Biotic and abiotic factors influencing diversification of herbivorous mammals

by

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To my parents, for allowing me to follow my dreams, and to Joe, for supporting me while I pursue them

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ABSTRACT

Both biotic and abiotic factors are known to control diversification. Though these factors are believed to operate at distinct temporal and spatial scales (i.e., the multilevel mixed model), often the scales at which key processes and outcomes of diversification operate are ambiguous or confused. To explore the dependence of factors promoting diversification on spatiotemporal scales as well as the biology and ecology of clades, my dissertation examined the interactive effects of lineage-specific traits with ecology and environment at multiple taxonomic, temporal, and spatial scales. I focused on the effects of a novel digestive strategy, foregut fermentation, in herbivorous mammals. In Chapter II, I tested predictions of a popular macroevolutionary model to evaluate the role of an abiotic factor, ecological opportunity, in the diversification of the foregut-fermenting Old World colobine monkeys. This work corroborated a growing body of work that the model is sensitive to the geographic scale of diversification, in particular to multiple dispersal-divergence events within a single radiation. In addition to the abiotic factor, I also found evidence for an important role of dietary specialization, a biotic factor, on the diversification of Asian colobines. Deviating from the current multilevel mixed model, these findings showed that both biotic and abiotic factors can be important controls on diversification at long timescales and large geographical scales. In Chapter III, I tested the effects of foregut fermentation on the relationship between ecological specialization and speciation rates in the terrestrial, herbivorous mammals. My findings indicated that foregut fermentation did mediate

speciation rates in mammals, supporting roles for both biotic and abiotic factors in determining differences in speciation among clades at intermediate temporal and geographical scales. In Chapter IV, I investigated the effects of environmental change, specifically historical climatic perturbations, and its interaction with digestive strategy on speciation rates of the terrestrial, herbivorous mammals. I found that climatic instability since the Last Glacial Maximum had stronger, multifarious effects on the richness of foregut-fermenting mammals. In contrast, hindgut herbivores experienced bounded instability across the continents on which they occur. These findings support important roles for both biotic and abiotic factors on species richness over short timescales and intermediate geographical scales. Overall, my findings from Chapters II-IV together show that not only are the effects of biotic and abiotic factors on diversity important on spatiotemporal scales not currently recognized in the multilevel mixed model, the effects of the factors themselves are likely to vary based on the biological and ecological differences found within and among clades.

CHAPTER I

INTRODUCTION

A longstanding question in evolutionary biology asks why some groups of organisms are phenomenally speciose with exceptional phenotypic diversity while others are depauperate in both aspects. Radiations span the continuum of species and phenotypic diversity, with the classic cases of adaptive radiation lying at one end with many species and morphological forms. Some groups such as the cichlids (Farias et al. 1999) are represented at both extremes of the continuum. In such cases the disparity in species and phenotypic richness among lineages sharing common ancestry implicates differing ecological and/or environmental contexts (Seehausen 2007), lineage-specific properties (Moyle et al. 2009), or the joint action of these two factors in the generation of disparate diversification outcomes.

Climatic and orographic events (Richardson et al. 2001) influence the probability of speciation and extinction by controlling the strength of gene flow between populations and the likelihood of population persistence. Furthermore, often populations encountering vacant or underutilized niches ("ecological opportunity") (Schluter 2000) are assumed to speciate rapidly due to the lack of ecological constraints posed by competition and predation (Seehausen 2007, Yoder et al. 2010). Radiations on islands and in water bodies that were initially depauperate of species highlight the importance of ecological opportunity in promoting phenotypic and species diversity (e.g., Grant and Grant 2006, Losos et al. 1998, Danley and Kocher 2001). However, lineage-specific traits also potentially influence diversification (Moyle et al. 2009). This dissertation examines the interaction between lineage-specific traits, ecology, and environment on the diversification and morphological evolution of exemplar clades. I apply state-of-the-art methods in phylogenetic comparative biology, morphometrics, and species distribution modeling to address these questions at varied taxonomic, temporal, and spatial scales. I focus on the effects of a novel digestive strategy, foregut fermentation, in the herbivorous mammals. Foregut fermentation evolved independently at least four times in the marsupials, sloths, artiodactyls, and primates and at least once in birds.

Foregut fermentation may operate as a "key innovation" (Simpson 1944, 1953) that contributed to the diversification of herbivorous mammals, similar to the decoupled pharyngeal jaws (Seehausen 2006) and mouth-brooding (Salzburger et al. 2005) of African cichlid fish, subdigital toepads of anole lizards (Losos 2009), and nitrile-specifier protein in pierid butterflies (Wheat et al. 2007). Key innovations are phenotypic novelties that allow lineages to exploit new or previously inaccessible resources upon their acquisition and are commonly invoked in cases of elevated speciation rates, species richness, and/or phenotypic diversity in a broad range of organisms (e.g., Berenbaum et al. 1996, Bond and Opell 1998, Lynch 2009, Vamosi and Vamosi 2010, Rutschmann et al. 2011).

In Chapter II, I test for temporal concordance between rates of diversification and morphological evolution to evaluate the role of ecological opportunity in the foregut-fermenting colobine monkeys (Tran 2014). The early burst model predicts that rates of diversification and morphological evolution are high early in a radiation but decline later due to reduced niche availability (Lovette and Bermingham 1999, Phillimore and Price 2008, Burbrink and Pyron 2010, Yoder et al. 2010). In conjunction with the biogeographic history of colobines, my findings suggest that constraints arising from dietary specialization and decreasing availability of new adaptive zones over time explain temporal changes in diversification but not morphological evolution in the Asian radiation. Due to the lack of appropriate forest habitat, ecological opportunity did not play a major role in the African radiation. Lastly, I attribute departures from the early burst model to the iterative series of diversification events that follow the monkeys' dispersal to Eurasia.

In Chapter III, I explore the effects of foregut fermentation on the relationship between niche specialization and speciation rate in the terrestrial, herbivorous mammals (in review). Speciation rates are predicted to be higher in ecological specialists than generalists if abiotic factors are the primary controls on species diversity but relatively lower if biotic interactions predominate (Vrba 1987, Bofarull et al. 2008, Stigall 2010, Baselga et al. 2011, Birand et al. 2012). I found that the positive relationship expected between ecological specialization and speciation in the purely abiotic model is recovered when foregut fermentation is included in the model. This result further supports joint roles for biotic and abiotic factors in determining differences in speciation rates among clades (Benton 2009).

In Chapter IV, I next investigate the effects of historical climatic perturbations and its interactions with digestive strategy on speciation rates of the terrestrial, herbivorous mammals. Long-term climatic oscillations are hypothesized to generate low species diversity while climatic stability promotes high species richness (Dynesius and Jansson 2000, Jansson and Dynesius 2002, Araujo et al. 2008, Abellan and Svenning 2014). I found that climatic instability since the Last Glacial Maximum had a stronger effect on the richness of foregut-fermenting mammals, an effect that varied with the particular component contributing to climatic instability. Unlike foregut fermenters, hindgut herbivores appear to be restricted within a common instability space regardless of their geographic origins. Differences in the instability-richness relationship between hindgut and foregut mammals suggest that the diversity of foregut herbivores has not equilibriated with respect to climatic change.

In Chapter V, I conclude with the implications of the preceding four chapters.

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CHAPTER II

THE ROLE OF ECOLOGICAL OPPORTUNITY IN SHAPING DISPARATE DIVERSIFICATION TRAJECTORIES IN A BICONTINENTAL PRIMATE RADIATION

ABSTRACT

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 data set of feeding morphology, I test predictions of the EO model to evaluate the role of ecological opportunity 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.

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 (Rabosky and Lovette 2008a; but see Etienne and Rosindell 2012). There is growing evidence that the availability of ecological opportunity can explain the "early burst" (Lovette and Bermingham 1999, Phillimore and Price 2008, Burbrink and Pyron 2010) of lineage accumulation produced by declining net diversification rate. In the ecological opportunity (EO) model, ample resources presented by key innovations, ecological release, or novel habitats (Hunter 1998, Schluter 2000, Yoder et al. 2010) are initially available for exploitation and promote rapid species proliferation (Losos et al. 1997, Schluter 2000, Harmon et al. 2008). However, speciation rate subsequently declines as the radiation progresses due to competition among daughter lineages for progressively saturated niche space ("niche filling"; Rabosky and Lovette 2008b) or as specialization constrains genetic variation (Gavrilets and Vose 2005, Gavrilets and Losos 2009).

Phenotypic and lineage diversification are coupled (Adams et al. 2009, Burbrink and Pyron 2010, Mahler et al. 2010, Slater et al. 2010, Burbrink et al. 2012a) if elevated morphological evolution generates forms that are capable of exploiting a broad range of niches, providing more opportunities for speciation via divergent selection (Schluter 1994, Schluter 2000). 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 (Schluter 2000, Harmon et al. 2003), 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 ecological opportunity had little influence on diversification. However, ecological opportunity 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 (Adams et al. 2009, Derryberry et al 2011, Burbink et al. 2012b, Frederich et al. 2013). In such cases, an ancillary approach that directly tests the effects of functional traits on diversification rates can resolve the relative impact of ecological opportunity on a radiation. If ecological opportunity was an important promoter of diversification, then phenotypic (e.g., niche-use) traits that increase access to ecological opportunity are expected to be associated with higher diversification rates. This is a crucial addition to the two standard predictions of the EO model.

Colobinae (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) (Delson 1994, Fleagle and Gilbert 2006). The species richness of colobines is second only to their sister group (Cercopithecinae) among all primates (*N*=52-59 species; Groves 2001, Wilson and Reeder 2005, IUCN 2008). 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 (Chivers 1994, Kay and Davies 1994, Waterman and Kool 1994, Alexander 1993, McNab 2002). Foregut fermentation may be a key innovation (Simpson 1944, 1953; Hunter 1998) that allowed colobines to invade folivore adaptive zones unavailable to other primates (i.e., ecological opportunity) 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 ecological opportunity in the radiation. Second, I test whether declining speciation or increasing extinction rate toward 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 ecological opportunity (i.e., forest habitat) in colobine monkeys.

MATERIALS AND METHODS

(a) Morphological data

Evolution of the cranium, mandible, and teeth is tightly correlated with diet due to the functional requirements of processing food (Kay 1975, Perez-Barberia and Gordon 1999, Dumont et al.

2012, Ross et al. 2012). 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 (Tables S2.1-S2.2).

Mandible shape was quantified from a Procrustes superimposition analysis of eight landmarks and 23 semilandmarks (Sheets 2003a, 2003b; Zelditch et al. 2004; Rohlf 2006; Marquez 2006) digitized from photographs (see Appendix 2.1 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, D.C., USA), Department of Mammalogy of the American Museum of Natural History (New York, 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 Appendix 2.1 for details). Then the data set 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 (Revell

2009) were used in subsequent analyses. The phylogenetic size-correction procedure was performed in the R (R Core Team 2012) package PHYTOOLS (Revell 2012).

(b) Phylogenetic data

Because a clade-specific, multilocus phylogeny of Colobinae with better species coverage is unavailable, I use the mammal supertree from (Fritz et al. 2009) updated from that of (Bininda-Emonds et al. 2007) that includes 57 recognized species of colobine monkeys (>96% of named species; Table S2.3). The supertree generally agrees with current phylogenetic hypotheses (Zhang and Ryder 1998, Li et al. 2004, Karanth et al. 2008, Sterner et al. 2006, Osterholz et al. 2008, Ting 2008, Ting et al. 2008, Roos et al. 2011) for this complex group, except for the placement of two Asian genera (see Appendix 2.1 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 (Moore et al. 2004), 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 (Kuhn et al. 2011) in BEAST v 1.7.4 (Drummond and Rambaut 2007). Use of these pseudo-posterior trees accounts for phylogenetic uncertainty in the original supertree. I also computed the maximum clade credibility (MCC) tree, which is the tree with the maximum product of posterior clade probabilities, of the 101 trees in TREEANNOTATOR v 1.7.4 (Drummond and Rambaut 2007).

(c) Tempo of lineage and morphological diversification

Because interspecific interactions that mediate the exploitation of ecological opportunity are expected to occur only between species that inhabit proximate geographic 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) data sets for the relevant analyses.

I compared semi-logarithmic lineage-through-time plots (Nee et al. 1992) 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 (Revell 2012). 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 (Pybus and Harvey 2000). The test was implemented in the R package LASER (Rabosky 2006a) assuming an approximately 3.4 percent 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 (Phillimore and Price 2008, Etienne et al. 2011). 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; Rabosky and Lovette 2008) using the second-order Akaike information criterion (AIC_c), 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) (Rabosky 2006b) using AIC_c to determine if density dependence affects speciation rate. The best model has the lowest AIC_c score. However, the fit of a model is significantly better only when the difference between AIC_c scores is greater than two units (Burnham 2002). Diversification models were fit in the LASER package.

I used the node-height test (Freckleton and Harvey 2006) to determine whether morphological evolution has slowed through time consistent with a niche-filling hypothesis. I computed absolute values of standardized independent contrasts (Felsenstein 1985) 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 (Freckleton and Harvey 2006).

To further evaluate patterns of morphological variation, I calculated disparity through time and morphological disparity indexes (MDI) with the R package GEIGER (Harmon et al. 2008) using the methods of Harmon et al. (2003) and Slater et al. (2010). 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 (Harmon et al. 2003). 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 ecological opportunity 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 (Table S2.4). Log-transformed values of these percentages were used to characterize the degree of folivory specialization. I used the QuaSSE method (FitzJohn 2010) 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 (φ) that captures temporal change in the rate of character evolution in half of these models. Differences between AIC_c scores greater than two units (Burnham 2002) were used to select between models. This method was implemented in the R package DIVERSITREE (FitzJohn 2012).

RESULTS

Lineage-through-time plots (Figure 2.1) establish a complex history of diversification in colobine monkeys. A trend of greater than expected lineage accumulation saturating toward the present is evident approximately 3.3 Ma in Asian colobines but not in the older African lineage (Figure 2.1). Examination of γ statistics for the pseudo-posterior trees corroborates these qualitative assessments. Although negative γ values (γ=-0.945±0.485 s.d.) (Figure S2.1) 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 (5,000 stimulated 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 My into the radiation rather than a true early-burst diversification (Figures 2.1, S2.1).

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=7.68x10^{-4}; CMD variables: b=0.0375, R^2=0.337, $F_{1,20}$=10.2, p=0.00458) (Figure S2.2). 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* (Figure S2.2). 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=0.0600; CMD variables: b=-0.0258, R^2=0.396, $F_{1,5}$=3.27, p=0.130) (Figure S2.2).

With the exception of African CMD traits, relative disparity of feeding morphology was generally much greater than expected under Brownian motion (Figure 2.2). 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 morphological disparity index 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 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: ΔAIC_c=1.36-4.77; Asian species: ΔAIC_c=1.96-

5.55) (Tables 2.1, S2.5). The exponential density-dependent model is 0.508 times as probable as the three-rate shift Yule model in the African clade (Tables 2.1, S2.5). Furthermore, a model with exponentially decreasing speciation rate but constant extinction received the lowest AIC_c score, but the fit is not significantly better than another model that allows extinction rate to vary (African species: ΔAIC_c=1.48; Asian species: ΔAIC_c=1.29) (Tables 2.1, S2.5). 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 (Kubo and Iwasa 1995, Paradis 2004, Maddison et al. 2007, FitzJohn 2010, Rabosky 2010).

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 (ΔAIC_c=3.16-25.1) (Tables 2.2, S2.6). 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 2.3). However, the expected rate of character evolution over time (described by the positive directional term φ=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 (ΔAIC_c=4.60-98.9) (Tables 2.2, S2.6). However, the failure here to reject the null hypothesis of no differential extinction due to dietary foliage is not informative about the role of extinction in the diversification process. Unless the character has a very strong effect, BiSSE-based methods have low power to reliably detect extinction rates on molecular phylogenies (Maddison et al. 2007, FitzJohn 2010).

DISCUSSION

(a) Lack of ecological opportunity likely underlies the weak radiation of African colobines

Because the lineage-through-time plot, MCCR test, and node-height tests provide no significant support for an early burst followed by a slowdown in speciation or morphological evolution (Figures 2.1, S2.2-S2.3), these processes were approximately constant-rate in the African lineage. Additionally, the QuaSSE analysis indicates that folivory does not promote rates of African speciation (Tables 2.2, S2.6), contrary to expectations if the evolution of foregut fermentation permitted access to highly-folivorous niches. Together these data lend no support for a significant influence of diet-related ecological opportunity in stimulating diversification of the living African colobines. Similar deviations from expectations of the EO model are found in other studies (Adams et al. 2009, Derryberry et al. 2011, Burbrink et al. 2012b) and are attributed to factors such as young clades not having sufficient time for density dependent effects to arise and sequential colonizations of new adaptive zones resulting in staggered rather than a single early burst of diversification (Burbrink et al. 2012b).

In this case a dearth of ecological opportunity may explain why colobines did not radiate as strongly in Africa. First, suitable tropical rainforest covered East Africa 12.6 Ma (Jacobs and Kabuye 1987) close to the divergence of African colobines but contracted and was partially replaced with grasslands several millions of years later because of aridification from the uplift of the central Tanganyikan plateau (Wasser and Lovett 1993, Sepulchre et al. 2006). Second, because historically more cercopithecine primates have co-occurred with colobines in Africa than Asia (Delson 1994, Fleagle and Gilbert 2006), interspecific competition for habitat and dietary resources may have depressed diversification of the African lineage despite the availability of potential niches. Lastly, constrained morphological diversification may have limited opportunities for speciation via divergent selection (Schluter 1994, 2000). 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 (Zhang 2006). Alternatively, the lack of divergence in feeding morphology may reflect constraints posed by the species' digestive strategy, since 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 (Delson 1994, Benefit 2000). Eight taxa are known from this time period (Delson 1994, Benefit 2000) and suggest that a potentially diverse radiation of African colobines was masked in the neontological data by extinction. A joint phylogenetic analysis of paleontological and neontological data will address whether this is the case, but unfortunately most extinct colobine taxa cannot yet be linked robustly to extant species (Delson 1994, Ting 2008).

