

Applications of Ecological Niche Modeling for Species Delimitation: A Review and Empirical Evaluation Using Day Geckos (*Phelsuma*) from Madagascar

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Abstract.—Although the systematic utility of ecological niche modeling is generally well known (e.g., concerning the recognition and discovery of areas of endemism for biogeographic analyses), there has been little discussion of applications concerning species delimitation, and to date, no empirical evaluation has been conducted. However, ecological niche modeling can provide compelling evidence for allopatry between populations, and can also detect divergent ecological niches between candidate species. Here we present results for two taxonomically problematic groups of *Phelsuma* day geckos from Madagascar, where we integrate ecological niche modeling with mitochondrial DNA and morphological data to evaluate species limits. Despite relatively modest levels of genetic and morphological divergence, for both species groups we find divergent ecological niches between closely related species and parapatric ecological niche models. Niche models based on the new species limits provide a better fit to the known distribution than models based upon the combined (lumped) species limits. Based on these results, we elevate three subspecies of *Phelsuma madagascariensis* to species rank and describe a new species of *Phelsuma* from the *P. dubia* species group. Our phylogeny continues to support a major endemic radiation of *Phelsuma* in Madagascar, with dispersals to Pemba Island and the Mascarene Islands. We conclude that ecological niche modeling offers great potential for species delimitation, especially for taxonomic groups exhibiting low vagility and localized endemism and for groups with more poorly known distributions. In particular, niche modeling should be especially sensitive for detecting recent parapatric speciation driven by ecological divergence, when the environmental gradients driving speciation are represented within the ecological niche models. [Biogeography; distribution modeling; evolution; mitochondrial DNA; morphology; speciation; systematics.]

The accurate identification of species (metapopulation lineages) during the early stages of postspeciation diversification (lineage divergence) has always presented systematists with unique challenges (Frost and Kluge, 1994; DeQueiroz, 1998, 2005; Wiens and Servedio, 2000; Coyne and Orr, 2004). For “cryptic” species lineages, morphological differences may be subtle, overlapping, or not yet fixed; pre- and postzygotic reproductive barriers may be incomplete; and lineage sorting of rapidly evolving molecular loci may be incomplete (Avice, 2000; Wiens and Servedio, 2000; Sites and Marshall, 2003; Futuyma, 2005). As a result, there has been considerable disagreement between researchers about the criteria that are used to recognize species, and as summarized by DeQueiroz (1998), this has also fueled the historical debate about the merits of alternative species concepts. Older and more divergent species can usually be readily recognized using many species criteria (concepts), but more recently evolved lineages qualify as species using far fewer species criteria. A practical yet conservative strategy taken by many researchers has been to apply a diversity of evidence to support the recognition of species (e.g., fixed or nonoverlapping differences in morphological, behavioral, or ecological characters, molecular divergence thresholds, additional quantitative methods, or geographic isolation), thereby meeting the requirements of several species criteria (e.g., see DeQueiroz, 1998). However, an inevitable consequence of this approach is that many of the most recent speciation events will go undetected.

In this paper, we explore the utility of applying ecological niche modeling methods, based on mapping environmental suitability (see Guisan and Thuiller, 2005, for a review of the discipline) to the issue of

species delimitation and, in particular, the recognition of cryptic species. To the best of our knowledge, this type of application for ecological niche modeling has only been discussed by Wiens and Graham (2005: 522–523). These authors describe how niche modeling can provide evidence for geographic isolation between populations (either based on conserved or divergent ecological niches), and hence can provide evidence supporting these populations as separate evolving lineages when gene flow is considered unlikely for the intervening unsuitable region. Although allopatric populations with divergent traits are often considered good candidates for species recognition (e.g., Frost and Hillis, 1990; Wiens, 2004), locality data may be too sparse to directly infer geographic isolation for the suspected candidate species, and the environmental suitability (for either species) in intermediate areas may be poorly known. However, through the application of ecological niche modeling, a much stronger case for geographic isolation can be made, by mapping the spatial distribution of environmental suitability of climatic variables. Here we apply this approach using empirical data for two gecko species groups in Madagascar.

Ecological Niche Modeling

Ecological niche models utilize associations between environmental variables and known species' occurrence localities to define abiotic conditions within which populations can be maintained (Guisan and Thuiller, 2005). Models have been variously termed “ecological niche” (Peterson et al., 1999) and “species distribution” (Elith et al., 2006) models, and although the interpretation of model output may vary (Peterson, 2006), the

methodological approach is essentially the same: (1) the study area is modeled as a map composed of grid cells at a specified resolution, (2) the dependent variable is the current known species' distribution, (3) a suite of environmental variables are collated to describe the characteristics of each cell, and (4) a function of the environmental variables is calibrated so as to classify the degree to which each cell is either suitable or unsuitable for the species (Hirzel et al., 2002). This approach makes it possible to map (and validate) areas of environmental suitability for a species based on the environmental (physical) conditions, even when species distributions are known from very limited locality data (Pearson et al., 2007). Models thus approximate a set of physical variables of Hutchinson's (1957) fundamental niche (Soberón and Peterson, 2005).

Model evaluation, using test localities that are not used for training the model, is important for detecting potential errors or poor predictive performance (Fielding and Bell, 1997). Evaluation identifies models that predict an excessively small or large area. Small-model predictions can represent model overfitting and will result in false-negative predictions of observed locality records. This is often the case when locality sampling is insufficient to capture the full range of environmental conditions occupied by a species. Large-model predictions result in the identification of areas that are unoccupied by the species (false-positive predictions), which may be caused by erroneous localities that are outside the actual species distribution, or may indicate range restriction due to dispersal barriers or biotic interactions such as competition and predation. Test data for model evaluation is commonly derived by partitioning known locality records into two data sets, one for model training and the other for testing. In cases where the number of the known localities is very low ($\sim <25$), training and test data sets can become very small (e.g., Anderson et al., 2002; Raxworthy et al., 2003; Anderson and Martínez-Meyer, 2004) and a jackknife data-partitioning approach can be used (Pearson et al., 2007). Several statistics have been applied to assess predictive performance on test data, some of which utilize both presence and absence records (e.g., Kappa, AUC), whereas others rely only on presence records (e.g., rate of false negatives; Fielding and Bell, 1997). In cases where only presence records are used, it is necessary to test that the prediction is statistically better than random with respect to the proportion of the study area that is predicted as "present" (Anderson et al., 2002).

Systematic Applications for Ecological Niche Modeling

Ecological niche modeling is already integrated into a broad variety of research disciplines (for a detailed review of the historical development and applications of ecological niche modeling, see Guisan and Thuiller, 2005), which include biological responses to climate change (Iverson and Prasad, 1998; Pearson and Dawson, 2003; Thomas et al., 2004; Thuiller et al., 2005a, Bonaccorso et al., 2006; Graham et al., 2006), invasive

species biology (Peterson, 2003; Thuiller et al., 2005b), conservation priority setting (Araújo and Williams, 2000; Ferrier et al., 2002; Anderson and Martínez-Meyer, 2004; Ortega-Huerta and Peterson, 2004), and ecology and evolutionary biology (Peterson et al., 1999; Anderson et al., 2002; Peterson and Holt, 2003; Rice et al., 2003; Graham et al., 2004b; Martínez-Meyer et al., 2004; Wiens et al., 2006; Kozak and Wiens, 2006). Because of the substantial biogeographic component that exists within the discipline of systematics, ecological niche modeling is now also playing an increasingly important role within phylogenetic research. These include the following systematic applications.

Recognition of areas of endemism.—Areas of endemism represent the OTUs for all vicariance biogeographic methods used in systematics. Their accurate identification is thus critical to these analyses. Criteria used for identification have been discussed by various authors (Axelius, 1991; Harold and Mooi, 1994; Morrone 1994; Linder, 2001; Szumik et al., 2004) but all are dependent upon first having an accurate understanding of the species distribution. In those cases where species localities are relatively rare, ecological niche modeling has powerful applications by providing an estimate of distributions that is more informative than a minimum area polygon, or subjective expert opinion. In addition, niche models can also be used to guide subsequent field surveys to accelerate the discovery of new populations, and further improve the understanding of species distributions (Raxworthy et al., 2003; Bourg, 2005; Guisan et al., 2005).

Recognition of erroneous localities.—As greater reliance is placed on mining diverse sources for locality data to determine species distributions (Graham et al., 2004a), another potentially valuable application for ecological niche modeling concerns the recognition of spatial error localities. These localities are outliers that fall outside the actual geographic distribution of the species, yet are reported in catalogs or the literature as accurate records. The recognition of these spatial error localities represents an important area of research that has not yet been well investigated (Graham et al., 2004a). We see potential promise in applying ecological niche modeling validation methods to this problem. As an example, we present here the situation found in the Malagasy cordylid lizard *Zonosaurus aeneus*, for which the locality Nosy Be (a near-offshore island) has been recently questioned (Vences et al., 1996; Raselimanana et al., 1999). Applying the jackknife validation method (Pearson et al., 2007) identifies the Nosy Be locality as an outlier: it is the only locality not predicted by niche models based on all other localities. Removing this locality also results in a dramatically different ecological niche model that provides a much better fit to the other locality records (Fig. 1).

Discovery of new areas of endemism and new species.—For some species, ecological niche modeling also leads to the discovery of isolated areas of environmental suitability that are not actually occupied by the species being modeled. An example of this is illustrated with a niche model for the Malagasy day gecko, *Phelsuma modesta* (Fig. 2).

