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Evolutionary biology

Evolutionary models demonstrate rapid and adaptive diversification of Australo-Papuan pythons

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Lineages may diversify when they encounter available ecological niches. Adaptive divergence by ecological opportunity often appears to follow the invasion of a new environment with open ecological space. This evolutionary process is hypothesized to explain the explosive diversification of numerous Australian vertebrate groups following the collision of the Eurasian and Australian plates 25 Mya. One of these groups is the pythons, which demonstrate their greatest phenotypic and ecological diversity in Australo-Papua (Australia and New Guinea). Here, using an updated and near complete time-calibrated phylogenomic hypothesis of the group, we show that following invasion of this region, pythons experienced a sudden burst of speciation rates coupled with multiple instances of accelerated phenotypic evolution in head and body shape and body size. These results are consistent with adaptive radiation theory with an initial rapid niche-filling phase and later slow-down approaching niche saturation. We discuss these findings in the context of other Australo-Papuan adaptive radiations and the importance of incorporating adaptive diversification systems that are not extraordinarily species-rich but ecomorphologically diverse to understand how biodiversity is generated.

1. Introduction

Lineages that encounter multiple available ecological niches may ultimately diversify to fill this ecological space, a process known as adaptive radiation [1,2]. This results in both an increase in speciation rates as the lineages diversify and the evolution of novel phenotypes as they adapt to the new ecological niches [3–5]. Colonization of an environmentally diverse region with less competition is a common precursor to adaptive radiation, and it has resulted in many spectacular radiations, both at small geographical scales [6,7] and when continents approach each other—facilitating biological exchanges [8–11].

Australo-Papua, the region comprising Australia, New Guinea and surrounding islands, broke apart completely from Antarctica in the early Eocene (around 45 Mya) and then began a long period of isolation from other major landmasses [12,13]. This time and isolation allowed for the diversification of many animal and plant groups including the iconic Australian marsupials and *Eucalyptus* trees, among many others [14–17]. However, many of the most diverse and emblematic groups in the region are descended from much more recent colonization events from Asia, coinciding with the collision of the Eurasian and Australian plates in the Oligocene around 25 Mya [18–20]. Squamate reptiles are extraordinarily diverse in the Australo-Papua region and the vast majority of this diversity is comparatively recent [19]. For example, agamid lizards, monitor lizards, blind snakes, elapid snakes and pythons are all groups that arrived to Australo-Papua probably sometime in the late Palaeogene and early Neogene

(20–30 Mya) and then diversified in both species number and ecological strategies [19,21–26].

Pythons are a clade of 40 constrictor snakes that display a remarkable level of ecomorphological diversity [25]. They have diversified into a number of ecomorphs that appear to be driven by microhabitat specialization, which is supported by findings of clade-wide convergence in morphology and ecology with New World boas and other snake lineages [27]. Despite being found from Africa to Australia, most of the species and ecological diversity are found east of Wallace's line in Australo-Papua. A recent study showed that pythons likely originated in Asia and later experienced a dramatic burst in morphological evolution accompanied by diverging ecological specialization when they crossed Wallace's line around 23 Mya [25]. This is consistent with adaptive radiation induced by ecological opportunity upon colonization of a new environment with open ecological niches [9].

Phenotypic and ecological aspects of python adaptive radiation have been well studied but the patterns of lineage diversification require further investigation. It is now possible to identify the signatures in phylogenetic trees left from evolutionary processes that can change rates of diversification [28,29], like adaptive radiation in response to ecological opportunity [9,30]. Theory predicts that when this happens there may be a sudden increase in speciation rates followed by a subsequent slow-down coinciding with niche space filling, termed diversity-dependent (DD) diversification [31,32]. Here, we implement a variety of lineage diversification analyses to investigate if pythons experienced an increase in speciation when they colonized Australo-Papua followed by a subsequent slow-down, which is expected if they adaptively radiated. However, because diversification patterns alone can fit a variety of evolutionary scenarios [33], we also investigate how rates of phenotypic evolution changed upon Australo-Papuan invasion. Although taxonomic diversification and phenotypic evolution are not necessarily coupled in adaptive diversification [34,35], synchronicity of these patterns with biogeographic milestones provides valuable evidence for the role of ecological opportunity in the generation of biodiversity.

