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**‘Chamaliens’ on the Hawaiian Islands: spatial risk assessment for the invasive Jackson’s chameleon (Chamaeleonidae)**DENNIS RÖDDER<sup>1</sup>, WOLFGANG BÖHME<sup>1</sup> & STEFAN LÖTTERS<sup>2</sup><sup>1</sup>) Zoological Research Museum Alexander Koenig, Department of Herpetology, Adenauerallee 160, 53113 Bonn, Germany<sup>2</sup>) Trier University, Department of Biogeography, Am Wissenschaftspark 25 + 27, 54296 Trier, Germany

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Alien species are of major concern to conservation biology, agriculture and the human society, as they may become invasive and successfully compete with native species, negatively influence crop production, and cause health problems. Several reptile species are considered invasive alien species, but most of them are little studied (KRAUS 2009). Amongst these species are a few chameleons. Apparently, several of the *Chamaeleo chamaeleo* (LINNAEUS, 1758) populations in the Mediterranean (e.g. Crete, Malta, Sicily) are non-autochthonous and their presence can be linked to historical trade routes (e.g. KLAVER 1981). *Chamaeleo africanus* LAURENTI, 1768 from northern Africa was translocated from the Nile delta onto the Peloponesos where it has maintained reproducing populations perhaps since antiquity (e.g. BÖHME et al. 1998, BÖHME 2000). More recently, the Malagasy *Furcifer pardalis* (CUVIER, 1829) has become invasive on Réunion Island (e.g. BOURGAT 1970).

One of the most successful invasive chameleons is Jackson’s chameleon, *Trioceros jacksonii* (BOULENGER, 1896), which is native to Afromontane Kenya and Tanzania (Fig. 1). Popular as a pet and commonly traded and imported by the thousands from Kenya and Tanzania (CARPENTER et al. 2004), this species was introduced to Oahu, Hawaiian Islands in 1972 (e.g. MCKEOWN 1991, WARING 1997). Apparently, established populations are referable to the large, up to 35 cm in total length, subspecies *T. j. xantholophus* (EASON, FERGUSON & HEBRARD, 1988) from Kenya and Tanzania (MCKEOWN 1991) (Fig. 2). As a result of inter-island transport which has only been restricted since 1997, Jackson’s chameleon currently has established wild populations on all the main islands including the island of Hawaii, Maui and Kauai as a result of multiple introductions and subsequent spread (Fig. 1; WARING 1997 cited in HAGEY et al. 2010). The species is especially common in wetter habitats at elevations from 100–1,000 m above sea level (MCKEOWN 1996, HOLLAND et al. 2009) and inhabits disturbed habitats as well as forested areas (MCKEOWN 1991, WARING 1997). The ecological impact of Hawaiian *T. jacksonii* has not been studied. Only recently, HOLLAND et

al. (2009) documented predation on endemic snail and insect species, including some threatened with extinction, and HAGEY et al. (2010) commented on its foraging strategy. Further studies on the natural history and distribution of *T. jacksonii* on Hawaiian Islands, coupled with monitoring and management efforts, are required.

GIS-based Species Distribution Models (SDMs) are a helpful tool towards these goals, as they focus on species’ potential distributions. In the case of invasive alien species, they can be understood as spatial risk assessments. Technically, a SDM assesses a species’ ecological niche and projects it into geographical space (RÖDDER et al. 2010a). Niche information is obtained at presence and sometimes absence sites of the study species; climatic niche information has been demonstrated to be a good predictor for invasion success in alien reptile species (e.g. BOMFORD et al. 2009; RÖDDER et al. 2009b). The resulting map shows similarities with the niche elsewhere, e.g. by different grid values, interpreted as ‘likelihood’ of the species’ potential occurrence (e.g. PETERSON & VIEGLAIS 2001, RÖDDER & LÖTTERS 2010). Projecting SDMs onto past or future climate scenarios may allow simulations of a species’ potential response to environmental changes (e.g. RÖDDER & SCHULTE 2010). For example, RÖDDER (2009) provided a spatial risk assessment for the invasive non-autochthonous frog *Eleutherodactylus coqui* on the Hawaiian Islands, suggesting range allocation towards higher elevations under future anthropogenic climate change, thus affecting protected areas.