(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 Mid-Late Miocene (Delson 1994, Fleagle and Gilbert 2006, Sterner et al. 2006, Roos et al. 2011). 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 (Figures 2.1, S2.2-S2.3) reflect a scenario of ecological release followed by niche saturation as colobines dispersed and then speciated *in situ* eastward and southward through Eurasia from Africa (Delson 1994, Fleagle and Gilbert 2006). The timing of divergences of extant Asian genera and of species (Figure S2.3) 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 (5.04 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) (Brandon-Jones 1996) and would have provided the dispersing ancestral colobines with ample ecological opportunity. However, Pleistocene glaciations led to widespread aridity and retreat of wet forests throughout Asia (Brandon-Jones 1996). 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 (Figures 2.2, S2.2). Frederich et al. (2013) show that rates of trait evolution accelerate rather than decelerate toward the present when radiations consist of *multiple* diversification events instead of a single event. Clades also are expected to exhibit ecological and morphological convergence (Frederich et al. 2013). 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 ecological opportunity encountered during the dispersal to Asia. Therefore, colobine biogeographic history and my findings jointly support an important role of ecological opportunity in the diversification of Asian species despite departures from the conventional EO model.

(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

(Tables 2.2, S2.6). Such a surprising relationship between a putative adaptation and speciation rate, however, has been uncovered in other studies (e.g., woodcreepers; Claramunt et al. 2012). This suggests that the decline in speciation rate (Tables 2.1, S2.5) 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 (Price et al. 2012), specialist species are expected to have elevated rates of speciation and extinction due to increased susceptibility to environmental change (Vrba 1987). Unique trophic specialists also can have elevated rates of morphological evolution (Martin and Wainwright 2011). In this case, folivory may be an evolutionary "dead-end" for colobines due to foliage being a much less nutritious food than other vegetative items (Dasilva 1992). Primates with low-quality diets offset energetic deficiencies with trade-offs such as longer rest periods (Chapman et al. 2007) and larger body size (Milton et al. 1980). I propose that highly-folivorous species, which have low-quality diets and thus tend to be larger, are 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 (Paradis et al. 2004, FitzJohn 2010). In summary, the QuaSSE analyses reveal that ecological opportunity 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; Rabosky et al. 2013) 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 ecological opportunity in radiations.

CONCLUSIONS

I find compelling evidence from neontological data that ecological opportunity shaped the diversification trajectory of only one of the two independent radiations of colobine monkeys. Depressed species diversification toward the present in the Asian radiation can be attributed to not only 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 ecological opportunity as a driver of diversification in systems with replicate radiations.

TABLES

Table 2.1. Fits of diversification models to phylogenetic data.

Log-likelihood and differences in AIC$_c$ (ΔAIC$_c$) of models that were fit to branching times derived from the MCC phylogeny of 57 species. Two constant-rate, density-independent (Yule, BD); two variable-rate, density-independent (Yule2rate, Yule3rate); and two variable-rate, density-dependent (DDX, DDL) variants of the birth-death model were evaluated. Three time-varying speciation (λ) and extinction (μ) models also were analyzed: exponentially decreasing speciation but constant extinction rate through time (SPVAR), exponentially increasing extinction but constant speciation (EXVAR), and decreasing speciation but increasing extinction rates (BOTHVAR). Significant best-supported models are indicated with bolded ΔAIC$_c$ values.

lineage		**Yule**	**Yule2Rate**	**Yule3Rate**	**BD**	**DDX**	**DDL**	**SPVAR**	**EXVAR**	**BOTHVAR**
African clade	**LnLik**	-11.926	-9.671	-5.042	-11.926	-10.220	-10.751	-11.188	-11.930	-11.153
	ΔAIC$_c$	2.076	3.440	**0.000**	4.768	**1.356**	2.419	**0.000**	**1.484**	3.747
Asian clade	**LnLik**	25.502	29.437	30.680	25.502	26.510	27.211	26.137	25.494	26.140
	ΔAIC$_c$	3.338	**0.000**	**1.964**	5.546	3.530	2.128	**0.000**	**1.285**	2.444

Table 2.2. Fits of the folivory-dependent speciation and extinction models.

Log-likelihood and ΔAIC_c of models in which rates of speciation (λ) and extinction (μ) 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 (φ) that describes temporal change in the rate of character evolution. Bolded ΔAIC_c values indicate significant best-supported models.

	African clade						Asian clade					
model	**φ value**	**LnLik**	**ΔAIC_c**	**φ value**	**LnLik**	**ΔAIC_c**	**φ value**	**LnLik**	**ΔAIC_c**	**φ value**	**LnLik**	**ΔAIC_c**
constant λ, constant μ	---	-43.268	**0.000**	0.007	-43.268	4.714	---	-92.926	3.161	0.002	-92.926	5.975
linear λ, constant μ	---	-43.210	4.598	0.102	-42.109	8.684	---	-92.910	5.945	0.738	-88.388	**0.000**
sigmoidal λ, constant μ	---	-43.215	19.695	0.009	-42.045	30.554	---	-92.397	11.431	0.064	-90.054	10.552
modal λ, constant μ	---	-42.101	17.467	0.009	-43.143	32.752	---	-92.306	11.251	0.062	-88.251	6.942
linear λ, linear μ	---	-43.265	10.995	-0.113	-43.044	19.352	---	-92.903	9.030	-0.568	-90.908	8.461
sigmoidal λ, sigmoidal μ	---	-43.215	98.895	-0.204	-41.194	226.854	---	-92.827	25.120	-0.583	-86.815	18.517
modal λ, modal μ	---	-42.065	96.594	0.010	-42.056	228.577	---	-89.176	17.820	0.527	-85.678	16.247
constant λ, linear μ	---	-43.268	4.714	0.000	-43.268	11.000	---	-92.926	5.975	0.002	-92.926	9.070
constant λ, sigmoidal μ	---	-43.267	19.800	-0.201	-43.204	32.873	---	-92.926	12.491	0.002	-92.926	16.292
constant λ, modal μ	---	-43.049	32.429	-0.023	-42.982	32.429	---	-92.926	12.491	0.002	-92.926	16.292

Table S2.1. Landmarks and semilandmarks of mandible shape.

Definitions of the 8 landmarks and 23 semilandmarks selected to describe mandible shape in this study. Each landmark is classified using Bookstein's (1991) typology: 1) a discrete point where structures meet, 2) a discrete maximum or minimum point on a curvature, and 3) a discrete point that is separated by a distance from another location.

landmark or semilandmark	definition	type
LM 1	Most superior point on coronoid process	2
LM 2	Most inferior point on mandibular notch	2
LM 3	Most superior point on condyloid process	2
LM 4	Most inferior point on posterior border of mandibular angle	3
LM 5	Most anterior point of contact between P_3 and alveolar ridge	1
LM 6	Point where a vertical line from landmark 5 intersects with inferior border of mandibular body	3
LM 7	Most anterior point of contact between M_2 and alveolar ridge	1
LM 8	Point of contact between alveolar ridge and anterior border of ramus	1
SLM 1-2	Between landmarks 1 and 2	
SLM 3-5	Between landmarks 2 and 3	
SLM 6-13	Between landmarks 3 and 4	
SLM 14-21	Between landmarks 4 and 6	
SLM 22-23	Between landmarks 1 and 8	

Table S2.2. Cranio-mandibular dental (CMD) characters.

Definitions of the 51 cranio-mandibular dental (CMD) characters measured to describe the non-shape components of feeding morphology. The acronyms of equivalent characters in the NYCEP PRIMO database (http://primo.nycep.org/) are provided alongside the names used in this study.

character	PRIMO character	definition	notes	used in analyses?
UI1L	UI1L	maxillary central incisor length	length = maximum distance between mesial and distal contact points, parallel to tooth row	N
UI1B	UI1W	maxillary central incisor breadth	breadth = maximum distance between buccal and lingual surfaces, perpendicular to mesiodistal diameter	N
UI2L	UI2L	maxillary lateral incisor length		N
UI2B	UI2W	maxillary lateral incisor breadth		N
UCL	UCL	maxillary canine length		N
UCB	UCW	maxillary canine breadth		N
UPM1L	UP3L	maxillary premolar 1 length		N
UPM1B	UP3W	maxillary premolar 1 breadth		N
UPM3L	UP4L	maxillary premolar 3 length		N
UPM3B	UP4W	maxillary premolar 3 breadth		N
UM1L	UM1L	maxillary molar 1 length		N
UM1B	UM1B	maxillary molar 1 breadth		N
UM2L	UM2L	maxillary molar 2 length		Y
UM2B	UM2B	maxillary molar 2 breadth		N
UM3L	UM3L	maxillary molar 3 length		Y
UM3B	UM3B	maxillary molar 3 breadth		N
LI1L	LI1L	mandibular central incisor length		N
LI1B	LI1W	mandibular central incisor breadth		N
LI2L	LI2L	mandibular lateral incisor length		N
LI2B	LI2W	mandibular lateral incisor breadth		N
LCL	LCL	mandibular canine length		N
LCB	LCW	mandibular canine breadth		N
LPM1L	LP3L	mandibular premolar 1 length		N

character	PRIMO character	definition	notes	used in analyses?
LPM3L	LP4L	mandibular premolar 3 length		Y
LPM3B	LP4W	mandibular premolar 3 breadth		Y
LM1L	LM1L	mandibular molar 1 length		Y
LM1B	LM1B	mandibular molar 1 breadth		N
LM2L	LM2L	mandibular molar 2 length		Y
LM2B	LM2B	mandibular molar 2 breadth		N
LM3L	LM3L	mandibular molar 3 length		Y
LM3B	LM3B	mandibular molar 3 breadth		N
UM1CH	UM1H	maxillary molar 1 crown height	from peak of paracone to dentino-enamel junction at base of crown	N
UM2CH	UM2H	maxillary molar 2 crown height		N
UM3CH	UM3H	maxillary molar 3 crown height		N
LM1CH	LM1H	mandibular molar 1 crown height	from peak of paraconid to dentino-enamel junction at base of crown	N
LM2CH	LM2H	mandibular molar 2 crown height		N
LM3CH	LM3H	mandibular molar 3 crown height		N
LIRL	LIRL	mandibular incisor row length	distance between distal edges of left and right lateral incisors at cemento-enamel junction	N
LPMRL	P4PL	mandibular premolar row length		Y
LMRL	M3ML	mandibular molar row length		Y
CONDYLL	CONDYLL	condyle length	maximum anterior-posterior length of mandibular condyle	N
CONDYLW	CONDYLW	condyle width	maximum mediolateral dimension of mandibular condyle	N
MAT	MAT	moment arm of temporal muscle	from mid-curvature of mandibular condyle to apex of coronoid process	N
MAM2	COGO	moment arm of masseter muscle (direct distance)	distance from top of mandibular condyle to inferior-most border of mandibular angle	Y
MANDL	IDGO	mandible length	from posterior edge of mandibular ramus to infradentale	Y
MANDH	MANDH	mandible height	height of mandibular corpus between M_1 and M_2	N
MANDSYM	SYML	mandible symphysis length	length of mandibular symphysis between inferior mandibular margin at midline and infradentale (highest point of gum between two central incisors of lower jaw)	Y

character	PRIMO character	definition	notes	used in analyses?
SYMW	SYMW	mandible symphysis width	symphyseal width (measured at widest point on symphysis perpendicular to SD)	N
PALL	PRST	palate length	prosthion (most anterior point on maxillary alveolar process, between central incisor teeth) to posterior nasal spine	Y
G I	GLIN	glabella to inion distance	distance from glabella (area on frontal bone between eyebrow ridges) to inion (most prominent projection of occipital bone at posterio-inferior part of skull	Y

Table S2.3. Taxonomy of colobine monkeys (subfamily Colobinae).

The recognized number of species and subspecies in each genus of the African and Asian clades according to three taxonomic authorities.

	Groves (2001)		Wilson and Reeder (2005)		IUCN (2008)	
genus	**no. species**	**no. subspecies**	**no. species**	**no. subspecies**	**no. species**	**no. subspecies**
Colobus	5	15	5	15	5	16
Piliocolobus	9	11	9	11	0	0
Procolobus	1	0	1	0	6 (8 unnamed)	15
total (African)	15	26	15	26	19	31
Nasalis	1	0	1	0	1	2
Presbytis	11	28	11	26	10	25
Pygathrix	3	0	3	0	3	0
Rhinopithecus	4	3	4	3	4	3
Semnopithecus	7	2	7	0	3	9
Simias	1	2	1	0	1	2
Trachypithecus	17	25	17	28	11	34
total (Asian)	44	60	44	57	33	75
total (all)	59	86	59	83	52	106

Table S2.4. Diet data of species.

The average percentages of total foliage (of young, mature, or indeterminate age) in the diets of 38 colobine species compiled from the literature.

species	% dietary foliage	reference(s)
Colobus angolensis	46.5	Maisels et al. 1994, Hayes et al. 1996, Fashing 2007, Kamilar and Paciulli 2008
Colobus guereza	74.7	Chivers 1994, Oates 1994, Hayes et al. 1996, Chapman and Pavelka 2005, Fashing 2007, Kamilar and Paciulli 2008
Colobus polykomos	55.5	Chivers 1994, Oates 1994, Fashing 2007, Kamilar and Paciulli
Colobus satanas	33.6	Oates 1994, Hayes et al. 1996, Brugiere et al. 2002, Fashing 2007, Kamilar and Paciulli 2008
Nasalis larvatus	53.7	Chivers 1994, Kirkpatrick 2007, Kamilar and Paciulli 2008
Piliocolobus badius	58.6	Oates 1994, Hayes et al. 1996, Chapman and Pavelka 2005, Fashing 2007, Kamilar and Paciulli 2008
Piliocolobus kirkii	64.8	Fashing 2007, Kamilar and Paciulli 2008
Piliocolobus pennantii	70.5	Chapman and Chapman 2000, Fashing 2007, Kamilar and Paciulli 2008
Piliocolobus preussi	89.0	Fashing 2007, Kamilar and Paciulli 2008
Piliocolobus rufomitratus	58.3	Fashing 2007, Kamilar and Paciulli 2008
Piliocolobus tephrosceles	83.0	Fashing 2007
Piliocolobus tholloni	63.3	Maisels et al. 1994, Fashing 2007
Presbytis comata	65.0	Kirkpatrick 2007, Kamilar and Paciulli 2008
Presbytis femoralis	29.0	Kirkpatrick 2007, Kamilar and Paciulli 2008
Presbytis hosei	73.5	Kirkpatrick 2007, Kamilar and Paciulli 2008
Presbytis melalophos	34.5	Chivers 1994
Presbytis potenziani	55.0	Fuentes 1996, Kirkpatrick 2007, Kamilar and Paciulli 2008
Presbytis rubicunda	36.8	Davies 1991, Chivers 1994, Kirkpatrick 2007, Kamilar and Paciulli 2008
Presbytis siamensis	35.7	Kirkpatrick 2007, Kamilar and Paciulli 2008
Presbytis thomasi	42.0	Kirkpatrick 2007, Kamilar and Paciulli 2008
Procolobus verus	75.8	Oates 1994, Hayes et al. 1996, Fashing 2007, Kamilar and Paciulli 2008
Pygathrix nemaeus	75.7	Chivers 1994, Kirkpatrick 1998, Lippold 1998, Kamilar and Paciulli 2008
Pygathrix nigripes	54.6	Hoang et al. 2009
Rhinopithecus avunculus	37.8	Boonratana and Le 1998; Kirkpatrick 1998, 2007; Kamilar and Paciulli 2008
Rhinopithecus bieti	6.0	Kirkpatrick 1998, Fashing 2007, Kamilar and Paciulli 2008

species	% dietary foliage	reference(s)
Rhinopithecus brelichi	63.1	Kirkpatrick 1998, 2007; Kamilar and Paciulli 2008; Xiang et al. 2012
Rhinopithecus roxellana	12.9	Kirkpatrick 1998, Guo et al. 2007
Semnopithecus dussumieri	48.5	Kirkpatrick 2007
Semnopithecus entellus	48.0	Chivers 1994
Semnopithecus priam	48.0	Kirkpatrick 2007
Simias concolor	60.0	Kamilar and Paciulli 2008
Trachypithecus auratus	52.3	Chivers 1994, Kirkpatrick 2007, Kamilar and Paciulli 2008
Trachypithecus francoisi	52.9	Kamilar and Paciulli 2008
Trachypithecus johnii	52.0	Kirkpatrick 2007, Kamilar and Paciulli 2008
Trachypithecus obscurus	55.8	Chivers 1994, Kirkpatrick 2007, Kamilar and Paciulli 2008
Trachypithecus phayrei	46.0	Kamilar and Paciulli 2008
Trachypithecus pileatus	58.0	Kirkpatrick 2007, Kamilar and Paciulli 2008
Trachypithecus vetulus	46.0	Chivers 1994, Dela 2007, Kirkpatrick 2007, Kamilar and Paciulli 2008

Table S2.5. Fits of diversification models to phylogenetic data.

Log-likelihood, AIC$_c$, and differences in AIC$_c$ (ΔAIC$_c$) of models that were fit to branching times derived from the maximum clade credibility (MCC) phylogeny of 57 species. Two constant-rate, density-independent (pure-birth [Yule], birth-death [BD]); two variable-rate, density-independent (multiple rate shift pure-birth [Yule2rate, Yule3rate]); and two variable-rate, density-dependent (exponential [DDX] and logistic [DDL] speciation) variants of the birth-death model were evaluated. Three time-varying speciation (λ) and extinction (μ) models also were analyzed: exponentially decreasing speciation rate but constant extinction through time (SPVAR), exponentially increasing extinction but constant speciation (EXVAR), and decreasing speciation but increasing extinction rates (BOTHVAR). Significant best-supported models are indicated with bolded ΔAIC$_c$ values.