2. Methods

We use a range of methods to detect diversification patterns consistent with adaptive radiation. To test our hypotheses on a well-sampled and updated phylogenetic tree with recent changes in python taxonomy [36,37], we built a species tree with Astral III v. 5.7.8 [38] using the gene trees for 33 species from 376 nuclear exons from Esquerré *et al.* [25], as well as a mitochondrial genome gene tree including 32 of those species and five species not sampled for the nuclear exons and not included in Esquerré *et al.* [25]. We time-calibrated this tree using MCMCTree from the PAML 4.9 package [39], using the dates inferred by Esquerré *et al.* as secondary calibrations. See electronic supplementary material for details. This time-calibrated tree contains 37 of the 40 (93%) currently recognized species: 27 for the Australo-Papuan clade, eight for the Afro-Asian clade and the two *Malayopython* species from Southeast Asia.

During an adaptive radiation, we often expect early bursts of diversification as lineages diversify to fill available niches. To visualize the diversification patterns, we constructed lineage through time (LTT) plots [40] of the Pythonidae and the Australo-Papuan clade separately and of the 95% confidence

interval (CI) of 1000 simulated trees under a pure-birth model and an early burst model (with a γ-statistic of −1). This was done with the functions *ltt95* and *pbtree* from the R package *phytools* [41]. As an additional more powerful tool to test the hypothesis that reaching Australo-Papua resulted in an increased rate of diversification with subsequent slow-down as a consequence of niche filling, we fitted constant rate (CR) and DD birth–death models to the Pythonidae and Australo-Papuan clade trees and performed a bootstrap-likelihood ratio test of DD against CR and computed the power of the test. This was done using the R package *DDD* [42,43].

In an attempt to identify diversification patterns associated with crossing biogeographic lines, we implemented a method based on graph theory that estimates the spectral density profile of a tree based on its Laplacian graph [44]. These spectral densities are used to identify different 'modalities' that can reflect distinct diversification patterns. In addition to fitting a model with the optimal number of modalities (i), we fitted models with 1 to (i) modalities to identify modalities in the tree that were consistent across all models. This was performed using the R package *RPANDA* [45]. Finally, we implemented the recently developed Bayesian method *cladogenetic diversification rate shift* (CLaDS) that aims to infer small changes in diversification rates by allowing rates to change at every speciation event [46,47]. At each speciation event in the tree, the two daughter lineages inherit speciation (λ) and extinction (μ) rates drawn from the joint probability distribution parametrized by the parental lineage's λ and μ. We implemented the CLaDS2 model that allows λ and μ to vary while maintaining the turnover constant and ran three MCMC sampling every 200 iterations until the Gelman statistic [48] was under 1.05 for every parameter, after discarding 25% of the chains as burnin. We specified a sampling fraction of 93%. This was run on the Julia package *PANDA* which implements a new version of CLaDS that runs much faster and more efficiently using data augmentation within a Bayesian MCMC [45,47].

To determine if shifts in lineage diversification rates were coupled with shifts in phenotypic evolution rates, we used the R package *RRPhylo* [49]. This program uses phylogenetic ridge regression to estimate branch-specific evolution rates and finds shifts towards higher or lower evolution rates across the phylogeny [49].

Linear measurements of body shape data and landmark coordinates for head shape data were taken from previous studies [25,27,50], which were size corrected (corrected for scale) using Procrustes superimposition for head shape landmark coordinates and log shape ratios for linear body shape measurements [50]. We did not perform allometric corrections as allometry is extremely variable and likely adaptive in pythons, and we see it as part of the evolutionary diversity [50]. Due to small morphological sampling sizes ($n < 5$) that resulted in overestimation of head and body shape evolutionary rates within the Australo-Papuan clade, we conservatively removed *Liasis savuensis* and *Simalia clastolepis*. We also analysed maximum snout–vent length as a measure of maximum body size. These data were obtained from the literature or from our own specimen measurements when these were larger than previously reported. With the analysis of maximum body size, we used the same character as a covariate, to avoid misleading inferences of increased evolutionary rates in lineages with larger body sizes.