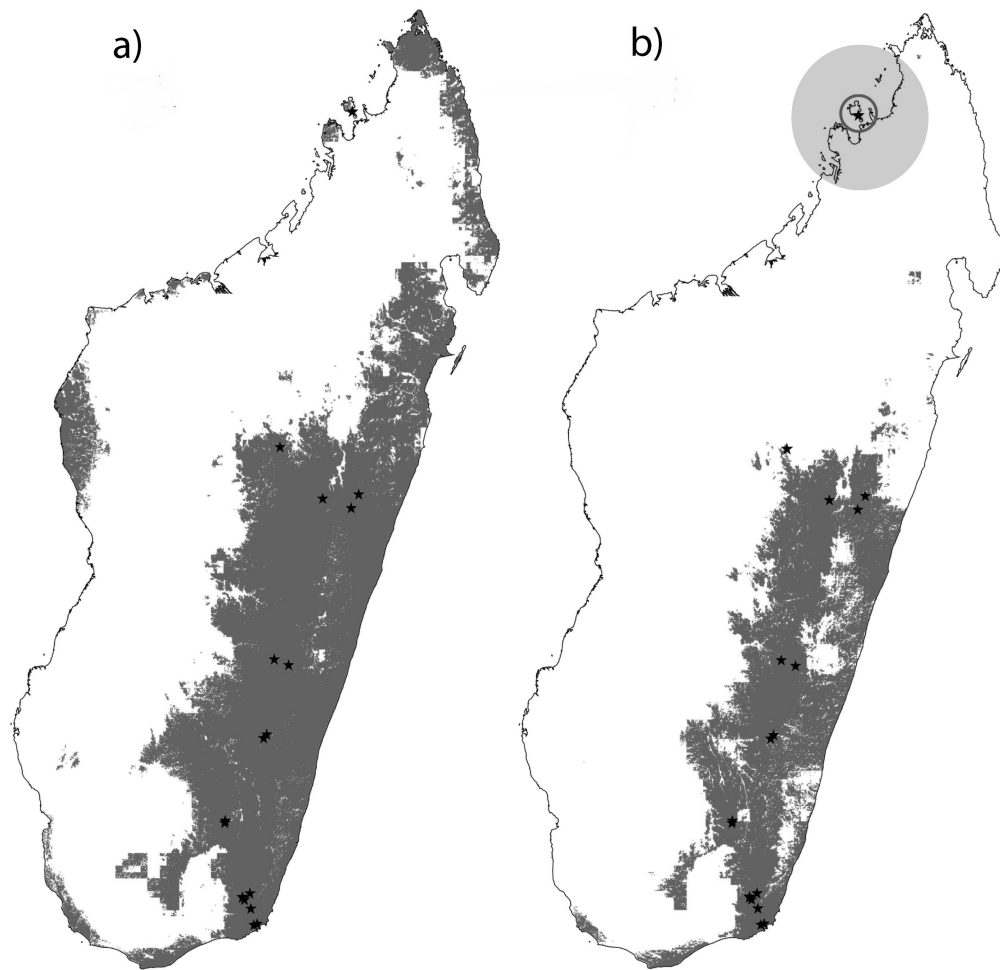


FIGURE 1. Using ecological niche models to identify erroneous localities. Two alternative niche models for *Zonosaurus aeneus*, based on (a) all localities and (b) all localities except Nosy Be in northwest Madagascar (circled). The Nosy Be locality has long been suspected as dubious (Vences et al., 1996; Raselimanana et al., 1999) and is the only locality not predicted by the jackknife model validation (see text). Localities indicated by star symbols.

The disjunct northern area of environmental suitability may be unoccupied as a result of biological interactions with other species (e.g., competition) or dispersal barriers that have prevented the species from occupying the disjunct area. In the latter case, these results have applications for predicting dispersal patterns of potentially invasive species (Peterson, 2003). For poorly surveyed regions (especially tropical regions with high levels of regional endemism), these disjunct areas of overprediction can also represent pockets of unrecognized local endemism that harbor unknown species (Raxworthy et al., 2003). Consequently, ecological niche modeling has the capacity to improve our understanding of patterns of endemism and accelerate the discovery process for new species. Beyond the obvious merits of species discovery (especially for conservation management), this ultimately will also result in phylogenetic and biogeographic analyses that benefit from greater taxonomic sampling, and that are spatially more informative.

Species delimitation.—Wiens and Graham (2005) have recently proposed that identifying geographic isolation

between allopatric populations using ecological niche modeling has practical importance for species delimitation. They argue that two populations separated by a region outside the climatic niche envelope of the two populations makes current gene flow unlikely and thus supports both populations being considered separate species. This scenario of geographic isolation between sister species can include situations where (1) niches are similar, with one species predicting the other species distribution (niche conservatism, as expected from classic allopatric speciation, see Peterson et al., 1999), or else (2) where niches are divergent, in which case interpredictivity of distributions between species is poor. Peterson and Holt (2003) have also used similar principles of predictivity to assess intraspecific niche differentiation between subspecies and populations.

Another potential method for using ecological niche modeling for species delimitation, which we develop here for the first time, concerns comparing niche models based on split and lumped taxonomic groupings. In cases of divergent ecological niches and a pair of valid

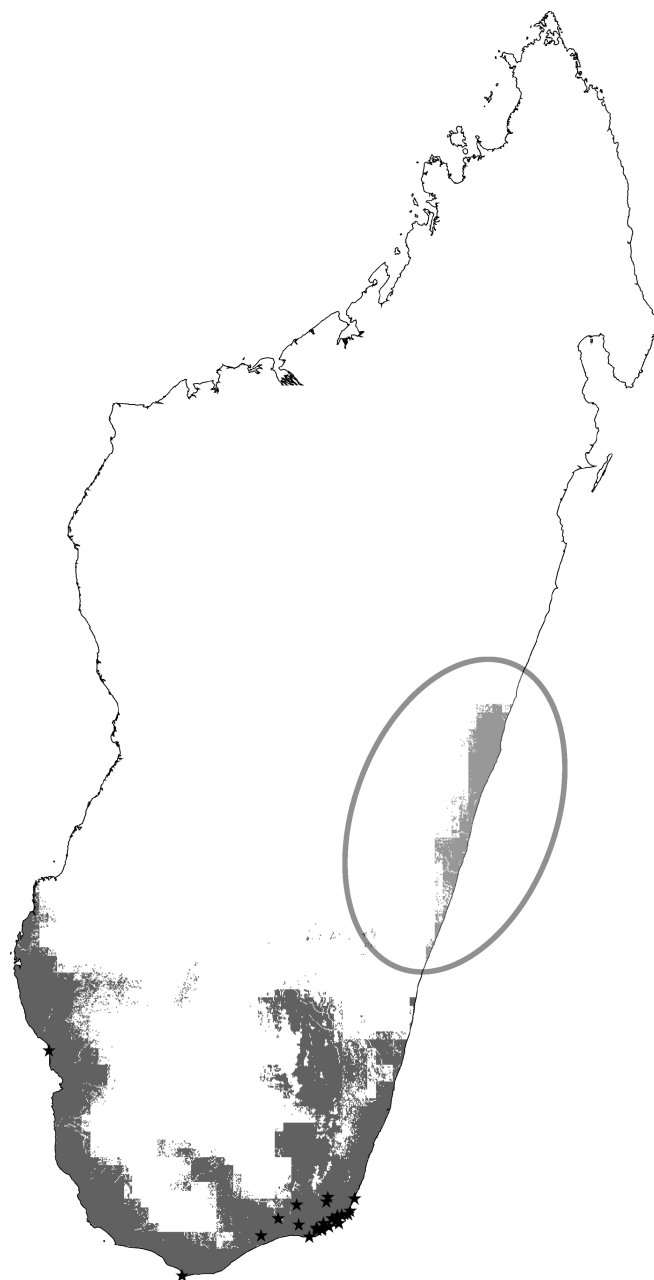


FIGURE 2. Using ecological niche models to identify areas of endemism. An ecological niche model for *Phelsuma modesta*. The disjunct northern area highlighted by the ellipse is actually not occupied by *Phelsuma modesta*. In Madagascar, these disjunct and unoccupied modeled areas often represent areas of localized endemism for other species (Raxworthy et al., 2003). In this case, this region was subsequently targeted for field surveys, which yielded the new species of *Phelsuma* described in this study. Localities indicated by star symbols.

species, when each candidate species is modeled separately these models should produce a better fit to the actual distribution than the ecological niche model for the two species combined. Under this scenario, the combined ecological niche model includes niche space that is not occupied by any of the candidate species, thus leading to excessive areas of overprediction (false-positive

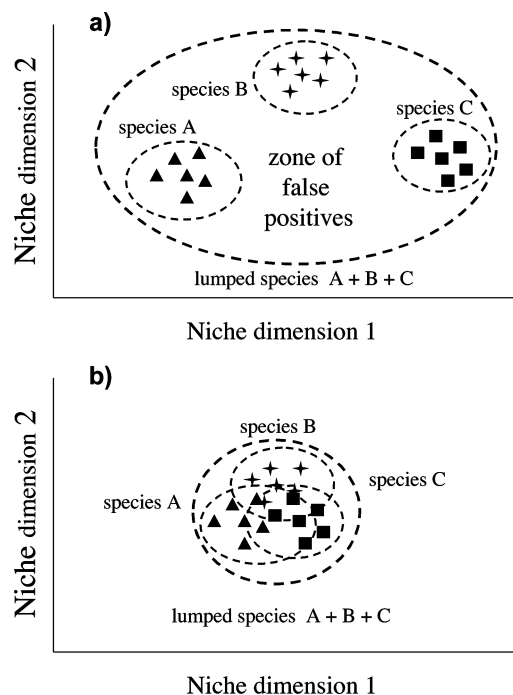


FIGURE 3. A theoretical representation of Hutchinson's (1957) hyperdimensional niche for three species, modeled as both three species and a single combined species. (a) When niches between the split species have diverged, the combined species niche may include unoccupied niche space that yields zones of false positives in distribution models. (b) When niches between the split species are similar (conservative), the combined species niche will be similar to each split species. This is the expected result from recent allopatric speciation, or from over splitting localities within a single species.

predictions). A graphical representation of this scenario is presented in Figure 3, illustrated using two dimensions of Hutchinson's (1957) hyperdimensional niche concept.