		Yule	**Yule2Rate**	**Yule3Rate**	**BD**	**DDX**	**DDL**	**SPVAR**	**EXVAR**	**BOTHVAR**
lineage	**no. of parameters**	1	3	5	2	2	2	3	3	4
African clade	**LnLik**	-11.926	-9.671	-5.042	-11.926	-10.220	-10.751	-11.188	-11.930	-11.153
	AIC$_c$	26.160	27.524	24.084	28.852	25.440	26.503	30.559	32.043	34.306
	ΔAIC$_c$	2.076	3.440	**0.000**	4.768	**1.356**	2.419	**0.000**	**1.484**	3.747
Asian clade	**LnLik**	25.502	29.437	30.680	25.502	26.510	27.211	26.137	25.494	26.140
	AIC$_c$	-48.904	-52.242	-50.279	-46.696	-48.712	-50.114	-45.642	-44.357	-43.199
	ΔAIC$_c$	3.338	**0.000**	**1.964**	5.546	3.530	2.128	**0.000**	**1.285**	2.444

Table S2.6. Fits of the folivory-dependent speciation and extinction models.

Log-likelihood, AIC$_c$, and differences in AIC$_c$ of models in which rates of speciation (λ) and extinction (μ) 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 (φ) that describes temporal change in the rate of character evolution. Bolded ΔAIC$_c$ values indicate significant best-supported models.

				African clade				Asian clade			
φ parameter	**λ model**	**μ model**	**no. of parameters**	**φ value**	**LnLik**	**AIC$_c$**	**ΔAIC$_c$**	**φ value**	**LnLik**	**AIC$_c$**	**ΔAIC$_c$**
no directional tendency	constant	constant	3		-43.268	95.535	**0.000**		-92.926	192.941	3.161
	linear	constant	4		-43.210	100.133	4.598		-92.910	195.725	5.945
	sigmoidal	constant	6		-43.215	115.230	19.695		-92.397	201.211	11.431
	modal	constant	6		-42.101	113.002	17.467		-92.306	201.031	11.251
	linear	linear	5		-43.265	106.530	10.995		-92.903	198.810	9.030
	sigmoidal	sigmoidal	9		-43.215	194.430	98.895		-92.827	214.900	25.120
	modal	modal	9		-42.065	192.129	96.594		-89.176	207.600	17.820
	constant	linear	4		-43.268	100.249	4.714		-92.926	195.755	5.975
	constant	sigmoidal	6		-43.267	115.335	19.800		-92.926	202.271	12.491
	constant	modal	6		-43.049	114.898	32.429		-92.926	202.271	12.491
directional tendency	constant	constant	4	0.007	-43.268	100.249	4.714	0.002	-92.926	195.755	5.975
	linear	constant	5	0.102	-42.109	104.219	8.684	0.738	-88.388	189.780	**0.000**
	sigmoidal	constant	7	0.009	-42.045	126.089	30.554	0.064	-90.054	200.332	10.552
	modal	constant	7	0.009	-43.143	128.287	32.752	0.062	-88.251	196.722	6.942
	linear	linear	6	-0.113	-43.044	114.887	19.352	-0.568	-90.908	198.241	8.461
	sigmoidal	sigmoidal	10	-0.204	-41.194	322.389	226.854	-0.583	-86.815	208.297	18.517
	modal	modal	10	0.010	-42.056	324.112	228.577	0.527	-85.678	206.027	16.247
	constant	linear	5	0.000	-43.268	106.535	11.000	0.002	-92.926	198.850	9.070
	constant	sigmoidal	7	-0.201	-43.204	128.408	32.873	0.002	-92.926	206.072	16.292
	constant	modal	7	-0.023	-42.982	127.964	32.429	0.002	-92.926	206.072	16.292

FIGURES

Figure 2.1. Lineage-through-time plots of the African and Asian clades.

Lineages from the distribution of 101 pseudo-posterior trees are plotted. Time proceeds from the past toward the present (0 Ma). Solid lines denote the median number of lineages; shaded areas represent the 95-percent confidence interval (CI) of the number of lineages. Dashed lines indicate the expected number of lineages under exponential growth with constant speciation and no extinction.

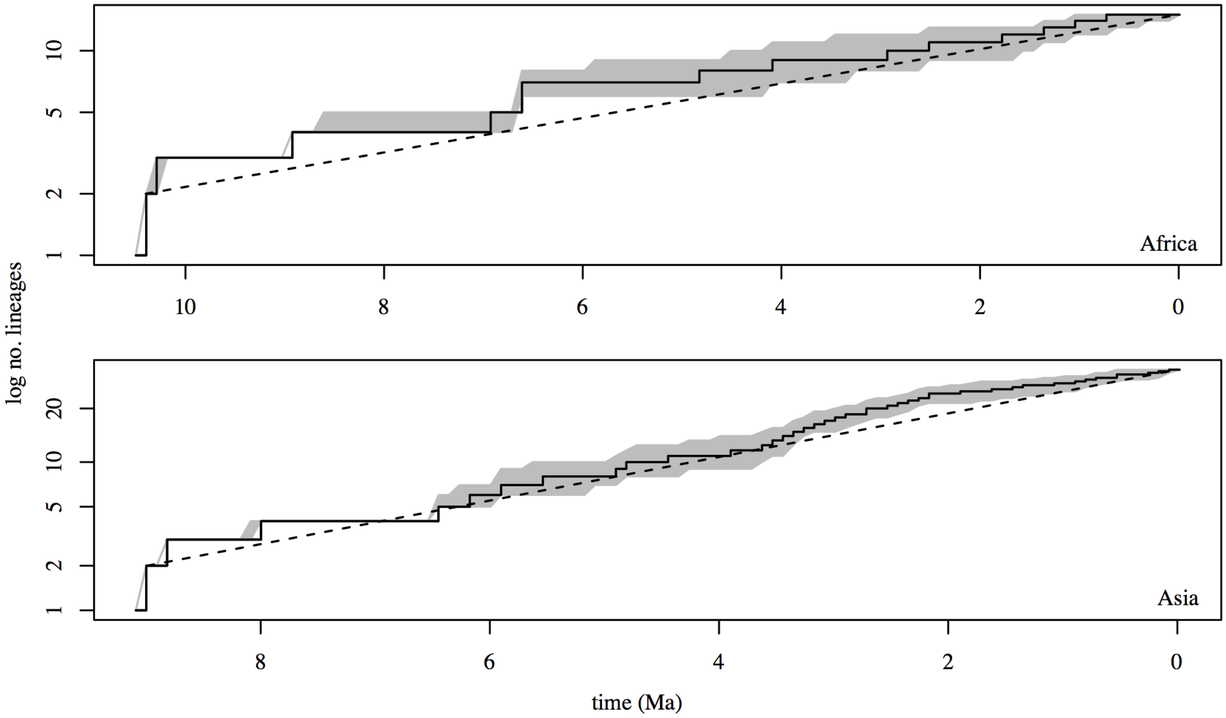


Figure 2.2. Disparity through time of feeding morphology.

Plots of disparity through time of (a) mandible shape and (b) CMD traits for the African and Asian clades. Time is relative from the past (0 Ma) to the present (1 Ma). 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-percent CI of the simulated disparities.

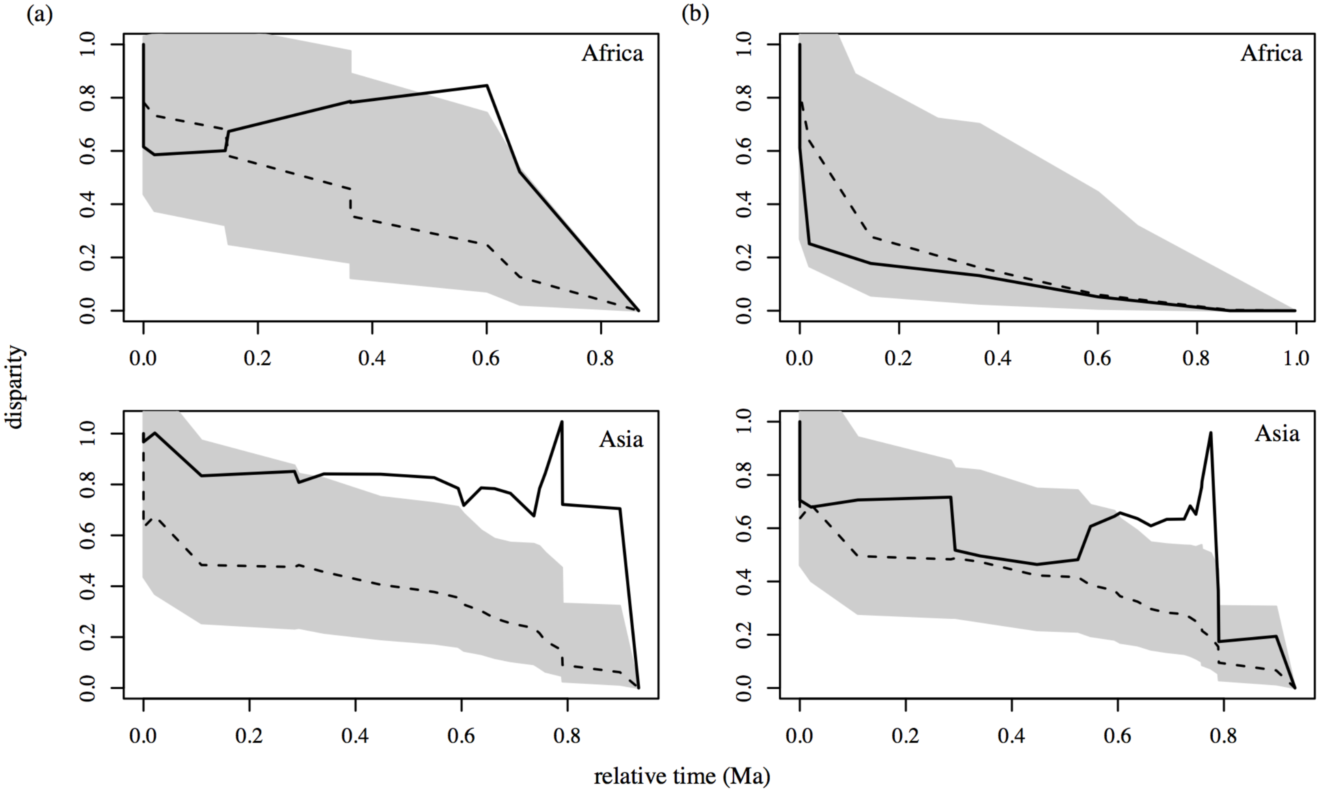


Figure 2.3. Folivory-dependent rates of speciation and extinction.

Plots of (a) speciation and (b) extinction rates as functions of folivory from the QuaSSE models with the lowest AIC$_c$ scores for the African and Asian clades.

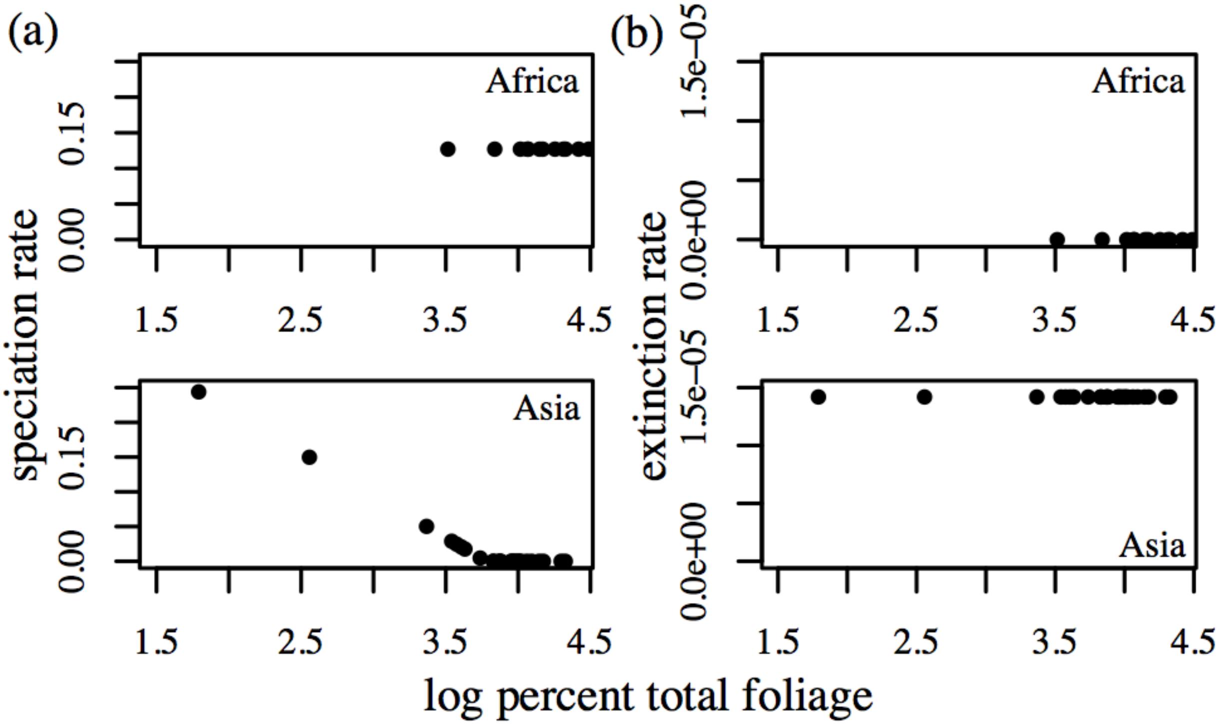


Figure S2.1. Gamma statistics for the phylogenies.

Distributions of gamma (γ) statistics for the 101 pseudo-posterior trees for the African and Asian clades. Dashed lines denote the value of 1.645 at which γ is significantly lower than expected under a pure-birth process.

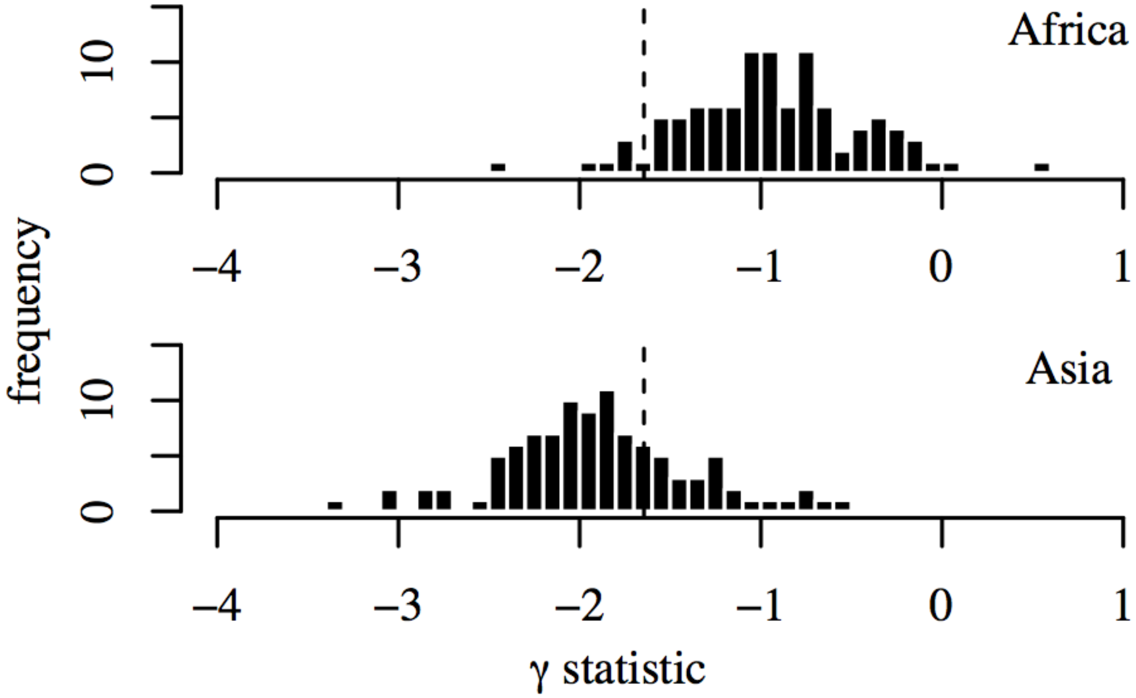


Figure S2.2. Node height tests of feeding morphology.

Plots of (a) mandible shape and (b) cranio-mandibular dental (CMD) contrasts against node heights from the MCC tree for the African and Asian clades. The outliers in the Asian CMD plot are contrasts between the ancestral nodes of *Presbytis* species and the *Semnopithecus*-*Trachypithecus* clade and between the surili species *Presbytis potenziani* and *P. rubicunda*.

