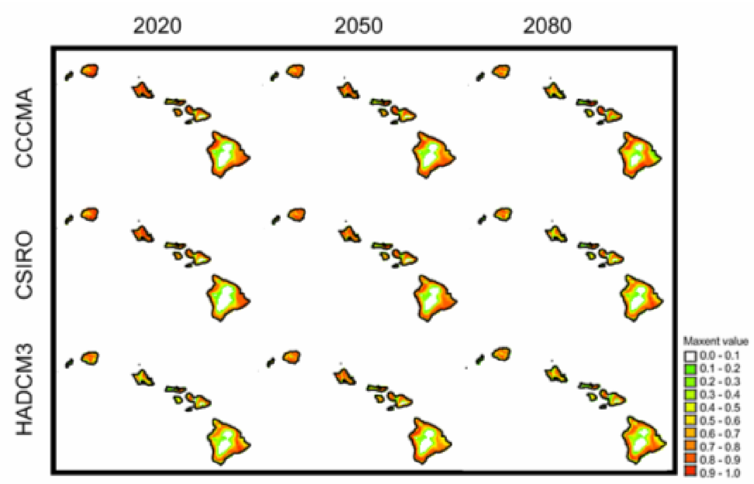

Figure 5. Potential distribution of *Eleutherodactylus coqui* under future climate change scenarios assuming A2a conditions. Higher Maxent values suggest higher climatic suitability.

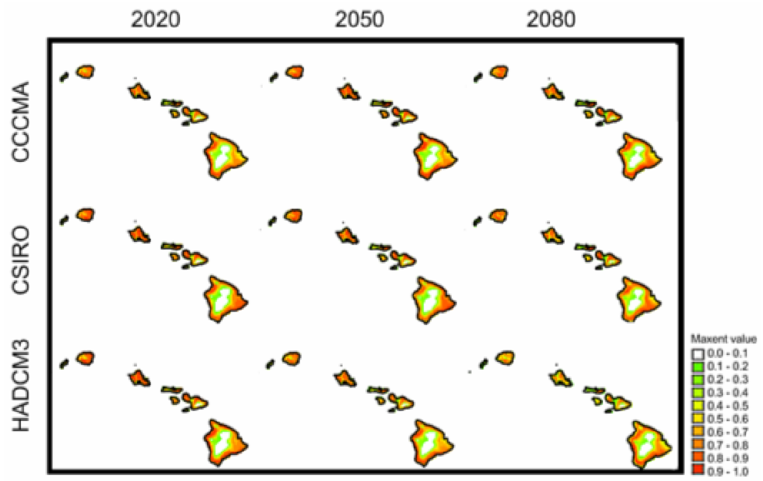

Figure 6. Potential distribution of *Eleutherodactylus coqui* under future climate change scenarios assuming B2a conditions. Higher Maxent values suggest higher climatic suitability.

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 has been 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 (Fig. 3) and protected areas on the major Hawaiian Islands (Fig. 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 & Campbell 2002). So, endemic species inhabiting these areas may not be threatened by the invader. Unfortunately, the entire islands of Kauai, Molokai, and Oahu, including all protected areas, provide suitable climatic conditions.

Applying future anthropogenic climate change scenarios, the models suggested an extension of the potential distribution of *E. coqui* towards higher altitudes in the Hawaiian Islands, and therefore into nature reserves which are currently free of *E. coqui*. The range alteration may already have started, since such a trend was recently observed by Kraus & Campbell (2002). The authors reported that *E. coqui* has expanded its altitudinal range on the Island of Hawaii form previous limits of 670 m to 1170 m asl, where it maintained feral populations which successfully survived the winters of 1999-2000 and 2000-2001. Kraus et al. (1999) and Kraus & 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 on 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 multi-million dollar floriculture and nursery industries because of quarantine restrictions and de-infestation measures that are required before plants can be exported (Kraus & Campbell 2002). This is especially important since *E. coqui* densities on the Island of Hawaii are the highest in the world (Stewart 1995, Stewart & Woolbright 1996, Woolbright et al. 2006). Populations of *E. coqui* are expanding (Kraus & 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 (Villanova University, USA) and Severus D. Covaciu-Marcov (Oradea University, Romania) for valuable comments on the manuscript. This work was funded by the "Graduiertenförderung des Landes Nordrhein-Westfalen".

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Submitted: 30 May 2008
/ Accepted: 21 August 2008