Taylor & Francis
Taylor & Francis Group

Research Article

Bayesian inference of species diffusion in the West African *Agama agama* species group (Reptilia, Agamidae)

ADAM D. LEACHÉ[1], JARED A. GRUMMER[1], MICHAEL MILLER[1], SNEHA KRISHNAN[1], MATTHEW K. FUJITA[2], WOLFGANG BÖHME[3], ANDREAS SCHMITZ[4], MATTHEW LEBRETON[5], IVAN INEICH[5], LAURENT CHIRIO[5], CALEB OFORI-BOATENG[6], EDEM A. ENIANG[7], ELI GREENBAUM[8], MARK-OLIVER RÖDEL[9] & PHILIPP WAGNER[10]

[1]Department of Biology & Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, 98195-1800, USA
[2]Department of Biology, University of Texas at Arlington, Arlington, TX, 76019, USA
[3]Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D53113, Bonn, Germany
[4]Natural History Museum of Geneva, Department of Herpetology and Ichthyology, C.P. 6434, CH-1211, Geneva 6, Switzerland
[5]Muséum National d'Histoire Naturelle & Sorbonne Universités, Département Systématique & Évolution (Reptiles), ISyEB (Institut de Systématique, Évolution, Biodiversité, UMR 7205 CNRS/UPMC/EPHE/MNHN), Paris, France
[6]Forestry Research Institute of Ghana, P.O. Box 63, Fumesua, Kumasi, Ghana
[7]Department of Forestry and Wildlife, University of Uyo, Akwa Ibom State, Nigeria
[8]Department of Biological Sciences, University of Texas at El Paso, 500 West University Ave., El Paso, TX, 79968, USA
[9]Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity, 10115, Berlin, Germany
[10]Zoologische Staatssammlung München, Münchhausenstr. 21, D81247, München, Germany

The savannah and tropical forest biomes of Africa have a long history of expansion and contraction, and the recent and rapid spread of dry savannah habitats has influenced the spatial and temporal diversification of vertebrate taxa across this region. We used a combination of species tree and phylogeographic methods to describe the spatio-temporal changes through time and across space (= species diffusion) in a clade of seven West African lizard species in the *Agama agama* species group. A Bayesian species tree diffusion approach was used to compare the relative rates at which species ranges changed across the landscape. We found that some species have high diffusion rates characterized by significant movement in their range location and minor changes to their overall range size, whereas other species show little movement in their range centre with an exponential increase in range size. This discrepancy between the rates that range locations shift versus change in their relative area could be linked to populations tracking their preferred habitats through time. A continuous Bayesian phylogeography approach using a relaxed random walk model was used to estimate the timing and rate of population size change and geographic diffusion in *A. picticauda*, the single species in the group with an extensive African distribution from Mauritania to Ethiopia. The mean dispersal rate of *A. picticauda* increased dramatically throughout the Pleistocene, and a Bayesian skyride analysis supports exponential population growth over this same time period. A comparison of genetic diversity across different loci and species suggests that *A. lebretoni* experienced a mitochondrial selective sweep that has caused a deficit of variation at this locus in relation to nuclear loci.

Key words: *Agama*, Bayesian, maximum-likelihood estimation, phylogeography, skyride, West Africa

Introduction

The savannah and tropical forest biomes of Africa have a dynamic and prolonged history of expansion and

contraction that intensified during the Pleistocene and resulted in the broad expansion of savannah (deMenocal, 1995; Dupont, 2011; Dupont & Weinelt, 1996; Hamilton & Taylor, 1991; Jacobs, 2004). Major shifts through time in the sizes, locations, and fragmentation levels of tropical forest and savannah biomes have created a rich setting to investigate the diversification of African species. Empirical studies have focused on the population dynamics of the forests (Allal et al., 2011; Hardy et al., 2013; Lowe,

Harris, Dormontt, & Dawson, 2010) and across a wide range of vertebrates, including birds (Fjeldsaå & Lovett, 1997; Fuchs & Bowie, 2015; Marks, 2010), mammals (Bobe & Behrensmeyer, 2004; Gonder et al., 2011; Lorenzen, Heller, & Siegismund, 2012; Mondol et al., 2015; Nicolas et al., 2008), snakes (Barlow et al., 2013; Freedman, Buermann, Lebreton, Chirio, & Smith, 2009; Wüster et al., 2007), lizards (Gonçalves et al., 2012; Leaché & Fujita, 2010; Measey & Tolley, 2011; Medina et al., 2016; Swart, Tolley, & Matthee, 2009), and frogs (Barej, Penner, Schmitz, & Rödel, 2015; Ernst, Schmitz, Wagner, Branquima, & Hoelting, 2015; Lawson, 2013; Loader et al., 2014).

The lizard genus *Agama* contains approximately 45 species that are a diverse and common component of the African biota. *Agama* lizards are diurnal insectivores that range in adult body size (snout–vent length) from approximately 47 mm to 133 mm (Leaché et al., 2014). Some species exhibit sexual size dimorphism and sexual dichromatism, and adult male breeding colouration is a conspicuous trait in the genus (Mediannikov, Trape, & Trape, 2012). Diversification within *Agama* is inferred to have started 18–27 Ma, and separate radiations in southern, eastern, western, and northern Africa have been diversifying for at least 7 million years (Leaché et al.,