3. Results

In the LTT plot (figure 1), the Pythonidae as a whole falls well within a pure-birth model of diversification, whereas the Australo-Papuan clade clearly fits an early burst pattern. For the Australo-Papuan clade, the maximum log-likelihood
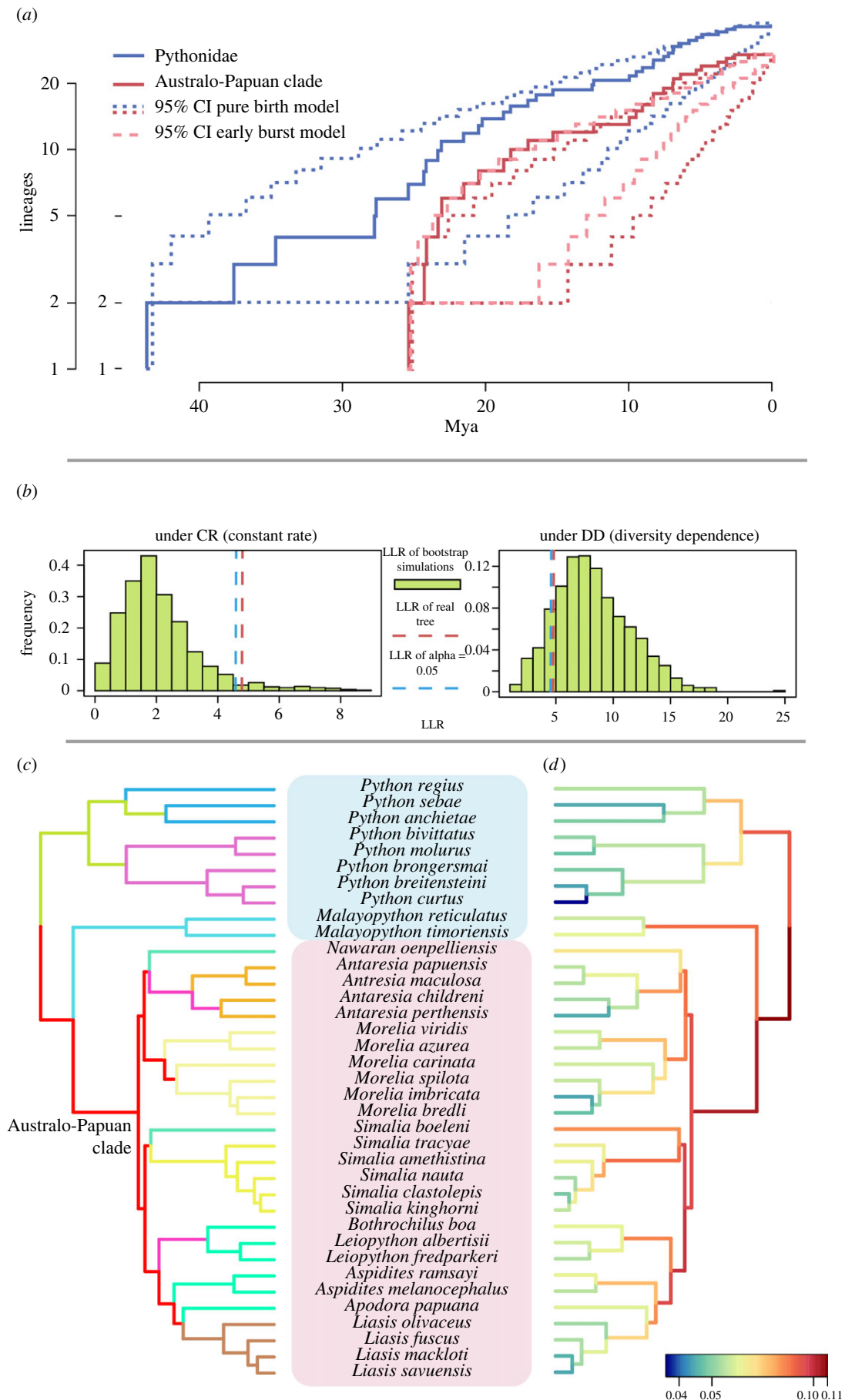
Figure 1. (*a*) LTT plots of the Pythonidae and the Australo-Papuan clade. Solid lines represent the observed tree and the dotted lines the 95% CI of 1000 simulated trees under a pure-birth model and under an early burst model. (*b*) LLRs inferred by DDD, for the Australo-Papuan clade and bootstrap simulations. (*c*) Pythonidae tree painted with the optimal nine diversification modalities estimated from its spectral distances profile. (*d*) The same tree with branches painted according to estimated speciation rates from *CLaDS*, as the legend on the bottom right.
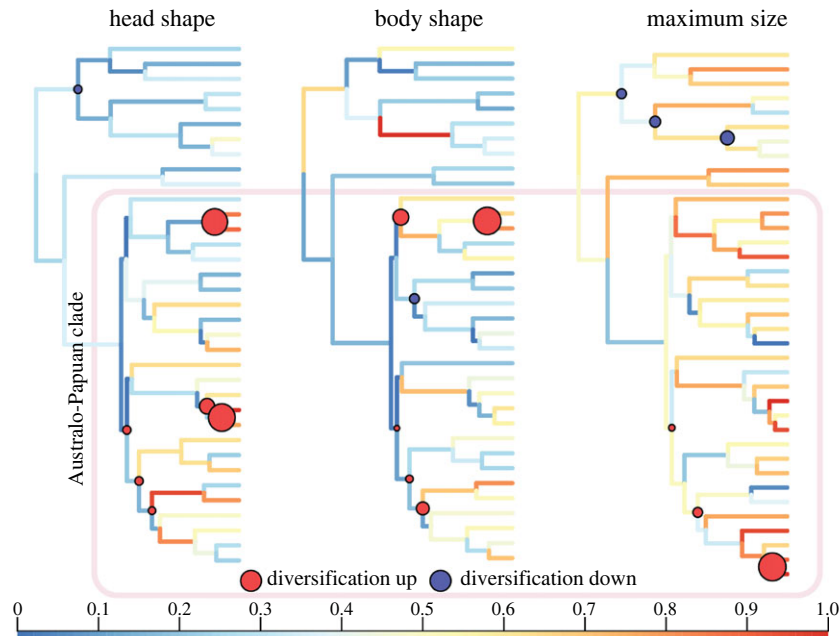
Figure 2. Rates of phenotypic evolution for head shape, body shape and maximum body size across the Pythonidae. Dots represent changes in evolutionary rates (red = positive; blue = negative). The dots are scaled by the relative size of the shift compared to all significant shifts (weather its positive or negative).

