

# Diversification and the adaptive radiation of the vangas of Madagascar

S. Reddy<sup>1,\*</sup>, A. Driskell<sup>2</sup>, D. L. Rabosky<sup>3</sup>, S. J. Hackett<sup>4</sup>  
and T. S. Schulenberg<sup>5</sup>

<sup>1</sup>Biology Department, Loyola University Chicago, Chicago, IL 60626, USA

<sup>2</sup>Smithsonian Institution Laboratory of Analytical Biology, Suitland, MD 20746, USA

<sup>3</sup>Department of Integrative Biology and Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

<sup>4</sup>Zoology Department, Field Museum of Natural History, Chicago, IL 60605, USA

<sup>5</sup>Cornell Lab of Ornithology, Ithaca, NY 14850, USA

The vangas of Madagascar exhibit extreme diversity in morphology and ecology. Recent studies have shown that several other Malagasy species also are part of this endemic radiation, even as the monophyly of the clade remains in question. Using DNA sequences from 13 genes and representatives of all 15 vanga genera, we find strong support for the monophyly of the Malagasy vangids and their inclusion in a family along with six aberrant genera of shrike-like corvids distributed in Asia and Africa. Biogeographic reconstructions of these lineages include both Asia and Africa as possible dispersal routes to Madagascar. To study patterns of speciation through time, we introduce a method that can accommodate phylogenetically non-random patterns of incomplete taxon sampling in diversification studies. We demonstrate that speciation rates in vangas decreased dramatically through time following the colonization of Madagascar. Foraging strategies of these birds show remarkable congruence with phylogenetic relationships, indicating that adaptations to feeding specializations played a role in the diversification of these birds. Vangas fit the model of an ‘adaptive radiation’ in that they show an explosive burst of speciation soon after colonization, increased diversification into novel niches and extraordinary ecomorphological diversity.

**Keywords:** passerines; phylogeny; diversification; foraging strategies; adaptive radiation

## 1. INTRODUCTION

Adaptive radiation involves both taxonomic and ecological diversification in response to ecological opportunity [1], but the extent to which the process underlies the diversity of species and phenotypes across the tree of life remains poorly understood [2]. Perhaps the best-known examples of island adaptive radiation in birds are Darwin’s finches (Thraupidae) and Hawaiian honeycreepers (Drepanidinae), but key tests of the adaptive radiation model have been applied to comparatively few insular avifaunas. The vangas (variously Vanginae or Vangidae) of Madagascar have been proposed to be a similar adaptive radiation [3,4], surpassing the finches in the number of species and rivalling both groups in ecomorphological disparity.

Variously a group of 15–21 species [5–7] endemic to Madagascar with one species extending into the Comoro Islands, vangas exhibit a great range of morphological, behavioural and ecological diversity. The composition of the group has long been a source of uncertainty. Evidence from recent phylogenetic investigations suggests that the subfamily is, if anything, larger and more diverse than previously recognized [3,8,9], while at the same time, others have questioned its monophyly [9,10]. The origins of this group have also been disputed [3,10,11]. Thus, while vangas are celebrated for their exceptional ecological

and phenotypic diversity, we are still unsure whether the group represents an endemic *in situ* radiation or whether their diversity is at least partly attributable to a diverse pool of colonizing lineages.

Madagascar, being an island of continental scale and origins, has a unique biogeographic history. It has been isolated since around 84 million years ago when it split from other Gondwana fragments and was last connected to India and the Seychelles block [12]. While some endemic lineages have been proposed to be Gondwanan relicts isolated on Madagascar when the supercontinent rifted [13–15], the origins of most of the vertebrate fauna post-date these Cretaceous tectonic events [15]. Relatively few colonization events have been hypothesized to have occurred into Madagascar, with most endemic lineages proposed to be colonizers of African origin from across the Mozambique channel [15,16]. Hypotheses of modes of colonization of most terrestrial groups include rafting across the Mozambique Channel [15,17–20] or via land-bridges that no longer exist [21,22], with the former receiving more support. Its proximity to Africa makes it reasonable to assume that much of the modern biota of Madagascar is derived from there, although an Asian component has been detected in some lineages [15,23–26]. Dispersals from Asia have been proposed to occur via stepping-stone islands across the Indian Ocean [25–27].

The avifauna of Madagascar is considered to be species-poor (*ca* 200 species) for its size [28], but about half of the species are endemic to the island. Vangas comprise one of the two larger endemic groups of passerines;

\*Author for correspondence (sreddy6@luc.edu).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2011.2380> or via <http://rspb.royalsocietypublishing.org>.

the other being the Bernieridae, a newly discovered clade comprising species formerly placed in three different families [29,30]. The vangas are primarily insectivorous, although some eat fruits and even small vertebrates [28]. One of the most remarkable features of vangas is the diversity in bill size and shape that probably indicate adaptations to foraging behaviours and diets. For instance, some species probe for insects in bark, much like woodpeckers [7,28]. Earlier authors [31] hypothesized that the lack of woodpeckers in Madagascar allowed vangas to radiate into this niche.

Molecular phylogenetic studies have shown that several other species endemic to Madagascar and previously classified in other families actually belong with the vangas [3,8]. These newly classified vangas had formerly been placed with nuthatches (*Hypositta*), sylviid warblers (*Newtonia*), babblers (*Mystacornis*), bulbuls (*Tylas*) and platysteirids (*Pseudobias*). These results, in concert with uncertainty over vanga monophyly, pose a number of challenges to understanding the evolutionary ecological origins of Madagascar's diverse avifauna. Further, if the newly constituted Vanginae is found to be monophyletic, the morphological and ecological diversity encompassed by this radiation is significantly expanded.

In this study, we asked whether Malagasy vangas show phylogenetic and ecological patterns consistent with adaptive radiation, meaning that they are a monophyletic group exhibiting morphological and ecological diversity consistent with a model of ecological opportunity. We first tested the monophyly of the Vanginae as well as the hypothesis that vangas are an endemic *in situ* radiation in Madagascar. We then determined their biogeographic origins by examining their closest relatives. We studied the role of the different foraging strategies or feeding niches in driving the evolution of this group. Finally, we tested whether patterns of lineage diversification through time are consistent with a model of adaptive radiation driven by ecological opportunity [2,4,32,33], as would be expected if colonization of an area with vacant niches played a role in the evolutionary history of this group. To address temporal patterns of diversification, we introduce a method for diversification studies that can accommodate incomplete taxon sampling, regardless of whether those species have been sampled randomly or non-randomly [34].