2014). The clade that is the focus of our study, the *A. agama* species group (*A. africana*, *A. agama*, *A. finchi*, *A. lebretoni*, *A. parafricana*, *A. paragama*, and *A. picticauda*), contains a subset of seven species belonging to a more inclusive West African clade that also includes *A. planiceps*, *A. boensis*, *A. sankaranica*, and *A. benueensis* (Leaché et al., 2014). The West African clade is estimated to have started diversifying 9–16 Ma, while the more exclusive *A. agama* species group began diversification 3–7 Ma (Leaché et al., 2014). The *A. agama* group is found in a variety of habitats, including both savannahs and the margins of tropical forests (Gonçalves et al., 2012; Mediannikov, Trape, & Trape, 2012), but sometimes also in urban settings. Fluctuations in habitat availability throughout the Pleistocene probably caused turbulent population histories in the *A. agama* group, which is distributed broadly throughout this region (Gonçalves et al., 2012). The distribution of the group extends from Mauritania and Sierra Leone in the west to Ethiopia and Kenya in the east, largely due to the broad range of one species, *A. picticauda* (Fig. 1). If climate cycles and shifts in vegetation structure had an impact on the *A. agama* group, then we might expect to discover genetic signatures of population size changes through time.
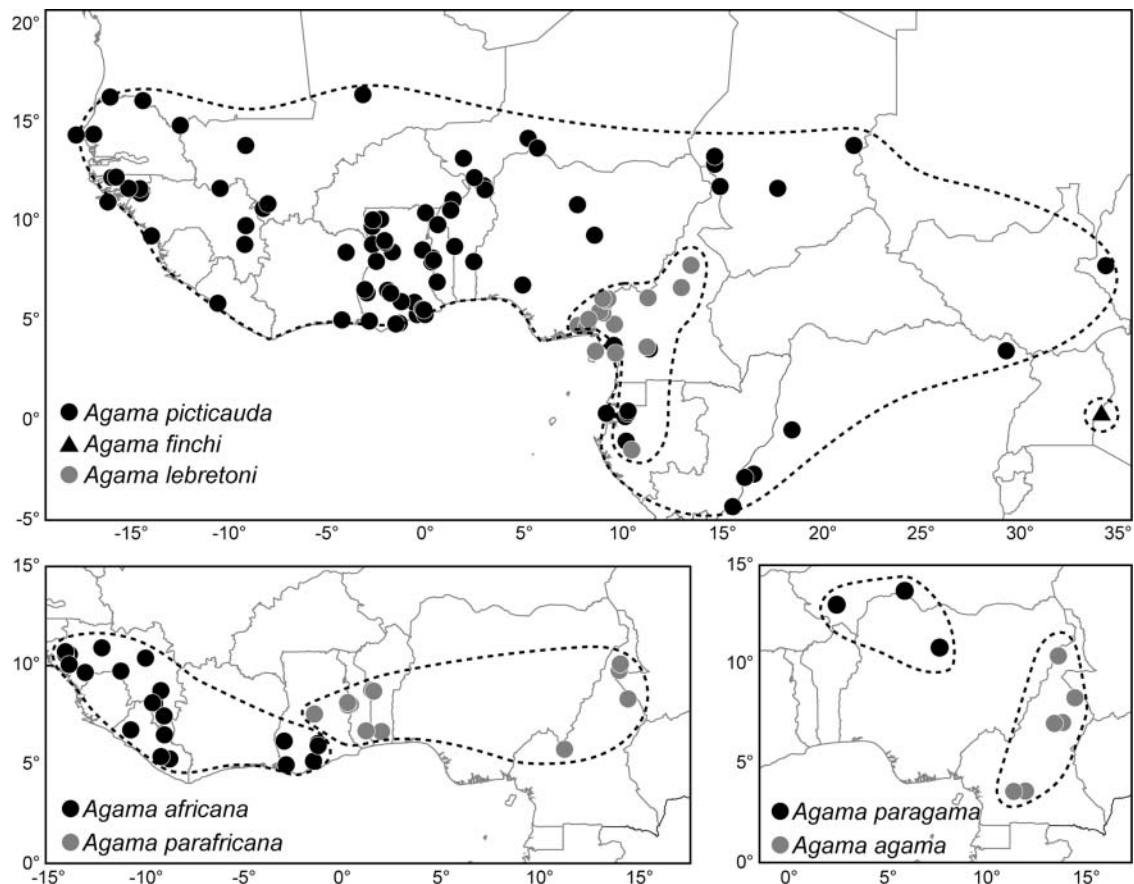
Fig. 1. Sampled populations for seven species in the *Agama agama* species group. Complete voucher information and locality data are provided in Appendix S1 (see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2016.1238018). Current distributions are shown in dashed lines.

The taxonomy, distribution, and phylogeny of the *Agama agama* group have been clarified as a result of molecular phylogenetic studies. Until recently, the majority of the species within the *A. agama* group were considered to be members of a single species, *A. agama* (Linnaeus, 1758), which previously contained over 10 subspecies (Wagner, Wilms, Bauer, & Böhme, 2009). The first phylogeographic study of the *A. agama* group discovered several instances of geographic overlap among phylogeographic groups and speculated that *A. agama* (sensu lato) contained multiple distinct lineages that co-occur throughout West Africa, and that overlapping species distributions could be explained by recent population expansions (Leaché et al., 2009). A subsequent molecular phylogenetic study of the group recognized *A. lebretoni* as a distinct species with a Central African distribution that included Cameroon, Gabon, and Bioko Island (Wagner, Barej, & Schmitz, 2009). An extensive phylogeographic study of West African *Agama* further subdivided *A. agama* (sensu lato) by elevating *A. africana* to the species level and describing two additional species, *A. parafricana* and *A. wagneri* (Mediannikov et al., 2012). We follow the taxonomy for *A. agama* published by Wagner et al. (2009), which restricted *A. agama* (sensu stricto) to Central Africa. According to this taxonomy, *A. wagneri* is not valid, and *A. picticauda* is available for the remaining populations distributed across West Africa (Leaché et al., 2014).

In this study, we investigate the spatial and temporal evolution of the *Agama agama* group. We use a Bayesian species tree diffusion approach to estimate species diffusion rates, which provide estimates for the locations and sizes of ancestral populations as well as the diffusion rates for extant species across the landscape (Nylinder et al., 2014). We use these estimates of historical species ranges to compare the relative rates at which species have moved across the landscape. We also apply a continuous phylogeographic approach using a relaxed random walk model (Lemey, Rambaut, Welch, & Suchard, 2010) to estimate the timing and rate of population size changes and geographic diffusion in the most broadly distributed species in the group, *A. picticauda*. The evolutionary perspectives of the species diffusion process provided by these methods are complementary; the species tree diffusion approach takes a broad evolutionary perspective, while the continuous phylogeographic method focuses on population-level inferences.

Materials and methods
Data collection
We sampled a total of 310 specimens from seven species that are part of the *Agama agama* species group (Fig. 1): *Agama africana* ($N = 27$), *A. agama* ($N = 11$), *A. finchi* ($N = 1$), *A. lebretoni* ($N = 42$), *A. parafricana* ($N = 25$), *A. paragama* ($N = 4$), and *A. picticauda* ($N = 200$). A complete list of examined specimens is provided in Appendix S1 (see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2016.1238018). Approval for animal research was provided by the University of Washington Office of Animal Welfare (IACUC #4209-01).

Agama finchi is perhaps the most morphologically distinctive member of the *A. agama* group (Böhme, Wagner, Malonza, Lötters, & Köhler, 2005); however, molecular phylogenetic studies have yet to support this species as distinct from *A. picticauda* (Leaché et al., 2009; Mediannikov et al., 2012). For the purposes of our phylogenetic and phylogeographic analyses, we considered *A. finchi* as a population of *A. picticauda.* However, we refrain from making any taxonomic changes to *A. finchi* until a more thorough species delimitation study can be conducted.

The sister species *A. planiceps* from Namibia was used to root trees in several of the phylogenetic analyses (see below). Most of our sampling was concentrated on *A. picticauda*, which is represented by samples from 17 countries (Fig. 1). We collected approximately 512 bp of the mitochondrial DNA (mtDNA) 16S rRNA gene (*16S*), and for a smaller set of samples we sequenced two nuclear genes, pinin (*PNN*; 911 bp, 66 samples) and RNA fingerprint protein 35 (*R35*; 649 bp, 64 samples). Molecular lab protocols for sequencing and sequence editing follow Leaché et al. (2009, 2014). Multiple sequence alignments were generated using Muscle v3.8 (Edgar, 2004) with default settings. New sequences are deposited on GenBank (accession numbers KX549470–KX549780).

Species tree diffusion
We inferred the ancestral locations of species and their subsequent spread throughout Africa using Bayesian species tree diffusion (Nylinder et al., 2014). The method quantifies the diffusion rate of species (both extant and ancestral) across a landscape in units of distance per time (km/Ma). This method requires a two-step process where species tree inference is followed by the estimation of the spatial and temporal diffusion of species. The method can accommodate phylogenetic uncertainty using a posterior distribution of species trees instead of a single point-estimate of phylogeny. We used data from a recently published phylogenetic study to obtain a posterior distribution of species trees for the *Agama agama* species group (Leaché et al., 2014). In that study, the species tree was estimated in *BEAST using a combination of mtDNA and nuclear genes, and the resulting posterior distribution was reduced to include only those trees that were congruent with a phylogeny estimated using 215 nuclear loci (Leaché et al., 2014). We used the reduced posterior distribution of species trees from the Leaché et al. (2014) study (206 trees in total), and removed all outgroup

species (and *A. finchi*) from the phylogeny using Mesquite (Maddison & Maddison, 2011).