In this paper, we develop SDMs for Jackson’s chameleon in the Hawaiian Islands under current and future climates based on the species’ climatic envelope at its invaded and native African distribution ranges. The goal is to appreciate the geographical potential of this species in its invaded range.

For SDM building, we used presence data from the native African and the invaded Hawaiian ranges of *Trioceros jacksonii* as available via the Global Biodiversity Information Facility (<http://www.gbif.org>) and HerpNet ([© 2011 Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V. \(DGHT\), Rheinbach, Germany  
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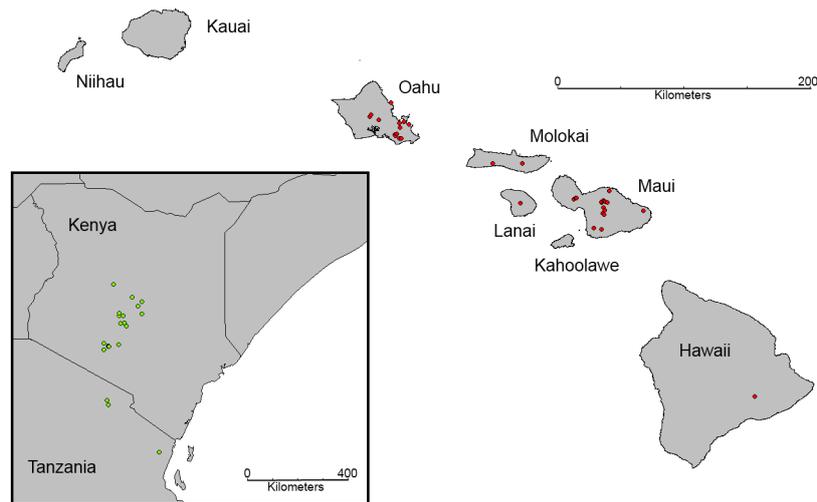


Figure 1. Species records used for model building in *T. jacksonii*'s invaded Hawaiian range and its native range in Kenya and Tanzania (insert).

www.herokuapp.org). When necessary, georeferencing of locality data was conducted with the BioGeoMancer (<http://bg.berkeley.edu/latest/>). DIVA-GIS 7.1.6 (HIJMAN et al. 2002; <http://www.diva-gis.org>) was used to check accuracy



Figure 2. Non-collected male *Trioceros jacksonii xantholophus* from Parklands in Nairobi.

of coordinates. Records were only considered if they could be unambiguously assigned to a single grid cell, leaving a total number of 81 presence records for modelling (Fig. 1).

Information on current climate, i.e., for the period 1950–2000, was obtained from the WorldClim database at a spatial resolution of 30 arc sec (HIJMAN et al. 2005; <http://www.worldclim.org>). For future climate, as expected for the year 2080, we downloaded interpolations of three different global change scenarios of the third and fourth assessments of the IPCC (2007); spatial resolution 30 arc sec (RAMIREZ & JARVIS 2008; <http://gisweb.ciat.cgiar.org/GCMPPage>). These anthropogenic climate change predictions, simulating conditions as expected in the two IPCC story lines A2a and B2a, were derived from simulations of three climate models CCCma-CGCM2 (FLATO et al. 2000, FLATO & BOER 2001), CSIRO-MK2 (GORDON & O'FARRELL 1997), and UKMO-HadCM3 (GORDON et al. 2000, POPE et al. 2000). Climate variables comprised monthly minimum and maximum temperatures, and average precipitation per month. Based on these, we computed 19 'bioclimatic' variables with DIVA-GIS; these are commonly used for species distribution modelling (e.g. BUSBY 1991, BEAUMONT et al. 2005). Since multicollinearity of predictor variables may hamper successful SDM projection through space or time (e.g. HEIKKINEN et al. 2006), we extracted all 'bioclimatic' values from the species records and performed a pair-wise correlation analysis based on Pearson's correlation coefficient with XLSTAT 2010 (<http://www.adinsoft.com>). For SDM computation, only variables with  $R^2 < 0.75$  were considered, resulting in a final variable set comprising 'mean monthly temperature range', 'temperature seasonality', 'maximum temperature of the warmest month', 'minimum temperature of the coldest month', 'annual temperature range', 'annual precipitation', 'precipitation in the wettest month', 'precipitation seasonality', 'precipitation in the warmest quarter' and 'precipitation in the coldest quarter'. It was suggested that these variables describe environmental conditions that are physiologically important to *T. jacksonii* (BENNETT 2004, ANDREWS 2008, LIN 1979, LIN & NELSON 1980).