## 2. METHODS

### (a) Phylogenetic analysis

We sampled all 15 genera and 16 out of 21 species of Vanginae (missing one species each of *Xenopirostris* and *Calicalicus* and three species of *Newtonia*), including all newly proposed members of this subfamily, and representatives of all potential relatives suggested by recent studies [3,10,35–38]. These included several African species of Playsteiridae and Malaconotidae, as well as Asian species proposed to be closely allied to vangas. In total, our phylogenetic dataset included 37 species, including 16 vangas, and nucleotide sequences from 13 genes, six mitochondrial and seven nuclear loci (see the electronic supplementary material for additional details).

We conducted phylogenetic analyses using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) methods. MP analyses were conducted in

PAUP\* [39] using heuristic searches to find the most parsimonious tree(s) and to calculate nodal support using bootstrap (see the electronic supplementary material). For ML, we conducted partitioned analyses in GARLI-PART v. 0.97 [40], and tested various partition schemes using MODELTEST v. 3.7 [41] (see the electronic supplementary material). We used the best partition scheme to also search for the best ML tree and calculate bootstrap support in RAxML v. 7.0.4 [42]. In RAxML, we conducted a rapid bootstrap of 1000 replicates using the GTRCAT model [43,44] and the best likelihood tree using the GTRGAMMA model on the separate partitions, each with distinct models but joint branch-length optimization. We performed Bayesian inference using MRBAYES v. 3.2 [45] using the same best partition scheme from the ML analysis and ran two Marko Chain Monte Carlo runs of four chains each for 20 million generations, sampling every 500th generation. We used default priors and unlinked all parameters across partitions except for branch-length calculations. Convergence of the two runs and stationarity were assessed using the AWTY tools [46]. A conservative burn-in of the first 4000 sampled generations was discarded.

We examined the robustness of our phylogenetic results by testing for topological instability and conflicts across the different loci. We used MESQUITE v. 2.74 [47] to look at possible effects of missing data and rogue taxa, which cause instability or reduced resolution (see the electronic supplementary material). We examined genome-wide signal for the recovered relationships by comparing single-gene analyses with the combined analysis and looked for significant conflict in terms of relationships that were highly supported in the single-gene trees that were not found in the combined analysis. We also conducted a gene-jackknifing analysis in which we removed one gene at a time and analysed the remaining data in order to examine whether any relationships were driven by single genes (see the electronic supplementary material).

### (b) Divergence times

We used the estimated dates in Barker *et al.* [35] for the split between Vireonidae and remaining corvid birds (node 10 in Barker *et al.* [35]) as well as the split of a clade of shrike-like birds including Vanginae and Malaconotidae (node 11 in Barker *et al.* [35]). Most other recent studies [48–50] of corvid birds have used the same calibration point to date divergences (the split of New Zealand from Gondwana at 82 million years corresponding to the basal divergence between *Acanthisitta* and all other passerines), therefore a range of potential calibrations was not available. Nevertheless, all of the studies using different analytical programmes have estimated roughly similar dates for those splitting events. We used r8s v. 1.71 [51] and both the non-parametric rate smoothing (NPRS) and penalized likelihood (PL) methods on the ML tree to estimate divergence times within vangas and their close relatives by setting the calibration point at the root of the tree (the split between vireos and other corvids) to 37 million years ago [35]. Details are provided in the electronic supplementary material.

### (c) Ancestral areas

We used Lagrange [52] to reconstruct ancestral areas using a likelihood method. We divided the globe into six relevant areas: Madagascar, Africa, tropical Asia, Eurasia (Palearctic), Australasia and Americas. Ranges of each terminal taxon

were assigned based on the geographical extent of the respective genera. In Lagrange, we allowed ancestral areas to include any combination of areas except for two combinations of non-adjacent areas—Madagascar & Americas; Africa & Americas. We input the chronogram calculated by PL in R8S to run the Lagrange analysis. We set the program to estimate baseline rates of dispersal and local extinction. Given the small number of species in our phylogeny, in concert with low number of transitions between geographical regions, we did not attempt to account for regional differences in speciation and extinction rates [32,53] and consequent effects on the reconstruction of geographical character states.

#### (d) Lineage diversification rates

Under the ecological opportunity model, lineage diversification rates are expected to slow through time after initial colonization because of diversity-dependent feedback on speciation and/or extinction rates [32,54,55]. Under this ‘early burst’ model, lineage diversification is high immediately after colonization of a new region, but slows through time as niches get occupied and as ecological opportunities for speciation are diminished. Thus, the ecological opportunity model predicts a temporal deceleration in speciation within the Malagasy vanga radiation. We tested whether diversification rates varied through time following colonization of Madagascar using time-dependent diversification models described previously [55,56]. We fitted two time-constant and two time-varying models of diversification to the time-calibrated Malagasy vanga subclade.

One challenge in testing for temporal variation in diversification rates for vangas is that our sampling is both incomplete and phylogenetically non-random. To address this issue, we implemented a method for accommodating missing taxa in diversification analyses regardless of whether they are randomly or non-randomly sampled. To impute the position of ‘missing’ speciation times in our phylogeny, we used a variant of the expectation-maximization (EM) algorithm that has been widely used to estimate missing data and latent variables in a variety of statistical applications [57]. We describe this method in detail in the electronic supplementary method. We also computed the gamma statistic [58], a measure of the distribution of speciation times in reconstructed phylogenetic trees. Gamma values significantly lower than those expected under constant-rate models of diversification imply a slowdown in speciation through time. See the electronic supplementary method for details.

#### (e) Foraging behaviour

The foraging behaviour of the vangas was described in depth by Schulenberg [28], Yamagishi & Nakamura [7] and Yamagishi & Eguchi [59]. We coded the foraging strategies employed by vangas and their close relatives as three main categories—gleaning, probing and sallying, as defined in Remsen & Robinson [60] (table 1). In cases where a taxon exhibits more than one mode, we coded this as a polymorphism. In cases where one behaviour is only rarely used, we examined coding as a polymorphism and as the dominant behaviour only. Both gave similar results in terms of reconstructing ancestral states. We used MESQUITE to reconstruct the ancestral states of these traits using parsimony optimization. Because we had polymorphisms, we were unable to perform likelihood reconstructions.

Table 1. Foraging behaviours of the Vangidae; the most frequently used techniques is listed first.

