The role of ecological opportunity in shaping disparate diversification trajectories in a bicontinental primate radiation

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Exceptional species and phenotypic diversity commonly are attributed to ecological opportunity (EO). The conventional EO model predicts that rates of lineage diversification and phenotypic evolution are elevated early in a radiation only to decline later in response to niche availability. Foregut fermentation is hypothesized to be a key innovation that allowed colobine monkeys (subfamily Colobinae), the only primates with this trait, to successfully colonize folivore adaptive zones unavailable to other herbivorous species. Therefore, diversification rates also are expected to be strongly linked with the evolution of traits related to folivory in these monkeys. Using dated molecular phylogenies and a dataset of feeding morphology, I test predictions of the EO model to evaluate the role of EO conferred by foregut fermentation in shaping the African and Asian colobine radiations. Findings from diversification methods coupled with colobine biogeographic history provide compelling evidence that decreasing availability of new adaptive zones during colonization of Asia together with constraints presented by dietary specialization underlie temporal changes in diversification in the Asian but not African clade. Additionally, departures from the EO model likely reflect iterative diversification events in Asia.

1. Introduction

Declining net diversification rate (i.e. the rate of species accumulation considering both speciation and extinction) is commonly observed in evolutionary radiations and results from decreasing rates of speciation and/or increasing extinction ([1]; but see [2]). There is growing evidence that the availability of ecological opportunity (EO) can explain the ‘early burst’ [3–5] of lineage accumulation produced by declining net diversification rate. In the EO model, ample resources presented by key innovations, ecological release or novel habitats [6–8] are initially available for exploitation and promote rapid species proliferation [7,9,10]. However, speciation rate subsequently declines as the radiation progresses owing to competition among daughter lineages for progressively saturated niche space (‘niche filling’; [11]) or as specialization constrains genetic variation [12,13].

Phenotypic and lineage diversification are coupled [5,14–17] if elevated morphological evolution generates forms that are capable of exploiting a broad range of niches, providing more opportunities for speciation via divergent selection [7,18]. Specific predictions of the EO model that follow from this include: (i) an early burst in morphological evolution should generate disparity in resource-use phenotypes that is partitioned primarily among rather than within subclades, such that subclades occupy different regions of morphological space [5,19], and (ii) rates of both net diversification and morphological evolution should decline temporally, consistent with early-burst dynamics. On the other hand, findings discordant with these predictions may be interpreted to indicate that phenotypic evolution and thus performance related to EO had little influence on diversification. However, EO may be difficult to detect when...
factors such as young lineage age or historical contingency reduce or erase the expected association between species diversity and morphological evolution [15,20–22]. In such cases, an ancillary approach that directly tests the effects of functional traits on diversification rates can resolve the relative impact of EO on a radiation. If EO was an important promoter of diversification, then phenotypic (e.g. niche-use) traits that increase access to EO are expected to be associated with higher diversification rates. This is a crucial addition to the two standard predictions of the EO model.

Colobines (colobine monkeys) is an excellent clade within the primates for interrogating the EO model. Colobines belong to the radiation of catarrhine primates that includes humans, the great apes, gibbons and other Old World monkeys. Two monophyletic lineages have radiated independently in Africa and Asia after the dispersal of the ancestral Asian colobine out of Africa in the Late Miocene (11.2–7.1 Ma) [23,24]. The species richness of colobines is second only to their sister group (Cercopithecinae) among all primates (N = 52–59 species; [25–27]). The highly folivorous colobines are the only primates that have evolved true foregut fermentation. Enlarged salivary glands and a multi-chambered stomach with cellulolytic bacteria allows these herbivorous monkeys to detoxify plant secondary compounds and extract available nutrients from leaves and other fibrous vegetation more efficiently than most hindgut-fermenting primates [28–32]. Foregut fermentation may be a key innovation [6,33,34] that allowed colobines to invade folivore adaptive zones unavailable to other primates (i.e. EO) and may explain their evolutionary success. Here, I first test the two predictions of the conventional EO model to determine whether lineage and morphological diversification are linked in colobine monkeys consistent with a central role of EO in the radiation. Second, I test whether declining speciation or increasing extinction rate towards the present generates the observed temporal decline in net diversification. Lastly, I link temporal trends in lineage accumulation and morphological evolution with dietary specialization in colobine monkeys. Following from the ancillary prediction of the EO model, I test for an association between high folivory and elevated diversification rate in this last analysis. Folivory specialization was selected as a niche-use trait for its high relevance to the hypothesized source of EO (i.e. forest habitat) in colobine monkeys.