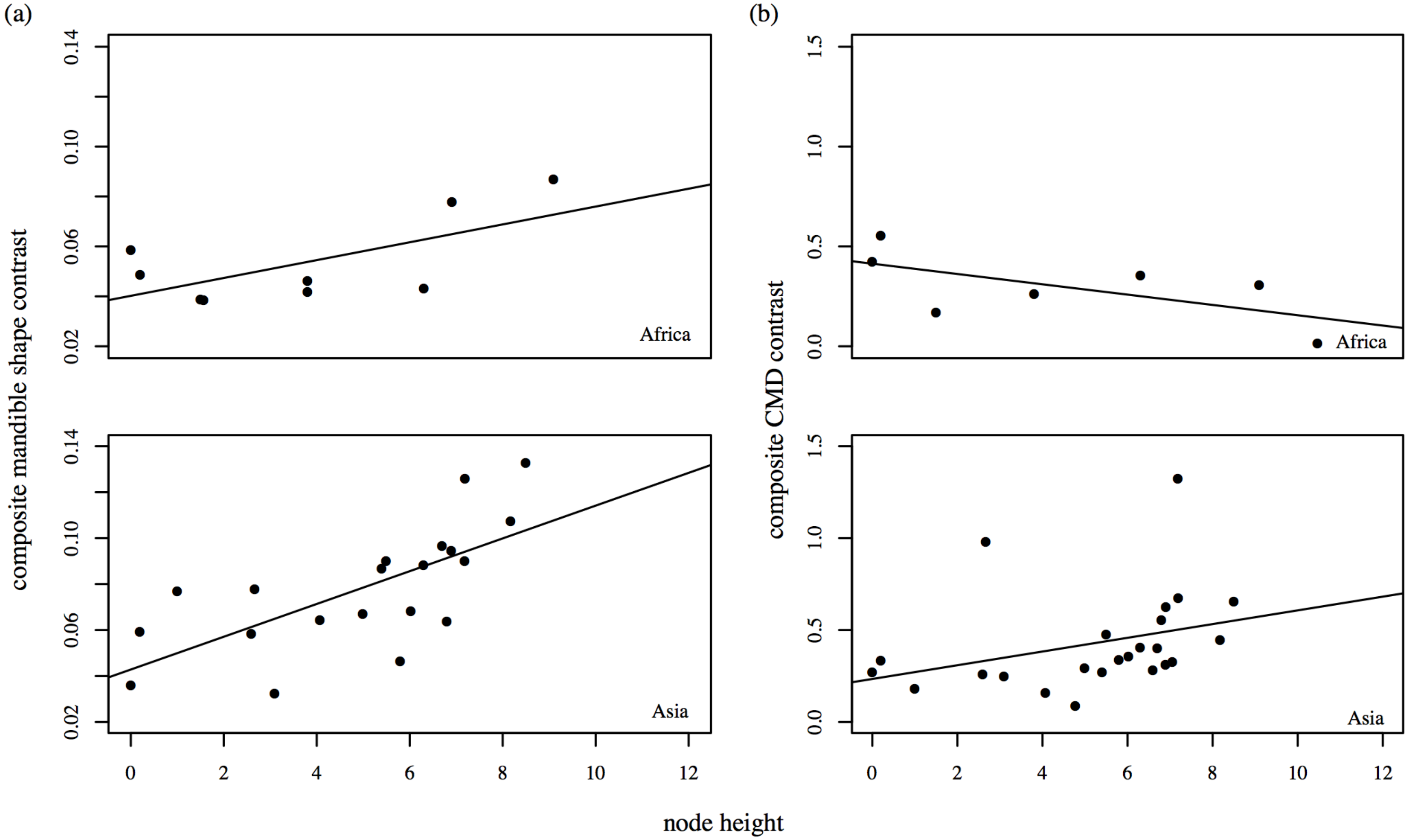
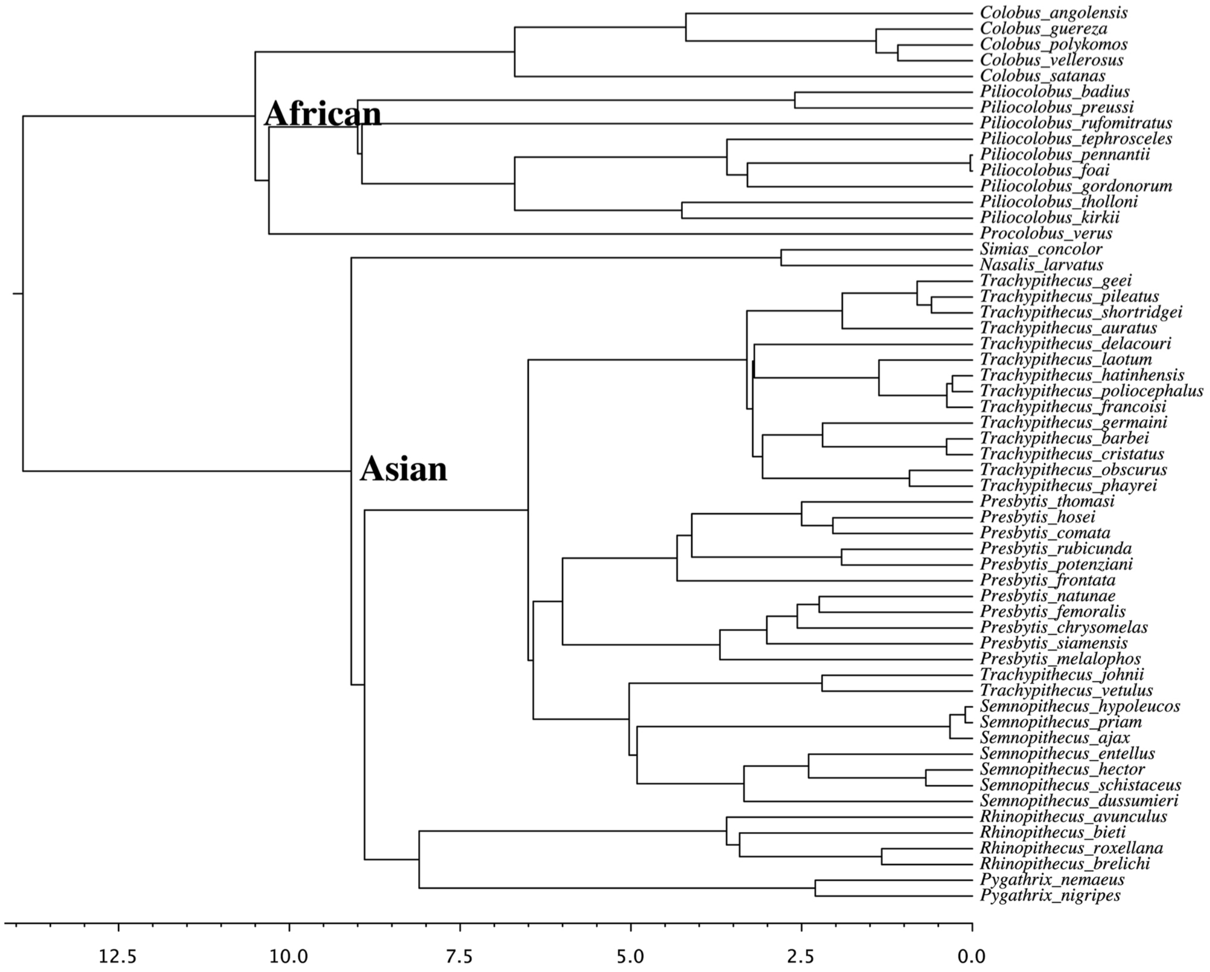


Figure S2.3. Phylogeny of Colobinae.

The maximum clade credibility (MCC) phylogeny of colobine monkeys (subfamily Colobinae) estimated from the distribution of 101 pseudo-posterior trees. The pseudo-posterior trees are from Kuhn et al. (2011).



APPENDIX

Appendix 2.1. Supporting methods and references.

(a) Morphological data

Each mandible was sampled at eight landmarks; an additional 23 semilandmarks were included to capture information about curvature (Rohlf 2006, Marquez 2006). Procrustes superimposition was done to remove variation due to position, scale, and orientation (Sheets 2003a, Zelditch et al. 2004). Semilandmarks were slid to minimize the Procrustes distance between specimens and the reference (Sheets 2003b). Measurements of 51 CMD variables were collected using a digital caliper (UPM Model No. 111-513 and Mitutoyo Model No. NTD12P-6") to 0.01 mm accuracy from 205 adult male museum specimens and supplemented with data from the PRIMO database (http://primo.nycep.org/).

(b) Phylogenetic data

The major disagreements between the supertree and colobine-specific phylogenies involve relationships in the Asian clade: the placement of the monotypic genus *Nasalis* in relation to other Asian genera (Sterner et al. 2006, Ting et al. 2008, Roos et al. 2011) and the placement of *Presbytis* in the langur or odd-nosed clade (Sterner et al. 2006, Ting et al. 2008, Roos et al. 2011). Such differences are not unexpected when potential bias stemming from limited species and molecular sampling in the colobine-specific phylogenies are considered. The supertree and specialist phylogenies agree on relationships within the African genus *Colobus* (Ting 2008) and the paraphyly of two *Trachypithecus* species (*T. johnii* and *T. vetulus*) that are more-closely related to *Semnopithecus* (Zhang and Ryder 1998, Li et al. 2004, Karanth et al. 2008, Osterholz et al. 2008).

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CHAPTER III

INTERACTION BETWEEN DIGESTIVE STRATEGY AND NICHE SPECIALIZATION PREDICTS SPECIATION RATES ACROSS HERBIVOROUS MAMMALS

ABSTRACT

Biotic and abiotic factors often are treated as mutually exclusive drivers of diversification processes. In this framework, ecological specialists are expected to have higher speciation rates than generalists if abiotic factors are the primary controls on species diversity but lower rates if biotic interactions are more important. Here, I show that the positive relationship between ecological specialization and speciation expected from the pure abiotic model is recovered when a species-specific trait, digestive strategy, is modeled in the terrestrial, herbivorous mammals (Mammalia). This result indicates that biotic and abiotic factors can operate in concert to generate the pattern expected from the strictly abiotic model. I also demonstrate that the effect of digestive strategy does not arise from higher speciation rates or broader ecological specialization in foregut-fermenting clades. Together, these findings suggest that a biological trait potentially played an important role in shaping mammal speciation in response to abiotic events.

INTRODUCTION

In the paleontological and neontological literature, two alternative frameworks seek to explain the drivers of species diversity (Benton 2009): the abiotic Court Jester (Barnosky 2001) and biotic Red Queen (Van Valen 1973) models. First, the Court Jester hypothesizes that physical factors such as climatic or tectonic change, not biotic interactions, primarily control speciation and extinction (Barnosky 2001). Under this model, rates of speciation and extinction are predicted to be higher in ecologically-specialized than generalist lineages. This expectation follows from the assumption that specialists are more susceptible to environmental perturbations, particularly to population isolation (Bofarull et al. 2008; Baselga et al. 2011; Birand et al. 2012). Population isolation potentially promotes speciation via vicariance or divergent selection and the extinction of species with fragmented populations, resulting in high speciation and extinction rates (Bofarull et al. 2008; Baselga et al. 2011; Birand et al. 2012). Generalists, on the other hand, are assumed to bear traits that buffer the effects of environmentally-induced reductions in population size and connectivity. High resistance to the effects of environmental perturbations potentially reduce the number of speciation and extinction events due to population isolation in generalists, resulting in low rates of speciation and extinction (Bofarull et al. 2008; Baselga et al. 2011; Birand et al. 2012). Therefore, when abiotic factors are the primary sources of selection, rates of speciation and extinction should increase with the degree of ecological specialization (Vrba 1987).

Second, the Red Queen model hypothesizes that negative interactions between species rather than physical factors are the predominant forces driving evolution (Van Valen 1973). In contrast to the Court Jester, little work has examined how rates of speciation and extinction should vary between specialists and generalists within the Red Queen paradigm. Van Valen (1973) suggested that species are continually involved in zero-sum interactions with other species in which none emerge victorious. When abiotic change is stochastic but constant, a consequence of these interactions are constant rates of evolution that are shared by members of higher taxa regardless of their age (Van Valen 1973; Stenseth and Smith 1984). However, the zero-sum assumption generates an evolutionary system whose behavior is particularly sensitive to any change in conditions (e.g., in the constancy of resources) (Smith 1976). In certain cases of inconstant environmental change resulting from the introduction of invasive species, competition may selectively induce extinction while suppressing divergence of specialized lineages (Stigall 2010). This translates into a positive correlation between ecological specialization and extinction rate but a negative correlation between the former and speciation rate in a Red Queen world. However, it is unclear how generalizable these relationships are across various systems obeying the Red Queen.

The Red Queen and Court Jester models are not mutually exclusive. Benton (2009) noted that biotic and abiotic factors might operate at different temporal and geographic scales. In the multi-level mixed model, the influence of biotic factors may be strongest over short time scales and small geographic regions (Benton 2009). Over longer time scales across larger regions and globally, environmental perturbations may prevail (Barnosky 2005; Benton 2009). Therefore, tests at the appropriate temporal and spatial scales may be key to being able to accurately distinguish between the two models (Barnosky 2001).

Among the extant mammals, rates of net diversification (speciation minus extinction) are significantly higher in herbivores than either carnivores or omnivores (Price et al. 2012).

Herbivorous mammals have evolved two primary suites of digestive physioanatomical adaptations for the fermentation of plant material: an enlarged cecum and/or colon in hindgut fermenters and a sacculated stomach in foregut fermenters (Gilchrist and Mackie 1984). The location of the specialized fermentation chamber in the gastrointestinal tract, either in the large intestine or before the true stomach, differentiates between hindgut and foregut-fermenting organisms. These two strategies involve trade-offs in diet quality, digestive efficiency, and other aspects (Gilchrist and Mackie 1984) with far-reaching implications across ecological and evolutionary scales.

Foregut fermentation evolved independently at least four times in mammals, in the: macropodiform marsupials (Macropodiformes: Macropodidae and Potoroidae), sloths (Bradypodidae and Megalonychidae), ruminant artiodactyls and tylopods (Artiodactyla: Ruminantia, Tylopoda, Tayassuidae, and Hippopotamidae), and colobine monkeys (Colobinae) (Chivers and Langer 1994; J. Fritz et al. 2009; Godoy-Vitorino et al. 2012; Haigler and Weimer 1991; Hume 1999, 2002; Lambert and Fellner 2011; Ley et al. 2008; Mackie et al. 1997, 1999; McNab 2002). Hindgut-fermenting herbivores include elephants, lagomorphs, and some rodents (Chivers and Langer 1994; J. Fritz et al. 2009; Godoy-Vitorino et al. 2012; Haigler and Weimer 1991; Hume 1999, 2002; Lambert and Fellner 2011; Ley et al. 2008; Mackie et al. 1997, 1999; McNab 2002). One herbivore, the giant panda, does not have specializations for fermenting plant matter (Van Soest 1994). Although food passage rates are reduced and some nutrients are lost to microbial metabolism, overall nutrient extraction is more efficient in foregut than hindgut fermentation (Langer 1987). Furthermore, endosymbiotic microbes in the foregut neutralize potentially toxic plant secondary compounds and can themselves be digested for additional proteins (Langer 1987). The foregut strategy potentially extends niche breadth by making a larger proportion of vegetation nutritionally accessible to herbivores. Thus, foregut lineages may persist across a wider range of resource regimes or be more ecologically generalized than hindgut fermenters (Langer 1984). Related hypotheses about the colonization and radiation of foregut-fermenting lineages in areas unsuitable or less desirable for other herbivores predict that the digestive novelty also is associated with elevated diversification (Langer 1984).

The putative effects of foregut fermentation, an evolutionary novelty, on ecological specialization and diversification in mammals suggest that a more synthetic explanation beyond the generalized expectations of the Red Queen and Court Jester models may be necessary. Because multiple lines of evidence suggest important roles for both biotic (Alroy et al. 2000) and abiotic (Cerling et al. 1997; Badgley et al. 2008; Maguire and Stigall 2009; Figueirido et al. 2012) factors in the diversification of mammals, tests of not only (1) whether, but also (2) how an intrinsic trait (here, digestive strategy) generates deviations in the relationship between niche specialization and diversification expected from the biotic-abiotic framework are necessary. Because of the difficulty with interpreting extinction rates from phylogenies of extant taxa (Paradis 2004; Rabosky 2010), here I focus only on speciation rate. To address the first part of my question, I combine geospatial and phylogenetic comparative methods to evaluate how niche specialization and speciation rate are correlated, when digestive strategy is and is not considered, in the herbivorous mammals. I then directly test for differences in specialization and speciation between foregut and hindgut lineages within a phylogenetic framework to determine where the effect of digestive strategy, if any, arises. Answers to these two questions ultimately demonstrate that biotic and abiotic drivers can operate in concert to jointly shape diversification dynamics.

METHODS

Phylogenies for niche and diversification analyses

The mammal supertree of S. Fritz et al. (2009) was selected to provide the phylogenetic structure for taxa in this study. It is the most comprehensive phylogeny of extant mammals to date with 5,021 species encompassing 93 percent of recognized species diversity (Wilson and Reeder 2005). Fully-resolved phylogenies ($N = 101$) (Kuhn et al. 2011) and the maximum clade credibility (MCC) phylogeny of this distribution were used in comparative analyses to avoid biases in diversification estimates arising from polytomies. Herbivorous species were identified using trophic data from Price et al. (2012) and the IUCN Red List (IUCN 2013). Despite often very complex differences between foregut and hindgut-fermenting species (Langer 1984), here I focus on a particular physioanatomical structure (i.e., stomach specializations for housing endosymbiotic bacteria) that defines foregut fermentation. Digestive strategy states were assigned to species according to which lineages are reported to possess foregut and hindgut fermentation (Chivers and Langer 1994; J. Fritz et al. 2009; Godoy-Vitorino et al. 2012; Haigler and Weimer 1991; Hume 1999, 2002; Lambert and Fellner 2011; Ley et al. 2008; Mackie et al. 1997, 1999; McNab 2002) (Table S3.1).

Selection of lineages

Lineages consisting of closely-related, herbivorous species with known hindgut or foregut fermentation state were chosen to compare niche use and speciation between the two groups. The selection criteria yielded 13 lineages of foregut fermenters (Antilocapridae, Bovidae, Bradypodidae, Camelidae, Cervidae, Colobinae, Giraffidae, Hippopotamidae, Macropodidae, Megalonychidae, Moschidae, Potoroidae, Tragulidae) and 33 lineages of hindgut fermenters (Atelidae, Bathyergidae, Capromyidae, Castoridae, Caviidae, Cebidae, Cercopithecinae, Chinchillidae, Cricetidae, Dasyproctidae, Elephantidae, Equidae, Hominidae, Hylobatidae, Hystricidae, Lemuridae, Leporidae, Muridae, Myocastoridae, Ochotonidae, Octodontidae, Pedetidae, Petromuridae, Phalangeridae, Phascolarctidae, Procaviidae, Pseudocheiridae, Rhinocerotidae, Sciuridae, Suidae, Tapiridae, Trichechidae, Vombatidae) (Figure 3.1).