The species tree diffusion analysis requires geographic distributions for each focal species as polygons in KML format. We generated species distribution polygons in Google Earth using the geographic records for species from our study (Appendix S1; Fig. 1). All priors for the species tree diffusion analyses were kept the same as in Nylinder et al. (2014). The default priors were sensible and worked well, but we did not perform a sensitivity analysis to determine whether the species diffusion results are sensitive to these choices. One exception was the prior on the standard deviation of branch diffusion rates, which was given a uniform prior with bounds (0,1000). Analyses using an exponential prior distribution with a mean of 2.712 for this parameter resulted in no diffusion of inferred ancestral ranges, indicating a large disparity in diffusion rates across branches in the species tree. We ran four independent species tree diffusion analyses in BEAST v1.8.0 (Drummond & Rambaut, 2007; Drummond, Suchard, Xie, & Rambaut, 2012) for 5×10^8 generations, sampling every 5×10^5 generations and discarding the first 10% of generations as burn-in. The MCMC begins at an arbitrary geographic starting location from within the distribution of each species, and changing these starting locations did not affect our results (data not shown). After ensuring adequate mixing of the MCMC chains in Tracer v1.5 (Rambaut & Drummond, 2007), we combined the four posterior distributions of trees using LogCombiner v1.8. The "timeslice" feature of the program Spread v1.0 (Bielejec, Rambaut, Suchard, & Lemey, 2011) was used to extract 80% high posterior density (HPD) ancestral geographic regions from the combined posterior probability distribution, which were then visualized as KML files in Google Earth. We calculated median diffusion rates for species (and ancestors) as diffusion distance per time unit (km/Ma), which provides a measure of the rate at which the centre of a species range shifts through time in relation to the most recent common ancestor (MRCA). We also used Google Earth to calculate the relative per cent change in the area of ranges as a function of time (km^2/Ma) to quantify changes in land area occupied by species through time.

relaxed random walk (RRW) model with individuals assigned GPS coordinates that can be found in Appendix S1 (see supplemental material online). A random "jitter" was added to each tip (window size 0.5) to aid in inference of individuals with identical GPS coordinates. We applied a fixed clock rate of 0.00836 substitutions/my, which was calculated by taking one half of the average pairwise uncorrected p-distances between all *A. picticauda* samples and individuals of the sister taxa (*A. agama* and *A. paragama*), and dividing that value by the mean age of the (*picticauda* + (*agama* + *paragama*)) clade. A strong prior assumption for the clock rate is required to establish the timing of population size changes. There is uncertainty in the age of the clade (ranging from approximately 1.5 to 3.7), and our reliance on the mean age does not account for this uncertainty.

We used marginal likelihood estimation (MLE) and Bayes factors (BF) to select the best coalescent prior and clock model for the data. We conducted marginal likelihood estimation using path sampling (PS) and stepping stone (SS) analyses in BEAST (Baele et al., 2012). Constant, expansion, and exponential models were first tested with analyses running for 2×10^7 generations, with sampling every 2×10^4 generations. For all models tested, MLE analyses were run for 50 path steps and 100 000 generations within each step. Bayes factors were calculated as two times the difference in marginal likelihood estimates between competing models, and significance was determined if the BF value was >10 (Kass & Raftery, 1995). For all analyses, two independent analyses were combined using LogCombiner. We used the best coalescent prior (exponential; see Table 1) to test the relaxed vs. strict clock with the same analysis parameters. The relaxed clock was favoured over the strict clock using PS (BF = 12.0), but only marginally by SS (BF = 9.7).

The final RRW analysis was performed with the HKY + Γ DNA substitution model, uncorrelated relaxed clock, and an exponential coalescent process. Two independent analyses were run for 2×10^8 generations, sampling every 2×10^5 generations, and then combined using Log-Combiner v1.8.1. We used the program Spread v1.0 (Bielejec et al., 2011) to produce KML files showing the 80% HPD regions of the diffusion of lineages through time on

Bayesian phylogeography

We inferred the diffusion of mitochondrial lineages through time using the continuous Bayesian phylogeography approach (Lemey et al., 2010). This method estimates population size changes through time, and also estimates ancestral population locations. For this analysis, we focused on the widespread species *A. picticauda*, where the dataset consisted of 201 individuals (including *A. finchi*) and 503 bp of the *16S* gene. We used the Gamma

Table 1. Marginal likelihood estimates and Bayes factor comparison of coalescent priors for *Agama picticauda*.

Model	Path sampling (PS)	Stepping stone (SS)	Bayes factor PS (SS)
Exponential	−1747.89	−1757.86	– (−)
Constant	−1758.02	−1767.66	20.3 (19.6)
Expansion	−1760.47	−1774.32	25.2 (32.9)

the landscape. We used the TimeSlicer function to estimate the mean diffusion rate across the genealogy at intervals of 50 000 years.

Population size trajectories

The effective population size is an indicator of genetic diversity within populations. We estimated changes in effective population size through time using Bayesian skyride plots (Minin, Bloomquist, & Suchard, 2008). These analyses were conducted for *A. picticauda* (including *A. finchi*) with the mtDNA data. We did not conduct analyses for the remaining species, because they either did not have enough samples, or because they lacked genetic variation (*A. lebretoni*). Posterior estimates for population size trajectories were obtained using BEAST v1.8.1. The prior for the root height of the tree was given a wide uniform distribution over the interval [1, 1000]. This prior is meant to accommodate the large variation in coalescent times that can be expected under the coalescent process. The MCMC was run for a total of 10×10^6 generations (sampling every 5 000 steps and excluding the first 10% as burn-in). We assessed convergence by examining parameter trends between two separate runs using Tracer. The two runs were combined before generating the Bayesian skyride plot in Tracer.

Selective sweeps

Identifying selective sweeps can be accomplished by contrasting the levels of genetic variation in mtDNA versus nuclear genes (Ballard & Rand, 2005). Genetic drift and the fixation of alleles in small populations is the likely outcome of a population bottleneck, and in such cases the genetic diversity of mtDNA and nuclear genes is expected to be low. However, if nuclear gene diversity exceeds that of mtDNA diversity, then a selective sweep is likely. We quantified genetic diversity by measuring the population size parameter $\theta = 4N\mu$, where N is the effective population size and μ is the mutation rate per site per generation. A biological interpretation of θ is the average proportion of different sites between two sequences sampled at random from the population. We calculated θ using the Bayesian coalescent program BPP v3.0 (Rannala & Yang, 2003; Yang, 2015). We conducted analyses separately for three species (*A. lebretoni*, *A. picticauda*, and *A. parafricana*) and for each dataset (mtDNA vs. nuclear genes). The prior for θ was assigned a mean value of 0.02 using a gamma (2 100) distribution. This prior assumes that there is, on average, 2% sequence divergence within populations (i.e., two sequences sampled at random from the population will differ by 2%). The analyses were run for 20 000 steps (sampling every other step) after an initial burn-in of 4 000 steps.

## Results

Species tree diffusion

The phylogenetic relationships among species and the ancestral locations of species and their subsequent spread throughout Africa are shown in Figs 2–7. The estimated ancestral areas overlap broadly in Nigeria and Cameroon. At 1 Ma, *A. africana* is beginning to extend to the west and has a parapatric distribution with respect to other lineages (Fig. 6), and by 0.01 Ma the distribution of *A. africana* is allopatric (Fig. 7). *Agama paragama* is also allopatric with all other lineages to the exclusion of *A. picticauda* at approximately 0.01 Ma (Fig. 7). Most of the estimated ranges remain relatively small with the exception of *A. picticauda*, which has a distribution that expands gradually starting 2 million years ago.