2. Material and methods

(a) Morphological data

Evolution of the cranium, mandible and teeth is tightly correlated with diet owing to the functional requirements of processing food [35–38]. Therefore, I examine two components of feeding morphology to test the role of dietary adaptations on the diversification of colobine morphology: (i) mandible shape and (ii) the length, breadth and/or height of select cranio-mandibular dental (CMD) characters averaged for each species (electronic supplementary material, tables S1 and S2).

Mandible shape was quantified from a Procrustes superimposition analysis of eight landmarks and 23 semilandmarks [39–43] digitized from photographs (see the electronic supplementary material, text S1 for details). Photographs of 160 adult male individuals representing 31 recognized species were taken at the Mammalogy Department of the Harvard University Museum of Comparative Zoology (Cambridge, USA), Mammal Division of the National Museum of Natural History (Washington, DC, USA), Department of Mammalogy of the American Museum of Natural History (New York City, USA) and Division of Mammals of the Field Museum of Natural History (Chicago, USA). Following superimposition, the data are 35-dimensional. The subsequent statistical analyses measure rates of divergence of multivariate shape within this 35-dimensional space.

Measurements of 51 CMD variables from 205 adult male museum specimens and the PRIMO database (http://primo.nycep.org/) were combined and averaged for 37 recognized species (see the electronic supplementary material, text S1 for details). Then the dataset was reduced to 15 total variables, including a proxy of size (glabella to inion distance), to minimize the amount of missing data per species. Residuals from least-squares regressions of log-transformed variables on the log-transformed size proxy that removed the influence of size while accounting for phylogenetic history [44] were used in subsequent analyses. The phylogenetic size-correction procedure was performed in the R [45] package phytools [46].

(b) Phylogenetic data

Because a clade-specific, multilocus phylogeny of Colobinae with better species coverage is unavailable, I use the mammal super-tree from Fritz et al. [47] updated from that of Bininda-Emonds et al. [48] that includes 57 recognized species of colobine monkeys (more than 96% of named species; electronic supplementary material, table S3). The supertree generally agrees with current phylogenetic hypotheses [49–56] for this complex group, except for the placement of two Asian genera (see the electronic supplementary material, text S1 for details). However, 11 of 85 colobine internodes in the supertree are unresolved and reflect a lack of information about phylogenetic relationships rather than near-simultaneous speciation events. Because these polytomies may bias estimates of diversification parameters [57], I use a distribution of 101 pseudo-posterior trees, in which polytomies have been resolved by simulating unknown branch lengths with a constant-rate birth-death model [58] in BEAST v. 1.7.4 [59]. Use of these pseudo-posterior trees accounts for phylogenetic uncertainty in the original supertree. I also computed the maximum clade credibility (MCC) tree (electronic supplementary material, text S2), which is the tree with the maximum product of posterior clade probabilities, of the 101 trees in TREEANNOTATOR v. 1.7.4 [59].

(c) Tempo of lineage and morphological diversification

Because interspecific interactions that mediate the exploitation of EO are expected to occur only between species that inhabit proximate geographical locations, all following analyses were performed separately for the two continental radiations. The number of species included in each analysis differs based on the trait considered. The MCC and all pseudo-posterior trees were pruned to include only those species that are represented in the clade-wide (57 species), mandible shape (31 species), CMD morphology (37 species) and diet (38 species) datasets for the relevant analyses.