for a CR model is −91.71, and for a DD model is −86.95. The test rejects the CR model ($p = 0.049$) which has a power of 0.88. A visual inspection of the log-likelihood ratios (LLR; figure 1) shows how the LLR for the Australo-Papuan tree lies closer to the mode of bootstrap simulations when fitting a DD model than a CR model.

Using the spectral distances profile from the Pythonidae tree, we identify 12 distinct modalities of diversification (figure 1; electronic supplementary material, figure S1). Testing varied numbers of possible modalities (from 1 to 12), we consistently recovered an independent modality assigned to the base of the Australo-Papuan radiation (electronic supplementary material, figure S1). The CLaDS model finds an increase in diversification rates in the Australo-Papuan radiation (figure 1).

The analysis on branch-specific rates of phenotypic evolution shows a trend towards increased rates of evolution in the Australo-Papuan radiation compared to the rest (figure 2). For head shape, there are six shifts towards higher rates, all within the Australo-Papuan radiation, and one shift towards a slower rate, which is at the base of the Afro-Asian radiation. For body shape, there are five shifts towards higher rates, all within the Australo-Papuan radiation, which also includes a single rate towards lower rates. For maximum size, the three shifts towards higher rates are within the Australo-Papuan radiation and the three towards lower rates are within the Afro-Asian radiation (figure 2).

4. Discussion

After crossing Wallace's line into Australo-Papua, pythons evolved an array of new phenotypes to match new ecological roles that were possibly never realized in Africa or Asia [25]. *Aspidites* evolved a semi-fossorial ecomorph almost losing the thermoreceptive organs that all other pythons have, with a phenotype so different that morphology-based phylogenetics placed it as the sister to all other pythons [51]. Water pythons (*Liasis mackloti* complex) and tree pythons (*Morelia*

viridis complex) evolved the most specialized aquatic and arboreal lifestyles, respectively [27], and dwarf pythons (*Antaresia*) diverged towards the smallest body sizes seen in the family [36]. Arrival in Australo-Papua resulted in considerable ecomorphological space expansion [25]. Here we now show that this colonization event led to increased rates of lineage diversification and phenotypic evolution—a pattern consistent with adaptive radiation.