Spatial data for characterization of species occurrences

A shapefile of the distributional ranges of terrestrial mammals was obtained from the 2013 IUCN Red List (IUCN 2013; http://www.iucnredlist.org/technical-documents/spatial-data). Each polygon in this shapefile represents a "limited of a species distribution", which indicates that the species likely occurs within the delimited area based on known occurrences and expert knowledge of the habitat preferences of the species. Records were filtered from the shapefile to include only areas in which species are likely native ("Origin" code 1), extant or extinct ("Presence" codes 1-2 and 4-5), and to occur regularly throughout the year or during the breeding or non-breeding season ("Seasonality" codes 1-3, 5).

To characterize species distributions more finely, occurrence records of species in the 46 lineages (Figure 3.1) were downloaded from the Global Biodiversity Information Facility (GBIF) database. Only records with the location filters of “georeferenced” and “with no known coordinate issues” were downloaded. For each species that was sampled in both the IUCN and GBIF data sets, GBIF occurrences were overlaid with the IUCN spatial polygon of the same species to determine which geographic coordinates fall within the known species distributional range. Only validated coordinates that were delimited within the corresponding species ranges were retained for further analysis. Of these, only species with five or more coordinates were further analyzed. A total of 155,817 records were obtained after applying this procedure, with a median of 93 occurrences per species (minimum = 5, maximum = 1,012). The spatial overlay analyses were performed in R v. 2.15.2 (R Core Team 2012) using the *sp* package (Pebesma and Bivand 2005). Both spatial data sets were converted to the WGS84 datum in ArcMap v. 10 (ESRI) prior to analysis.

Estimation of species and lineage niche specialization

To capture both dietary and habitat dimensions of mammalian niches, I selected the resource-use variables of diet breadth and environmental disparity to characterize per-lineage niche specialization. Data on the diet breadth (i.e., the number of food items in the diet) of species were collected from the PanTHERIA database (Jones et al. 2009). Then, values were averaged across all extant species in each clade to obtain per-lineage diet breadths.

PanTHERIA defines the number of items in a species' diet using the following categories: “vertebrate”, “invertebrate”, “fruit”, “flowers/nectar/pollen”, “leaves/branches/bark”, “seeds”, “grass”, and “roots/tubers”. Therefore, herbivores have a maximum diet breadth of six. Species with diet breadths greater than six were removed from the analysis, because they likely were misclassified as herbivores or their diet breadths were erroneously coded. Though admittedly coarse in resolution, this classification of diet includes the major food items that would comprise part of herbivorous species' diets across the different taxonomic groups. This feature of the data set allows comparison across a broad variety of species, for which diet breadth based on other measures (e.g., taxonomic diversity of plants eaten) potentially would be heavily biased by the geographic locations for which data are available. However, one major limitation of PanTHERIA's classification scheme is that it likely will not capture the full range of variation in species' diets, in particular those of species with highly specialized dietary items that do not fall within any of the six vegetative categories (e.g., fungus or lichen). This limitation has the effect of decreasing diet breadth values, making the analyses of the relationship between diet breadth and speciation more conservative.

Another potential limitation of the diet data is the quality of the classification itself. To check the quality of the PanTHERIA data, diet breadths of a subset of the lineages in the analysis were reclassified in this study and compared to the database values. An exhaustive literature search for each primate species was performed using the search term "((genus AND species) AND diet*) under "Topic" in Web of Science. Then, all dietary items were recorded for each species from each journal article with the appropriate information. Lastly, the number of dietary items were tabulated across the literature sources for each species using the PanTHERIA classification scheme (Table S3.2). This procedure found dietary information appropriate for classification into the six categories for 88 percent (15/17) of the primate species in the analysis. A linear regression of the diet breadths classified in this study and the PanTHERIA values indicates that the data are not significantly correlated ($\beta = 0.125$, $R^2 = -0.0693$, $F_{1,13} = 0.0930$, $p = 0.765$) (Figure S3.1). This exercise indicates that diet breadths may vary based on the sources used and the individual reviewing the data, and so diet data from PanTHERIA were considered inappropriate for use in the following analyses.

The environmental disparity of each species and lineage was computed as the maximum pairwise dissimilarity at 19 climatic and net primary productivity variables (i.e., a 20-dimensional habitat space) (Table S3.3) among the species' observed occurrences and among species within a clade, respectively. Maximum rather than mean disparity was chosen to capture the fullest extent of the realized niches of species and clades. Based on the validation analysis of PanTHERIA diet data, only environmental disparity (hereafter referred to as “niche specialization”) was considered in subsequent analyses.

The environmental variables chosen for this analysis were: 19 annual bioclimatic variables from the WorldClim database (~1950-2000, 5 arc-minute or 10 km resolution) (Hijmans et al. 2005) and annual net primary productivity (NPP) derived from Moderate-resolution Imaging Spectroradiometer (MODIS) imaging data (2000-2012, 30 arc-second or 1 km resolution) (Zhao et al. 2005). The bioclimatic variables capture annual trends and variation in temperature and precipitation. As the difference between the total amount of plant biomass that is converted from solar energy and the chemical energy that is consumed during plant respiration, NPP represents the amount of energy that potentially is available to herbivores. A raster of median values across the 12-year NPP data was written in ARCMAP. Then, the 20 raster grids were resampled to the same resolution as the bioclimatic data in ARCMAP for further analysis. The coarser resolution was selected due to the prohibitive computational demands of processing the 1-km data sets for all species in the 46 clades. For each species with occurrence data, values of the 20 variables were extracted at each validated geographic coordinate. Lastly, medians, which are less sensitive to extreme values than are means, of the 20 variables across all coordinates were computed for each species to estimate per-lineage disparities. All environmental raster data sets were converted to the WGS84 datum in ARCMAP prior to analysis. Disparity was computed with the *tip.disparity* function from the R package GEIGER (Harmon et al. 2008) modified to calculate maximum rather than mean pairwise dissimilarity. Of the 668 species that were in both the IUCN and GBIF data sets, only 197 (76 percent of the 259 known herbivorous species) had no missing data at any of the environmental variables and were suitable for the per-lineage disparity calculations. These 197 species represent 39 of the 46 original lineages. Table 3.1 lists the lineages and the number of species sampled for each in the final data set.

Estimating habitat breadth as disparity over the 20 environmental variables has several advantages and disadvantages. First, the resolution of the variables may not be sufficiently fine to capture real differences between taxa. That is, taxa may partition habitat space at scales beyond that which can be captured by the disparity metric used in this study. Second, not all the variables may be relevant for differentiating the ecological niches of taxa. For example, species may be specialists on some niche axes but generalists on others (Emery 2012). Despite these disadvantages, the variables analyzed in this study maximize the availability of standardized data for more species and over a larger geographic area than other possible habitat variables.

Because underestimation of lineage-wide disparities might result from missing or under-sampled species occurrence data or distributional ranges, regressions of lineage disparity on the proportion of species that was sampled and that is endangered or extinct in each lineage were performed to assess this issue. The conservation statuses of species in each lineage were obtained from the 2013 IUCN Red List. The number of species that are classified as being “endangered”, “critically endangered”, “extinct in the wild”, or “extinct” was tabulated for each lineage. Then the sum of these numbers relative to the total number of sampled species was calculated for each lineage. Similarly, the proportion of species sampled was calculated as the number of species that was used to estimate lineage disparity over the total number of species in each lineage. However, lineage disparities are not significantly correlated with either of these variables in phylogenetic regressions (species sampled: $\beta = 1.81.4 \times 10^3$, $R^2 = 0.0229$, $F_{1,37} = 1.89$, $p = 0.178$; species status: $\beta = -1.74 \times 10^3$, $R^2 = -0.00974$, $F_{1,37} = 1.02$, $p = 0.431$).

Estimates of diversification parameters using the BAMM model

Because of its ability to model temporal and among-lineage heterogeneity in evolutionary rates, the Bayesian Analysis of Macroevolutionary Mixtures (BAMM) model (Rabosky 2013) was applied to the MCC phylogeny of 5,021 species to estimate per-lineage speciation rates. The BAMM model estimates regimes of heterogenous diversification parameters on a phylogeny without requiring *a priori* information about the location of rate shifts. This study focused only on speciation rate, since it is difficult to interpret extinction from phylogenies of extant taxa

(Paradis 2004; Rabosky 2010). In lieu of a global sampling fraction applied to the entire phylogeny, sampling fractions were calculated using the taxonomy (Wilson and Reeder 2005) of each genus. Four reversible-jump Metropolis-coupled MCMC chains were allowed to run for 1.50×10^9 generations using the default priors and were sampled every 10^6 iterations. Seventeen percent of the posterior samples were discarded prior to further analysis after assessing convergence diagnostics using the R package CODA (Plummer et al. 2006). The MCMC analysis was performed using the BAMM v. 2.0 software (Rabosky 2014). Speciation rates, model-averaged across the posterior distribution of models, were estimated for each lineage using the R package BAMMTOOLS (Rabosky et al. 2014) and compared between foregut and hindgut groups in phylogenetic analysis of variance tests in GEIGER. It must be noted here that analysis of extant-only molecular phylogenies promotes a perceptual bias that richness increases with time regardless of the true diversity dynamics of a clade (Ricklefs 2007). Therefore, speciation rates from BAMM and related models must be interpreted with this in mind.

Phylogenetic comparative analyses

Linear models that account for the phylogenetic non-independence of comparative data were fit to assess the correlation between per-lineage niche specialization and speciation rates using phylogenetic generalized least-squares (pGLS) regression (Grafen 1989) and the MCC phylogeny in the R package CAPER (Orme 2013). Maximum likelihood was specified to optimize the branch length transformations (Pagel's λ and δ) (Pagel 1999) for the pGLS procedures. The fit of models with and without digestive strategy as a factor, and with and without an interaction term between niche specialization and digestive strategy, was assessed using the second-order

Akaike Information Criterion (AICc) corrected for finite sample size in CAPER. The preferred model within the set of candidate models has the minimum AICc value (Burnham and Anderson 2002).

RESULTS

How are niche specialization and speciation rate correlated?

For herbivorous mammals, phylogenetic generalized least-squares (pGLS) regression indicates that the degree of niche specialization and speciation rate are not significantly correlated ($\beta = 6.92 \times 10^{-6}$, $R^2 = 0.0436$, $F_{1,37} = 2.73$, $p = 0.107$) (Figure 3.2, Table 3.2). This result supports neither the strictly abiotic Court Jester nor the strictly biotic Red Queen model. However, the relationship becomes significantly positive when digestive strategy is included as a factor in the model ($\beta = 2.20 \times 10^{-5}$, $R^2 = 0.228$, $F_{3,35} = 4.74$, $p = 0.00706$) (Figure 3.2). This interaction-term model is preferred over the single-term model ($AICc_{niche*strategy,\ df = 4} = —31.7$ v. $AICc_{niche,\ df = 2} = -27.0$). Therefore, the effect of niche specialization on speciation rate is dependent on the mode of digestive fermentation. Because smaller values of environmental disparity indicate greater niche specialization, these results indicate that generalism is associated with higher speciation rates in foregut fermenters ($\beta_{foregut} = -3.60 \times 10^{-1}$). Conversely, generalist hindgut fermenters have relatively lower speciation rates. The positive correlation between the degree of ecological specialization and speciation expected under the Court Jester is recovered only for hindgut fermenters. while the relationship found for foregut fermenters is more consistent with the Red Queen.

Niche specialization does not differ between foregut and hindgut fermenters

The effect of digestive mode on the niche specialization-speciation relationship can arise from differences between foregut and hindgut clades in either the degree of ecological specialization or the magnitude of speciation rates. However, per-lineage niche specialization does not significantly vary between foregut and hindgut groups ($F_{1,37} = 0.33053$, $p = 0.749$) (Figure 3.3).

Clade speciation rates do not differ between digestive strategies

Because digestive strategy does not appear to mediate the relationship between niche specialization and speciation rate through differences in specialization, I tested whether speciation rates vary between the foregut and hindgut groups. The BAMM analysis indicates that clade-averaged speciation rates are not significantly different between foregut and hindgut-fermenting lineages ($\lambda_{\text{foregut}} = 0.122$, $\lambda_{\text{hindgut}} = 0.101$; $F_{1,37} = 1.46$, $p = 0.447$) (Figure 3.4).

DISCUSSION

The degree of niche specialization is predicted to affect diversification dynamics in distinct ways depending on whether biotic or abiotic controls on species diversity prevail. When extrinsic, abiotic factors such as climate change are the primary selection pressures, specialized niche use is expected to promote higher rates of speciation and extinction relative to the rates of generalists (Vrba 1987). This hypothesis assumes that specialist clades are more susceptible to changes in the extrinsic environment (e.g., to disproportionally suffer from population decline or isolation induced by climate change) than generalist clades (Baselga et al. 2011). Results from recent studies (Fernandez and Vrba 2005; Bofarull et al. 2008; Cantalapiedra et al. 2011; Cano et al.

2012) that evaluated the extent of specialization, measured as the number of biomes occupied by species in various mammal groups including the terrestrial herbivores, have supported this prediction. Here, I find that the positive relationship between degree of niche specialization and speciation rate expected due to extrinsic selection pressures is recovered, however, only when the mode of digestive fermentation is considered. Neither differences in niche specialization nor speciation between foregut and hindgut-fermenting clades appear to underlie the interactive effect of digestive strategy and niche specialization found here.

Although my results indicate that foregut fermentation is not associated with broader niche use in mammals, they do not rule out this possibility. First, the definition of the "niche" considered here may be limited. Diet is a more intuitive metric with which to test the resource use of species as a function of their digestive strategy. With the appropriate data, an explicit analysis of diet breadth holds great potential for resolving the question of whether niche specialization varies with fermentation mode. Second, the niche estimates examined here are static snapshots of a highly responsive trait. The approaches taken in this study do not model temporal changes in niche that are induced by climatic and other environmental perturbations during the individual clade histories (a range of ca. 9.09 - 65.8 My). Although niche conservatism may be prevalent over short to intermediate timescales (10 - 10^6 Yr) (Peterson 2011), it is unclear the extent to which present-day estimates depart from historical niches beyond the expectation that the degree of departure should vary among mammals according to idiosyncrasies in biogeographic history, biology, and other factors. Niche conservatism above the species level seems to be more strongly controlled by life history traits than extrinsic factors (Hadly et al. 2009). For example, the range sizes of North American mammals remained constant at the genus and family levels over a time period during which species within the clades experienced range shifts and extinctions due to climate change (Hadly et al. 2009). If this is the case, niches above the species level (as were examined here) may be more robust to the effects of extrinsic changes. However, it has been shown that niche conservatism at the species and genus levels over deep time (10^5 – 10^6 Yr) is sensitive to the presence of biotic drivers, such as the introduction of invasive species (Stigall 2014). Nevertheless, the lack of correlation between environmental disparity and the number of species that are at risk in each lineage (see Methods) suggests that changes in niche due to anthropogenic activities, at the very least, are not likely to be a prominent factor affecting the niche estimates considered here.

Furthermore, the data and analyses used in this study may not fully capture the true diversification histories of herbivorous mammals without the incorporation of fossil information. In future, new studies, particularly ones that aim to test the effects of past events on diversification dynamics, must integrate neontological and paleontological data using statistical approaches (e.g., Doyle and Donoghue 1987; Paradis 2004; Heath et al. 2014) in order to more fully understand the historical events that have structured the diversities and distributions of living mammals.

Resilience in the face of abiotic change is an integral feature of ecological specialization that influences the persistence (Kammer et al. 1997) and proliferation (Ozinga et al. 2013) of taxa across scales (but see Colles et al. [2013]) but that is not examined here. Global climatic and environmental changes since the Eocene promoted an increase in the diversity of artiodactyls but a decline in the hindgut-fermenting perissodactyls (Cifelli 1981; Langer 1987; Janis 1989). Consequently, the extant artiodactyls are 14 times as diverse as the perissodactyls (Wilson and Reeder 2005; IUCN 2013). The macropodiform marsupials are less arboreal than the hindgut-fermenting phalangerids, suggesting that the former were not as adversely affected as more forest-adapted fauna by the expansion of open grasslands in east-central Australia during the Plio-Pleistocene (Bryne et al. 2011). Nevertheless, historical climate changes have left detectable signatures of genetic structuring in macropodiforms that are forest-adapted (Macqueen et al. 2011). The radiation of colobine monkeys throughout South and Southeast Asia coincided with the expansion of moist forests during a period of high global temperatures in the Miocene (Brandon-Jones 1996). Changes in the availability of moist forest may have contributed to the greater diversity of the foregut-fermenting colobine rather than the hindgut-fermenting cercopithecine monkeys in Asia (IUCN 2013).

Such comparisons between foregut and hindgut sister groups suggest that the responses of foregut clades to ecological opportunity (Purvis et al. 2011) and environmental change may hold the keys to understanding the digestive novelty's impact on speciation. In other words, foregut fermentation may benefit herbivores by allowing them to successfully exploit ecological opportunity arising from environmental change, in ways that hindgut fermenters cannot (Langer 1984). The higher speciation rates predicted for foregut-fermenting generalists found here would support a scenario in which generalists radiated after colonizing novel habitats or niches. In contrast, the positive specialization-speciation relationship recovered for hindgut fermenters suggests that generalism may not be a route toward increase diversity in those herbivores. If abiotic drivers are the primary forces controlling hindgut speciation rates, as the present results suggest, than generalism may be the consequence of environmental perturbations in hindgut-fermenting lineages. Climatic oscillations are predicted to select against specialization (Dynesius and Jansson 2000). Results for hindgut and foregut mammals together indicate that there is a role for the Court Jester alongside biotic factors in explanations of diversity changes in herbivorous mammals. Therefore, further studies that explicitly test the linkage between digestive strategy and climate-dependent speciation rates (Condamine et al. 2013) are necessary.