I compared semi-logarithmic lineage-through-time plots [60] with a null Yule (pure-birth) model to determine whether the rate of increase in the number of lineages has changed through time using the phytools package [46]. The slope of these curves is a straight line if net diversification rate was constant through time. To detect a temporal slowdown in diversification, I assessed the summary statistic gamma (γ) with the Monte Carlo constant-rates (MCCR) test. The γ statistic compares the observed positions of internodes in a phylogeny to that expected under a pure-birth process [61]. The test was implemented in the R package LASER [62] assuming an approximately 3.4% incomplete taxon sampling based on the species coverage of the pseudo-posterior phylogenies.
Declining net diversification results from changes in speciation and/or extinction rate that may reflect diversity-dependent processes such as niche-filling [4, 63]. To test whether changes in lineage accumulation are driven by decreasing speciation or increasing extinction, I compared the fits of three time-varying speciation and extinction models (SPVAR, EXVAR and BOTHVAR; [1]) using the second-order Akaike information criterion (AICc), which corrects for small sample sizes by penalizing complex models more heavily than the AIC. I also evaluated six diversification models (rate-constant Yule and birth-death, exponential and linear density-dependent, and two rate-shift Yule models) [64] using AICc to determine whether density dependence affects speciation rate. The best model has the lowest AICc score. However, the fit of a model is significantly better only when the difference between AICc scores is greater than two units [65]. Diversification models were fit in the LASER package.

I used the node-height test [66] to determine whether morphological evolution has slowed through time consistent with a niche-filling hypothesis. I computed absolute values of standardized independent contrasts [67] of the two components of feeding morphology and correlated them with the heights of their respective nodes. A significant negative relationship between node height and contrast values indicates that the rate of trait evolution decreased as the number of species increased in a radiation [66].

To further evaluate patterns of morphological variation, I calculated disparity through time and the morphological disparity index (MDI) with the R package GEER [68] using the methods of Harmon et al. [19] and Slater et al. [14]. Relative disparity quantifies how the variety of morphological forms in a clade occupies morphospace. Values near zero indicate that disparity is high among subclades relative to within subclades, whereas values near one indicate that disparity primarily is partitioned within subclades. Expected relative disparity was estimated using 10,000 simulations under a Brownian motion model. MDI describes the difference in relative disparity of a clade with the expectation from Brownian motion [19]. Negative MDI values indicate that clade disparity is lower than expected under Brownian motion and suggest that the clade has undergone rapid adaptive radiation since subclades occupy different regions of morphospace.

(d) Folivory-dependent diversification
Because the acquisition of foregut fermentation is proposed to have increased the efficiency of folivory in colobines, I test whether speciation and extinction rates vary according to the extent of folivory specialization in extant species. Under the EO hypothesis, highly folivorous (i.e. specialized) lineages are expected to have elevated diversification rates if foregut fermentation permitted access to new arboreal adaptive zones. Data on the percentage of total dietary foliage were collected from the literature and averaged for each of 38 species (electronic supplementary material, table S4). Log-transformed values of these percentages were used to characterize the degree of folivory specialization. I used the QuaSE method [69] and MCC phylogeny to estimate the effect of folivory as a constant, linear, sigmoidal or modal function on speciation and extinction rates under Brownian motion (N = 20 models). I included a directional term (θ) that captures temporal change in the rate of character evolution in half of these models. Differences between AICc scores greater than two units [65] were used to select between models. This method was implemented in the R package DIVERSITree [70].