Estimates for the diffusion rates of species are shown in Figs 8–9. The species with the largest diffusion distances (shifts in range centre per unit time, Fig. 8) are *A. africana* (*c*. 1,200 km/Ma) and *A. paragama* (*c*. 500 km/Ma). The diffusion rates for the remaining species are < 300 km/Ma, and the estimates for the ancestors are < 100 km/Ma. The relative per cent change in the area of ranges as a function of time (km²/Ma) was quantified to estimate changes in land area occupied by species (Fig. 9). Whereas *A. africana* had the largest diffusion distance, the relative area increase was only approximately 50% (Fig. 9). The largest relative area change was approximately 225% in *A. picticauda*. Three species had reduced range areas through time (*A. lebretoni*, *A. paragama*, and *A. agama*).

Bayesian phylogeography and population size trajectory

The *16S* alignment (512bp) contained 108 unique haplotypes, 88 variable sites, and an average pairwise sequence divergence of 2.89%. Within *A. picticauda* there were 67 unique haplotypes (from 201 total, including *A. finchi*), 42 variable sites, and an average pairwise sequence divergence of 1.42%. The results of the continuous Bayesian phylogeography analysis of *A. picticauda* using the RRW model are shown in Figs 10–12. Unlike the species tree diffusion analysis that estimates the ancestral area for the lineage in Cameroon and Nigeria (Figs 2–7), the continuous phylogeography approach excludes Cameroon from the ancestral area and places the ancestor in Ghana, Togo, Benin, and Nigeria (Fig. 10). At 0.5 Ma the population is estimated to extend to extreme Western Africa (Fig. 11). The present distribution for *A. picticauda* is shown in Fig. 12.

The Bayesian skyride analysis supports an exponential growth for *A. picticauda* (Fig. 13); the population size increases by nearly two orders of magnitude over a 2 million year period. This increase in the effective population
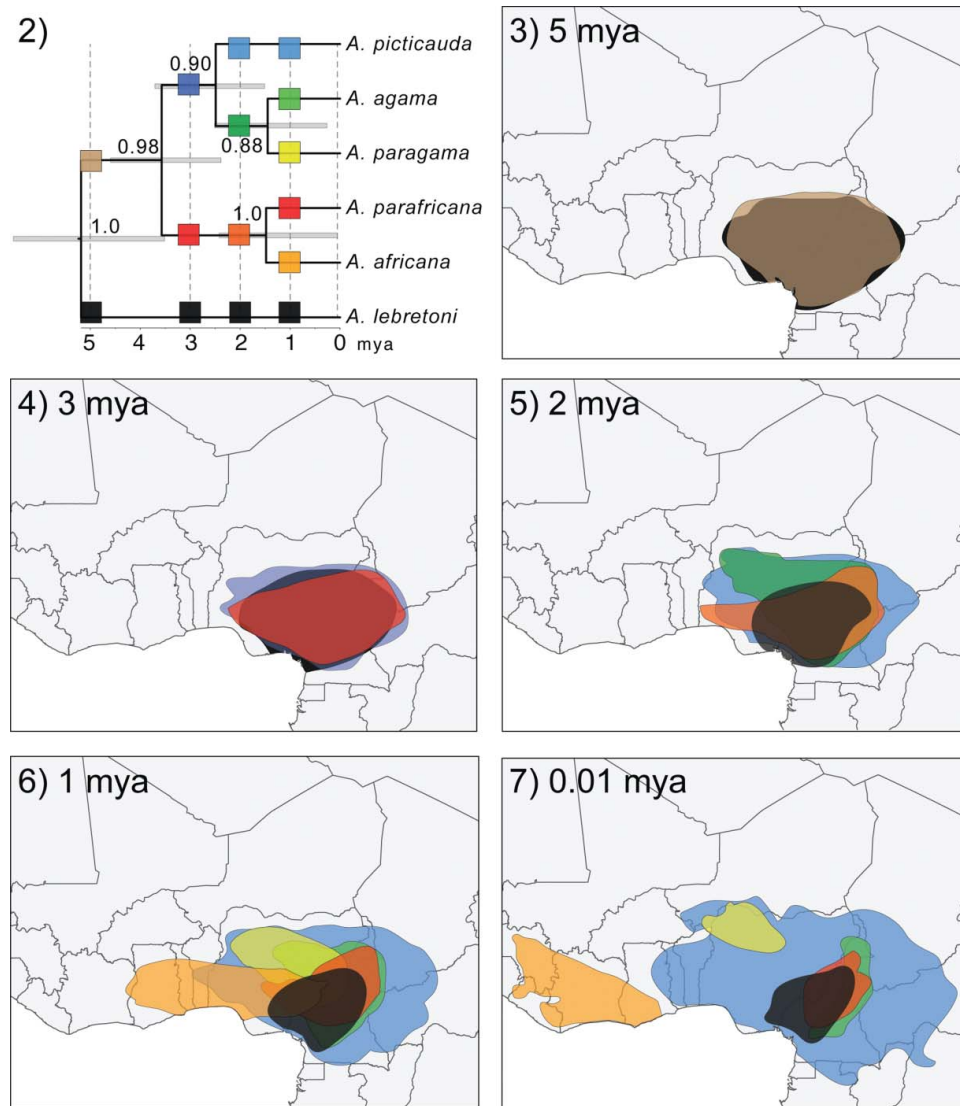
Fig. 2–7. Species tree diffusion in the *Agama agama* group. **2,** species tree with Bayesian posterior probability support values shown on the nodes along with estimated area reconstructions at five time slices. **3–7,** the 80% highest-posterior density (HPD) areas for ancestral populations estimated at five time-slices, colour-coded according to the species tree in Fig. 2.

size is matched with an increase in the mean diffusion rate estimated by the Bayesian phylogeographic analysis (Figs 13–14). The mean diffusion rate of *A. picticauda* is estimated to have been stable at around 1 000 km/Ma at the start of the population history (Fig. 14). Starting at 1 Ma the diffusion rate increases, and within the last 250 kya the diffusion rate doubles to over 3 000 km/Ma.

Selective Sweeps

We contrast levels of genetic variation in mtDNA versus nuclear genes with the coalescent estimator of population size θ in Table 2. The expected relationship of higher genetic diversity in mtDNA versus nuclear loci was observed in *A. africana* and *A. picticauda*. However, the

nuclear gene diversity estimates for *A. lebretoni* (θ = 0.00294) exceeded that of mtDNA diversity (θ = 0.00171). These results suggest that a selective sweep could be responsible for removing mtDNA genetic variation from *A. lebretoni*.

