Diversification and the adaptive radiation of the vangas of Madagascar


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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 corvoids 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 colonizing 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 (Drepanidinacae), 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 rivaling 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 relics isolated on Madagascar when the supercontinent rifted [13–15], the origins of most of the vertebrate fauna postdate 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 landbridges 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;
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 is an 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 (Pseudobrias). 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 Caliscalix 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 Acantitis 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 88s 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

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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 88s 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.

(c) 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.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Foraging behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artamella</td>
<td>probing, gleaning</td>
</tr>
<tr>
<td>Caliculus</td>
<td>gleaning</td>
</tr>
<tr>
<td>Cyanolanius</td>
<td>gleaning, sallying</td>
</tr>
<tr>
<td>Euryxenos</td>
<td>sallying</td>
</tr>
<tr>
<td>Falcidea</td>
<td>probing</td>
</tr>
<tr>
<td>Hypositita</td>
<td>gleaning</td>
</tr>
<tr>
<td>Leptopenus</td>
<td>gleaning, sallying</td>
</tr>
<tr>
<td>Mystacornis</td>
<td>gleaning, probing occasionally</td>
</tr>
<tr>
<td>Newtonia</td>
<td>gleaning</td>
</tr>
<tr>
<td>Oriola</td>
<td>probing, gleaning</td>
</tr>
<tr>
<td>Pseudobias</td>
<td>sallying</td>
</tr>
<tr>
<td>Schetra</td>
<td>sallying</td>
</tr>
<tr>
<td>Tylas</td>
<td>gleaning, sallying</td>
</tr>
<tr>
<td>Vanga</td>
<td>sallying</td>
</tr>
<tr>
<td>Xenopirostris</td>
<td>probing, gleaning</td>
</tr>
<tr>
<td>Philentoma</td>
<td>gleaning; rarely sallying</td>
</tr>
<tr>
<td>Prionops</td>
<td>gleaning, sallying</td>
</tr>
<tr>
<td>Bias</td>
<td>sallying</td>
</tr>
<tr>
<td>Megabaya</td>
<td>sallying</td>
</tr>
<tr>
<td>Tephrodornis</td>
<td>gleaning, rarely sallying</td>
</tr>
<tr>
<td>Hemipus</td>
<td>gleaning, sallying</td>
</tr>
</tbody>
</table>

*aThere 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). 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, Megabayas [6,7]), Malaconotidae (Prionops [5]), Prionopidae (Prionops, Philetoma, Tephrodornis [6]) and Campephagidae (Hemipus [5,6]), and incertae sedis (Philetoma, Tephrodornis [5]). In MP, these taxa fall into two groups with Tephrodornis, Hemipus, Bias, Megabayas in one clade as sister to the Malagasy vangas (Vanginae) and the clade of Philetoma + Prionops being sister to this larger clade. In ML and BI, Philetoma 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 vang-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).
Timing and biogeography

The divergence timing analysis shows that vangas reached Madagascar roughly 20 Ma (PL = 19.9; NPRS = 18.8, confidence intervals are shown in the electronic supplementary material, figure S3; figure 2). Diversification at the base of the clade including vangas and their shrike-like relatives (N45) happened relatively quickly, with this clade splitting from remaining corvoids at 24.2 Ma (PL; NPRS = 22.85) and subsequently colonizing Madagascar roughly four million years later. Accordingly, although we analysed a more finely sampled dataset of shrike-like corvoids, our dates are consistent with the results obtained for these nodes by Barker et al. [35] and Beresford et al. [48], the studies from which we derived our calibrations, and other recent studies that used somewhat different methods [61].

Results of the Lagrange ancestral area analysis are shown in figure 2. For all nodes, Lagrange reports multiple possible reconstructions within two likelihood units, however the reconstructions show have about the twice the relative probability as the next most likely reconstruction (except for N40; see below). We predicted the ancestral areas of nodes within the clade of Asian-African-Malagasy shrike-like birds (node N45, figure 2). Lagrange predicts that the basal node of this lineage (N45) gave rise to descendants in Asia and Africa (Malaconotidae and Aegithinidae) and Africa (Platysteiridae, Vangidae). The ancestral distribution of Vangidae (N44) is Africa. In the first divergence within Vangidae (N40), there are two reconstructions with similar likelihoods and near relative probabilities—the first predicts the ancestral area in the top to be Asia + Madagascar and the bottom to be Africa (46% relative probability); the second predicts the ancestral area in the top to be Asia and the bottom to be Asia + Africa. The first reconstruction implies dispersal from Africa to Asia and Madagascar, although it is equivocal if this dispersal is from Africa to Asia and then Madagascar, or to Madagascar then Asia, or simultaneously to Asia and Madagascar. The second reconstruction also implies dispersal from
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 Vanginae 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 Vanginae (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
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 corvoid 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 Corvuids. 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
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Table 2. Diversification-through-time patterns in Malagasy vangas. The λ model and the μ 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.

<table>
<thead>
<tr>
<th>model name</th>
<th>λ model (t) = λ</th>
<th>μ model (t) = 0</th>
<th>np</th>
<th>LogLik</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>pure birth</td>
<td>λ(t) = λ</td>
<td>μ(t) = μ</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>birth–death</td>
<td>λ(t) = λ</td>
<td>μ(t) = μc^{−kt}</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>exponential, with extinction</td>
<td>λ(t) = λc^{−kt}</td>
<td>μ(t) = μc^{−kt}</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>exponential, no extinction</td>
<td>λ(t) = λc^{−kt}</td>
<td>μ(t) = 0</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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 Hypoissa). 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-Oriolita-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, sallys 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
Adaptation into unoccupied and novel ecological niches. Adaptations led to further speciation. Both lines of evidence for this group are due to common ancestry and that these early lineages was high and declined dramatically over time, presumably owing to the occupation and saturation of 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.

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