Our results point to an increased burst of speciation when pythons arrived in Australo-Papua, with a gradual slow-down towards the present (figure 1). We find that diversification rates have been higher in Australo-Papua and that the diversification mode lies closer to a DD model than a CR (figure 1). We find support for a unique diversification modality, as well as increased speciation rates, at the base of the Australo-Papuan clade (figure 1). These patterns are consistent with niche filling or diversity dependence [8,52–54]. However, our lineage diversification inferences on pythons acquire a lot more evolutionary significance when combined with what we know about their biogeographic and phenotypic evolution (figure 2).

Aside from an increase in speciation rates, early evolution of morphological diversity is also an important property of adaptive radiation, as has been postulated for eutherian mammals [55], Caribbean anole lizards [56] and Darwin's famous finches [57]. Although this pattern seems to be rare in empirical data [58], Australo-Papuan pythons rapidly evolved a variety of phenotypes soon after crossing Wallace's line [25]. Importantly, this considerable evolution of novel and diverging morphologies has been shown to match adaptations to a variety of different microhabitats [27]. The combination of early divergence into different ecotypes with an increase in speciation rates upon crossing an important biogeographic line is strongly indicative of Australo-Papua providing ecological opportunity for adaptive radiation. After the early ecomorphological divergence and as the speciation rates slow-down, speciation events towards the tip more likely represent allopatric speciation since these ecologically similar species are distributed in allopatry [59].

The main caveat of our findings is the low statistical power derived from the small number of tips in the python phylogeny, which is why it is important to interpret lineage diversification patterns of small radiations in conjunction with other lines of evidence. Adaptive radiation resulting in hundreds of biologically diverse species within a few million years provides truly fascinating opportunities for evolutionary biologists, but these are rare [2,60]. Most groups radiate into much more modest clades, for example, the famous Darwin's finches. This clade comprises only 14 species that diversified across the Galapagos volcanic archipelago and evolved different beak shapes that exploit different food resources [57]. Their diversification was rapid and adaptive, but due to reasons likely involving time, geographical area and available ecological niches they have not evolved into a particularly species-rich clade. Furthermore, animals like large constrictor snakes occupy high trophic levels where niche availability is more limited [61], and we should not expect apex predators to diversity into a myriad of sympatric species. Boas [27], monitor lizards [26] and different carnivoran mammal radiations [62], also exhibit patterns of adaptive radiation without diversifying into hundreds of species. Adaptive radiations resulting in a more limited number of species that diverged and specialized seem to be far more common than the extraordinary text-book examples of Caribbean anoles and African lake cichlids [54,63,64]. Incorporating these clades as models to understand the processes that generate biodiversity is vital for a comprehensive treatment of the study of adaptive radiation.

There can be alternative explanations for the speciation patterns we find in pythons. Speciation rates are not necessarily linked to an enhancement in ecological space [65,66], and slow-downs in diversifications rates are common throughout the tree of life and are not necessarily related to biotic factors [28,29]. Time dependence, protracted speciation and tree reconstruction methodological issues can all result in inferred diversification slow-downs [28]. Moreover, branching patterns themselves have been shown ineffective in discriminating between DD and time-dependent diversification models effectively [67]. Finally, the higher diversity of pythons in Australo-Papua might be related to more stochastic factors than ecological opportunity. However, the repeated radiation events among squamate reptiles after invading Australo-Papua [64] offer strong evidence that crossing these biogeographic barriers results in increased diversification and rates of trait evolution. Most of the snake and large lizard diversity in Australo-Papua shares the python's history of an Afro-Asian origin but reaches their highest diversity after the crossing of Wallace's line around 20–30 Mya [19,21,22,24–26,68]. This includes, among others, the ecomorphologically diverse agamid and varanid lizards [22,26,69], and all of the region's snake clades, including the mega-diverse elapids and the cryptic blindsnakes [21,24,25,68]. Moreover, our findings of matching increased phenotypic evolutionary rates and lineage diversification also strongly support a role of ecological opportunity.

Australo-Papua offers a large and environmentally heterogeneous area, which combined with the presence of fewer similar organisms competing for niche space, offered ample opportunity for ecological specialization and also allopatric speciation [70,71]. This study adds to the body of evidence showing that Australo-Papua is an incredible land of ecological opportunity with much of its extraordinary contemporary diversity drawn from Laurasian rather than Gondwanan origins.

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