Discussion

Species tree diffusion

Biogeographic reconstructions of species that are continuously distributed across a landscape are difficult because they typically require the partitioning of species into discrete geographic areas (Ronquist & Sanmartín, 2011). Previous analyses of *Agama* biogeography took this
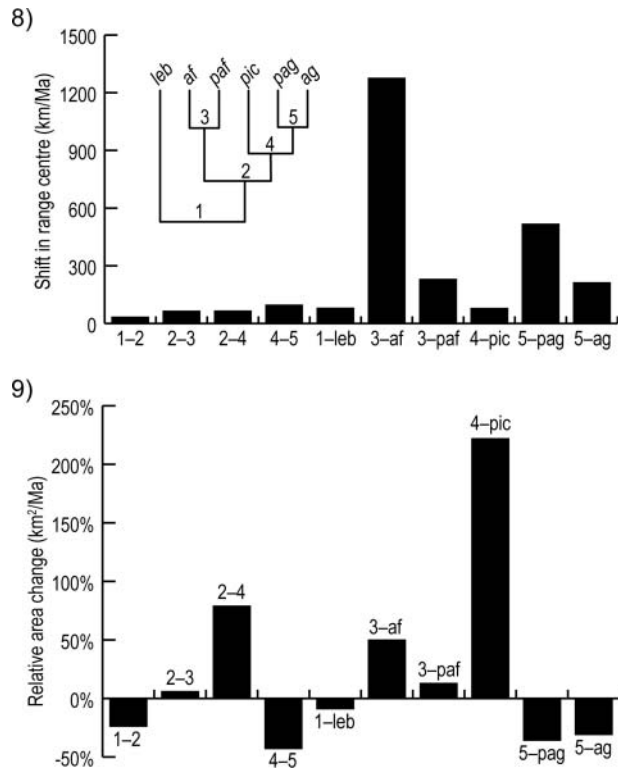
Fig. 8–9. Species tree diffusion estimates for each species (extant and ancestral) in the *Agama agama* species group. **8**, the y-axis is presented as the median diffusion distance of the estimated range centre per time unit (km/Ma). **9**, the y-axis is presented as the relative change in range area per unit time (km²/Ma). Positive and negative values indicate range area increases and decreases, respectively. Species are abbreviated as follows: *lebretoni* (leb), *africana* (af), *parafricana* (paf), *picticauda* (pic), *paragama* (pag), *agama* (ag). Inferred distributions are shown in Figs 3–7.
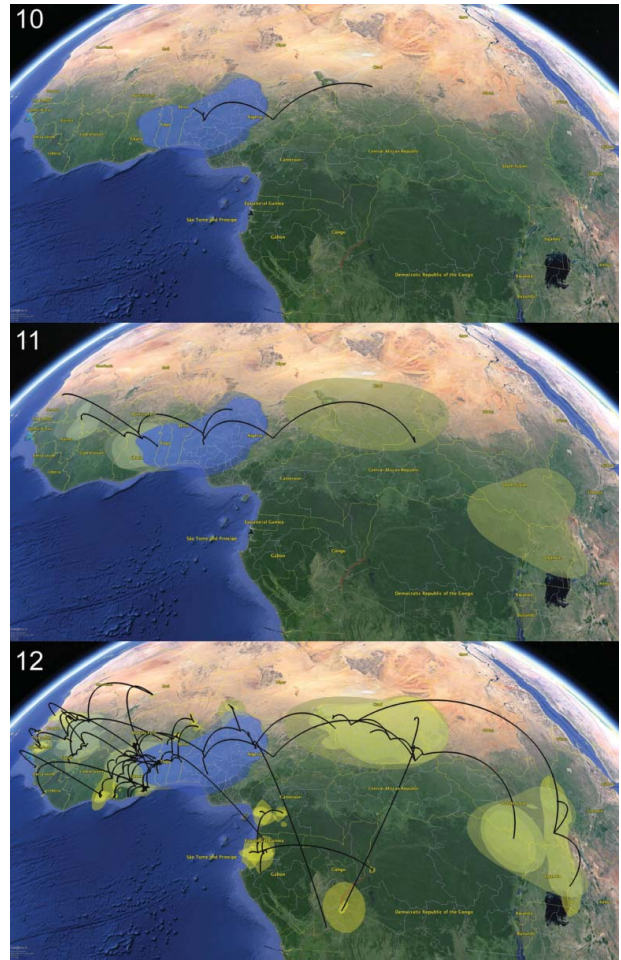
Fig. 10–12. Bayesian phylogeographic projections for *Agama picticauda* at three time slices: **10**, 1 Ma, **11**, 0.5 Ma, and **12**, present time. The MCC gene tree is represented with black lines. Older diffusion events are shown in blue, and more recent ones are shown in yellow.
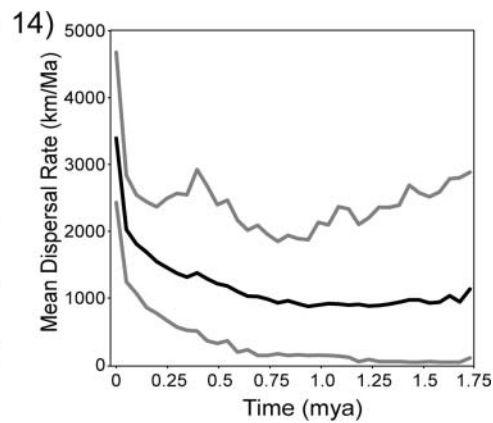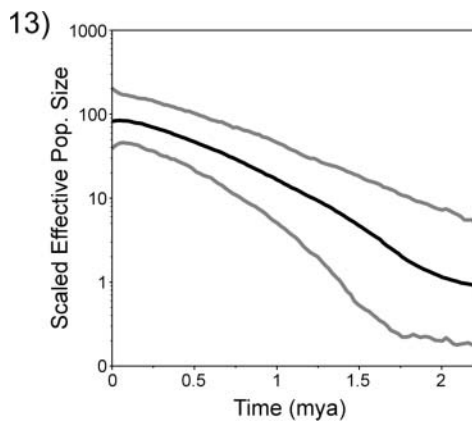
Fig. 13–14. Estimates for historical population size dynamics in *Agama picticauda*. **13**, effective population size trajectory based on a Bayesian skyride analysis of mtDNA. The median population size is shown with a black line, and the 95% HPD is shown with grey lines. **14**, diffusion rate through time (km/Ma) based on a relaxed random walk analysis of mtDNA. The mean diffusion rate is shown with a black line, and the 95% HPD is shown with grey lines. Note the different time intervals (x-axes) between (a) and (b).

approach by assigning species to discrete geographic areas of Africa (Leaché et al., 2014). The discrete approach to biogeography is useful for identifying ancestral areas at a coarse scale, but the Bayesian species tree diffusion approach can provide similar inferences without the need for pre-defining discrete areas of analysis (Nylinder et al., 2014). The continuous biogeography approach offers the additional advantage of providing estimates of species diffusion rates across the landscape, which can help test predictions about species responses to habitat shifts.

We estimated species diffusion rates for a clade containing six species of *Agama*, and found heterogeneous patterns of species diffusion. Several species showed relatively rapid shifts in the location of their range (as measured by the rate of change in their range centre), while some species have maintained relatively stable range centres through time (Figs 8–9). The species diffusion rate is useful for making inferences about range centre movements; however, it is necessary to separate species diffusion rate dynamics more fully to understand the spatial and temporal history of species diffusion. Examining estimates of range shifts and relative range change estimates reveals interesting patterns of species diffusion in the *A. agama* group (Figs 8–9). The most interesting comparison is between *A. africana* and *A. picticauda*; the range centre of *africana* moved quickly (over 1200 km/Ma), but only experienced a 50% increase in area over that time period, whereas *A. picticauda* increased in range by over 200% while maintaining a relatively stable range centre (Figs 8–9). Further studies are needed to investigate whether or not there is an ecological basis for these differences. *Agama picticauda* is a particularly successful colonizer and human commensal (see discussion below), and this could contribute to their quick spread throughout Africa in relation to other members of the *A. agama* group. Another issue that deserves more attention is the extensive overlap in the ancestral species distributions through time (Figs 2–7). The ancestral ranges support sympatric distributions for long time periods, yet it is unlikely that sympatric speciation is responsible for the diversification history of the group. It is more likely that vicariant and/or ecological speciation was the major driver of diversification in the *A. agama* group, as was shown for other North African *Agama* species (Gonçalves et al., 2012).