3. Results
Lineage-through-time plots (figure 1) establish a complex history of diversification in colobine monkeys. A trend of greater than expected lineage accumulation saturating towards the present is evident approximately 3.3 Ma in Asian colobines but not in the older African lineage (figure 1). Examination of γ statistics for the pseudo-posterior trees corroborates these qualitative assessments. Although negative γ values (γ = −0.945 ± 0.485 s.d.) (electronic supplementary material, figure S1) suggest that speciation rates declined over time consistent with early-burst diversification in the African lineage, the observed statistics are not significantly different from values for phylogenies simulated under a birth-death process that accounts for incomplete taxon sampling (5000 simulated phylogenies per tree; p = 0.161 ± 0.114). Only γ values for Asian colobines indicate a significant slowdown in net diversification rate (γ = −1.89 ± 0.523, p = 0.0348 ± 0.0457), but this likely corresponds to rate declines following the period of elevated lineage accumulation approximately 6 Myr into the radiation rather than a true early-burst diversification (figure 1; electronic supplementary material, figure S1).
Concordant with late shifts in the acceleration and subsequent slowdown of net diversification rate, significant positive relationships between node height and independent contrasts of feeding morphology indicate that the rate of morphological evolution has increased rather than decreased through time in Asian colobines (shape: $b = 0.00713$, $R^2 = 0.476$, $F_{1,18} = 16.3$, $p = 7.68 \times 10^{-4}$; CMD variables: $b = 0.0375$, $R^2 = 0.337$, $F_{1,20} = 10.2$, $p = 0.00458$) (electronic supplementary material, figure S2). The node-height test of CMD variables was significant in the Asian lineage after removal of two outlier contrasts between the ancestral nodes of *Presbytis* species and the *Semnopithecus–Trachypithecus* clade and between the surili species *Presbytis potenziani* and *P. rubicunda* (electronic supplementary material, figure S2). Only in the African clade does the node-height test of CMD variables appear to support the early-burst model, although the negative slope is non-significant (shape: $b = 0.00358$, $R^2 = 0.418$, $F_{1,7} = 5.02$, $p = 0.060$; CMD variables: $b = -0.0258$, $R^2 = 0.396$, $F_{1,5} = 3.27$, $p = 0.130$) (electronic supplementary material, figure S2).

With the exception of African CMD traits, relative disparity of feeding morphology was generally much greater than expected under Brownian motion (figure 2). This indicates that morphological disparity primarily was partitioned within rather than among subclades during most of colobine history, such that subclades occupied a greater than expected proportion of morphospace (i.e. high convergence rather than the predicted divergence among subclades). High values of the MDI for both lineages reflect the elevated convergence in morphological traits (African shape: MDI = 0.220, $p = 0.0469$; Asian shape: MDI = 0.414, $p = 0.00220$; Asian CMD variables: MDI = 0.162, $p = 0.0757$). Morphological disparity of CMD traits in the African lineage non-significantly departs from this general trend but in the expected direction, such that among-subclade disparity was higher than that within subclades (MDI = −0.0561, $p = 0.170$).

Comparisons of $\text{AIC}_c$ scores among six rate-constant and rate-variable birth-death models for each lineage show that rather than density dependence having a strong effect on the temporal decline in lineage accumulation, a pure-birth model with either two or three shifts in speciation rate received the most support (African species: $\Delta \text{AIC}_c = 1.36–4.77$; Asian species: $\Delta \text{AIC}_c = 1.96–5.55$) (table 1; electronic supplementary material, table S5). The exponential density-dependent model is 5.08 times as probable as the three-rate-shift Yule model in the African clade (table 1; electronic supplementary material, table S5). Furthermore, a model with exponentially decreasing speciation rate but constant extinction received the lowest $\text{AIC}_c$ score, but the fit is not significantly better than another model that allows extinction rate to vary (African species: $\Delta \text{AIC}_c = 1.48$; Asian species: $\Delta \text{AIC}_c = 1.29$) (table 1; electronic supplementary material, table S5). Because estimates of extinction rates on phylogenies of extant taxa from these and similar methods (e.g. QuaSSE) have large variances and bias, they must be interpreted with caution without additional data from the fossil record [69,71–74].