<i>Artamella</i>	probing, gleaning
<i>Calicalicus</i>	gleaning
<i>Cyanolanius</i>	gleaning, sallying
<i>Euryceros</i>	sallying
<i>Falcula</i>	probing
<i>Hypositta</i>	gleaning
<i>Leptopterus</i>	gleaning, sallying
<i>Mystacornis</i>	gleaning, probing occasionally <sup>a</sup>
<i>Newtonia</i>	gleaning
<i>Oriolia</i>	probing, gleaning
<i>Pseudobias</i>	sallying
<i>Schetba</i>	sallying
<i>Tylas</i>	gleaning, sallying
<i>Vanga</i>	sallying
<i>Xenopirostris</i>	probing, gleaning
<i>Philentoma</i>	gleaning; rarely sallying
<i>Prionops</i>	gleaning, sallying
<i>Bias</i>	sallying
<i>Megabyas</i>	sallying
<i>Tephrodornis</i>	gleaning, rarely sallying
<i>Hemipus</i>	gleaning, sallying

<sup>a</sup>There is evidence that *Mystacornis* uses probing behaviour to forage on the ground by sticking its bill into moss and dead material; this behaviour is somewhat different from that of the other vangas who probe, which tend to also manipulate the substrate by chiselling and stripping bark, etc.

### 3. RESULTS

#### (a) Phylogenetic analysis

Our dataset had a total of 37 taxa and 11 118 aligned nucleotides from 13 genes, including four mitochondrial protein-coding genes (CYTB, ND2, ND3, COI), two rRNAs (12s, 16s), three nuclear exons (RAG1, RAG2, CMOS) and four nuclear introns (GAPDH, LDH, FIB5, MYO). All MP, ML and BI analyses of the combined dataset show that vangas are a monophyletic radiation endemic to Madagascar (figure 1 and electronic supplementary material, figures S1 and S2). This includes all the species in the traditional classification of the subfamily as well the newly proposed members such as *Mystacornis*, *Newtonia*, *Tylas* and *Pseudobias*. Nodal support for the monophyly of vangas is high in ML (96 Bootstrap (BS)) and BI (0.99 Posterior Probability (PP)), but not in MP (less than 50 BS).

The closest relatives of vangas are a group of six Asian and African genera formerly placed in several different families at various times, including the Platysteiridae (*Bias*, *Megabyas* [6,7]), Malaconotidae (*Prionops* [5]), Prionopidae (*Prionops*, *Philentoma*, *Tephrodornis* [6]) and Campephagidae (*Hemipus* [5,6]), and *incertae sedis* (*Philentoma*, *Tephrodornis* [5]). In MP, these taxa fall into two groups with *Tephrodornis*, *Hemipus*, *Bias*, *Megabyas* in one clade as sister to the Malagasy vangas (Vanginae) and the clade of *Philentoma* + *Prionops* being sister to this larger clade. In ML and BI, *Philentoma* is consistently found as the sister species of Vanginae, although only with low support, and the remaining five are monophyletic, again with low support. The clade of vangas + the six relatives (hereby the Vangidae or vanga-shrikes) are found consistently in all analyses with high support (100 BS in ML, 1.0 PP in BI and 85 BS in MP). We found that the phylogenetic results were largely consistent across the different data partitions and analyses (see the electronic supplementary material).





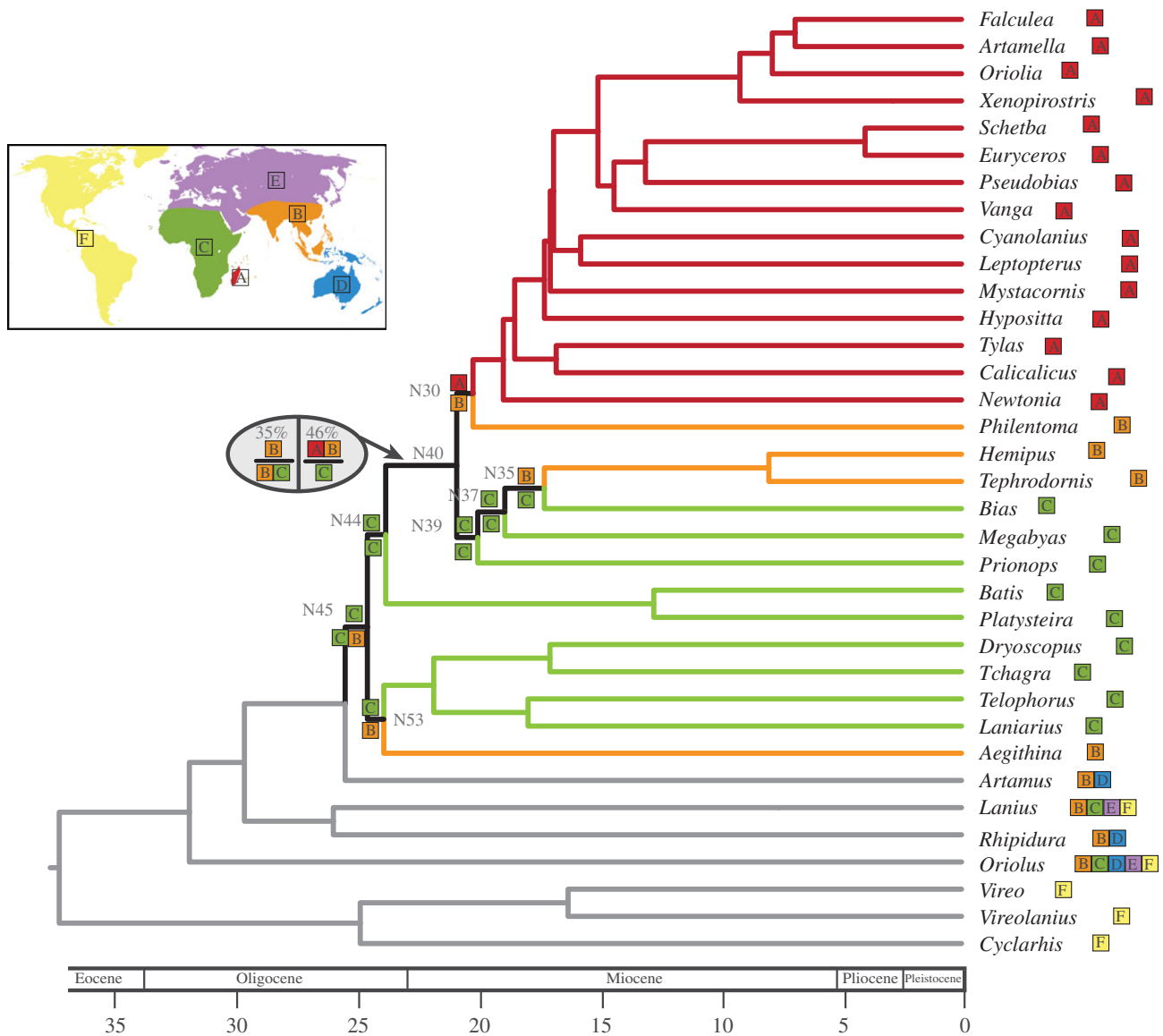


Figure 2. Chronogram using penalized likelihood and ancestral area reconstruction using Lagrange. Nodes show the ancestral area(s) reconstruction with the highest likelihood of the descendant lineages on either side of split. Numbers at nodes prefixed with an 'N' refer to node numbers referenced in the text. For all nodes except N40, the reconstructions shown have about twice the relative probability (see the electronic supplementary material) as the next most likely. Coloured branches are used when all the descendant lineages are only found in a single area. Geographical areas are as follows: A (red), Madagascar; B (orange), Asia; C (green), Africa; D (blue), Australia; E (purple), Eurasia; F (yellow), Americas.