Bayesian phylogeography and population trajectory

Our species tree diffusion analyses provide estimates for species movement through time and space, and we augmented those estimates with population data for *A. picticauda* with Bayesian phylogeographic inference. We investigated the phylogeographic history of the most wide-ranging species in the group, *A. picticauda*, to estimate the timing and rate of population size changes and population diffusion.

The species tree diffusion and Bayesian phylogeography methods differ with respect to the inferred location of the ancestral population of *A. picticauda*, with the former placing the population near Cameroon, and the latter placing it between Ghana and Nigeria. It is difficult to determine which, if either, estimate is more accurate. The species tree approach has the advantage of including information about the distributions of closely related species, whereas the phylogeographic approach includes detailed population data that are lacking from the species tree method. Regardless of discrepancies in the ancestral range estimates, both methods support a rapid increase in the diffusion of *A. picticauda* across Africa. The mean dispersal rate increases rapidly within the last 0.25 Myr, and the Bayesian skyride analyses supports an exponential increase in the effective population size (Figs 13–14). The projected distribution also increases dramatically within the last 0.5 million years (Figs 10–12).

Species in the *Agama agama* group are successful colonizers of offshore islands and other areas around the globe (Borroto-Páez, Bosch, Fabres, & Osmany, 2015; Guillermet, Couteyen, & Probst, 1998; Wagner, Bauer, Wilms, Barts, & Böhme, 2012). For example, *A. lebretoni* occurs off the coast of the Gulf of Guinea on Bioko Island (Wagner et al., 2009). This island is a short distance from the mainland (*c*. 32 km) and could have been connected to the mainland during the Pleistocene (Lee, Halliday, Fitton, & Poli, 1994). The mtDNA selective sweep that has occurred in *A. lebretoni* prevents us from examining the timing of their arrival on Bioko with this quickly evolving locus. *Agama picticauda* is documented from the Bijagós archipelago off the coast of Guinea-Bissau where it appears to be restricted to trees along coastal areas (Auliya, Wagner, & Böhme, 2012). This species is also found on the Cape Verde Islands, and that population is presumed to have originated from Mali (Vasconcelos, Rocha, Brito, Carranza, & Harris, 2009). Other island colonization events, including those of Madagascar and Grande Comore Island are attributable to the *A. agama* group, but determining the species and/or population of origin is difficult without a genetic analysis (Wagner, Glaw, Glaw, & Böhme, 2009). There is also a documented case of the accidental transport of an *A. agama* (sensu lato) to the Maltese Islands that was imported with a shipment of beer (Schembri & Schembri, 1984), and *A. lebretoni* to Spain (Sancho & Pauwels, 2015). Although the source populations are currently undetermined, *A. picticauda* is now considered a widespread and dominant non-indigenous species in Florida, USA, where animals originating from the pet trade were released into the wild (Enge, Krysko, & Talley, 2004; Krysko et al., 2011).

Selective sweep

A selective sweeps occurs when adaptive alleles spread through a population. These adaptive alleles may arise from pre-existing variation, independently through recurrent mutations, or through hybridization with other species (Messer & Petrov, 2013). Selective sweeps involve positive selection on beneficial mutations, ultimately reducing the genetic diversity at certain loci (Rato, Carranza, Perera, & Harris, 2013). Mitochondrial genes are useful markers for identifying the presence of selective sweeps. Since all mitochondrial genes are linked together, selection pressure on any of the genes could lead to fixation of the entire mitochondrial genome (Amato, Brooks, & Fu, 2007). The high mutation rate and non-recombining nature of mtDNA allows for genetic hitchhiking, which has the potential to cause strong selective sweeps (Rato et al., 2013). Reductions in mtDNA diversity have no effect on the nuclear genome, therefore discrepancies between effective population size estimates from mtDNA and nuclear loci can be good indicators of possible selective sweep events (Jäckel, Mora, & Dobler, 2013). We found evidence for a mitochondrial selective sweep in *Agama lebretoni*; variation in nuclear loci exceeded that of mtDNA diversity (Table 2). A general trend in animals is that nuclear loci tend to exhibit much lower levels of variation than mitochondrial genes, primarily due to the faster mutation rate of mtDNA. Thus, to observe a much smaller nuclear theta compared with mtDNA theta is exceptional, and indicates that mitochondrial genes exhibited a selective sweep rather than a shared demographic history with the nuclear genome.

Hybridization and population bottlenecks have contributed to selective sweeps of mtDNA in some reptile species. Introgressed mitochondrial genomes are better adapted to the particular environmental conditions experienced by the recipient species. Studies of the Moorish gecko genome by Rato et al. (2013) revealed that mitochondrial selective sweeps resulted in genetic hitchhiking and the fixation of mtDNA haplotypes. A study by Amato

et al. (2007) attributes low mtDNA diversity of wood turtles to a bottleneck effect during Pleistocene glaciations, followed by a rapid expansion. However, this study also notes that it is possible that the low variation of mtDNA may be due to a not-yet known reason, since low variation has been observed among many other turtle species (Lamb & Avise, 1992). McGuire et al. (2007) noted a possible selective sweep in the mitochondrial genes of crotaphytid lizards. The mtDNA of the studied population had undergone repeated introgressions that were mediated by hybridization (McGuire et al., 2007). Investigating the ecological niches, physiology, and mitochondrial respiration of *Agama* lizards will help determine whether certain mitochondrial genotypes are better adapted to particular environments (Roberts, Vo, Fujita, Moritz, & Kearney, 2012).

Disclosure statement

No potential conflict of interest was reported by the authors.

Table 2. Coalescent estimates of population sizes (θ).

Species	θ mtDNA	θ nuclear loci
Agama lebretoni	0.00171 (0.00014–0.00383)	0.00294 (0.00147–0.00533)
A. africana	0.00784 (0.00295–0.01390)	0.00390 (0.00106–0.00757)
A. picticauda	0.02920 (0.01870–0.03970)	0.00700 (0.00409–0.01040)

θ values are reported as the mean and 95% highest posterior density (95% HPD). Two loci were included in the nuclear θ estimate, *PNN* and *R35*.

Supplemental data

Supplemental data for this article can be accessed here: http://dx.doi.org/10.1080/14772000.2016.1238018.

References

Allal, F., Sanou, H., Millet, L., Vaillant, A., Camus-Kulandaivelu, L., Logossa, Z. A., … Bouvet, J. M. (2011). Past climate changes explain the phylogeography of *Vitellaria paradoxa* over Africa. *Heredity*, *107*, 174–186.

Amato, M. L., Brooks, R, J., & Fu, J. (2007). A phylogeographic analysis of populations of the wood turtle (*Glyptemys insculpta*) throughout its range. *Molecular Ecology, 2*, 570–581.

Auliya, M., Wagner, P., & Böhme, W. (2012). The herpetofauna of the Bijagós archipelago, Guinea-Bissau (West Africa) and a first country-wide checklist. *Bonn zoological Bulletin, 61*, 255–281.

Baele, G., Lemey, P., Bedford, T., Rambaut, A., Suchard, M. A., & Alekseyenko, A. V. (2012). Improving the accuracy of demographic and molecular clock model comparison while accommodating phylogenetic uncertainty. *Molecular Biology and Evolution, 29*, 2157–2167.