Contrary to expectations of high folivory elevating diversification rate, a model in which speciation rate varies as a negative rather than positive linear function of dietary foliage with constant extinction has the strongest support among the 20 trait-dependent speciation and extinction models tested for Asian colobines ($\Delta \text{AIC}_c = 3.16–25.1$) (table 2; electronic supplementary material, table S6). Less folivorous Asian species have exceptionally elevated rates of speciation and therefore higher net diversification rates than species that consume a larger proportion of leaves in their diet (figure 3). However, the expected rate of character evolution over time (described by the positive directional term $\Phi = 0.738$) of this best-fit model suggests that folivory has increased along lineages in the Asian clade. Dietary foliage likely has no effect on either speciation or extinction rate in African species.

*Figure 2. Plots of disparity through time of (a) mandible shape and (b) CMD traits for the (i) African and (ii) Asian clades. Time is relative from the past (0 Myr) to the present (1 Myr). Solid lines indicate the mean empirical relative disparity, dashed lines the median expected relative disparity estimated from 10 000 simulations under Brownian motion, and the shaded area the 95% CI of the simulated disparities.*
decreasing speciation but increasing extinction rates (BOTHV AR). Significant best-supported models are indicated with italic exponentially decreasing speciation but constant extinction rate through time (SPV AR), exponentially increasing extinction but constant speciation (EXV AR) and decreasing speciation but increasing extinction rates (BOTHV AR). Significant best-supported models are indicated with italic $\Delta$AIC$_c$ values.

<table>
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<tr>
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High convergence in feeding morphology among African, as well as Asian, subclades suggests that either functional responses to ecological pressures are constrained or that feeding on items such as leaves, fruits and seeds likely requires a limited set of solutions at the characters measured in this study. The latter is consistent with evidence that the gene encoding pancreatic ribonuclease, which digests cellulolytic bacteria, evolved parallel amino acid changes in African and Asian species [78]. Alternatively, the lack of divergence in feeding morphology may reflect constraints posed by the species’ digestive strategy, as both foregut fermentation and the mandible, in particular, are strongly tied to the processing of tough plant parts such as leaves and unripe seeds. Analysis of characters that are not coupled with foregut fermentation may help adjudicate between these alternative interpretations.

Alternately, the lack of strong support for early bursts in species and morphological diversification in the African clade may reflect extinctions in the Early Pleistocene of large-bodied, Pliocene-origin colobines, which included arboreal, semi-terrestrial and terrestrial forms [23,79]. Eight taxa are known from this time period [23,79] and suggest that a potentially diverse radiation of African colobines was masked in the neontological data by extinction. A joint phylogenetic analysis of palaeontological and neontological data will address whether this is the case, but unfortunately most extinct colobine taxa cannot yet be linked robustly to extant species [23,52].

(b) Colonization of new areas was a source of ecological opportunity for Asian species

Although I did not find strong support for the morphological predictions of the conventional EO model (i.e. high morphological disparity among subclades and negative relationships between node height and absolute values of independent contrasts of feeding morphology), my findings from the diversification and morphological analyses are consistent with a delay in the rapid radiation of the Asian lineage until colonization of South and Southeast Asia in the Middle–Late Miocene [23,24,49,51]. Specifically, the temporal lag in rate elevation and subsequent slowdown of lineage accumulation as well as accelerated evolutionary rates of feeding morphology in this group (figure 1; electronic supplementary material, figures S1 and S2) reflect a scenario of ecological
Table 2. Log-likelihood and AICc of models in which rates of speciation (l) and extinction (m) varied as functions of folivory specialization, defined as the natural logarithm of the average percentage of total foliage in each species' diet. Models were evaluated with and without a directional parameter (F) that describes temporal change in the rate of character evolution. Italic DAICc values indicate significant best-supported models.