Africa to Asia and then subsequently to Madagascar. From the African Vangidae (N39), there is a dispersal to Asia at N37 along the lineage leading to *Hemipus* and *Tephrodornis*.

### (c) Foraging behaviour

Optimizing and reconstructing ancestral states of foraging strategies show that the vangas first colonizing Madagascar were gleaners (figure 3). The basal divergences within Vangiinae show these lineages to be mainly gleaners or generalist gleaners and salliers (figure 3), like their continental relatives (table 1). Probing vangas are united in one clade, as are vangas who are aerial or sallying specialists (figure 3). These two clades are sisters, a consistently well-supported relationship.

### (d) Diversification rates

We used our implementation of the EM algorithm to estimate the positions of the five 'missing' speciation events in the Malagasy Vangiinae (see §2). In each case,

the 'expectation' step consisted of simulating subclades under the relevant diversification model, conditional on the full (sampled plus missing) diversity as well as the age of the subclade. These missing speciation times were then used jointly with the observed data to update parameters of the diversification model.

We found strong support for declining rates of speciation through time during the radiation of the Malagasy clade (table 2). The time-constant models provided a poor fit to the observed data (table 2) and the overall-best fit model specified an exponential decline in the rate of speciation through time (figure 4). Consistent with previous studies [56,62], extinction rates were estimated to be near zero under both time-constant and time-varying models of diversification.

Gamma statistics [58] computed for the Malagasy radiation provide further evidence for a slowing of speciation through time following the colonization of Madagascar. The observed gamma statistic ( $-3.32$ ) is highly unlikely if

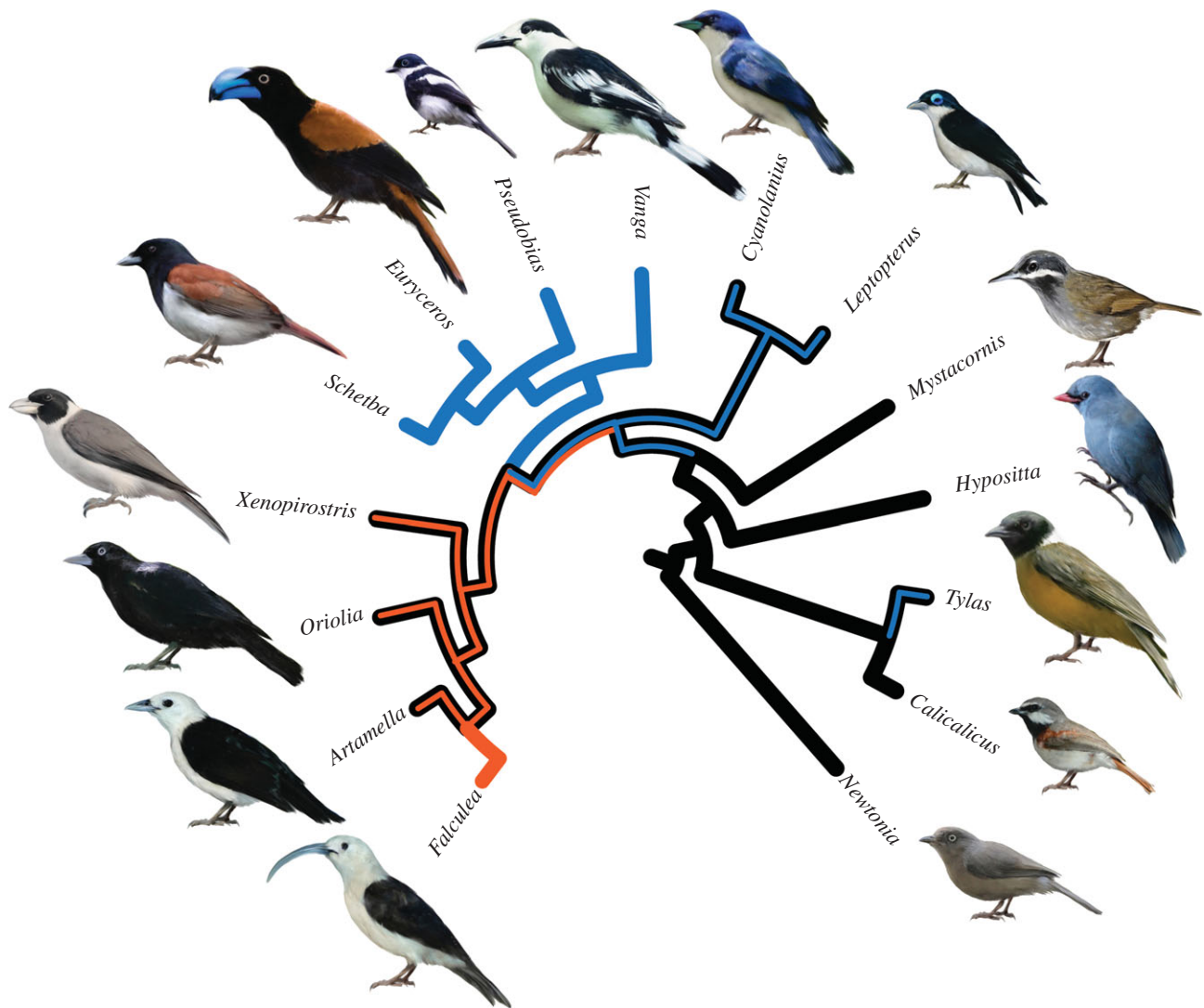


Figure 3. The radiation of Vanginae and optimized foraging behaviour (table 1): black, gleaning; blue, sallying; red, probing. Illustrations of birds by Velizar Simeonovski.

speciation rates have been constant through time, under both random taxon sampling ( $p < 0.001$ ) as well as 'phylogenetically overdispersed' taxon sampling ( $p = 0.017$ ). This latter sampling model (see the electronic supplementary material) assumed a 'worst case' scenario for non-random taxon sampling, where only the most phylogenetically divergent subset of lineages was included in the analysis. These results are unlikely to be due to saturation of mtDNA: the observed gamma statistic was  $-3.52$  for the PL-smoothed phylogeny constructed after excluding third codon positions from mtDNA protein coding genes. Finally, it is unlikely that this slowdown in diversification could have resulted from recent (post-Pleistocene) extinction of many vanga species or from the presence of unsampled (cryptic) species diversity. In the electronic supplementary material, figure S4, we demonstrate that at least 60 additional species of Malagasy vangas would have to be present (or to have recently gone extinct) to generate a gamma statistic of equal magnitude if speciation rates have truly been constant over time.