Ballard, J. W. O., & Rand, D. M. (2005). The population biology of mitochondrial DNA and its phylogenetic implications. *Annual Review of Ecology, Evolution, and Systematics*, *36*, 621–642.

Barej, M. F., Penner, J., Schmitz, A., & Rödel, M.-O. (2015). Multiple genetic lineages challenge the monospecific status of the West African endemic frog-family Odontobatrachidae. *BioMed Central Evolutionary Biology, 15*, 67.

Barlow, A., Baker, K., Hendry, C. R., Peppin, L., Phelps, T., Tolley, K. A., … Wüster, W. (2013). Phylogeography of the widespread African puff adder (*Bitis arietans*) reveals multiple Pleistocene refugia in southern Africa. *Molecular Ecology*, *22*, 1134–1157.

Bielejec, F., Rambaut, A., Suchard, M. A., & Lemey, P. (2011). SPREAD: Spatial phylogenetic reconstruction of evolutionary dynamics. *Bioinformatics*, *27*, 2910–2912.

Bobe, R., & Behrensmeyer, A. K. (2004). The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus Homo. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *207*, 399–420.

Böhme, W., Wagner, P., Malonza, P., Lötters, S., & Köhler, J. (2005). A new species of the *Agama agama* group (Squamata: Agamidae) from western Kenya, East Africa, with comments on *Agama lionotus* Boulenger, 1896. *Russian Journal of Herpetology*, *12*, 143–150.

Borroto-Páez, R., Bosch, R. A., Fabres, B. A., & Osmany, A. G. (2015). Introduced amphibians and reptiles in the Cuban Archipelago. *Herpetological Conservation and Biology, 10*, 985–1012.

deMenocal, P. B. (1995). Plio-Pleistocene African climate. *Science, 270*, 53–59.

Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BioMed Central Evolutionary Biology, 7*, 214.

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973.

Dupont, L. M. (2011). Orbital scale vegetation change in Africa. *Quaternary Science Reviews, 30*, 3589–3602.

Dupont, L. M., & Weinelt, M. (1996). Vegetation history of the savanna corridor between the Guinean and the Congolian rain forest during the last 150,000 years. *Vegetation History & Archaeobotany, 5*, 273–292.

Edgar, R. C. (2004). MUSCLE: A multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, *32*, 1792–1797.

Enge, K. M., Krysko, K. L., & Talley, B. L. (2004). Distribution and ecology of the introduced african rainbow lizard, *Agama agama africana* (Saura: Agamidae), in Florida. *Florida Scientist*, *67*, 303–310.

Ernst, R., Schmitz, A., Wagner, P., Branquima, M. F., & Hoelting, M. (2015). A window to Central African forest history: Distribution of the *Xenopus fraseri* subgroup south of the Congo Basin, including a first country record of *Xenopus andrei* from Angola. *Salamandra*, *51*, 147–155.

Fjeldsaå, J., & Lovett, J. C. (1997). Geographical patterns of old and young species in African forest biota: The significance of specific montane areas as evolutionary centres. *Biodiversity & Conservation*, *6*, 325–346.

Freedman, A. H., Buermann, W., Lebreton, M., Chirio, L., & Smith, T. B. (2009). Modeling the effects of anthropogenic habitat change on savanna snake invasions into African rainforest. *Conservation Biology*, *23*, 81–92.

Fuchs, J., & Bowie, R. C. (2015). Concordant genetic structure in two species of woodpecker distributed across the primary West African biogeographic barriers. *Molecular Phylogenetics and Evolution*, *88*, 64–74.

Gonçalves, D. V., Brito, J. C., Crochet, P. A., Geniez, P., Padial, J. M., & Harris, D. J. (2012). Phylogeny of North African *Agama* lizards (Reptilia: Agamidae) and the role of the Sahara desert in vertebrate speciation. *Molecular Phylogenetics and Evolution*, *64*, 582–591.

Gonder, M. K., Locatelli, S., Ghobrial, L., Mitchell, M. W., Kujawski, J. T., Lankester, F. J., … Tishkoff, S. A. (2011). Evidence from Cameroon reveals differences in the genetic structure and histories of chimpanzee populations. *Proceedings of the National Academy of Sciences (USA)*, *108*, 4766–4771.

Guillermet, C., Couteyen, S., & Probst, J.-M. (1998). Une nouvelle espèce de reptile naturalisée à La Réunion, l'Agame des colons *Agama agama* (Linnaeus). *Bulletin Phaethon, 8*, 67–69.

Hamilton, A. C., & Taylor, D. (1991). History of climate and forests in tropical Africa during the last 8 million years. *Climatic Change, 19*, 65–78.

Hardy, O. J., Born, C., Budde, K., Daïnou, K., Dauby, G., Duminil, J., … Lowe, A. J. (2013). Comparative phylogeography of African rain forest trees: A review of genetic signatures of vegetation history in the Guineo-Congolian region. *Comptes Rendus Geoscience*, *345*, 284–296.

Jäckel, R., Mora, D., & Dobler, S. (2013). Evidence for selective sweeps by *Wolbachia* infections: Phylogeny of *Altica* leaf beetles and their reproductive parasites. *Molecular Ecology*, *22*, 4241–4255.

Jacobs, B. F. (2004). Paleobotanical studies from Tropical Africa: Relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society B, 359*, 1573–1583.

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association, 90*, 773–795.

Krysko, K. L., Burgess, J. P., Rochford, M. R., Gillette, C. R., Cueva, D., Enge, … Nielsen, S. V. (2011). Verified non-indigenous amphibians and reptiles in Florida from 1863

through 2010: Outlining the invasion process and identifying invasion pathways and stages. *Zootaxa, 3028*, 1–64.

Lamb, T., & Avise, J. C. (1992). Molecular and population genetic aspects of mitochondrial DNA variability in the diamondback terrapin. *Malaclemys terrapin. Journal of Heredity*, *83*, 262–269.

Lawson, L. P. (2013). Diversification in a biodiversity hot spot: Landscape correlates of phylogeographic patterns in the African spotted reed frog. *Molecular Ecology*, *22*, 1947–1960.

Leaché, A. D., Chong, R. A., Papenfuss, T. J., Wagner, P., Böhme, W., Schmitz, A., … Baha El Din, S. (2009). Phylogeny of the genus *Agama* based on mitochondrial DNA sequence data. *Bonner zoologische Beiträge, 56*, 273–278.

Leaché, A. D., & Fujita, M. K. (2010). Bayesian species delimitation in West African forest geckos (*Hemidactylus fasciatus*). *Proceedings of the Royal Society of London B: Biological Sciences*, *277*, 3071–3077.

Leaché, A. D., Wagner, P., Linkem, C. W., Böhme, W., Papenfuss, T. J., Chong, R. A., … Burbrink, F. T. (2014). A hybrid phylogenetic-phylogenomic approach for species tree estimation in African *Agama* lizards with applications to biogeography, character evolution, and diversification. *Molecular Phylogenetics and Evolution*, *79*, 215–230.

Lee, D.-C., Halliday, A. N., Fitton, J. G., & Poli, G. (1994). Isotopic variations with distance and time in the volcanic islands of the Cameroon line: Evidence for a mantle plume origin. *Earth and Planetary Science Letters*, *123*, 119–138.

Lemey, P., Rambaut, A., Welch, J. J., & Suchard, M. A. (2010). Phylogeography takes a relaxed random walk in continuous space and time. *Molecular Biology and Evolution*, *27*, 1877–1885.

Linnæus, C. (1758). Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. *Edito decima. Tomus 1*, Stockholm: Laurenti Salvi, Holmiæ.