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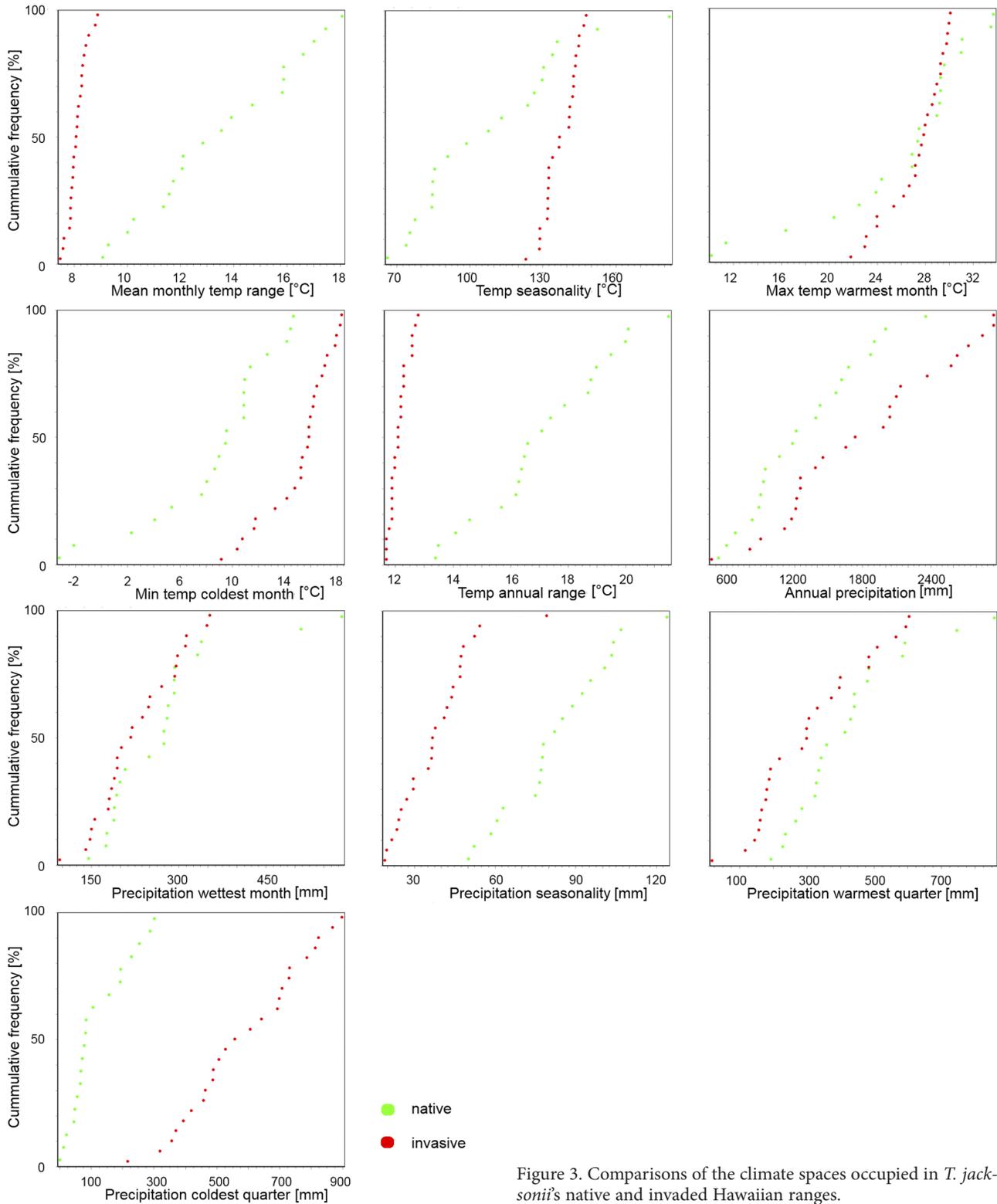