#### 4. DISCUSSION

##### (a) *Vangidae*

The origin of shrike-like corvid birds in Madagascar has long fascinated ornithologists. Our study uncovers a novel

group of species that are closely related to Malagasy vangas, which we place in the family Vangidae together with the vangas. This study is the first to show with strong support that the closest relatives of the Malagasy vangas (Vanginae) consist of species from both Africa and Asia.

The genera allied with the Malagasy vangas—*Philentoma*, *Tephrodornis*, *Hemipus*, *Bias*, *Megabyas* and *Prionops*—have all been notoriously hard to place within the Corvids. They have been variously placed in several different oscine families, including Campephagidae, Malaconotidae, Platysteiridae and Prionopidae. This is the first study to bring all these aberrant taxa together in a phylogenetic analysis. We also find consistent, yet not strong, support for *Philentoma* to be the sister group to the Malagasy vangas, similar to Jonsson *et al.* [61].

##### (b) *Monophyly of Vanginae*

We find consistent support for the Vanginae being a monophyletic radiation endemic to Madagascar. Basal divergences in the Vanginae and Vangidae were rapid, leaving little signal to recover these deep branches. Data from 13 genes were needed to recover a strongly supported monophyletic Vanginae. As apparent from the gene-jackknifing and single-gene analyses, low support

Table 2. Diversification-through-time patterns in Malagasy vangas. The  $\lambda$  model and the  $\mu$  model give functional forms of speciation and extinction rates, respectively, through time under each fitted model; np is the number of parameters in each model and LogLik is log likelihood.

model name	$\lambda$ model	$\mu$ model	np	LogLik	AIC	$\Delta$ AIC
pure birth	$\lambda(t) = \lambda$	$\mu(t) = 0$	1	-25.2	52.4	13.8
birth–death	$\lambda(t) = \lambda$	$\mu(t) = \mu$	2	-25.2	54.4	15.8
exponential, with extinction	$\lambda(t) = \lambda_0 e^{-kt}$	$\mu(t) = \mu_0 e^{-zt}$	4	-17.1	42.2	3.6
exponential, no extinction	$\lambda(t) = \lambda_0 e^{-kt}$	$\mu(t) = 0$	2	-17.3	38.6	0

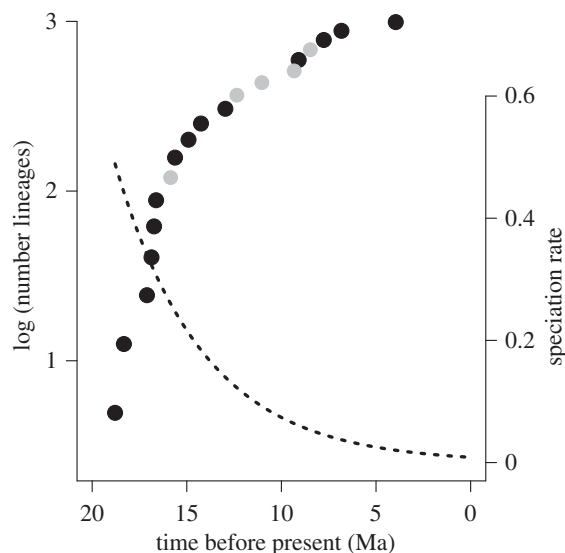


Figure 4. Tempo and mode of lineage diversification in Malagasy vangas. Black circles denote observed lineage-accumulation curve; grey circles are the locations of ‘missing’ speciation events estimated using the EM algorithm under the best-fit diversification model. ML estimate of speciation-through-time under exponential decline model is indicated by the dashed line.

for the monophyly of this group with less data indicates poor signal at these basal, fast-paced divergence events.

Many of the relationships within Vanginae receive significant support, yet the placement of some species is weak, including many of the more ‘unstable’ taxa in our study as well as most of the taxa more recently identified to be part of the vanga radiation (i.e. *Newtonia*, *Mystacornis* and *Hypositta*). Eleven of the 15 genera of vangas are monotypic. Previously, three of these taxa, *Leptopterus*, *Cyanolanius*, *Artamella*, were categorized as congeners (in the genus *Leptopterus*). These taxa are not recovered as a monophyletic group and are instead distributed throughout the radiation. This is just one more example of how the extreme morphological differences between taxa have confused phylogenetic analyses and classifications. Our study samples only one set of congeneric species, *Xenopirostris damii* and *Xenopirostris xenopirostris*, which show a young divergence time. However in comparison, two considerably morphological divergent species, *Euryceros* and *Schetba*, show only a slightly greater genetic divergence (figure 1).

### (c) Adaptive foraging strategies

A majority of Vangidae species glean arthropods from the surfaces of leaves or bark. This seems to be the primitive condition, with all of the early-diverging lineages of Vanginae exhibiting this behaviour and some of these

lineages being generalists in terms of using gleaning, as well as an alternative behaviour, such as sallying. In a more derived clade of vangas, there is a split between species that probe versus species that specialize in sallying foraging techniques. All species in the *Artamella-Falculea-Oriolia-Xenopirostris* clade forage regularly if not primarily by probing with subsurface manoeuvres directed at bark or other woody substrates. This clade includes species with some of the most notable specialized bill morphologies among the vangas, including the deep, laterally compressed bills of the three species of *Xenopirostris* and the long, deeply curved (sickle-shaped) bill of *Falculea*. Species of vangas in this clade are important components of forest bird communities on Madagascar, with two or three species of probing vangas present at most sites (representing 5–14% of the passerine species diversity) [28]. Earlier authors [31] noted that *Falculea* filled a vacant woodpecker niche on Madagascar, but it was not recognized previously that *Falculea* is embedded within a small radiation of vangas with similar behaviours. The four taxa that use primarily sallying or aerial manoeuvres also are included in a single clade. Three of these taxa (*Vanga*, *Schetba* and *Euryceros*) sally to the ground or to foliage; perhaps the most specialized member of this clade, *Pseudobias*, sallies to air and to foliage. This study is the first to identify these taxa as a monophyletic group.