Although ecological niche modeling in geographic space is well suited to determining geographic isolation between candidate cryptic species, to date we are not aware of empirical examples that have applied this method to this specific application. In this study, we explore the potential for ecological niche modeling to inform species delimitation using two species groups of *Phelsuma* day geckos from Madagascar.

Phelsuma Groups Targeted for Empirical Study

This study considers two taxonomically problematic species groups of *Phelsuma* day geckos in Madagascar. The first is the *Phelsuma madagascariensis* species group, which currently includes four recognized subspecies: *P. m. madagascariensis* (Gray, 1831), *P. m. grandis* Gray 1870, *P. m. kochi* Mertens 1954, and *P. m. boehmei* Meier 1982. Previously, the following subspecies have been synonymized: *P. m. martensi* Mertens, 1962 (= *P. m. madagascariensis*), *P. m. venusta* Wermuth, 1965 (= *P. m. grandis*); and *P. m. notissima* Mertens 1970 (= *P. m. kochi*; Meier and Böhme, 1991; Uetz, 2006). The subspecies *P. m. boehmei* (only known from the type locality, Perinet) is considered similar to the nominate form *P. m. madagascariensis*.

The reported diagnostic character for this subspecies, dark skin between body tubercles, has been previously recorded for coastal *P. m. madagascariensis* (see Glaw and Vences, 1994), and *P. m. boehmei* is considered part of a *P. m. madagascariensis* “megasubspecies” by Meier (1982) and Meier and Böhme (1991). Putative morphologically intermediate forms have also been reported between *P. m. kochi* and *P. m. grandis* (Meier and Böhme (1991) and *P. m. madagascariensis* and *P. m. grandis* (Krüger, 1996). More recently, support for the specific status of two subspecies, *P. m. grandis* and *P. m. kochi*, was provided by mtDNA results that found these forms paraphyletic with respect to *P. abbottii* (Madagascar and Aldabra) and *P. parkeri* (Pemba Island, East African coast) (Austin et al., 2004; Rocha et al., 2007). However, no formal taxonomic changes have yet been proposed.

The second targeted group is the *Phelsuma dubia* species group. In addition to *P. dubia* (Boettger, 1881), which is distributed in Madagascar, the Comoros, Zanzibar, and coastal East Africa, a second Madagascar species, *P. hielscheri* (Rösler et al., 2001) was recently described based on five specimens from two localities and considered closely related to *P. dubia* (it had been previously confused with this species). Other authors have also discussed the status of these species and populations (Glaw et al., 1999; Berghof, 2001), and a recent mtDNA analysis (Rocha et al., 2007) has investigated genetic variation between *P. dubia* populations in the Comoros and Zanzibar. During our 2006 survey of sites of potential unrecognized endemism along the southeast coast of Madagascar (identified by Raxworthy et al., 2003), we found *Phelsuma* of the *dubia* group that we suspected to represent a new species. We here include these specimens as part of a broad assessment of species limits within the *dubia* group for Madagascar. For both these groups, in addition to species delimitation, we also discuss support for alternative geographic modes of speciation and consider niche evolution between sister species.

MATERIALS AND METHODS

Field Surveys, Localities, and Morphology

Phelsuma field surveys were timed for the austral summer (between January and April) for the period of peak rainfall and for months with above mean annual temperatures (Jury, 2003). Geckos were collected by searching vegetation (palms, bamboo, and trees) up to approximately 10 m height, primarily by day. Specimens were also opportunistically collected at night when found roosting on branches or palm fronds. Survey sites were selected based on combinations of the following criteria: (1) occurrence of primary habitats (almost always mixed with anthropogenic habitats); (2) inclusion of regions of potential unknown endemism identified by ecological niche modeling (following Raxworthy et al., 2003); (3) inclusion of different massif systems; (4) inclusion of broad elevational transects when available; and (5) status as national protected areas. Descriptions of the massifs, protected areas, and the distribution of primary habitats are given in Goodman and Benstead (2003). Photographs of

representative specimens were taken soon after capture to record natural coloration. All color descriptions are based on diurnal photographs taken of captured animals, where animals were first allowed to acclimate before photography (*Phelsuma* day geckos can quickly change the intensity of their coloration). The following information was recorded at the time of capture for each individual: date, time, longitude-latitude-elevation (recorded using a GPS, altimeter, or 1:100,000 topographic maps), and microhabitat. Voucher specimens were euthanized and fixed in 10% buffered formalin and later transferred to 70% alcohol. Liver and/or thigh muscle were removed from representative specimens and frozen in liquid nitrogen or preserved in alcohol or tissue buffer. Voucher specimens are deposited at the American Museum of Natural History (AMNH), the University of Michigan Museum of Zoology (UMMZ), and the University of Antananarivo Department of Animal Biology (UADBA).

The localities used for niche modeling were compiled based on those for voucher specimens held at AMNH and UMMZ, and supplemented with literature records that could be georeferenced: *madagascariensis* group: Meier and Böhme (1991), Kuchling (1993), Glaw and Vences (1994), Van Heygen (2004); and the *dubia* group: Glaw et al. (1999), Berghof (2001), Rösler et al. (2001). Literature records were evaluated carefully to check species identification and localities, and other literature records were excluded if there was uncertainty about localities or identifications. Localities are provided in the supplemental appendix (www.systematicbiology.org). We consider *P. m. boehmei*, known from a single locality, as *P. m. madagascariensis* (see Proposed Taxonomic Changes, below). Because of the resolution of the environmental layers (1 km²), where specimens of the same species had been collected in close proximity to each other, only one occurrence record per grid cell was included.

All morphological measurements were made on preserved specimens. Measurements were made to the nearest mm using a ruler or to the nearest 0.1 mm using a reticle and binocular microscope. Snout-vent length is abbreviated as SVL. All scale nomenclature and other specific gecko morphology follows previously used descriptions (Raxworthy and Nussbaum, 1994; Nussbaum et al., 2000). Abbreviations for field series are RAN, Ronald A. Nussbaum; RAX, Christopher J. Raxworthy. Standard institutional abbreviations are used (Leviton et al., 1985) with the addition of UADBA for the University of Antananarivo Department of Animal Biology.

Phylogenetic Analyses

Two taxa, *Rhoptropella ocellata* and *Lygodactylus* sp., were used as outgroups for phylogenetic analyses based on the results of Austin et al. (2004). The ingroup *Phelsuma* terminals included all our tissue samples for the *P. madagascariensis* and *P. dubia* group from Madagascar, and putative or previously supported closely related species (with available tissues or sequences) from Madagascar and elsewhere in the Indian Ocean (Austin et al., 2004; Rocha et al., 2007). This group of species was

selected to provide comparative material for assessing the specific status of our target taxa. The current species diversity for *Phelsuma* (including extinct species) is 38 species (Uetz, 2006). Localities, morphological voucher numbers, tissue numbers, and GenBank numbers of all samples are provided in the supplemental appendix (available at www.systematicbiology.org).

DNA from either frozen or ethanol preserved (70%) tissue samples was isolated using the QIAGEN DNAeasy spin columns. DNA from formalin-fixed museum specimens was extracted using a modified method from Fang et al. (2002) and precautionary steps were taken to prevent contamination (Glenn et al., 2002). To allow for the inclusion of non-Malagasy *Phelsuma* from previous studies (Austin et al., 2004; Rocha et al., 2007), our sequencing efforts focused on the mitochondrial 12S rRNA and cytochrome *b* genes. PCR amplification was performed under locus-specific parameters (Austin et al., 2004). All sequences were initially aligned using Sequencher v4.5 (Gene Codes, Inc.). Alignments were fine-tuned by eye, by amino acids (cyt-*b*), or to a secondary structure (12S rRNA: Houde et al., 1999). BLAST searches (NCBI) were performed for each contig to identify any potential contamination. PCR amplification was performed under locus-specific parameters. PCR cleanup, cycle sequencing reactions, and analysis were done using standard protocols previously described (Ingram et al., 2004). All sequences have been deposited in the NCBI GenBank database (accession numbers EF424440 to EF424466 and EF434870). The data set was partitioned by gene, codon position (for cyt-*b*), and stems and loops (for the 12S rRNA locus) for Bayesian analysis. The reading frames of cytochrome *b* were confirmed using MacClade v3.08 (Maddison and Maddison, 2002). Both loci were analyzed individually and combined (although because these mtDNA loci are genetically linked, a combined analysis was considered straightforward).

Maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods were used to analyze these data using PAUP*4.0b10 (MP: Swofford, 2002), Garli v0.942 (ML: Zwickl, 2006), and MrBayes v3.1.2 (BI: Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Under MP, all analyses were performed using equal weighting and the heuristic search option with 1000 replicate searches, random addition of taxa, and TBR branch swapping, with the steepest descent option not in effect. To determine the appropriate model of evolution for maximum likelihood and Bayesian analyses, a hierarchical likelihood ratio test (hLRT) was performed using ModelTest v3.06 (Posada and Crandall, 1998). For the ML analyses, four independent searches were performed with Garli default settings, except for the genthreshfortopterm, stopgen, and stoptime, which were increased to 20,000, 500,000, and 5,000,000, respectively. The likelihood scores from the "best tree" recovered using Garli were optimized using PAUP*. Bayesian posterior probabilities were calculated using the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) sampling approach in MrBayes v3.01 (Huelsenbeck and Ronquist, 2001). Four independent

searches were performed for each data set; each search consisted of a cold chain and three heated chains (temp = 0.2). All searches started with random trees and uniform prior probabilities for all possible trees. For the combined data set, data were partitioned by codon (cyt-*b*) and stems and loops (12S rRNA) and each partition was allowed to evolve at a different rate (Ronquist and Huelsenbeck, 2003). For all data sets, Markov chains were run for 2×10^7 generations and trees were sampled every 100 generations. To determine that stationarity had been reached, we compared the fluctuating values of the likelihood from the four independent searches using TRACER v1.3 (Rambaut and Drummond, 2003). The "burn-in" value was conservatively set at 2000; the first 2000 (200,000 generations) trees were eliminated from the approximation of posterior probabilities. The trees retained from each run were combined and a 50% majority rule consensus tree was produced to determine nodal posterior probabilities. The topologies recovered from MP, ML, and BI analyses for each data set were compared using the Shimodaira-Hasegawa (S-H) test (Shimodaira and Hasagawa, 1999) in PAUP*. Bootstrap proportions (BP; Felsenstein, 1985), decay indices (DI; Bremer, 1988), and posterior probabilities (PP; Ronquist and Huelsenbeck, 2003) were used as relative measures of nodal support. Bootstrap analyses were initiated using 1000 replicates, each with 10 random addition sequences and TBR branch-swapping using PAUP*. Decay indices were generated using TreeRot v.2 (Sorenson, 1999). Data matrices and trees have been submitted to TreeBase (accessions S1796 and M3280).

Ecological Niche Models

We applied the maximum entropy method (Maxent; Phillips et al., 2006), which requires only presence (not absence) species records and has been shown to perform well in comparison with other approaches (Elith et al., 2006), especially at low sample sizes (Hernandez et al., 2006; Pearson et al., 2007). Maxent characterizes probability distributions from incomplete information and is applied here to estimate the unknown probability distribution defining a species' distribution across the study area. The approach is to find the probability distribution of maximum entropy (that which is closest to uniform) subject to constraints imposed by the known distribution of the species and environmental conditions across the study area (Phillips et al., 2004, 2006). Because our study area contains a very large number of cells (~600,000), the implementation that we used took a random sample of 100,000 cells from the landscape to represent the environmental conditions present in the region. We implemented Maxent models using version 2.3 of software developed by S. Phillips and colleagues (for free download see <http://www.cs.princeton.edu/~schapire/maxent>). Selection of the convergence threshold, maximum number of iterations, regularization values, and features was carried out automatically by the software following default rules. Regularization is a variable selection method employed in Maxent to reduce the likelihood of overfitting.

Maxent assigns a probability of occurrence to each cell in the study area. However, because each cell's probability tends to be extremely small we generate model output as cumulative probabilities, wherein the value of a given grid cell is the sum of that cell and all other cells with equal or lower probability, multiplied by 100 to give a percentage (Phillips et al., 2006). Model output is thus a continuous variable ranging from 0 to 100, indicating relative suitability. To facilitate model analysis, we created binary predictions of presence and absence by classifying as "present" any cell with suitability greater than or equal to the lowest value associated with an observed presence record (Pearson et al., 2007).

Maxent models were built using environmental variables extracted from a database of digital layers relating to three principal traits: temperature, precipitation, and topography (Table 1). All environmental variables were resampled to an oblique Mercator projection at 1 km² resolution. Eleven temperature variables were extracted from the WorldClim data set (Hijmans et al., 2005; <http://www.worldclim.org>), which was generated by interpolation of climate data from weather stations (~117 stations in Madagascar). Four precipitation variables were derived from NOAA's Famine Early Warning System (FEWS) data archive (<http://www.cpc.ncep.noaa.gov/products/fews/data.html>). The FEWS precipitation estimates were generated using a method that incorporates data from models, satellite images, and surface data recorders (see Pearson et al., 2007). Five topographical variables were taken from the U.S. Geological Survey's Hydro1k database (<http://edcdaac.usgs.gov/topo30/hydro/index.asp>; see Pearson et al., 2007).

TABLE 1. The environmental layers used for ecological niche modeling.

Environmental variables and data sources
1. Annual mean temperature ^a
2. Mean diurnal range (mean of monthly [max. temperature – min. temperature]) ^a
3. Maximum temperature of the warmest month ^a
4. Minimum temperature of the coldest month ^a
5. Annual temperature range (variable 3 – variable 4) ^a
6. Isothermality [(variable 2/variable 5) × 100] ^a
7. Temperature seasonality (standard deviation × 100) ^a
8. Mean temperature of the wettest quarter ^a
9. Mean temperature of the driest quarter ^a
10. Mean temperature of the warmest quarter ^a
11. Mean temperature of the coldest quarter ^a
12. Mean annual precipitation ^b
13. Mean February precipitation ^b
14. Mean August precipitation ^b
15. Precipitation seasonality (coefficient of variation) ^b
16. Elevation ^c
17. Slope ^c
18. Aspect: northness ^{c,d}
19. Aspect: eastness ^{c,d}
20. Compound topographic index (wetness index) ^c

Data sources: ^aWorldClim (Hijmans et al., 2005); ^bNOAA Famine Early Warning System; ^cU.S. Geological Survey HYDRO1k database. ^dNorthness and eastness variables were generated from aspect using the transformations described in Pearson et al. (2007; supplemental appendix, available at www.systematicbiology.org).

Evaluation of the predictive ability of Maxent models (model validation) was based on two methods: when locality sample sizes exceeded 10 they were split 75:25 into training and test data partitions, with five replicate tests of random data partitions. For each replicate, we calculated the number of test localities omitted from the prediction and applied a binomial test to check statistical significance with regard to the proportion of the study area that was predicted as present. For smaller sample sizes (<25 localities) we also used the jackknife test as described by Pearson et al. (2007). In this case, to minimize effects of spatial autocorrelation, only training localities separated by at least 10 km from the jackknife test locality were used. Model evaluation was restricted to using only presence records. These evaluation results were used to compare ecological niche models based on lumped and split species limits.

RESULTS

Phelsuma Phylogeny

Approximately 1131 bp and 850 bp of the *cyt-b* and 12S rRNA mitochondrial genes, respectively, were analyzed for 34 individuals. For the *cyt-b* gene, 583 (52%) characters were variable and 160 (27% of 583) were parsimony informative. A heuristic search under maximum parsimony recovered a single most parsimonious tree (not shown; tree length [TL] = 1920, consistency index [CI] = 0.470, retention index [RI] = 0.592). For the 12S gene, 357 (42%) were variable and 283 (79% of 241) were parsimony informative. A heuristic search under maximum parsimony recovered 12 equally parsimonious trees (not shown: TL = 540, CI = 0.613, RI = 0.436). Under ML, the general time-reversible (Yang, 1994), corrected for among-site rate variation using the discrete gamma distribution and invariable sites (GTR+Γ+I), was significantly better than all simpler models (MODELTEST; *P*-value <0.001) for both *cyt-b* and 12S.

To allow comparisons between these two mitochondrial data sets, the phylogenies were trimmed to include only samples represented in both data sets. Based on the S-H test, the ML trees from each dataset were not significantly different (*P*-value = 0.10). This result and strong overall topological congruence between the recovered phylogenies (for all methods) provided support for analyses of the combined data set. The combined MP analysis resulted in four equally parsimonious trees (TL = 2753, CI = 0.516, RI = 0.662). For the combined analyses, the likelihood and Bayesian analyses recovered identical topologies (Fig. 4). Although the topology recovered from the MP analysis differed slightly, it was not statistically significant (S-H test; *P* = 0.221). The specific differences in topologies are described below.

Phelsuma madagascariensis Group

The ecological niche model based on all *Phelsuma madagascariensis* group records (64 localities) is shown in Figure 5a. Model validation statistics based on five replicate