Figure 3. Comparisons of the climate spaces occupied in *T. jacksonii*'s native and invaded Hawaiian ranges.

For SDM development, Maxent 3.2.2 was applied (PHILLIPS et al. 2006, PHILLIPS & DUDÍK 2008), a machine-learning algorithm following the principle of maximum entropy (JAYNES 1957). Maxent has been successfully applied in studies assessing possible spreads of invasive alien species (GIOVANELLI et al. 2007, RÖDDE & LÖTTERS 2010), pathogens (RÖDDE et al. 2009a, LÖTTERS et al. 2010

“2009”), and potential impact of climate change (RÖDDE & WEINSHEIMER 2009, RÖDDE et al. 2010b). In most cases, Maxent outperforms comparable SDM methods, even when the sample size is small (HERNANDEZ et al. 2006, WISZ et al. 2008). This was further confirmed by Maxent's ability to predict previously unknown populations in poorly known species (PEARSON et al. 2007, WEINSHEIMER et

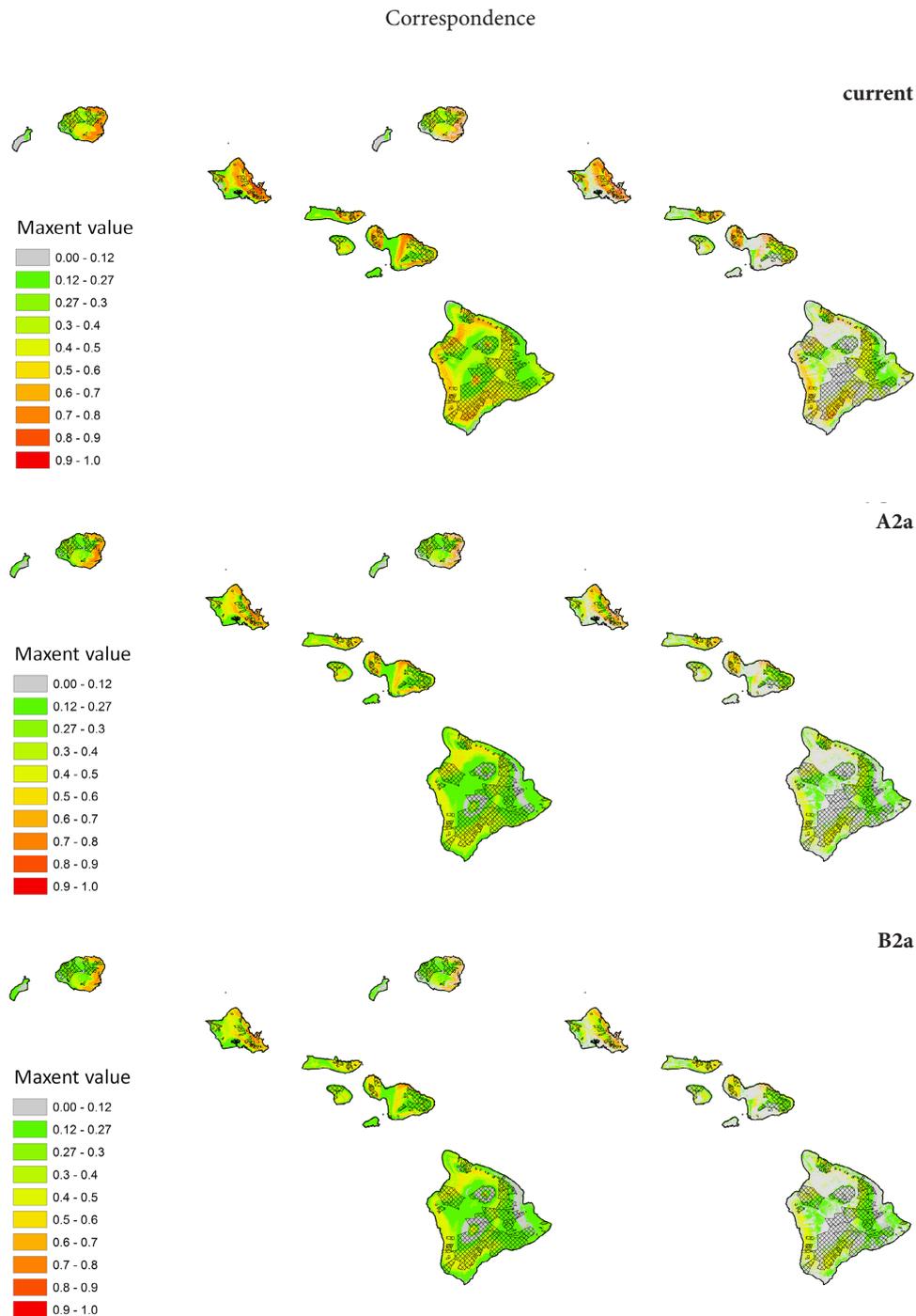


Figure 4. Potential distribution of Jackson's chameleon on the Hawaiian Islands under current climate and two future anthropogenic climate change scenarios (A2a, B2a), based on a Maxent Species Distribution Model and bioclimatic conditions at the species' native African occurrence. Warmer colours indicated higher suitability to the species when considering climate conditions only (each left) and when considering climate as well as land cover (each right). Established reserves are indicated as crosshatched areas.