### (d) Diversification of vangas and their relatives

The closest relatives of vangas are a group of shrike-like birds found primarily in the Old World tropics. Our biogeographic analysis shows that the Malagasy vanga radiation has connections to Asia as well as Africa. Most Malagasy fauna (birds, mammals, reptiles, etc.) were previously proposed to be derived from Africa, the closest mainland source. Our study tested different possibilities and provides evidence to substantiate the hypothesis of an Asian origin. Though the connection to Asia might be surprising, this is similar to patterns in other endemic radiations of Madagascar, both avian and non-avian [26,63–65].

Although our analysis is equivocal in terms of distinguishing the particular route of the vanga dispersal to Madagascar, all three scenarios of dispersal are intriguing: from Africa to Asia via Madagascar, to Madagascar via Asia, and simultaneously to Asia and Madagascar. The possibility of *Philentoma* arriving in Asia via Madagascar is intriguing because a lineage colonizing a mainland area from an island is considered a rare occurrence and has only recently been demonstrated [61,66].

Within the closest relatives of vangas, all genera have low species diversity, with one genus (*Prionops*) containing seven species, three genera (*Philentoma*, *Hemipus* and *Tephrodornis*) comprised of two species each, and two



genera (*Bias* and *Megabyas*) being monotypic. All of these taxa are distributed in continental regions and even together do not equate the level of species diversity that radiated from the lineage that colonized Madagascar. This suggests these taxa did not diversify in these continental regions as successfully as vangas on Madagascar, perhaps owing to competition with other lineages, whereas the vangas on Madagascar probably encountered a depauperate avifauna and unoccupied niches upon colonization.

### (e) Adaptive radiation in vangas

Increased diversification in the Vanginae correlates with the colonization of Madagascar. There is also remarkable congruence between feeding strategies and the phylogeny of this group. Given this, it is reasonable to assert that expanding and specializing feeding behaviours played a large role in the diversification and adaptive radiation of these groups within Madagascar, leading to the extreme morphological differentiation. Interestingly, the basal lineages of the Vangidae, both continental and Malagasy, all use a generalist or gleaning strategy and exhibit a great diversity in terms of plumage but do not show as much variation in bills compared with the more derived vanga groups.

Adaptive radiations, regardless of whether one views them as part of a continuum [67] or exceptional [1,2,4], have intriguing properties from which to study evolution. Our study shows that the incredible diversity of forms encompassed in the vangas of Madagascar arose as an *in situ* radiation and exhibits a pattern of diversification consistent with the ecological opportunity model. Upon colonization of Madagascar, the speciation rate of the early lineages was high and declined dramatically over time, presumably owing to the occupation and saturation of niches. We also show that foraging specializations in this group are due to common ancestry and that these adaptations led to further speciation. Both lines of evidence point towards speciation in vangas being driven by adaptation into unoccupied and novel ecological niches.

We thank Velizar Simeonovski for his extraordinary illustrations of birds. Fieldwork in Madagascar was authorized by the Direction des Eaux et Forests and the Commission Tripartite. For samples and logistics, we acknowledge the Field Museum of Natural History and, in particular, Steve Goodman. For helpful comments, we are grateful to John Bates, Cathy Bechtoldt, Nick Block, Josh Engel, Irby Lovette, Peter Makovicky, Rick Ree, V. V. Robin, Jason Weckstein, Dave Willard and Ben Winger. We also thank Associate Editor Trevor Price, Per Alström, and an anonymous reviewer for suggesting significant improvements to the paper. Laboratory work was conducted at the Pritzker Laboratory of Molecular Systematics at the Field Museum of Natural History and at the Laboratory of Analytical Biology at the Smithsonian Institution. This research was supported by grants from Sigma Xi, the University of Chicago (Neirman Fund), the American Museum of Natural History (Frank M. Chapman Fund), the Field Museum of Natural History (Reichelderfer Fund) and the National Science Foundation (DEB-0962078). Data generated in this study were deposited into GenBank (JQ239173-JQ239370).

### REFERENCES

- Glor, R. E. 2010 Phylogenetic insights on adaptive radiation. *Annu. Rev. Ecol. Evol. Syst.* **41**, 251–270. (doi:10.1146/annurev.ecolsys.39.110707.173447)
- Schluter, D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
- Yamagishi, S., Honda, M., Eguchi, K. & Thorstrom, R. 2001 Extreme endemic radiation of the Malagasy vangas (Aves: Passeriformes). *J. Mol. Evol.* **53**, 39–46.
- Losos, J. B. & Mahler, D. L. 2010 Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. In *Evolution since Darwin: the first 150 years* (eds M. A. Bell, D. J. Futuyma, W. F. Eanes & J. S. Levinton), pp. 381–420. Sunderland, MA: Sinauer.
- Dickinson, E. C. (ed.) 2003 *The Howard and Moore complete checklist of the birds of the World, revised and enlarged*. 3rd edn. London, UK: Christopher Helm.
- Clements, J. F. 2007 *The Clements checklist of birds of the world*, 6th edn. Ithaca, NY: Cornell University Press.
- Yamagishi, S. & Nakamura, M. 2009 Family Vangidae (Vangas). In *Handbook of the birds of the world. Bush-Shrikes to Old World Sparrows*, vol. 14 (eds J. del Hoyo, A. Elliott & D. Christie), pp. 142–171. Barcelona, Spain: Lynx Edicions.
- Johansson, U. S., Bowie, R. C., Hackett, S. J. & Schulenberg, T. S. 2008 The phylogenetic affinities of Crossley's babbler (*Mystacornis crossleyi*): adding a new niche to the vanga radiation of Madagascar. *Biol. Lett.* **4**, 677–680. (doi:10.1098/rsbl.2008.0444)
- Schulenberg, T. S. 1995. Evolutionary history of the vangas (Vangidae) of Madagascar. *PhD Committee on Evolutionary Biology*. University of Chicago, Chicago, IL, USA.
- Manegold, A. 2008 Composition and phylogenetic affinities of vangas (Vangidae, Oscines, Passeriformes) based on morphological characters. *J. Zool. Syst. Evol. Res.* **46**, 267–277. (doi:10.1111/j.1439-0469.2008.00458.x)
- Sibley, C. G. & Ahlquist, J. A. 1990 *Phylogeny and classification of birds*. New Haven, CT: Yale University Press.
- Plummer, P. S. & Belle, E. R. 1995 Mesozoic tectonostratigraphic evolution of the Seychelles microcontinent. *Sediment. Geol.* **96**, 73–91. (doi:10.1016/0037-0738(94)00127-G)
- Cracraft, J. 2001 Avian evolution, Gondwana biogeography and the Cretaceous–Tertiary mass extinction event. *Proc. R. Soc. Lond. B* **268**, 459–469. (doi:10.1098/rspb.2000.1368)
- Noonan, B. P. & Chippindale, P. T. 2006 Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic land bridge. *Am. Nat.* **168**, 730–741. (doi:10.1086/509052)
- Yoder, A. D. & Nowak, M. D. 2006 Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annu. Rev. Ecol. Evol. Syst.* **37**, 405–431. (doi:10.1146/annurev.ecolsys.37.091305.110239)
- Simpson, G. G. 1940 Mammals and land bridges. *J. Wash. Acad. Sci.* **30**, 137–163.
- Ali, J. R. & Huber, M. 2010 Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* **463**, 653–656. (doi:10.1038/nature08706)
- Fuller, S., Schwarz, M. & Tierney, S. 2005 Phylogenetics of the allopapine bee genus *Braunsapis*: historical biogeography and long-range dispersal over water. *J. Biogeogr.* **32**, 2135–2144. (doi:10.1111/j.1365-2699.2005.01354.x)
- Vences, M., Vieites, D. R., Glaw, F., Brinkmann, H., Kosuch, J., Veith, M. & Meyer, A. 2003 Multiple overseas dispersal in amphibians. *Proc. R. Soc. Lond. B* **270**, 2435–2442. (doi:10.1098/rspb.2003.2516)
- Yoder, A. D., Burns, M. M., Zehr, S., Delefosse, T., Veron, G., Goodman, S. M. & Flynn, J. J. 2003 Single origin of Malagasy Carnivora from an African ancestor. *Nature* **421**, 734–737. (doi:10.1038/nature01303)
- McCall, R. A. 1997 Implications of recent geological investigations of the Mozambique Channel for the