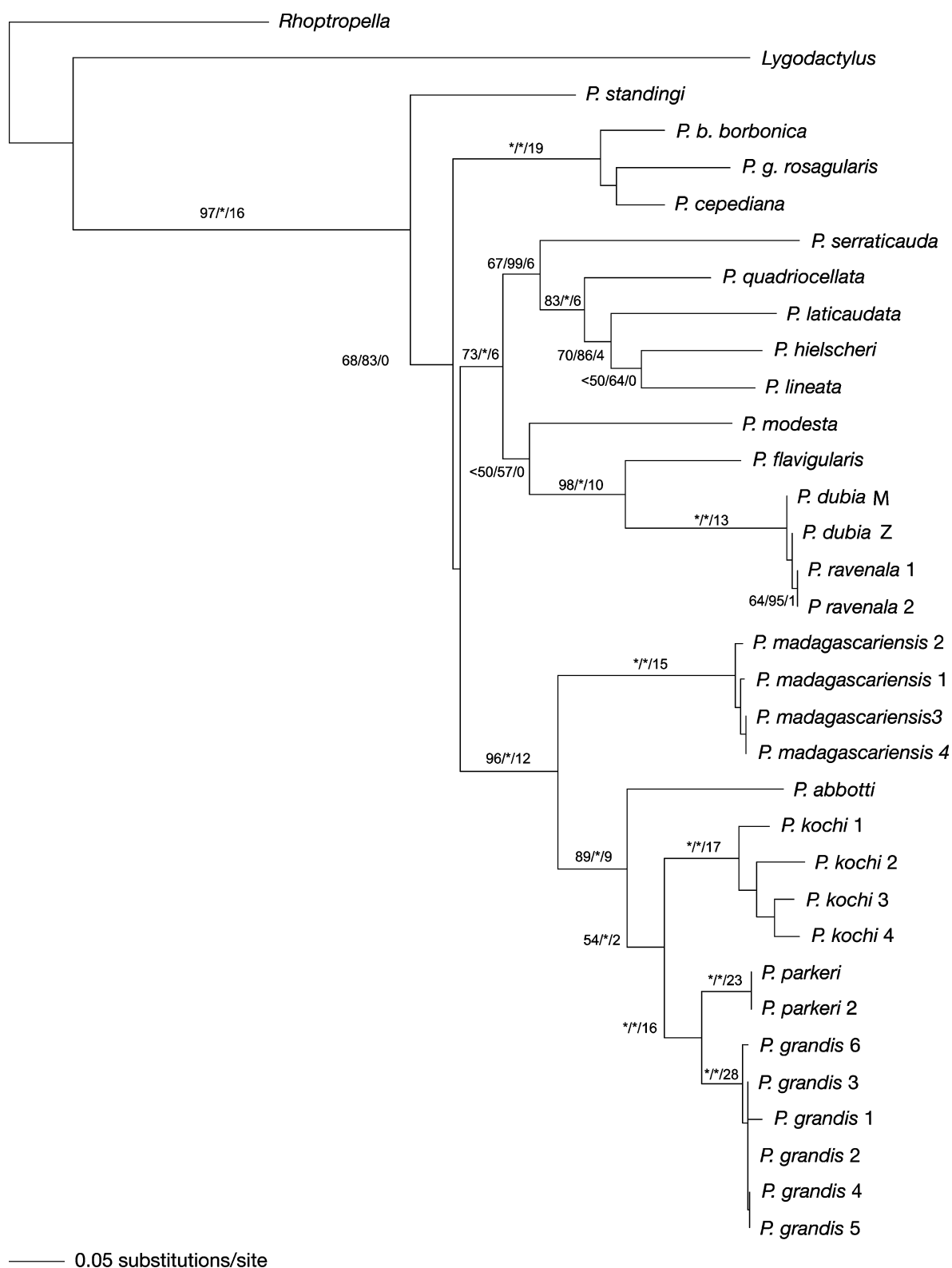


FIGURE 4. Maximum likelihood phylogeny under GTR+ Γ +I ($-\ln L = 13,765.409$, $\alpha = 0.98021$ proportion of invariable sites = 0.35260) based on 1981 bp of combined data (12S rRNA and *cyt-b*). All Bayesian analyses recovered a similar topology. Maximum parsimony recovered an almost identical topology (see text for details). Values above branches are MP bootstrap proportions, Bayesian posterior probabilities, and Bremer decay indices. M = Madagascar; Z = Zanzibar. Taxon numbers correspond to those used in the supplemental appendix (available at www.systematicbiology.org).

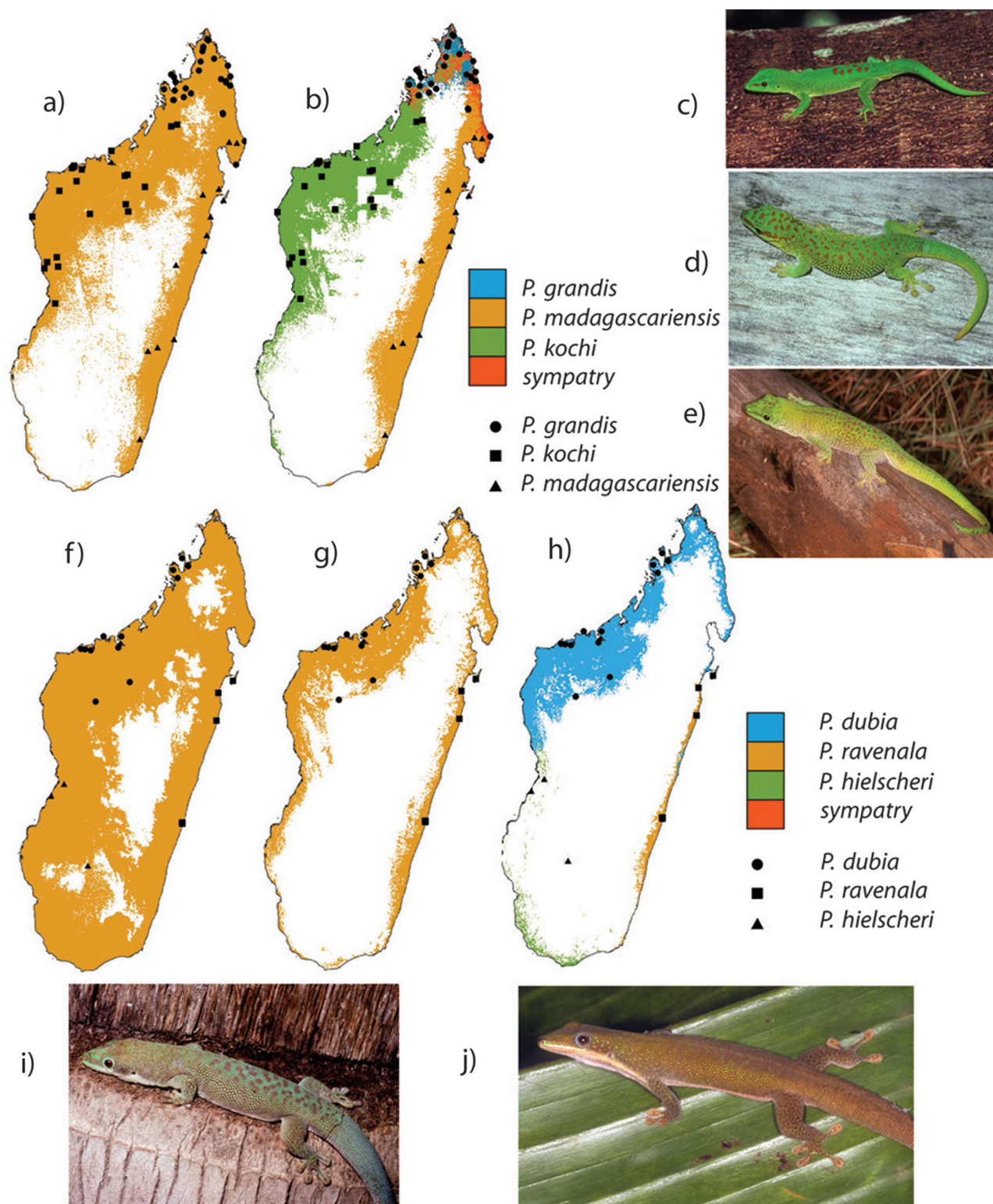


FIGURE 5. (a) The single ecological niche model based on all localities, when treating the *Phelsuma madagascariensis* subspecies group as consisting of a single species (*P. m. madagascariensis*, *P. m. grandis*, *P. m. kochi*). (b) The three overlaid ecological niche models, when treating each subspecies as a valid species. (c) *Phelsuma grandis* (Manongarivo). (d) *Phelsuma madagascariensis* (Masoala, UMMZ 208192). (e) *Phelsuma kochi* (Ambohibola). (f) The single ecological niche model based on all localities, when treating the *Phelsuma dubia* species group as a single species (including *P. dubia* + *P. hielscheri* + *P. ravenala* sp. nov.). (g) The *Phelsuma dubia* species group ecological niche model, when excluding the three *P. hielscheri* localities. (h) The three overlaid ecological niche models, when treating *Phelsuma hielscheri*, *P. dubia* (west coast), and *P. ravenala* sp. nov. (east coast) as valid species. (i) *Phelsuma dubia* (Ambanja). (j) *Phelsuma ravenala* sp. nov. (Mananjary).

random partitions of the localities into test (25%) and training (75%) data and the binomial test were as follows: omission error = 0–0.188 (0–3 from 12 test localities omitted), and $P < 0.01$ in all replicates. These validation replicate results are statistically significant (correct prediction of test points is better than random, based on model area compared to the total area of Madagascar), but inspection of the model reveals extensive areas of prediction within the interior of the island where no records exist (potential zones of false positives). Most of the interior of the island substantially exceeds the maximum known elevation of 1000 m for *P. madagascariensis* (Raxworthy, personal observation). Modeling each subspecies separately results in the overlaid ecological niche models shown in Figure 5b. Model validation statistics for *P. m. grandis* (28 localities): omission error = 0–0.571 (0–4 from seven), and $P < 0.001$ in all replicates. Model validation statistics for *P. m. kochi* (22 localities): omission error = 0–0.6 (0–3 from five), and $P < 0.05$ in three of five replicates. Model validation statistics for *P. m. madagascariensis* (14 localities): omission error = 0–0.34 (0–1 from three), and $P < 0.01$ in four of five replicates. Jackknife validation (for taxa with <25 localities): *P. m. madagascariensis* omission error = 2 of 14, $P < 0.001$; *P. m. kochi* omission error = 5 of 22, $P < 0.001$. In contrast to the combined model (Fig. 5a) the three subspecies models generate a much better fit to the known distribution, with almost all the interior regions of Madagascar now shown to be absent for these subspecies. Also, despite smaller locality sample sizes, these three subspecies ecological niche models are statistically significant in almost all replicates and in all jackknife tests. These findings are consistent with each subspecies having evolved its own distinct niche space, and correspondingly, the models having parapatric or allopatric spatial distributions (site sympatry between subspecies is unknown in the field). The combined modeled niche space for the three subspecies includes substantial niche space that is actually unoccupied. These results are thus consistent with each subspecies representing a separate species lineage.