Loader, S. P., Sara Ceccarelli, F., Menegon, M., Howell, K. M., Kassahun, R., Mengistu, A. A., … Larson, J. G. (2014). Persistence and stability of Eastern Afromontane forests: Evidence from brevicipitid frogs. *Journal of Biogeography*, *41*, 1781–1792.

Lorenzen, E. D., Heller, R., & Siegismund, H. R. (2012). Comparative phylogeography of African savannah ungulates. *Molecular Ecology*, *21*, 3656–3670.

Lowe, A. J., Harris, D., Dormontt, E., & Dawson, I. K. (2010). Testing putative African tropical forest refugia using chloroplast and nuclear DNA phylogeography. *Tropical Plant Biology*, *3*, 50–58.

McGuire, J. A., Linkem, C. W., Koo, M. S., Hutchison, D. W., Lappin, A. K., Orange, D. I., … Jaeger, J. R. (2007). Mitochondrial introgression and incomplete lineage sorting through space and time: Phylogenetics of crotaphytid lizards. *Evolution*, *61*, 2879–2897.

Maddison, W. P., & Maddison, D. R. (2015). *Mesquite: A modular system for evolutionary analysis*. Version 2.75. 2011. Retrieved from http://mesquiteproject.org (accessed 14 September 2016).

Marks, B. D. (2010). Are lowland rainforests really evolutionary museums? Phylogeography of the green hylia (*Hylia prasina*) in the Afrotropics. *Molecular Phylogenetics and Evolution*, *55*, 178–184.

Measey, G. J., & Tolley, K. A. (2011). Sequential fragmentation of Pleistocene forests in an East Africa biodiversity hotspot: Chameleons as a model to track forest history. *Public Library of Science ONE*, *6*, e26606.

Mediannikov, O., Trape, S., & Trape, J. F. (2012). A molecular study of the genus *Agama* (Squamata: Agamidae) in West Africa, with description of two new species and a review of the taxonomy, geographic distribution, and ecology of currently recognized species. *Russian Journal of Herpetology*, *19*, 115–142.

Medina, M. F., Bauer, A. M., Branch, W. R., Schmitz, A., Conradie, W., Nagy, Z. T., … Greenbaum, E. (2016). Molecular phylogeny of *Panaspis* and *Afroblepharus* skinks (Squamata: Scincidae) in the savannas of sub-Saharan Africa. *Molecular Phylogenetics and Evolution, 100*, 409–423.

Messer, P. W., & Petrov, D. A. (2013). Population genomics of rapid adaptation by soft selective sweeps. *Trends in Ecology & Evolution*, *28*, 659–669.

Minin, V. N., Bloomquist, E. W., & Suchard, M. A. (2008). Smooth skyride through a rough skyline: Bayesian coalescent-based inference of population dynamics. *Molecular Biology and Evolution*, *25*, 1459–1471.

Mondol, S., Moltke, I., Hart, J., Keigwin, M., Brown, L., Stephens, M., & Wasser, S. K. (2015). New evidence for hybrid zones of forest and savanna elephants in Central and West Africa. *Molecular Ecology*, *24*, 6134–6147.

Nicolas, V., Bryja, J., Akpatou, B., Konecny, A., Lecompte, E., Colyn, M., … Granjon, L. (2008). Comparative phylogeography of two sibling species of forest dwelling rodent (*Praomys rostratus* and *P. tullbergi*) in West Africa: Different reactions to past forest fragmentation. *Molecular Ecology*, *17*, 5118–5134.

Nylinder, S., Lemey, P., De Bruyn, M., Suchard, M. A., Pfeil, B. E., Walsh, N., & Anderberg, A. A. (2014). On the biogeography of *Centipeda*: A species-tree diffusion approach. *Systematic Biology*, *63*, 178–191.

Rambaut, A., & Drummond, A. J. (2007). *Tracer* v1. 5. Retrieved from http://beast.bio.ed.ac.uk/ (accessed 14 September 2016).

Rannala, B., & Yang, Z. (2003). Bayes estimation of species divergence times and ancestral population sizes using DNA sequences from multiple loci. *Genetics*, *164*, 1645–1656.

Rato, C., Carranza, S., Perera, A., & Harris, D. J. (2013). Evolutionary patterns of the mitochondrial genome in the Moorish gecko. *Tarentola mauritanica. Gene*, *512*, 166–173.

Roberts, J. A., Vo, H. D., Fujita, M. K., Moritz, C., & Kearney, M. (2012). Physiological implications of genomic state in parthenogenetic lizards of reciprocal hybrid origin. *Journal of Evolutionary Biology*, *25*, 252–263.

Ronquist, F., & Sanmartín, I. (2011). Phylogenetic methods in biogeography. *Annual Review of Ecology, Evolution, and Systematics*, *42*, 441.

Sancho, V., & Pauwels, O. S. G. (2015). An accidental importation of an Afrotropical anthropophilic lizard (Squamata: Agamaidae: *Agama lebretoni*) into Spain. *Bulletin of the Chicago Herpetological Society, 50*, 218–219.

Schembri, S. P., & Schembri, P. J. (1984). On the occurrence of *Agama agama* (L.) (Reptilia: Agamidae) in the Maltese Islands. *Societa Veneziana di Scienze Naturali Lavori, 9*, 89–91.

Swart, B. L., Tolley, K. A., & Matthee, C. A. (2009). Climate change drives speciation in the southern rock agama (*Agama atra*) in the Cape Floristic Region, South Africa. *Journal of Biogeography*, *36*, 78–87.

Vasconcelos, R., Rocha, S., Brito, J. C., Carranza, S., & Harris, D. J. (2009). First report of introduced African rainbow lizard *Agama agama* (Linnaeus, 1758) in the Cape Verde Islands. *Herpetozoa*, *21*, 183–186.

Wagner, P., Barej, M. F., & Schmitz, A. (2009). Studies on African *Agama* VII. A new species of the *Agama agama*-group (Linnaeus, 1758) (Sauria: Agamidae) from Cameroon & Gabon, with comments on *Agama mehelyi* Tornier, 1902. *Bonner zoologische Beiträge*, *56*, 285–297.

Wagner, P., Glaw, F., Glaw, K., & Böhme, W. (2009). Studies on African *Agama* IV: First record of *Agama agama* (Sauria: Agamidae) from Madagascar and identity of the alien population on Grande Comore Island. *Herpetology Notes*, *2*, 73–77.

Wagner, P., Wilms, T. M., Bauer, A., & Böhme, W. (2009). Studies on African *Agama* V. On the origin of *Lacerta agama* Linnaeus, 1758 (Squamata: Agamidae). *Bonner zoologische Beiträge*, *56*, 215–223.

Wagner, P., Bauer, A. M., Wilms, T. M., Barts, M., & Böhme, W. (2012). Miscellanea Accrodontia: Notes on nomenclature, taxonomy and distribution. *Russian Journal of Herpetology, 19*, 177–189.

Wüster, W., Crookes, S., Ineich, I., Mané, Y., Pook, C. E., Trape, J. F., & Broadley, D. G. (2007). The phylogeny of cobras inferred from mitochondrial DNA sequences: Evolution of venom spitting and the phylogeography of the African spitting cobras (Serpentes: Elapidae: *Naja nigricollis* complex). *Molecular Phylogenetics and Evolution*, *45*, 437–453.

Yang, Z. (2015). A tutorial of BPP for species tree estimation and species delimitation. *Current Zoology, 61*, 854–865.

Associate Editor: Mark Wilkinson