- mammalian colonization of Madagascar. *Proc. R. Soc. Lond. B* **264**, 663–665. (doi:10.1098/rspb.1997.0094)
- 22 Wit, M. J. 2003 Madagascar: heads it's a continent, tails it's an island. *Ann. Rev. Earth Planet Sci.* **31**, 213–248. (doi:10.1146/annurev.earth.31.100901.141337)
- 23 Keith, S. 1980 Origins of the avifauna of the Malagasy region. In *Proceedings of the 4th Pan African Ornithological Congress* (ed. D. N. Johnson), pp. 99–108. Johannesburg, South Africa: South African Ornithological Society.
- 24 Marks, B. D. & Willard, D. E. 2005 Phylogenetic relationships of the Madagascar pygmy kingfisher (*Ispidina madagascariensis*). *Auk* **122**, 1271–1280. (doi:10.1642/0004-8038(2005)122[1271:PROTMP]2.0.CO;2)
- 25 Warren, B. H., Strasberg, D., Bruggemann, J., Prys-Jones, R. & Thébaud, C. 2010 Why does the biota of the Madagascar region have such a strong Asiatic flavour? *Cladistics* **26**, 526–538. (doi:10.1111/j.1096-0031.2009.00300.x)
- 26 Warren, B. H., Bermingham, E., Prys-Jones, R. P. & Thébaud, C. 2005 Tracking island colonization history and phenotypic shifts in Indian Ocean bulbuls (*Hypsipetes*: Pycnonotidae). *Biol. J. Linn. Soc.* **85**, 271–287. (doi:10.1111/j.1095-8312.2005.00492.x)
- 27 Sheldon, F. H., Lohman, D. J., Lim, H. C., Zou, F., Goodman, S. M., Prawiradilaga, D. M., Winker, K., Braile, T. M. & Moyle, R. G. 2009 Phylogeography of the magpie-robin species complex (Aves: Turdidae: *Copsychus*) reveals a Philippine species, an interesting isolating barrier and unusual dispersal patterns in the Indian Ocean and Southeast Asia. *J. Biogeogr.* **36**, 1070–1083. (doi:10.1111/j.1365-2699.2009.02087.x)
- 28 Schulenberg, T. S. 2003 Vangidae, vangas. In *The natural history of Madagascar* (eds S. M. Goodman & J. P. Benstead), pp. 1138–1143. Chicago, IL: University of Chicago Press.
- 29 Cibois, A., Slikas, B., Schulenberg, T. S. & Pasquet, E. 2001 An endemic radiation of Malagasy songbirds is revealed by mitochondrial DNA sequence data. *Evolution* **55**, 1198–1206. (doi:10.1111/j.0014-3820.2001.tb00639.x)
- 30 Cibois, A., Normand, D., Gregory, S. M. S. & Pasquet, E. 2010 Bernieridae (Aves: Passeriformes): a family-group name for the Malagasy sylvioid radiation. *Zootaxa* **2554**, 65–68.
- 31 Moreau, R. E. 1966 *The bird faunas of Africa and its islands*. London, UK: Academic Press.
- 32 Rabosky, D. L. & Glor, R. E. 2010 Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proc. Natl Acad. Sci. USA* **107**, 22 178–22 183. (doi:10.1073/pnas.1007606107)
- 33 Yoder, J. B. et al. 2010 Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol.* **23**, 1581–1596. (doi:10.1111/j.1420-9101.2010.02029.x)
- 34 Brock, C. D., Harmon, L. J. & Alfaro, M. E. 2011 Testing for temporal variation in diversification rates when sampling is incomplete and nonrandom. *Syst. Biol.* **60**, 410–419. (doi:10.1093/sysbio/syr007)
- 35 Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. 2004 Phylogeny and diversification of the largest avian radiation. *Proc. Natl Acad. Sci. USA* **101**, 11 040–11 045. (doi:10.1073/pnas.0401892101)
- 36 Fuchs, J., Bowie, R. C., Fjeldsa, J. & Pasquet, E. 2004 Phylogenetic relationships of the African bush-shrikes and helmet-shrikes (Passeriformes: Malaconotidae). *Mol. Phylogenet. Evol.* **33**, 428–439. (doi:10.1016/j.ympev.2004.06.014)
- 37 Fuchs, J., Cruaud, C., Couloux, A. & Pasquet, E. 2007 Complex biogeographic history of the cuckoo-shrikes and allies (Passeriformes: Campephagidae) revealed by mitochondrial and nuclear sequence data. *Mol. Phylogenet. Evol.* **44**, 138–153. (doi:10.1016/j.ympev.2006.10.014)
- 38 Moyle, R., Cracraft, J., Lakim, M., Nais, J. & Sheldon, F. 2006 Reconsideration of the phylogenetic relationships of the enigmatic Bornean Bristlehead (*Pityriasis gymmcephala*). *Mol. Phylogenet. Evol.* **39**, 893–898. (doi:10.1016/j.ympev.2006.01.024)
- 39 Swofford, D. L. 2003 *PAUP\**. *Phylogenetic analysis using parsimony (\*and Other Methods)*, Version 4b10. Sunderland, MA: Sinauer Associates.
- 40 Zwickl, D. J. 2006 Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. *PhD dissertation*. University of Texas at Austin, Austin, TX, USA.
- 41 Posada, D. & Crandall, K. A. 1998 Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818. (doi:10.1093/bioinformatics/14.9.817)
- 42 Stamatakis, A. 2006 RAXML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**, 2688–2690. (doi:10.1093/bioinformatics/btl446)
- 43 Stamatakis, A., Hoover, P. & Rougemont, J. 2008 A rapid bootstrap algorithm for the RAXML web-servers. *Syst. Biol.* **57**, 758–771. (doi:10.1080/10635150802429642)
- 44 Stamatakis, A. 2006 Phylogenetic models of rate heterogeneity: a high performance computing perspective. In *Proc. of the 20th International Parallel and Distributed Processing Symposium (IPDPS)*, Rhodes Island, Greece, 25–29 April 2006. (doi:10.1109/IPDPS.2006.1639535)
- 45 Ronquist, F. & Huelsenbeck, J. P. 2003 MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**, 1572–1574. (doi:10.1093/bioinformatics/btg180)
- 46 Nylander, J. A., Wilgenbusch, J. C., Warren, D. L. & Swofford, D. L. 2008 AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* **24**, 581–583. (doi:10.1093/bioinformatics/btm388)
- 47 Maddison, W. P. & Maddison, D. R. 2010 Mesquite: a modular system for evolutionary analysis. Version 2.73. See <http://mesquiteproject.org>.
- 48 Beresford, P., Barker, F. K., Ryan, P. G. & Crowe, T. M. 2005 African endemics span the tree of songbirds (Passeri): molecular systematics of several evolutionary 'enigmas'. *Proc. R. Soc. B* **272**, 849–858. (doi:10.1098/rspb.2004.2997)
- 49 Fuchs, J., Fjeldsa, J., Bowie, R. C., Voelker, G. & Pasquet, E. 2006 The African warbler genus *Hyltiota* as a lost lineage in the Oscine songbird tree: molecular support for an African origin of the Passerida. *Mol. Phylogenet. Evol.* **39**, 186–197. (doi:10.1016/j.ympev.2005.07.020)
- 50 Njabo, K. Y., Bowie, R. C. & Sorenson, M. D. 2008 Phylogeny, biogeography and taxonomy of the African wattle-eyes (Aves: Passeriformes: Platysteiridae). *Mol. Phylogenet. Evol.* **48**, 136–149. (doi:10.1016/j.ympev.2008.01.013)
- 51 Sanderson, M. J. 2003 r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics* **19**, 301–302. (doi:10.1093/bioinformatics/19.2.301)
- 52 Ree, R. H. & Smith, S. A. 2008 Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* **57**, 4–14. (doi:10.1080/10635150701883881)
- 53 Goldberg, E. E., Lancaster, L. T. & Ree, R. H. 2011 Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* **60**, 451–465. (doi:10.1093/sysbio/syr046)
- 54 Phillimore, A. B. & Price, T. D. 2008 Density-dependent cladogenesis in birds. *PLoS Biol.* **6**, e71. (doi:10.1371/journal.pbio.0060071)