al. 2010) and even species that are likely to be new to science (RAXWORTHY et al. 2003). Next to species presence records, Maxent requires a set of pseudo-absence records for SDM computation. The selection of these is a crucial step towards successful model building (PHILLIPS 2008, MATEO et al. 2010, VANDERWAL et al. 2009). Herein, we randomly selected 20 pseudo-absence records per species record within a circular buffer of 10 km as recommended by MATEO et al. (2010). This results in a set of pseudo-absence records with a similar spatial structure as present in

the species records, equalling the target group background approach suggested by PHILLIPS et al. (2009).

For model evaluation, 70 % of the species records were used for model training and the remaining 30 % for model testing via the Area Under Curve (AUC), referring to the Receiver Operating characteristic Curve (PHILLIPS et al. 2006, FIELDING & BELL 1997). Furthermore, Maxent allows tracing back the relative contribution of each variable to the final model, and so facilitates comparisons with physiological properties of the target species. As data splits may affect

the model due to the exclusion of some species records that represent features not present in the remaining records, this procedure was repeated 100 times and averages were computed subsequently. Land cover data for the Hawaii Islands were obtained from the Coastal Service Center of the National Oceanic and Atmospheric Administration (<http://www.csc.noaa.gov/crs/lca/hawaii.html>); land cover classes included high- and low-intensity development, cultivated land, grassland, evergreen forest, scrub/shrub, palustrine emergent wetlands, unconsolidated shoreline, bare land, and water. Information on current reserve networks was adopted from the Office of Planning, State of Hawaii.