For the combined mitochondrial data, almost identical relationships for the *P. madagascariensis* subspecies and closely related species (*P. abbottii* and *P. parkeri*) were recovered in all analyses (MP, ML, BI), with *P. parkeri* and *P. m. grandis* forming a clade. *P. abbottii* is sister to a *P. parkeri* + *P. m. grandis* + *P. m. kochi* clade (ML, BI) or forms a polytomy with the *P. m. kochi* clade and *P. parkeri* + *P. m. grandis* clade (MP). *P. m. madagascariensis* is sister to all other members of this entire *P. madagascariensis* group clade in all analyses. As a result, *P. abbottii* and *P. parkeri* render the *P. madagascariensis* subspecies group paraphyletic. The average uncorrected *P*-distances (cyt-*b* / 12S) between these taxa are *P. m. grandis* vs. *P. parkeri* (0.08918/0.03588); and *P. m. grandis* + *P. parkeri* + *P. abbottii* + *P. kochi* clade –vs. *P. m. madagascariensis* (0.19733/0.1086). The molecular results thus support the ecological niche modeling results, and are consistent with each *P. madagascariensis* subspecies representing a separate species.

Morphological examination of the *P. madagascariensis* subspecies also finds the following character variation that can be used to diagnose each form: size of tubercles (rounded scales) on the body flanks compared to the mid-dorsal region, extent of the reddish eye-stripe, the dorsal coloration of the body, comparative size of neck tubercles compared to surrounding tubercles, development of chevron markings on the throat, and maximum adult SVL. These characters are described in detail below in “Proposed Taxonomic Changes.” As with the molecular data, the morphological results support the ecological niche modeling results and are consistent with each subspecies representing a separate species lineage that is diagnosable using morphology.

Phelsuma dubia Group

The ecological niche model based on all *Phelsuma dubia* group records (21 localities): *Phelsuma dubia* + *P. hielscheri* + *P. ravenala* sp. nov. (see below) is shown in Figure 5f. Model validation statistics based on five replicate partitions of the localities into test (25%) and training data and the binomial test are as follows: omission error = 0–0.4 (0–2 from five), and $P < 0.05$ in one of five replicates. The majority of validation replicates are not statistically significant, and inspection of the model reveals extensive areas of prediction within the interior and south of the island where no records exist (potential zones of false positives). After removing the *P. hielscheri* records, we modeled the *Phelsuma dubia* group again, resulting in the model shown in Figure 5g. Model validation statistics for *P. dubia* + *P. ravenala* sp. nov. (18 localities) are omission error = 0–0.75 (0–3 from four), and $P < 0.01$ in three of five replicates. In contrast to the combined *Phelsuma dubia* + *P. hielscheri* + *P. ravenala* sp. nov. model (Fig. 5f), the majority of *Phelsuma dubia* + *P. ravenala* sp. nov. validation replicates are statistically significant and the model provides a much better fit for distribution, with almost all the interior and southern regions of Madagascar now shown to be absent. However, it is also apparent that the localities now fall into two clusters: an eastern *P. ravenala* sp. nov. group and a western-northwestern coastal *P. dubia* group, which are separated from each other by a coastal region of northern and northeastern Madagascar that lacks localities. In addition, the southern distribution limits along both coasts appear too extensive—especially for the western coastal populations. Modeling *P. dubia*, *P. ravenala* sp. nov., and *P. hielscheri* separately results in the three overlaid niche models shown in Figure 5h. Model validation statistics for western coastal *P. dubia* (12 localities) are omission error = 0–1.0 (0–3 from three), and $P < 0.01$ in four of five replicates. The two other taxa had sample sizes that were too small to validate with replicate partition testing. Jackknife validation statistics for the western coastal *P. dubia* (12 localities) are omission error = 2 of 12, and $P < 0.001$ for all replicates. Statistics for the eastern coastal *P. ravenala* sp. nov. (6 localities) are omission error = 4 of six, and $P < 0.001$ for all replicates. The *P. hielscheri* locality sample size (three) was too small

for validation. These models for eastern and western coastal forms of *P. dubia* provide a better fit for distribution, with almost all of the interior and southern regions of Madagascar now removed from the prediction. This finding is consistent with *P. hielscheri*, the eastern *P. ravenala* sp. nov., and western *P. dubia* each having evolved to occupy different environmental niche space, and correspondingly, the modeled distributions being parapatric and allopatric to each other (sympatry between *P. dubia* and *P. hielscheri* is unknown in the field). The combined modeled niche space for the three species/populations includes substantial niche space that is actually unoccupied (with low validation statistical support), which is indicative of divergent species niches. These results are thus consistent with *P. hielscheri*, the eastern *P. ravenala* sp. nov., and western *P. dubia* each representing separate species.

The combined mtDNA phylogenetic relationship recovered under ML and BI for western Madagascar and Zanzibar populations of *P. dubia*, *P. hielscheri*, *P. ravenala* sp. nov., and closely related species, *P. flavigularis* and *P. modesta* is shown in Figure 4. This topology differs from the MP analysis in the placement of *P. modesta* placed basal to the *P. quadriocellata*–*P. lineata* clade in the MP analysis, and *P. hielscheri* sister to *P. laticauda*. The Zanzibar *P. dubia* specimen is sister to the two *P. ravenala* sp. nov. samples, and this clade is sister to the western Madagascar *P. dubia* sample (ML, BI). For the MP results, the Zanzibar *P. dubia* specimen forms a polytomy with the *P. dubia* from Madagascar and the *P. ravenala* sp. nov. clade. In all analyses these species are sister to *P. flavigularis*. Remarkably, in all analyses, *P. hielscheri* does not form a sister clade with *P. dubia* but instead is recovered as sister to *P. lineata* or *P. laticauda* (see above). The uncorrected *P*-distances (cyt-*b*, 12S) are *P. ravenala* sp. nov.–*P. dubia* (Zanzibar = Z; na/0.0028), *P. ravenala* sp. nov.–*P. dubia* (Western Madagascar = W; na/0.0047), *P. dubia*–*P. hielscheri*, (0.2148/na). The uncorrected average *P*-distances (cyt-*b*, 12S) between *P. dubia* and *P. flavigularis* is 0.1874/0.0855, and the smallest distance (0.1455/na) is between *P. lineata* and *P. hielscheri*. These molecular results support the ecological niche modeling results, and are consistent with *P. hielscheri*, *P. dubia*, and *P. ravenala* sp. nov. each representing separate species in Madagascar. However, the 12S genetic divergence exhibited between populations of *P. dubia* and *P. ravenala* sp. nov. in Madagascar suggests a recent divergence. Morphological examination of *P. dubia*, *P. hielscheri*, and *P. ravenala* sp. nov. also finds the following character variation that can be used to diagnose each taxon: number of scales around the midbody, body color, maximum number of femoral pores, and surface form of the scales on the ventral surface of abdomen (Table 2). These characters are described in detail below in “Proposed Taxonomic Changes.” As with the molecular data, the morphological results support the ecological niche modeling results, and are consistent with *P. dubia*, *P. hielscheri*, and *P. ravenala* sp. nov. representing separate species lineages that are diagnosable using morphology.

TABLE 2. Adult variation in *Phelsuma ravenala* sp. nov., *P. dubia*, and *P. hielscheri*. All measurements in mm. *Phelsuma dubia* data taken from the following specimens: UMMZ 201547–201552, 208022–208023, 208025, 216606, 219295–219300. *P. hielscheri* data taken from Rösler et al. (2001) and UMMZ 216604–05. ps = nostril center posterior to suture between rostral and first supralabial.

Character	Species			
	<i>P. ravenala</i> sp. nov.		<i>P. dubia</i>	<i>P. hielscheri</i>
	Holotype	AMNH	UMMZ	Types/UMMZ
Total n	1	17	15	7
Male SVL (n)	61 (1)	49–61 (8)	42–62 (11)	50–73 (5)
Female SVL (n)	—	50–57 (9)	48–57 (4)	50–64 (2)
Tail length ^a	59	40–68	46–75	54–88
Supralabials	10	10–11	10–12	10–11
Infralabials	10	9–10	9–10	8–10
Nostril position	ps	ps	ps	ps
Scansors 4th toe	17	16–18	16–19	16–17
Femoral pores	27	8–27	15–31	25–30
Scales around body	75	68–76	78–86	86–98

^aIncludes regenerated tails.

PROPOSED TAXONOMIC CHANGES

Phelsuma madagascariensis Group

Based upon the results from ecological niche modeling, mtDNA, and morphology, we here formally propose to elevate the following three *P. madagascariensis* subspecies: *P. m. madagascariensis*, *P. m. grandis*, and *P. m. kochi*, to species rank. An identification key for these taxa is provided below (see also Fig. 5c to e). We also propose that the subspecies *P. m. boehmei*, known only from the type locality (Perinet), is considered a junior synonym of the nominate form *P. madagascariensis*. The reported diagnostic character for this subspecies, dark skin between tubercles, has been previously recorded for coastal *P. m. madagascariensis* (see Glaw and Vences, 1994). Examination of the *P. m. madagascariensis* that we have collected (UMMZ 192428, 196856, 208192, 216702; AMNH R-155736–40) also reveals individual variation in the darkness of skin color between the dorsal tubercles, and we thus consider *P. m. boehmei* as a junior synonym of the nominate species.