<table>
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<th>φ value</th>
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(c) Folivory depresses speciation in Asian colobines

Here, folivory is hypothesized to confer an advantage to colobines during their colonization of new habitats in Asia but unexpectedly has a negative rather than positive effect on speciation rate (table 2; electronic supplementary material, table S6). Such a surprising relationship between a putative adaptation and speciation rate, however, has been uncovered in other studies (e.g. woodcreepers; [81]). This suggests that the decline in speciation rate (table 1; electronic supplementary material, table S5) likely driving the temporal slowdown in lineage accumulation in Asia is associated with increased exploitation of leaves by Asian species. Although generalist herbivores have high rates of net diversification and transition to other trophic niches [82], specialist species are expected to have elevated rates of speciation and extinction owing to increased susceptibility to environmental change [83]. Unique trophic specialists can also have elevated rates of morphological evolution [84]. In this case, folivory may be an evolutionary ‘dead-end’ for colobines owing to foliage being a much less nutritious food than other vegetative items [85]. Primates with low-quality diets offset energetic deficiencies with trade-offs such as longer rest periods [86] and larger body size [87]. I propose that highly folivorous species, which have low-quality diets and thus tend to be larger, are release followed by niche saturation as colobines dispersed and then speciated in situ eastward and southward through Eurasia from Africa [23,24]. The timing of divergences of extant Asian genera and of species (electronic supplementary material, figure S3) generally track the putative dispersal route of the ancestral Asian colobine. Langurs (genus *Semnopithecus*) that are distributed in South Asia near the front of the proposed dispersal route diverged (5.0 Ma) before most other groups that presently occur further east and south in China, peninsular southeast Asia and Indonesia (6.0–2.3 Ma). Moist forests expanded in southeast Asia when global temperatures and sea level rose in the Early Miocene (23.8–16.4 Ma) [80] and would have provided the dispersing ancestral colobines with ample EO. However, Pleistocene glaciations led to widespread aridity and retreat of wet forests throughout Asia [80]. Slowed lineage diversification in the Asian clade is coincident with this period of forest contraction.

I find that rates of feeding morphology evolution have increased rather than slowed through time and morphological convergence rather than divergence among subclades was the norm in the Asian lineage (figure 2; electronic supplementary material, figure S2). Frederich et al. [22] show that rates of trait evolution accelerate rather than decelerate towards the present when radiations consist of multiple diversification events instead of a single event. Clades are also expected to exhibit ecological and morphological convergence [22]. This dynamic explains why rates of morphological evolution in Asian colobines diverge from those predicted by the conventional EO model. Departures from the model (i.e. positive relationships from node-height tests and high among-subclade morphological convergence) actually reflect the iterative nature of diversification in the Asian lineage and are consistent with graduated in situ speciation promoted by EO encountered during the dispersal to Asia. Therefore, colobine biogeographic history and my findings jointly support an important role of EO in the diversification of Asian species despite departures from the conventional EO model.
less likely to diversify than their less folivorous, smaller counterparts. This is consistent with findings that net diversification declines with increasing body size in primates \([69,88]\). In summary, the QuaSSE analyses reveal that EO in the form of factors other than folivory specialization likely structured diversification in Asian colobines. This study shows that in conjunction with tests of indirect predictions, QuaSSE and similar methods (e.g. BAMM \([89]\)) that directly estimate relationships between rates of trait evolution and diversification have great potential to provide deeper insights on the roles of specific factors of EO in radiations.

5. Conclusion
I find compelling evidence from neontological data that EO shaped the diversification trajectory of only one of the two independent radiations of colobine monkeys. Depressed species diversification towards the present in the Asian radiation can be attributed not only to decreasing availability of new adaptive zones but also to constraints presented by dietary specialization, while departures from the conventional EO model reflect the dynamics of iterative diversification events. In conclusion, this study emphasizes the need to perform analyses of lineage accumulation and morphological evolution separately for geographically independent lineages rather than for the clade as a whole to robustly detect the influence of EO as a driver of diversification in systems with replicate radiations.

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