Although digestive strategy is not associated with differential speciation rates in herbivorous mammals, the effect of a codistributed character (such as body size) cannot be ruled out (Maddison et al. 2007; FitzJohn et al. 2009). Body size (BM) often is viewed as a composite measure of such fundamental, intrinsic factors as physiology, morphology, life history, and ecology (Collar et al. 2011). Because of the mismatched scaling of gut capacity and energetic demand to body mass (BM^1 and $BM^{3/4}$, respectively), smaller animals require more energy per unit of body mass than larger animals (Clauss et al. 2003). This physiological constraint theoretically allows larger herbivores to select diets of lower nutritional quality than smaller animals (the “Jarman-Bell Principle”) (Clauss et al. 2003; but see Muller et al. 2013). Because the forestomach increases efficiency by delaying the passage of ingested food (Clauss et al. 2003), it may reduce the total energetic requirements of and therefore more strongly promote the survival of smaller-bodied, foregut than hindgut-fermenting animals. Net diversification rates generally decrease with increasing body size in primates (Paradis 2005), but the synergistic effects of body size and digestive strategy on mammalian diversification requires further investigation.

In conclusion, the Court Jester and Red Queen models often are presented as dichotomous alternatives. However, evidence from this study suggests that abiotic factors alone do not adequately explain diversification dynamics within the terrestrial, herbivorous mammals at the taxonomic, temporal, and geographic scales examined here. Rather, support is found for the multilevel mixed model (Benton 2009; Stigall 2013), in which both biotic and abiotic factors prevail at large temporal and geographic scales. Furthermore, my finding that digestive strategy mediates the diversification outcomes of terrestrial, herbivorous lineages (Table 3.2) highlights that investigations of the relative influences of biotic versus abiotic factors on patterns of species diversity cannot be predicated on “all else being equal” (i.e., hypotheses must be informed by the relevant, and idiosyncratic, traits of taxa) (Ezard et al. 2011).

TABLES

Table 3.1. Lineages of terrestrial, herbivorous mammals that were analyzed in this study. Clades ($N = 39$) for which per-lineage environmental disparities could be calculated with no missing data. Key: S_{total} = number of described species in each lineage, $S_{analyzed}$ (%) = percentage of species included in the niche and comparative analyses, disparity = environmental disparity, λ = speciation rate estimated from BAMM model.

lineage	digestive strategy	S_{total}	$S_{analyzed}$ (%)	disparity	λ
Antilocapridae	foregut	1	100.00	3.22E+08	0.136
Atelidae	hindgut	24	29.17	4.26E+08	0.175
Bathyergidae	hindgut	16	6.25	2.68E+08	0.086
Bovidae	foregut	143	39.16	7.49E+08	0.160
Camelidae	foregut	4	50.00	4.05E+08	0.065
Capromyidae	hindgut	20	5.00	5.74E+07	0.140
Castoridae	hindgut	2	50.00	5.29E+08	0.071
Caviidae	hindgut	18	27.78	5.29E+08	0.128
Cebidae	hindgut	56	1.79	3.66E+07	0.175
Cervidae	foregut	51	41.18	8.03E+08	0.180
Chinchillidae	hindgut	7	14.29	4.06E+08	0.085
Colobinae	foregut	59	16.95	3.66E+08	0.213
Cricetidae	hindgut	681	0.29	3.48E+08	0.136
Dasyproctidae	hindgut	13	15.38	3.29E+08	0.087
Elephantidae	hindgut	3	66.67	4.85E+08	0.064
Equidae	hindgut	8	62.50	5.32E+08	0.216
Giraffidae	foregut	2	50.00	2.89E+08	0.153
Hippopotamidae	foregut	2	50.00	3.36E+08	0.065
Hominidae	hindgut	7	28.57	9.66E+07	0.173
Hystricidae	hindgut	11	36.36	5.66E+08	0.085
Lemuridae	hindgut	19	15.79	2.16E+08	0.067
Leporidae	hindgut	61	31.15	7.83E+08	0.098
Macropodidae	foregut	65	23.08	8.42E+08	0.164
Megalonychidae	foregut	2	50.00	3.86E+08	0.069
Muridae	hindgut	730	0.14	4.42E+08	0.098
Ochotonidae	hindgut	30	10.00	3.93E+08	0.067
Octodontidae	hindgut	13	15.38	3.20E+08	0.123
Pedetidae	hindgut	2	50.00	2.75E+08	0.069
Petromuridae	hindgut	1	100.00	2.67E+08	0.085
Phalangeridae	hindgut	27	18.52	5.93E+08	0.065
Phascolarctidae	hindgut	1	100.00	4.89E+08	0.067
Potoroidae	foregut	10	10.00	1.23E+08	0.065
Procaviidae	hindgut	4	75.00	4.57E+08	0.064
Pseudocheiridae	hindgut	17	29.41	7.92E+08	0.065
Rhinocerotidae	hindgut	5	40.00	3.76E+08	0.065
Sciuridae	hindgut	278	1.08	5.15E+08	0.144
Tapiridae	hindgut	4	75.00	3.58E+08	0.065
Tragulidae	foregut	8	37.50	2.52E+08	0.066
Vombatidae	hindgut	3	33.33	2.45E+08	0.066

Table 3.2. Phylogenetic generalized least-squares regressions.

Shown are results from the three pGLS models fit to the lineage data.

model	term	***β***	**std. error**	***t*-value**	***p***	**R^2**	**F**	**overall *p***	**AICc**
disparity only	intercept	-1.198	0.105	-11.372	<0.001	0.044	2.733	0.107	-26.984
	disparity	6.92E-06	4.19E-06	1.653	0.107				
disparity + strategy, interaction	intercept	-1.042	0.124	-8.403	<0.001	0.228	4.739	0.007	-31.712
	disparity	-2.26E-06	4.86E-06	-0.465	0.645				
	$\text{strategy}_{\text{foregut}}$	-0.360	0.159	-2.267	0.030				
	$\text{disparity*strategy}_{\text{foregut}}$	2.20E-05	7.30E-06	3.012	0.005				
disparity + strategy, no interaction	intercept	-1.218	0.109	-11.162	<0.001	0.039	1.780	0.183	-25.340
	disparity	6.98E-06	4.16E-06	1.676	0.102				
	$\text{strategy}_{\text{foregut}}$	0.064	0.078	0.820	0.418				

Table S3.1. List of sources for trophic level and fermentation state of species considered in this study.

species	trophic	trophic source	order	family	subfamily	strategy	strategy source(s)
Antilocapra americana	herbivore	Price et al. 2012	Artiodactyla	Antilocapridae		foregut	Mackie et al. 1997; Fritz et al. 2009
Aepyceros melampus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Aepycerotinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Alcelaphus buselaphus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Alcelaphinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Connochaetes gnou	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Alcelaphinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Connochaetes taurinus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Alcelaphinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Damaliscus lunatus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Alcelaphinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Damaliscus pygargus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Alcelaphinae	foregut	Fritz et al. 2009
Antidorcas marsupialis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Antilope cervicapra	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Eudorcas thomsonii	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Gazella gazella	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Litocranius walleri	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012

species	trophic	trophic source	order	family	subfamily	strategy	strategy source(s)
Madoqua guentheri	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Madoqua kirkii	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Nanger granti	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Neotragus batesi	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Neotragus pygmaeus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Oreotragus oreotragus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Ourebia ourebi	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Procapra gutturosa	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Raphicerus campestris	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Raphicerus melanotis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Raphicerus sharpei	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Dorcatragus megalotis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Fritz et al. 2009
Gazella dorcas	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Fritz et al. 2009
Nanger dama	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Fritz et al. 2009
Saiga tatarica	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Antilopinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Bison bison	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Bos javanicus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Boselaphus tragocamelus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Syncerus caffer	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Tetracerus quadricornis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Tragelaphus angasii	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009

species	trophic	trophic source	order	family	subfamily	strategy	strategy source(s)
Tragelaphus buxtoni	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Tragelaphus eurycerus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Tragelaphus imberbis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Tragelaphus scriptus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Tragelaphus spekii	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Tragelaphus strepsiceros	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Bubalus depressicornis	herbivore	IUCN 2014	Artiodactyla	Bovidae	Bovinae	foregut	Fritz et al. 2009
Bison bonasus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Fritz et al. 2009
Bos frontalis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Fritz et al. 2009
Bos grunniens	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Fritz et al. 2009
Bos taurus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Fritz et al. 2009
Bubalus bubalis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Fritz et al. 2009
Taurotragus oryx	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Bovinae	foregut	Fritz et al. 2009
Ammotragus lervia	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Budorcas taxicolor	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Hemitragus jemlahicus	herbivore	IUCN 2014	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Naemorhedus goral	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Fritz et al. 2009
Oreamnos americanus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Ovibos moschatus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Ovis ammon	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Ovis canadensis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Ovis dalli	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Pseudois nayaur	herbivore	IUCN 2014	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Rupicapra rupicapra	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Capra falconeri	herbivore	IUCN 2014	Artiodactyla	Bovidae	Caprinae	foregut	Fritz et al. 2009
Capra hircus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Fritz et al. 2009
Capra ibex	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Capricornis sumatraensis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Caprinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002

species	trophic	trophic source	order	family	subfamily	strategy	strategy source(s)
Cephalophus callipygus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Cephalophinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Cephalophus natalensis	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Cephalophinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Cephalophus nigrifrons	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Cephalophinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Cephalophus spadix	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Cephalophinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Sylvicapra grimmia	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Cephalophinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Rucervus duvaucelii	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Elaphurus davidianus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Cervinae	foregut	Fritz et al. 2009
Hippotragus equinus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Hippotraginae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Hippotragus niger	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Hippotraginae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Oryx gazella	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Hippotraginae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Addax nasomaculatus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Hippotraginae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Oryx dammah	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Hippotraginae	foregut	Fritz et al. 2009
Kobus ellipsiprymnus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Reduncinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Kobus kob	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Reduncinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Kobus leche	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Reduncinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Kobus vardonii	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Reduncinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Pelea capreolus	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Reduncinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Redunca arundinum	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Reduncinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Redunca fulvorufula	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Reduncinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012

species	trophic	trophic source	order	family	subfamily	strategy	strategy source(s)
Redunca redunca	herbivore	Price et al. 2012	Artiodactyla	Bovidae	Reduncinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Vicugna vicugna	herbivore	Price et al. 2012	Artiodactyla	Camelidae		foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Camelus bactrianus	herbivore	Price et al. 2012	Artiodactyla	Camelidae		foregut	Fritz et al. 2009
Camelus dromedarius	herbivore	Price et al. 2012	Artiodactyla	Camelidae		foregut	Fritz et al. 2009
Lama glama	herbivore	Price et al. 2012	Artiodactyla	Camelidae		foregut	Fritz et al. 2009
Lama guanicoe	herbivore	IUCN 2014	Artiodactyla	Camelidae		foregut	Fritz et al. 2009
Alces alces	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Alces americanus	herbivore	IUCN 2014	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Blastocerus dichotomus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Hippocamelus antisensis	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Hippocamelus bisulcus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Mazama americana	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Mazama gouazoubira	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Odocoileus hemionus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Odocoileus virginianus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Ozotoceros bezoarticus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Pudu puda	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Rangifer tarandus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Capreolus capreolus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Capreolinae	foregut	Fritz et al. 2009
Axis porcinus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012

species	trophic	trophic source	order	family	subfamily	strategy	strategy source(s)
Cervus elaphus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Cervus nippon	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Muntiacus atherodes	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Muntiacus muntjak	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Rusa unicolor	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Przewalskium albirostris	herbivore	IUCN 2014	Artiodactyla	Cervidae	Cervinae	foregut	Fritz et al. 2009
Axis axis	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Fritz et al. 2009
Dama dama	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Elaphodus cephalophus	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Fritz et al. 2009
Muntiacus reevesi	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Rucervus eldii	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Fritz et al. 2009
Rusa timorensis	herbivore	Price et al. 2012	Artiodactyla	Cervidae	Cervinae	foregut	Fritz et al. 2009
Giraffa camelopardalis	herbivore	Price et al. 2012	Artiodactyla	Giraffidae		foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009; Godoy-Vitorino et al. 2012
Okapia johnstoni	herbivore	Price et al. 2012	Artiodactyla	Giraffidae		foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Hexaprotodon liberiensis	herbivore	Price et al. 2012	Artiodactyla	Hippopotamidae		foregut	Fritz et al. 2009
Hippopotamus amphibius	herbivore	Price et al. 2012	Artiodactyla	Hippopotamidae		foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Moschus moschiferus	herbivore	Price et al. 2012	Artiodactyla	Moschidae		foregut	Mackie et al. 1997
Hyemoschus aquaticus	herbivore	Price et al. 2012	Artiodactyla	Tragulidae		foregut	Hume 2002
Tragulus javanicus	herbivore	Price et al. 2012	Artiodactyla	Tragulidae		foregut	Hume 2002; Fritz et al. 2009
Tragulus napu	herbivore	IUCN 2014	Artiodactyla	Tragulidae		foregut	Hume 2002
Phacochoerus aethiopicus	herbivore	Price et al. 2012	Artiodactyla	Suidae	Suinae	hindgut	Fritz et al. 2009
Lagorchestes hirsutus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Hume 2002; McNab 2002
Macropus agilis	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009

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Macropus giganteus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Macropus parma	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Macropus parryi	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Macropus robustus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Macropus rufus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Onychogalea fraenata	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Petrogale persephone	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Petrogale xanthopus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Setonix brachyurus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Hume 2002; McNab 2002
Thylogale stigmatica	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Wallabia bicolor	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Macropus fuliginosus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Fritz et al. 2009
Macropus rufogriseus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Macropodinae	foregut	Fritz et al. 2009
Lagostrophus fasciatus	herbivore	Price et al. 2012	Diprotodontia	Macropodidae	Sthenurinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Bettongia penicillata	herbivore	Price et al. 2012	Diprotodontia	Potoroidae		foregut	Fritz et al. 2009
Ailurops ursinus	herbivore	IUCN 2014	Diprotodontia	Phalangeridae	Ailuropinae	hindgut	Hume 1999
Phalanger orientalis	herbivore	Price et al. 2012	Diprotodontia	Phalangeridae	Phalangerinae	hindgut	Hume 1999
Trichosurus caninus	herbivore	Price et al. 2012	Diprotodontia	Phalangeridae	Phalangerinae	hindgut	Hume 1999
Trichosurus vulpecula	herbivore	Price et al. 2012	Diprotodontia	Phalangeridae	Phalangerinae	hindgut	Hume 1999
Wyulda squamicaudata	herbivore	Price et al. 2012	Diprotodontia	Phalangeridae	Phalangerinae	hindgut	Hume 1999
Phascolarctos cinereus	herbivore	Price et al. 2012	Diprotodontia	Phascolarctidae		hindgut	Hume 1999; Fritz et al. 2009
Petauroides volans	herbivore	Price et al. 2012	Diprotodontia	Pseudocheiridae	Hemibelideinae	hindgut	Hume 1999
Petropseudes dahli	herbivore	Price et al. 2012	Diprotodontia	Pseudocheiridae	Pseudocheirinae	hindgut	Hume 1999
Pseudocheirus peregrinus	herbivore	Price et al. 2012	Diprotodontia	Pseudocheiridae	Pseudocheirinae	hindgut	Hume 1999
Pseudochirulus forbesi	herbivore	Price et al. 2012	Diprotodontia	Pseudocheiridae	Pseudocheirinae	hindgut	Hume 1999
Pseudochirops albertisii	herbivore	IUCN 2014	Diprotodontia	Pseudocheiridae	Pseudochiropsinae	hindgut	Hume 1999
Vombatus ursinus	herbivore	Price et al. 2012	Diprotodontia	Vombatidae		hindgut	Fritz et al. 2009
Dendrohyrax dorsalis	herbivore	Price et al. 2012	Hyracoidea	Procaviidae		hindgut	McNab 2002
Heterohyrax brucei	herbivore	Price et al. 2012	Hyracoidea	Procaviidae		hindgut	McNab 2002
Procavia capensis	herbivore	Price et al. 2012	Hyracoidea	Procaviidae		hindgut	McNab 2002; Fritz et al. 2009
Brachylagus idahoensis	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus alleni	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus americanus	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009