Identification key for the *Phelsuma madagascariensis* group in Madagascar:

- 1a. Tubercles on the body flanks greatly enlarged compared to mid-dorsal tubercles, many exceeding 1 mm horizontal diameter in adult; reddish eye stripe extends from nostril through eye to neck *P. madagascariensis*
- 1b. Tubercles on the body flanks moderately enlarged compared to mid-dorsal tubercles, but rarely exceed 1 mm horizontal diameter in adult; reddish eye stripe extends from nostril to eye only 2
- 2a. Brilliant green body, including lower flanks, which are never mottled with brown and white; field of slightly enlarged neck tubercles posterior to ear

- opening; weak, dark double chevron marking often absent on throat, adult SVL may exceed 100 mm *P. grandis*
- 2b. Pale lime green body, with lower flanks mottled with brown and white; no obvious field of enlarged neck tubercles posterior to ear opening; weak dark double chevron marking often visible on throat, adult SVL typically <100 mm *P. kochi*

Phelsuma dubia Group

Our results from ecological niche modeling, mtDNA, and morphology all support the recognition of *P. dubia*, *P. hielscheri*, and *P. ravenala* sp. nov. as separate valid species. The type locality for *Phelsuma dubia* is the near-offshore island of Nosy Be, in northwestern Madagascar and the holotype has been both recently rediscovered and redescribed (Mertens, 1973; Glaw et al., 1999). Consequently, the east coast form represents a new species, which we here describe.

NEW SPECIES DESCRIPTION

Phelsuma ravenala sp. nov. (Fig. 5)

Holotype.—AMNH R-155718 (RAX 8676), a mature male, collected 14 February 2006, outskirts of Mananjary Town, 21°12.004'S, 48°21.254'E, 20 m elevation, by Mananjary Fivondronana, Fianarantsoa Province, Madagascar, by N. Rabibisoa, J. Rafanomezantsoa, A. Rakoton-drazafy, P. Razafimahatratra, and C. J. Raxworthy.

Paratypes.—UADBA RAX 8651, 8675; collected 13 to 14 February 2006, Mananjary Town, 21°13'S, 48°20'E, 10 m elevation, all other data as holotype. AMNH R-155719-35 (RAX 8679-8682, 8684-8686, 8725, 8728, 8731-8733, 8735-8738, 8742) and UADBA RAX 8677-78, 8683, 8724, 8726-8727, 8729-8730, 8734, 8739-8741, 8743-8745; collected 14 to 15 February 2006, at same locality and by same collectors as holotype.

Diagnosis.—A medium-sized (adults 49 to 61 mm SVL) *Phelsuma* with slender form, head and body not strongly flattened dorsoventrally. In life, dorsal ground color green with reddish brown spots on body; throat white and lacking dark chevrons. Median dorsal cleft in rostral scale; nostril above first supralabial, not in contact with rostral; smooth (unkeeled) scales on ventral surface of abdomen and tail; dorsolateral scales much larger than dorsal scales, 68 to 76 scales around midbody; males with up to 27 femoral pores; subcaudal scales less than twice as wide as long.

Phelsuma ravenala sp. nov. differs from all other *Phelsuma* species by a combination of subcaudal scales less than twice as wide as long, ventral scales of abdomen smooth, body lacks a prominent black lateral line, SVL < 70 mm, enlarged dorsolateral body scales compared to dorsal granules, 68 to 76 scales around midbody, dorsal coloration green, and throat coloration white without dark chevrons. *Phelsuma ravenala* sp. nov. is phenetically most similar to *P. dubia* and *P. hielscheri* but can be distinguished by the lower number of scales around mid-

body (68 to 76 versus 78 to 98), body color (green versus grayish or greenish-blue, Fig. 5i, j), and the lower maximum number of femoral pores (27 versus 30 to 31). It also differs from *P. hielscheri*, two other similar species *P. flavigularis*, and *P. berghofi* by the form of the scales on the ventral surface of the abdomen (smooth vs. keeled). It also differs from *P. flavigularis* and *P. berghofi* by color of the throat (white versus yellow).

Description of holotype.—Specimen in excellent condition, but right forelimb missing (removed as a tissue sample). Right hemipene everted. Tail regenerated for 59 mm. Measurements and features of scalation in Table 2.

Body and head not strongly flattened dorsoventrally. Distinct rostral cleft in dorsal process of rostral scale. Three postrostral scales posterior to rostral and between nasal scales. Nostril center positioned above the first supralabial scale, posterior to the suture between the rostral and first supralabial scales. Three postnasals on each side. Dorsal and lateral scales of head smooth, nearly flattened in profile, but becoming increasingly rounded in profile on the posterior regions of the head. Dorsal scales of neck and body tuberculate; vertebral and dorsolateral scales keeled. Dorsolateral body scales much larger than dorsal scales. Dorsal scales of fore- and hind limbs weakly keeled. Regenerated portion of tail without keeled scales or tail whorls. Two tail whorls evident on original tail, with each whorl including six transverse scale rows in dorsal view. Subcaudal scales less than twice as long as wide. Scales of lateral portion of body weakly keeled. All ventral scales smooth, except narrow transverse band of weakly keeled scales in the pectoral area.

Coloration after eight months in preservative: ground color of dorsum of head, neck, body, tail and limbs brownish, with weak orange blotches on dorsal body that are most prominent on the posterior half, where some fuse to form short transverse bars. Weak orange blotch between eyes, and a smaller spot on midline of the anterior snout. Ring of scales around eyes grey. Iris gray. Lips (supra- and infralabials) white. Venter of chin, throat, limbs, tail, and body white with a sharp transition to the darker dorsal coloration.

Coloration in life.—Ground color of dorsal and lateral surfaces of head, body, limbs, and tail metallic green, with darker greenish brown skin color between body tubercles that are most obvious on flanks. A red line runs from the eye to snout tip, with a smaller red spot on the midline of the anterior snout. Bright blue ring of scales surrounds eye, iris bright red. Upper lips with greenish sheen. Lower lips white. Neck with small scattered pale green flecks. Irregular dark reddish brown spots on dorsal body, most prominent on the posterior half, where some fuse to form short transverse bars. Upper surfaces of limbs with small brown spots. Venter white.

Variation.—Morphometric and meristic variation of the types are summarized in Table 2. Some individuals in life have traces of a slightly darker lateral line on the neck and in the groin area, which can still be seen in preservation in a few specimens (e.g., AMNH R-155720, 155725). The only ontogenetic variation in coloration now seen

in preservation is the slightly pale yellow tail, which is found in the juvenile coloration of smallest specimen examined, AMNH R-155722 (RAX 8682), with an SVL of 25 mm. There is no obvious sexual dichromatism and no sexual dimorphism, except that males have femoral pores and may reach a slightly larger size (see Table 2).

Etymology.—The specific name “*ravenala*” is the Malagasy name for the Traveller’s Palm *Ravenala madagascariensis*, which appears to represent the major habitat for this species of day gecko.

Distribution.—The Mananjary region, and possibly the east coast of Madagascar as far north as Nosy Boraha (Isle Ste. Marie) (see Berghof, 2001).

Habitat.—All specimens of *Phelsuma ravenala* sp. nov. were seen on the trunks or frond stems of Traveller’s Palms (*Ravenala madagascariensis*) growing in plantations, grassland, or gardens around and within the town of Mananjary (0 to 20 m elevation). Geckos only occupied Traveller’s Palms exceeding approximately 6 m in total height, and were caught up to a height of 8 m above ground.

Remarks.—Excluding Traveller’s Palms, we conducted intensive searches for *Phelsuma* in other palm trees (primarily coconut), banana plants, and *Pandanus* screw palms in anthropogenic areas and degraded littoral forest in the Mananjary region. These searches yielded *Phelsuma pusilla* and *Phelsuma madagascariensis* (the latter only in littoral forest) but we did not find other *Phelsuma ravenala* sp. nov., and we tentatively conclude that this species may be a specialist of the Traveller’s Palm (similar to *P. berghofi*, pers. obs.). *Phelsuma ravenala* sp. nov. uses palm axils as places to take refuge, and possibly their more slender body plan (compared to *P. dubia*) facilitates entry into these areas. They were frequently seen licking plant fluids associated with palm fruits. As many as five individual *Phelsuma ravenala* sp. nov. were found inhabiting a single plant, however we never found this species associated together with other *Phelsuma* species at the type locality.

DISCUSSION

Species Delimitation

We find that ecological niche modeling has considerable utility in recognizing closely related species in *Phelsuma*. Morphological or molecular data were first used as a guide for partitioning localities between suspected species. Subsequently, using both the lumped and split taxonomic groupings, ecological niche models were compared for predictive performance. In both our empirical studies, these species complexes were found to include taxa that occupied divergent niche space.

The detection of the new species, *P. ravenala*, represents an example where, despite low levels of molecular divergence with its sister species *P. dubia*, niche differences, morphologically diagnostic characters, and disjunct distributions all supported both lineages representing separate species. These findings thus suggest that for some species, niches have the potential to evolve

relatively rapidly. Interestingly, the area of coastal endemism in southeast Madagascar occupied by *P. ravenala* corresponds to part of the niche model prediction for the related species *Phelsuma modesta*. The *P. modesta* niche model includes a disjunct unoccupied area north of its actual distribution, which corresponds closely to the southern distribution of *P. ravenala* sp. nov. that includes the type locality (compare Figs. 2 and 5h). Indeed, the type locality for *P. ravenala*, Mananjary, was originally selected for survey based upon the *P. modesta* niche model and others, as part of a larger scale test of using ecological niche models to identify previously unrecognized areas of local endemism (Raxworthy et al., 2003).