- 55 Rabosky, D. L. & Lovette, I. J. 2008 Density-dependent diversification in North American wood warblers. *Proc. R. Soc. B* **275**, 2363–2371. (doi:10.1098/rspb.2008.0630)
- 56 Rabosky, D. L. & Lovette, I. J. 2008 Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* **62**, 1866–1875. (doi:10.1111/j.1558-5646.2008.00409.x)
- 57 Dempster, A. P., Laird, N. & Rubin, D. 1977 Maximum likelihood from incomplete data via the EM algorithm. *J. R. Stat. Soc. Lond. B* **39**, 1–38.
- 58 Pybus, O. G. & Harvey, P. H. 2000 Testing macro-evolutionary models using incomplete molecular phylogenies. *Proc. R. Soc. Lond. B* **267**, 2267–2272. (doi:10.1098/rspb.2000.1278)
- 59 Yamagishi, S. & Eguchi, K. 1996 Comparative foraging ecology of Madagascar vangids (Vangidae). *Ibis* **138**, 283–290. (doi:10.1111/j.1474-919X.1996.tb04340.x)
- 60 Remsen Jr, J. V. & Robinson, S. K. 1990 A classification scheme for foraging behavior of birds in terrestrial habitats. In *Avian foraging: theory, methodology, and applications* (eds M. L. Morrison, C. J. Ralph, J. Verner & J. R. Jehl). Studies in avian biology, vol. 13, pp. 144–160. See [http://elibrary.unm.edu/sora/Condor/cooper/sab\\_013.pdf](http://elibrary.unm.edu/sora/Condor/cooper/sab_013.pdf).
- 61 Jonsson, K. A., Fabre, P. H., Ricklefs, R. E. & Fjeldsa, J. 2011 Major global radiation of corvid birds originated in the proto-Papuan archipelago. *Proc. Natl Acad. Sci. USA* **108**, 2328–2333. (doi:10.1073/pnas.1018956108)
- 62 Morlon, H., Potts, M. D. & Plotkin, J. B. 2010 Inferring the dynamics of diversification: a coalescent approach. *PLoS Biol.* **8**, e1000493. (doi:10.1371/journal.pbio.1000493)
- 63 Renner, S. S. 2004 Multiple Miocene Melastomataceae dispersal between Madagascar, Africa and India. *Phil. Trans. R. Soc. Lond. B* **359**, 1485–1494. (doi:10.1098/rstb.2004.1530)
- 64 Sparks, J. 2004 Molecular phylogeny and biogeography of the Malagasy and South Asian cichlids (Teleostei: Perciformes: Cichlidae). *Mol. Phylogenet. Evol.* **30**, 599–614. (doi:10.1016/S1055-7903(03)00225-2)
- 65 Vences, M., Freyhof, J., Sonnenberg, R., Kosuch, J. & Veith, M. 2001 Reconciling fossils and molecules: Cenozoic divergence of cichlid fishes and the biogeography of Madagascar. *J. Biogeogr.* **28**, 1091–1099. (doi:10.1046/j.1365-2699.2001.00624.x)
- 66 Filardi, C. E. & Moyle, R. G. 2005 Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature* **438**, 216–219. (doi:10.1038/nature04057)
- 67 Olson, M. E. & Arroyo-Santos, A. 2009 Thinking in continua: beyond the ‘adaptive radiation’ metaphor. *BioEssays* **31**, 1337–1346. (doi:10.1002/bies.200900102)