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Lepus californicus	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus callotis	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus flavigularis	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus microtis	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus othus	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus townsendii	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Oryctolagus cuniculus	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Romerolagus diazi	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus aquaticus	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus audubonii	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus bachmani	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus brasiliensis	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus cunicularius	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus floridanus	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus nuttallii	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus palustris	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Sylvilagus transitionalis	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus capensis	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Lepus europaeus	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Fritz et al. 2009
Pronolagus crassicaudatus	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Pronolagus rupestris	herbivore	Price et al. 2012	Lagomorpha	Leporidae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Ochotona collaris	herbivore	Price et al. 2012	Lagomorpha	Ochotonidae		hindgut	Haigler and Weimer 1991

species	**trophic**	**trophic source**	**order**	**family**	**subfamily**	**strategy**	**strategy source(s)**
Ochotona dauurica	herbivore	Price et al. 2012	Lagomorpha	Ochotonidae		hindgut	Haigler and Weimer 1991
Ochotona princeps	herbivore	Price et al. 2012	Lagomorpha	Ochotonidae		hindgut	Haigler and Weimer 1991
Equus grevyi	herbivore	Price et al. 2012	Perissodactyla	Equidae		hindgut	Haigler and Weimer 1991; McNab 2002; Ley et al. 2008; Fritz et al. 2009
Equus hemionus	herbivore	IUCN 2014	Perissodactyla	Equidae		hindgut	Fritz et al. 2009
Equus zebra	herbivore	IUCN 2014	Perissodactyla	Equidae		hindgut	Haigler and Weimer 1991; McNab 2002; Ley et al. 2008; Fritz et al. 2009
Equus kiang	herbivore	IUCN 2014	Perissodactyla	Equidae		hindgut	Fritz et al. 2009
Equus burchellii	herbivore	Price et al. 2012	Perissodactyla	Equidae		hindgut	Fritz et al. 2009
Equus quagga	herbivore	IUCN 2014	Perissodactyla	Equidae		hindgut	Fritz et al. 2009
Ceratotherium simum	herbivore	Price et al. 2012	Perissodactyla	Rhinocerotidae		hindgut	Haigler and Weimer 1991; McNab 2002; Ley et al. 2008; Fritz et al. 2009
Diceros bicornis	herbivore	Price et al. 2012	Perissodactyla	Rhinocerotidae		hindgut	Haigler and Weimer 1991; McNab 2002; Ley et al. 2008; Fritz et al. 2009
Rhinoceros unicornis	herbivore	Price et al. 2012	Perissodactyla	Rhinocerotidae		hindgut	Fritz et al. 2009
Tapirus bairdii	herbivore	Price et al. 2012	Perissodactyla	Tapiridae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Tapirus indicus	herbivore	Price et al. 2012	Perissodactyla	Tapiridae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Tapirus pinchaque	herbivore	Price et al. 2012	Perissodactyla	Tapiridae		hindgut	Haigler and Weimer 1991; McNab 2002; Fritz et al. 2009
Tapirus terrestris	herbivore	Price et al. 2012	Perissodactyla	Tapiridae		hindgut	Fritz et al. 2009
Bradypus torquatus	herbivore	Price et al. 2012	Pilosa	Bradypodidae		foregut	Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Choloepus hoffmanni	herbivore	Price et al. 2012	Pilosa	Megalonychidae		foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Colobus guereza	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Colobus polykomos	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Colobus satanas	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Godoy-Vitorino et al. 2012
Nasalis larvatus	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Presbytis comata	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Presbytis melalophos	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Presbytis rubicunda	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Procolobus verus	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Pygathrix nemaeus	herbivore	IUCN 2014	Primates	Cercopithecidae	Colobinae	foregut	Fritz et al. 2009
Pygathrix nigripes	herbivore	IUCN 2014	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Semnopithecus entellus	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009

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Trachypithecus cristatus	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Fritz et al. 2009
Trachypithecus johnii	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Trachypithecus obscurus	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002; Fritz et al. 2009
Trachypithecus vetulus	herbivore	Price et al. 2012	Primates	Cercopithecidae	Colobinae	foregut	Mackie et al. 1997; Hume 2002; McNab 2002
Alouatta caraya	herbivore	Price et al. 2012	Primates	Atelidae	Alouattinae	hindgut	Committee on Animal Nutrition; National Research Council Staff; Ad Hoc Committee on Nonhuman Primate Nutrition; Board on Agriculture and Natural Resources Staff; Division on Earth and Life Studies Staff 2003
Alouatta guariba	herbivore	Price et al. 2012	Primates	Atelidae	Alouattinae	hindgut	Committee on Animal Nutrition; National Research Council Staff; Ad Hoc Committee on Nonhuman Primate Nutrition; Board on Agriculture and Natural Resources Staff; Division on Earth and Life Studies Staff 2003
Alouatta palliata	herbivore	Price et al. 2012	Primates	Atelidae	Alouattinae	hindgut	Committee on Animal Nutrition; National Research Council Staff; Ad Hoc Committee on Nonhuman Primate Nutrition; Board on Agriculture and Natural Resources Staff; Division on Earth and Life Studies Staff 2003; Fritz et al. 2009
Alouatta pigra	herbivore	Price et al. 2012	Primates	Atelidae	Alouattinae	hindgut	Committee on Animal Nutrition; National Research Council Staff; Ad Hoc Committee on Nonhuman Primate Nutrition; Board on Agriculture and Natural Resources Staff; Division on Earth and Life Studies Staff 2003
Ateles belzebuth	herbivore	Price et al. 2012	Primates	Atelidae	Atelinae	hindgut	Chivers and Langer 1994
Ateles chamek	herbivore	Price et al. 2012	Primates	Atelidae	Atelinae	hindgut	Chivers and Langer 1994
Ateles geoffroyi	herbivore	Price et al. 2012	Primates	Atelidae	Atelinae	hindgut	Chivers and Langer 1994
Pithecia pithecia	herbivore	Price et al. 2012	Primates	Cebidae	Pitheciinae	hindgut	Fritz et al. 2009
Papio hamadryas	herbivore	Price et al. 2012	Primates	Cercopithecidae	Cercopithecinae	hindgut	Lambert and Fellner 2010
Gorilla beringei	herbivore	IUCN 2014	Primates	Hominidae		hindgut	Ley et al. 2008
Gorilla gorilla	herbivore	Price et al. 2012	Primates	Hominidae		hindgut	Ley et al. 2008; Fritz et al. 2009
Pan paniscus	herbivore	Price et al. 2012	Primates	Hominidae		hindgut	Ley et al. 2008; Fritz et al. 2009
Hylobates moloch	herbivore	Price et al. 2012	Primates	Hylobatidae		hindgut	Fritz et al. 2009
Hapalemur griseus	herbivore	Price et al. 2012	Primates	Lemuridae		hindgut	Fritz et al. 2009
Varecia variegata	herbivore	Price et al. 2012	Primates	Lemuridae		hindgut	Fritz et al. 2009
Eulemur macaco	herbivore	Price et al. 2012	Primates	Lemuridae		hindgut	Ley et al. 2008
Lemur catta	herbivore	Price et al. 2012	Primates	Lemuridae		hindgut	Fritz et al. 2009
Elephas maximus	herbivore	Price et al. 2012	Proboscidea	Elephantidae		hindgut	McNab 2002; Ley et al. 2008; Fritz et al. 2009
Loxodonta africana	herbivore	Price et al. 2012	Proboscidea	Elephantidae		hindgut	McNab 2002; Ley et al. 2008; Fritz et al. 2009
Heterocephalus glaber	herbivore	Price et al. 2012	Rodentia	Bathyergidae	Heterocephalinae	hindgut	Ley et al. 2008; Fritz et al. 2009

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Capromys pilorides	herbivore	IUCN 2014	Rodentia	Capromyidae	Capromyinae	hindgut	Fritz et al. 2009
Castor canadensis	herbivore	Price et al. 2012	Rodentia	Castoridae		hindgut	Haigler and Weimer 1991; Fritz et al. 2009
Cavia aperea	herbivore	Price et al. 2012	Rodentia	Caviidae	Caviinae	hindgut	Mackie et al. 1999; Fritz et al. 2009
Microcavia australis	herbivore	Price et al. 2012	Rodentia	Caviidae	Caviinae	hindgut	Mackie et al. 1999
Dolichotis patagonum	herbivore	Price et al. 2012	Rodentia	Caviidae	Dolichotinae	hindgut	Mackie et al. 1999; Fritz et al. 2009
Kerodon rupestris	herbivore	IUCN 2014	Rodentia	Caviidae	Hydrochoerinae	hindgut	Mackie et al. 1999; Fritz et al. 2009
Hydrochoerus hydrochaeris	herbivore	Price et al. 2012	Rodentia	Caviidae		hindgut	Mackie et al. 1999; Fritz et al. 2009
Lagostomus maximus	herbivore	Price et al. 2012	Rodentia	Chinchillidae		hindgut	Fritz et al. 2009
Chinchilla chinchilla	herbivore	IUCN 2014	Rodentia	Chinchillidae		hindgut	Fritz et al. 2009
Cricetomys emini	herbivore	Price et al. 2012	Rodentia	Cricetidae	Cricetomyinae	hindgut	Fritz et al. 2009
Graphiurus murinus	herbivore	Price et al. 2012	Rodentia	Cricetidae	Graphiurinae	hindgut	Fritz et al. 2009
Hypogeomys antimena	herbivore	IUCN 2014	Rodentia	Cricetidae	Nesomyinae	hindgut	Fritz et al. 2009
Dasyprocta azarae	herbivore	IUCN 2014	Rodentia	Dasyproctidae		hindgut	Fritz et al. 2009
Dasyprocta leporina	herbivore	Price et al. 2012	Rodentia	Dasyproctidae		hindgut	Fritz et al. 2009
Hystrix africaeaustralis	herbivore	Price et al. 2012	Rodentia	Hystricidae		hindgut	Haigler and Weimer 1991; Fritz et al. 2009
Atherurus africanus	herbivore	Price et al. 2012	Rodentia	Hystricidae		hindgut	Haigler and Weimer 1991; Fritz et al. 2009
Hystrix brachyura	herbivore	Price et al. 2012	Rodentia	Hystricidae		hindgut	Haigler and Weimer 1991
Trichys fasciculata	herbivore	Price et al. 2012	Rodentia	Hystricidae		hindgut	Haigler and Weimer 1991
Mastomys natalensis	herbivore	Price et al. 2012	Rodentia	Muridae	Murinae	hindgut	Fritz et al. 2009
Myocastor coypus	herbivore	Price et al. 2012	Rodentia	Myocastoridae		hindgut	Fritz et al. 2009
Spalacopus cyanus	herbivore	Price et al. 2012	Rodentia	Octodontidae		hindgut	Fritz et al. 2009
Octodon degus	herbivore	Price et al. 2012	Rodentia	Octodontidae		hindgut	Fritz et al. 2009
Pedetes capensis	herbivore	Price et al. 2012	Rodentia	Pedetidae		hindgut	Fritz et al. 2009
Petromus typicus	herbivore	Price et al. 2012	Rodentia	Petromuridae		hindgut	Fritz et al. 2009
Sciurus variegatoides	herbivore	Price et al. 2012	Rodentia	Sciuridae	Sciurinae	hindgut	Fritz et al. 2009
Cynomys ludovicianus	herbivore	Price et al. 2012	Rodentia	Sciuridae	Xerinae	hindgut	Fritz et al. 2009
Marmota marmota	herbivore	IUCN 2014	Rodentia	Sciuridae	Xerinae	hindgut	Fritz et al. 2009
Marmota bobak	herbivore	IUCN 2014	Rodentia	Sciuridae	Xerinae	hindgut	Fritz et al. 2009
Trichechus manatus	herbivore	Price et al. 2012	Sirenia	Trichechidae		hindgut	Fritz et al. 2009

Table S3.2. List of dietary items in primate species' diets, reclassified using the PanTHERIA scheme.

species	items	fruit	flowers/nectar/pollen	leaves/branches/bark	seeds	grass	roots/tubers	diet breadth
Alouatta belzebul	bark, flower, fruit, leaf, petiole, pseudobulb, pseudofruit, twig, wood	1	1	1				3
Alouatta caraya	bark, bract, flower, fruit, leaf, petiole, pine cone, stem	1	1	1				3
Alouatta guariba	flower, fruit, leaf, pine cone, seed	1	1	1	1			4
Alouatta palliata	flower, fruit, leaf, leaf bud, petiole, shoot	1	1	1				3
Alouatta pigra	flower, fruit, leaf, stem	1	1	1				3
Aotus azarae	flower, fruit, leaf	1	1	1				3
Aotus nancymaae	flower, fruit, leaf	1	1	1				3
Ateles belzebuth	aril, flower, fruit, inflorescence, infructescence, leaf, mesocarp, petiole, seed	1	1	1	1			4
Ateles chamek	flower, fruit, leaf, vegetative material	1	1	1				3
Ateles geoffroyi	bark, bud, decayed wood, flower, fruit, leaf, leaf bud, palm heart, pith, sap, stem	1	1	1				3
Ateles hybridus								
Avahi laniger	leaf			1				1
Avahi meridionalis								
Brachyteles arachnoides								
Cacajao calvus	flower/nectar, pulp, seed	1	1		1			3
Cacajao melanocephalus	seed				1			1
Callicebus personatus	flower, fruit, leaf, seed, shoot	1	1	1	1			4
Cebus apella	flower, fruit, leaf, stem	1	1	1				3
Cebus capucinus	fruit, leaf	1		1				2
Cercocebus galeritus	fruit, seed	1			1			2
Cercopithecus ascanius	fruit, leaf	1		1				2
Cercopithecus mitis	fruit, leaf	1		1				2
Cheirogaleus major	leaf			1				1
Chiropotes albinasus	seed				1			1
Chiropotes chiropotes	flower, fruit, leaf, seed	1	1	1	1			4
Chiropotes satanas	aril, flower, fruit, petiole, seed, seedlet, twig	1	1	1	1			4
Chlorocebus djamdjamensis	flower, fruit, leaf, root, shoot, stem	1	1	1			1	4
Colobus angolensis	arillated seed, flower, fruit pulp, leaf, seed	1	1	1	1			4
Colobus guereza	bark, flower, fruit, leaf, seed	1	1	1	1			4
Colobus polykomos	fruit, leaf, liana leaf, seed, seed/fruit	1	1	1	1			4
Colobus satanas	leaf, seed			1	1			2
Colobus vellerosus								
Eulemur collaris	flower, fruit, leaf	1	1	1				3

species	items	fruit	flowers/nectar/pollen	leaves/branches/bark	seeds	grass	roots/tubers	diet breadth
Eulemur fulvus	bamboo pitch, bamboo stem, leaf, leaf base, shoot			1				1
Eulemur macaco	bark, flower, fruit, gum, leaf, stem	1	1	1				3
Eulemur rubriventer	flower, fruit	1	1					2
Hapalemur aureus	branch, branch shoot, fruit, leaf, leaf base, petiole, shoot, stem, stem pith, young stem	1		1				2
Hapalemur griseus	leaf			1				1
Indri indri	leaf			1				1
Lagothrix lagotricha	fruit	1						1
Lemur catta	floral bud, flower, fruit, leaf, leaf bud, mature stem, seed, shoot, stalk, stem, wood	1	1	1	1			4
Lepilemur mustelinus	leaf			1				1
Macaca fuscata	bark, bud		1	1				2
Macaca radiata								
Macaca silenus								
Mandrillus leucophaeus	fruit pulp, fruit with seed, seed	1			1			2
Microcebus rufus	fruit	1						1
Nasalis larvatus	flower, fruit, leaf, seed, shoot, spore	1	1	1	1			4
Papio anubis	fruit, pith, root	1		1			1	3
Papio cynocephalus	corm, flower, fruit, legume, pod, seed, shoot	1	1		1		1	4
Papio hamadryas	blade, flower, fruit, fruit epicarp and mesocarp, fruit pod, gum, latex, leaf, leaf blade, root, root bulb, root sheath, seed, seed head, stem	1	1	1	1		1	5
Papio ursinus	fruit, inflorescence, leaf, leaf or shoot, seed, stem, underground storage organ	1	1	1	1		1	5
Piliocolobus badius	arillated seed, flower, fruit, fruit pulp, leaf, seed, seed/fruit	1	1	1	1			4
Piliocolobus preussi	flower, fruit, leaf	1	1	1				3
Piliocolobus rufomitratus	bark, flower, fruit, leaf, leaf bud, petiole	1	1	1				3
Pithecia irrorata	aril, flower, fruit, leaf, pulp, seed	1	1	1	1			4
Presbytis melalophos								
Presbytis potenziani	bark, flower, fruit, leaf, tuber	1	1	1			1	4
Presbytis rubicunda	bud, flower, flower bud, flower bud/flower, fruit, leaf, pith, pulp, seed, skin	1	1	1	1			4
Procolobus verus	flower, fruit, fruit/seed, leaf	1	1	1	1			4
Prolemur simus	branch, branch shoot, culm pith, flower, fruit, leaf, leaf base, petiole, pith, shoot, stem, stem pith	1	1	1				3
Propithecus diadema	flower, flower bud, fruit, leaf, seed	1	1	1	1			4
Propithecus edwardsi	fruit	1						1

species	items	fruit	flowers/nectar/pollen	leaves/branches/bark	seeds	grass	roots/tubers	diet breadth
Propithecus perrieri	bud, flower, fruit, leaf, petiole, seed	1	1	1	1			4
Propithecus tattersalli								
Propithecus verreauxi	floral bud, flower, fruit, leaf, leaf bud, petiole, seed, shoot, stalk, stem, wood	1	1	1	1			4
Pygathrix cinerea	flower, fruit, leaf, seed	1	1	1	1			4
Rhinopithecus bieti	all, bark, bud, catkin, flower, flower bud, fruit, fungus, leaf, lichen, petiole, pith, seed, shoot, tuber	1	1	1	1		1	5
Rhinopithecus brelichi								
Rhinopithecus roxellana	bark, bud, carpospore, flower, fruit, inflorescence, leaf, petiole, seed, twig	1	1	1	1			4
Semnopithecus entellus	bark, cone, dry seed, flower, flower bud, fruit, internode, latex, leaf, leaf bud, leaf gall, needle, node, petiole, ripe, root, seed, shoot	1	1	1	1		1	5
Simias concolor	bark, flower, fruit, leaf, tuber	1	1	1			1	4
Trachypithecus cristatus	bud, flower, flower and bud, fruit, leaf	1	1	1				3
Trachypithecus delacouri	flower, fruit, leaf, leaf bud, seed, stem	1	1	1	1			4
Trachypithecus francoisi	bark, bud, flower, fruit, leaf, petiole, root, seed, stem	1	1	1	1		1	5
Trachypithecus hatinhensis								
Trachypithecus johnii	flower, fruit, leaf, stem	1	1	1				3
Trachypithecus vetulus	flower, fruit, leaf, leaf stem, seed	1	1	1	1			4
Varecia variegata	flower, fruit, fruit skin, leaf, seed	1	1	1	1			4

Table S3.3. Description of variables used to compute the maximum environmental disparity metric.