Despite these advances, one of the remaining challenges with the species delimitation approach that we present here concerns the assessment of the ecological niche model quality in the lumped vs. split species complexes. Obtaining allopatric or parapatric models for the split species could be deemed sufficient argument alone for species delimitation. But ideally, the lumped species localities should also result in an inferior ecological niche model, when compared to the predictive performance of the models based on the split species localities. Both *Phelsuma* species groups produced inferior models for the lumped species (showing substantial erroneous prediction in the interior regions of the island), yet this was only clearly reflected by the model validation statistics in one of the two groups that we studied (*P. dubia* group). Thus, we also assessed model quality by expert opinion: in our case utilizing negative distribution data from other surveys conducted by CJR and others within the interior of Madagascar. A potential solution for model validation might therefore be the inclusion of negative locality data. However, as has been reported elsewhere, there are also substantial pitfalls concerning the use of negative locality data, especially for more poorly surveyed regions (Anderson, 2003).

We expect that ecological niche modeling will have greatest utility for species delimitation in groups that show high levels of local endemism (especially tropical species with low vagility and inhabiting regions with steep environmental gradients) and for cryptic species that exhibit low levels of molecular divergence and little morphological divergence. This species delimitation technique will be especially valuable for detecting ecologically mediated parapatric speciation, when the environmental gradient variables driving speciation are also used for ecological niche modeling. If results for other taxonomic groups prove similar to those that we report here for *Phelsuma*, this technique may offer great potential in detecting recent ecologically driven speciation events.

Niche Evolution and Speciation

Contrasting results have been recently reported concerning the degree of plasticity shown by ecological niches between closely related species. Some authors, including Peterson et al. (1999) and Kozak and Wiens (2006), have found niches to be conservative between

sister species, and suggested that the lack of niche evolution facilitates speciation by producing allopatric distributions in response to changing environmental conditions. Other authors have found considerable niche plasticity between sister species or closely related species (Losos et al., 2003; Graham et al., 2004b) or else no general relationship between phylogenetic similarity and niche similarity (Knouft et al. 2006). Furthermore, evidence for intraspecific niche variation has been reported by Peterson and Holt (2003).

However, even in the case of conservative niches, ecological niche modeling may still detect evidence for cryptic species. This is the situation when species distributions are modeled with disjunct areas, and a case for genetic isolation between these allopatric populations can be made (Wiens and Graham, 2005). We did not obtain empirical results of conservative niches and allopatric sister species (conservative niches being recognized here based on a criteria of substantial niche model overlap, see also Peterson et al., 1999), but conservative niches have been found for sister taxa of montane salamanders in the Appalachian Highlands (Kozak and Wiens, 2006). These authors (and Wiens and Graham, 2005) also propose that in order to test whether niche conservatism drives allopatric lineage splitting, the niche characteristics of sister species and the intervening absence localities should be compared, and that the intervening areas should be the more divergent. However, for our *Phelsuma* sister species (within Madagascar), the parapatric model distributions that we report here do not suggest lineage divergences being driven by isolation.

Our results find that in both species groups of *Phelsuma*, closely related taxa occupy divergent niches that show little spatial overlap when projected in geographic space. The most striking example of ecological divergence is shown by the *P. dubia*–*P. ravenala* species pair, which show low levels of genetic divergence (0.47%, 12S uncorrected *P* distance) but that occupy different environmental and geographic space (Fig. 5h). Similarly, for the *P. madagascariensis* species group, the three former Madagascar subspecies that we consider valid species occupy divergent niches that show little spatial overlap. These findings suggest that niche divergence can evolve comparatively quickly when compared to morphology or genetic divergence, and we suspect (based upon similar patterns of endemism), that many low-vagility species groups in Madagascar have closely related species occupying divergent environmental space.

The apparent close association of *P. ravenala* with the Traveller's Palm (*Ravenala madagascariensis*) is intriguing. We have also observed a similar association for *P. berghofi*, a species that appears closely related (based on phenetic similarity) to *P. ravenala*, *P. flavigularis*, and *P. dubia*. However, it is not clear if the Mananjary population (type locality) and other suspected more northerly populations of *P. ravenala* are restricted to *Ravenala*. In particular, Berghof (2001) has reported *P. dubia* as occupying *Ravenala* and coconut palms at Mananjary and also

occupying coconut palms at Toamasina (Tamatave) and Nosy Boraha (Isle Ste. Marie). For the ecological niche modeling, we tentatively assigned the populations at these two latter sites to *P. ravenala*. However, because Toamasina and Nosy Boraha are heavily frequented by boat traffic, these populations could otherwise represent human-introduced *P. dubia*, as suspected for *P. dubia* in the Comoro Islands (Rocha et al., 2007). By comparison, *P. dubia* in western Madagascar occurs on a wide variety of palm trees, including coconut (Raxworthy, pers obs). Thus, although our observations at Mananjary are suggestive, contradictory evidence does not support *P. ravenala* being an obligate *Ravenala* palm specialist. It is also worth noting that this palm occupies primary, secondary, and anthropogenic humid habitats across Madagascar, and thus has a wide distribution that is far greater than the current known distribution of *Phelsuma ravenala*.

Concerning the speciation history for both these species groups in Madagascar, and because distributional data alone are always open to multiple interpretations (Moritz et al., 2000), we examine here support for alternative speciation scenarios. These include (1) allopatry established by rivers creating barriers to dispersal (Martin, 1972; Pastorini et al., 2005); (2) allopatry established by populations becoming isolated within watersheds (Wilmé et al., 2006); and (3) ecologically mediated parapatric speciation (see Smith et al., 1997; Schneider et al., 1999; Moritz et al., 2000; Via, 2001; Ogden and Thorpe, 2002) based on an ancestral coastal population distributed along an environmental gradient.

For continental Madagascar, the scenario of allopatric speciation via a river barrier does not find strong support because (1) Madagascar's coastal area is covered by hundreds of bisecting rivers and consequently coastal species have distributions that traverse many river drainages; (2) species distribution breaks do not correspond to the largest river systems; and (3) in the case of *P. madagascariensis* and *P. grandis*, we have found both occupying the same side of the same river drainage: the northern bank of the Ankavanana and Onive River, Masoala, but not at the same site (see also Krüger, 1996, for similar observations).

Wilmé et al. (2006) recently proposed that during glacial periods, orographic precipitation maintained mesic conditions at higher elevations in river valleys, which were occupied by species retreating from increased aridity at lower elevations. Consequently, they suggest that endemism evolved within the most isolated mesic areas of watersheds. However, we find that none of the *Phelsuma* distributions we report here are confined to any of the watershed areas of endemism that were identified by Wilmé et al. (2006).

For these *Phelsuma* species, parapatric speciation scenarios are more parsimonious than the preceding two allopatric scenarios in terms of minimizing assumptions of either range expansion or contraction. Niche differences between species are consistent with an ecologically mediated form of parapatric speciation (disruptive selection for different niches; see Schluter, 2001), and these species

are distributed on significant environmental gradients. The latitudinal range seen in these coastal *Phelsuma* distributions results in these species straddling significant gradients for both rainfall and temperature under current climatic conditions (Jury, 2003; Hijmans et al., 2005). In addition, based on the descriptions of paleoclimate models for Madagascar (Wells, 2003) similar gradients appear to have existed throughout the Cenozoic. Conversely, however, some of the steepest climatic gradients in Madagascar are based on elevation, and it is therefore surprising to see no evidence for montane parapatric speciation within these groups, if parapatric speciation is dominant. Kozak and Wiens (2006) have proposed a test for parapatric speciation by comparing correlations of genetic variation with geographic distance vs. climatic distance (measured as Euclidean distance within a principal-components analysis of climatic variables). Their expectation is that climatic distance should be more strongly correlated to genetic variation when parapatric speciation is being driven by environmental gradients (assuming that climatic distance is a good surrogate for the actual environmental gradient driving speciation). However, additional genetic sampling will be required before such an evaluation can be conducted on these *Phelsuma* species.

Concerning our phylogenetic results for the other *Phelsuma* species, these are largely congruent with Austin et al. (2004) and Rocha et al. (2007), and find support for a major Madagascar radiation of *Phelsuma*, with additional oceanic dispersals from Madagascar for the Mascarene Island clade (*Phelsuma cepedianana*, *P. borbonica*, and *P. guimbeaui*), *P. parkeri* on Pemba Island, the population of *P. abbottii* on Aldabra, and the populations of *P. dubia* on the Comoros, Zanzibar, and in East Africa. In the case of *Phelsuma parkeri*, the relatively high levels of divergence we find compared to its sister taxa, *P. grandis*, suggests a comparatively ancient origin on Pemba Island for *P. parkeri*. A lack of geographic structure found between *P. dubia* populations on different Comoros islands and a specimen from Zanzibar has led Rocha et al. (2007) to suspect a recent and possibly anthropogenic colonizations from Madagascar. Further study will be needed to establish the phylogenetic relationships between these island populations and the *P. dubia* and *P. ravenala* populations in Madagascar. Our preliminary analysis based on 12S mtDNA (not shown) finds the Zanzibar specimen falling in a clade with *P. ravenala* and the other Comoros specimens forming a polytomy with *P. dubia* from Northwest Madagascar. However, the inclusion of many more species is needed to explore the full biogeographic history of this group, especially concerning continental speciation within Madagascar itself.

Nevertheless, based on the findings of this study, we anticipate that this new application of ecological niche modeling will greatly facilitate species delimitation, and thus also aid the recognition of both additional species diversity and more recent speciation events. In addition, through combining phylogenetic data with ecological niche models, for more recently diverged sister species, we also expect this approach to offer exciting new op-

portunities for exploring the processes of continental speciation.

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