Comparisons of the occupied climate space in *T. jacksonii*'s native and invaded Hawaiian ranges revealed that the highest similarities existed in the 'precipitation in the wettest month' and the 'precipitation in the warmest quarter' and the greatest differences in the 'mean monthly temperature range', 'annual temperature range' and the 'precipitation in the coldest quarter' (Fig. 3). The 'minimum temperature of the coldest month' experienced within *T. jacksonii*'s invaded range is well above its critical thermal minimum ( $5.3 \pm 0.5$  °C,  $n = 8$ , BENNETT 2004), but well below its voluntary minimum temperature ( $29.1 \pm 0.32$  °C,  $n = 7$ , BENNETT 2004). Its preferred body temperature ( $32.1 \pm 0.24$  °C,  $n = 7$ , BENNETT 2004), voluntary maximum body temperature ( $34.2 \pm 0.31$ ,  $n = 7$ , BENNETT 2004), panting threshold ( $36.2 \pm 0.67$ ,  $n = 5$ , BENNETT 2004), and critical thermal maximum ( $41.0 \pm 0.15$ ,  $n = 8$ , BENNETT 2004;  $42.0 \pm 0.91$  °C,  $n = 10$ , LIN 1980) are slightly higher than the maximum temperature of the warmest month within its invaded range. Differences of up to 6 °C may be compensated by heliothermic thermoregulation, and feeding activity may occur at temperatures as low as 10 °C (BENNETT 2004), however.

It has been suggested that climatic conditions supporting successful reproduction and balanced sex ratios can be strong predictors for the geographic range limits of reptile species (e.g. RÖDDER et al. 2009b). In *T. jacksonii*, reproduction is clearly associated with higher precipitation during the long wet season in East Africa (LIN 1979, LIN & NELSON 1981). Although the amount of annual precipitation is quite similar in the chameleons' native and invaded ranges, precipitation seasonality is much more pronounced in its native range. Thus, the higher monthly precipitation in its Hawaiian range may even facilitate circannual breeding.

Following the terminology of SWETS (1988), we received 'good' average AUC values for the SDM-based on current climate ( $AUC_{\text{training}} = 0.86$ ;  $AUC_{\text{test}} = 0.78$ ). The minimum prediction value of the training records was 0.12, and the lowest 10 percentile was 0.27. Analysis of variable contributions in the model revealed that on average the 'precipitation in the coldest quarter' had the highest explanative power (30.2 %), followed by the 'mean monthly temperature range' (26.1 %), and the 'precipitation seasonality' (12.8 %). Average contributions of all other variables were < 10 %. Our SDM suggests that, under current 'bioclimatic' conditions, Jackson's chameleon may find suitable areas nearly everywhere on the Hawaiian Islands, including many reserves, even when the availability of suitable microhabitats in terms of land cover is considered (Fig. 3). The situation is not likely to change under future anthro-

pogenic climate change with A2a and B2a scenarios, which forecast nearly identical and only slightly less suitable conditions for *T. jacksonii* (Fig. 4).

Invasive Hawaiian Jackson's chameleons are suggested to interact with native biota, at least as a predator to endemic fauna (HOLLAND et al. 2009). While the impact of this species is poorly understood, we here provide evidence how severe the problem may be or may become as *T. jacksonii* finds suitable habitat almost all over the Hawaiian Islands. This emphasizes, in concert with HOLLAND et al. (2009), the severity of a problem that should no longer be neglected. Besides the impact on potential prey invertebrates, it should be considered hypothetically that *T. jacksonii* might compete with other local fauna for food resources.

The potential invasion success and expected damage to the native fauna may be unparalleled by other invasive chameleons, although potential distribution and ecological impact studies remain limited (e.g. DIMAKI et al. 2001). At least the spatial potential of *Chamaeleo africanus* in mainland Greece may be limited as, despite of the species' occurrence on the Peloponesos since historical times, there is no indication of past or present dispersal (W. BÖHME, unpubl. data). Likewise, the Réunion population of *Furcifer pardalis* is suggested to be restricted to a small, particularly dry and hot area on the western coast near St. Paul, although this species has recently been found elsewhere on the island, but its invasion success there remains unknown (E. KOCH, pers. comm., March 2010). Invasion success was apparently limited in *Furcifer oustaleti* (MOCQUARD, 1894), which was translocated from Madagascar to near Nairobi, Kenya, but where this species has not been documented since 1974 (SPAWLS et al. 2002). *Trioceros jacksonii* seems to be exceptional among chameleons for its invasive potential, as shown by its successful colonisation of the Hawaiian Archipelago.

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