"BIO" variables are from the WorldClim database (Hijmans et al. 2005). All raster data sets were converted to the same resolution (5 arc-minutes) prior to analysis.

variable	description	original resolution	source
BIO1	annual mean temperature	5 arc-minutes	Hijmans et al. 2005
BIO2	mean diurnal range	5 arc-minutes	Hijmans et al. 2005
BIO3	isothermality	5 arc-minutes	Hijmans et al. 2005
BIO4	temperature seasonality	5 arc-minutes	Hijmans et al. 2005
BIO5	maximum temperature of warmest month	5 arc-minutes	Hijmans et al. 2005
BIO6	minimum temperature of coldest month	5 arc-minutes	Hijmans et al. 2005
BIO7	temperature annual range	5 arc-minutes	Hijmans et al. 2005
BIO8	mean temperature of wettest quarter	5 arc-minutes	Hijmans et al. 2005
BIO9	mean temperature of driest quarter	5 arc-minutes	Hijmans et al. 2005
BIO10	mean temperature of warmest quarter	5 arc-minutes	Hijmans et al. 2005
BIO11	mean temperature of coldest quarter	5 arc-minutes	Hijmans et al. 2005
BIO12	annual precipitation	5 arc-minutes	Hijmans et al. 2005
BIO13	precipitation of wettest month	5 arc-minutes	Hijmans et al. 2005
BIO14	precipitation of driest month	5 arc-minutes	Hijmans et al. 2005
BIO15	precipitation seasonality	5 arc-minutes	Hijmans et al. 2005
BIO16	precipitation of wettest quarter	5 arc-minutes	Hijmans et al. 2005
BIO17	precipitation of driest quarter	5 arc-minutes	Hijmans et al. 2005
BIO18	precipitation of warmest quarter	5 arc-minutes	Hijmans et al. 2005
BIO19	precipitation of coldest quarter	5 arc-minutes	Hijmans et al. 2005
MOD17A3NPP	annual median net primary production (2000-2012)	30 arc-seconds	Zhao et al. 2005

FIGURES

Figure 3.1. Cladogram of 46 lineages of terrestrial, herbivorous mammals selected for comparative analyses.

Numbers to left of clade names are total known species richness of clades (Wilson and Reeder 2005; IUCN 2013). Foregut-fermenting lineages are indicated with an asterisk.

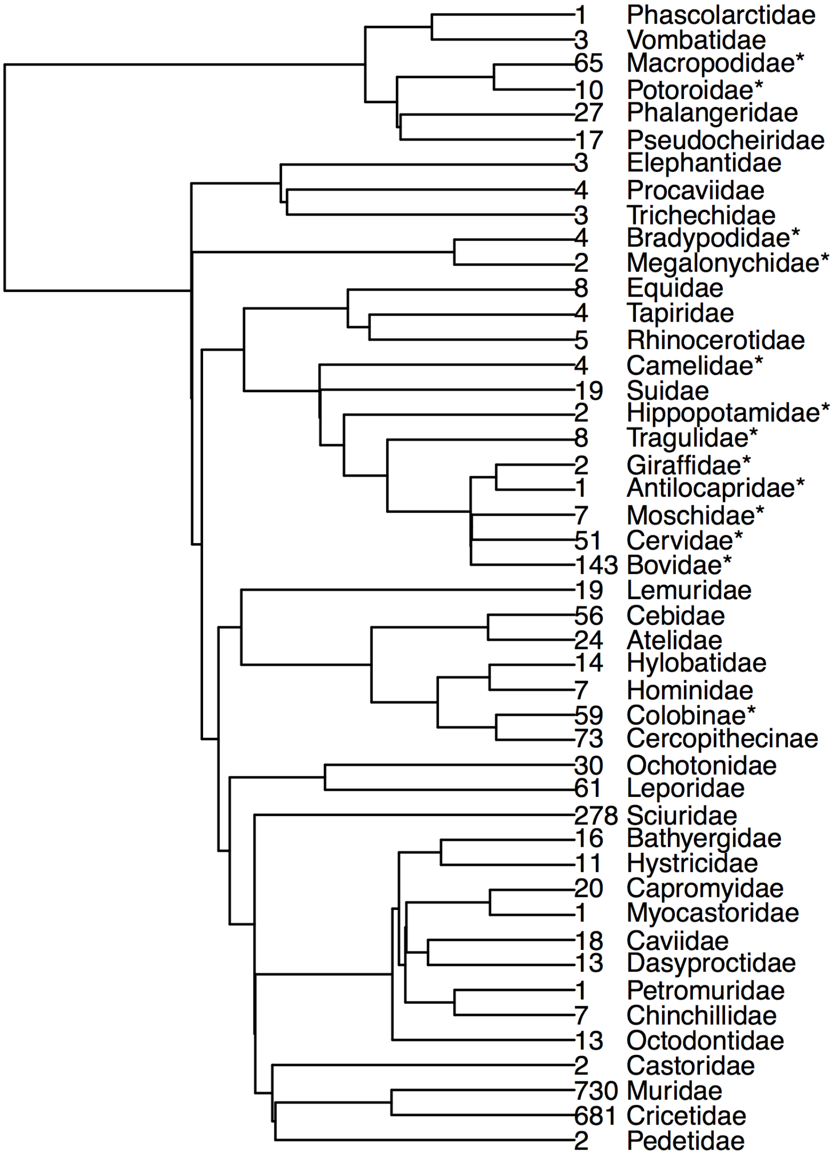


Figure 3.2. Relationship between niche specialization and speciation.

The effect of niche specialization on speciation rate was modeled using phylogenetic generalized least-squares regression at the clade level (*N* = 46). Niche specialization was measured by maximum environmental disparity. Here, lineages with low values of disparity are considered ecological specialists while those with high values are generalists. Speciation rates estimated from the BAMM model were $\log_{10}$-transformed prior to analysis. The dashed and solid lines indicate the relationship including and excluding digestive strategy as a factor, respectively. Foregut-fermenting clades are coded in white while hindgut clades are in black. The clade-level relationship with digestive strategy as a factor with an interaction term is significant ($p = 0.00706$) (Table 2).

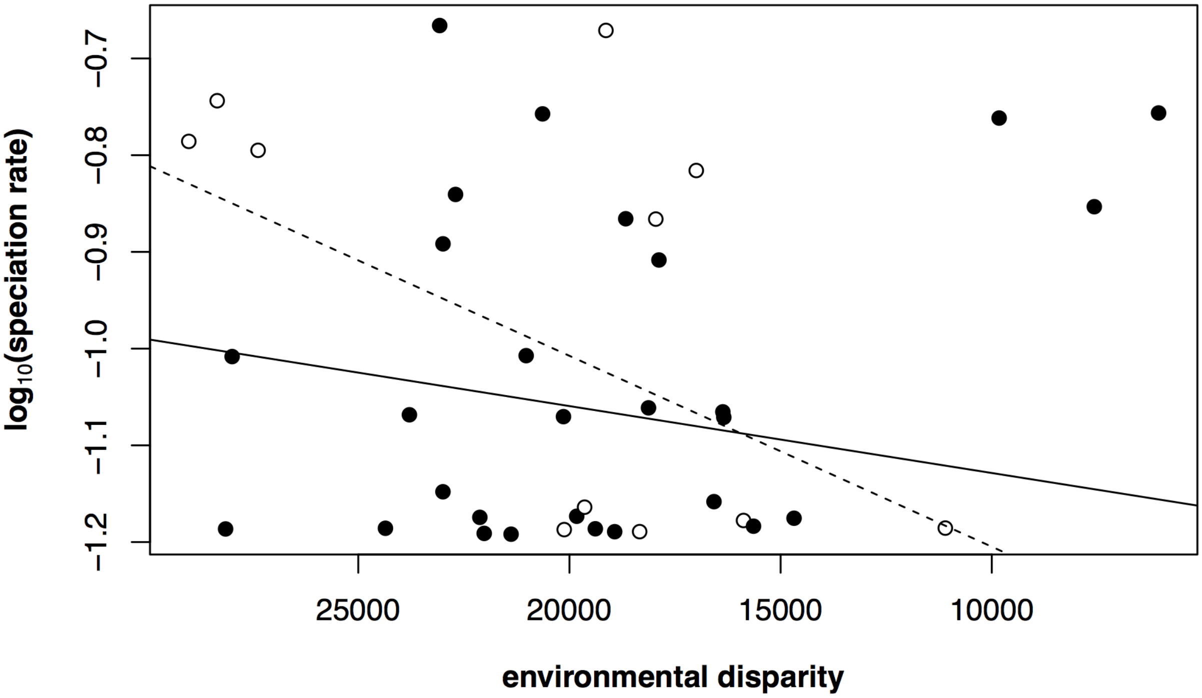


Figure 3.3. Differences in niche specialization between foregut and hindgut-fermenting clades.

Per-lineage niche specialization of the two groups was compared using phylogenetic analysis of variance. Again, niche specialization was measured with the disparity variable. Per-lineage disparities are not significantly different between foregut and hindgut-fermenting lineages (*p* = 0.749).

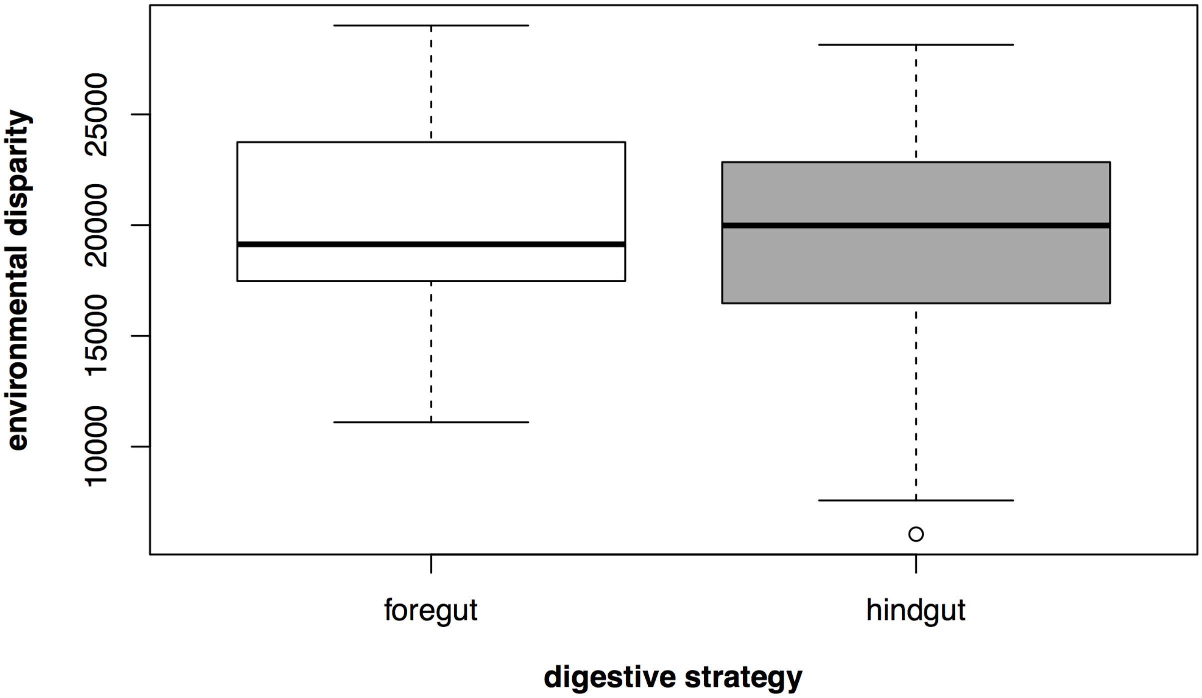


Figure 3.4. Differences in speciation between foregut and hindgut-fermenting clades. Speciation rates were compared between the two groups using phylogenetic analysis of variance. Shown are box-plots of $\log_{10}$-transformed speciation rates. Lower and upper whiskers represent the minimum and maximum data, respectively, within $\log_{10}(1.5)$ of the interquartile range of the data. Per-lineage speciation rates are not significantly different between foregut and hindgut-fermenting lineages ($p = 0.447$).

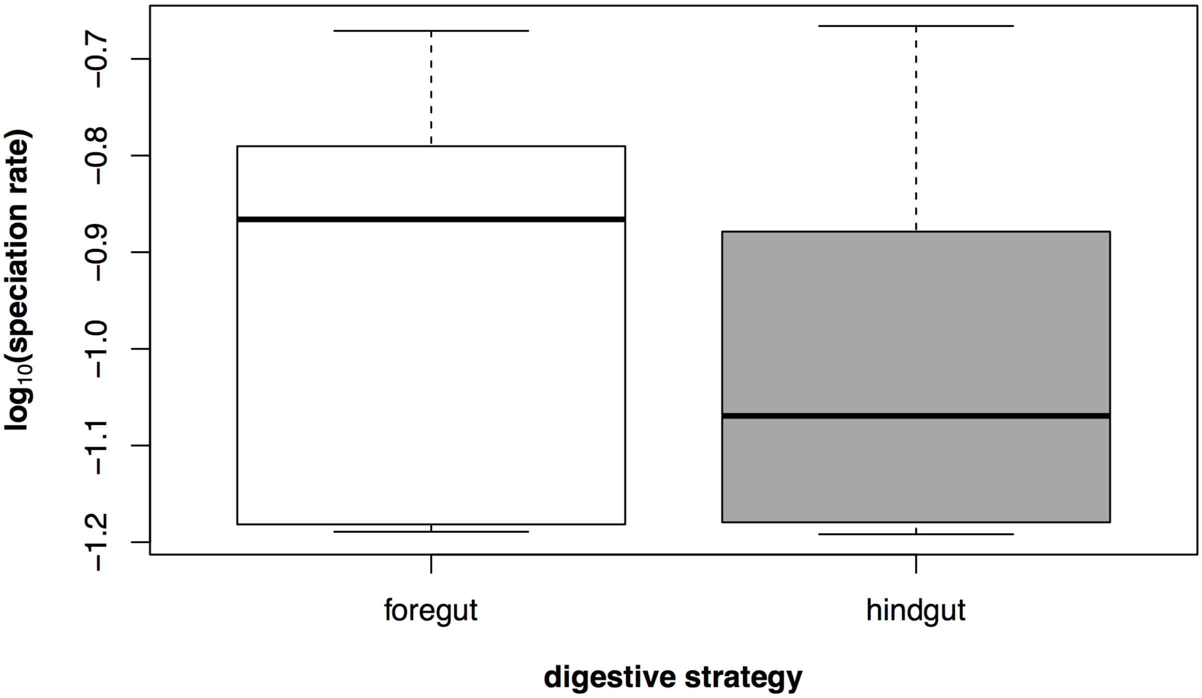
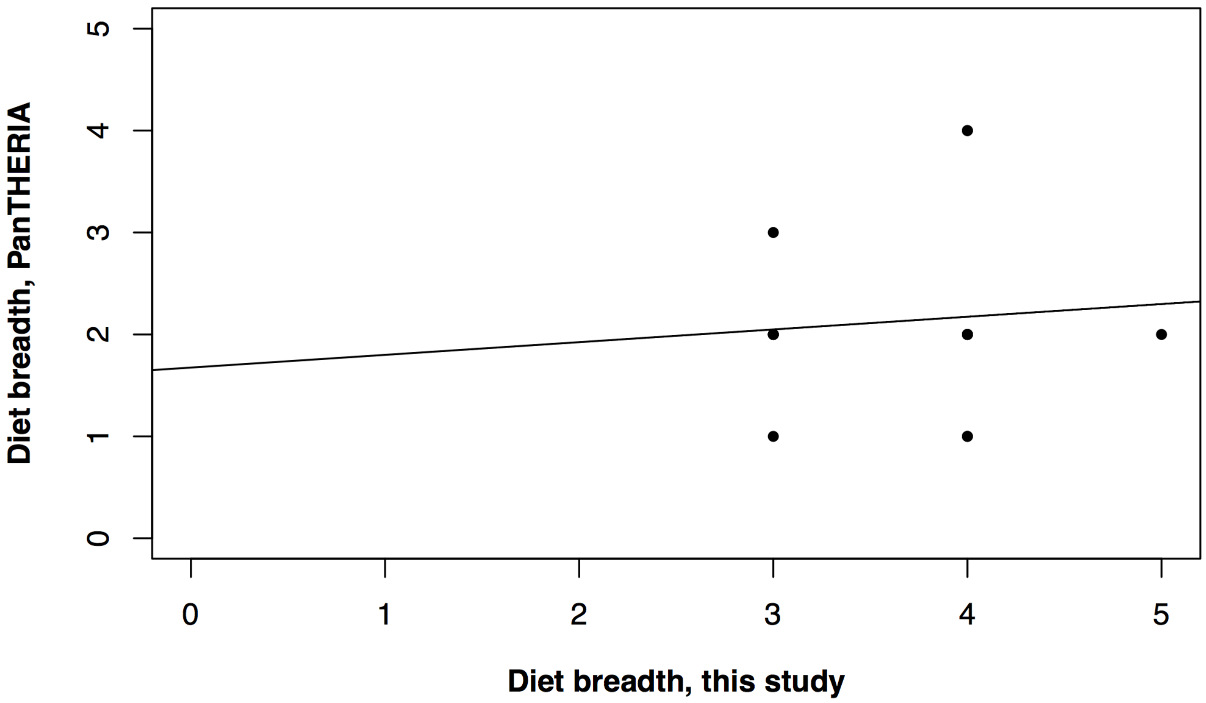


Figure S3.1. Scatterplot of diet breadth reclassified in this study and data from PanTHERIA for primates.



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CHAPTER IV

BOUNDS OF HISTORICAL CLIMATIC INSTABILITY DIFFER AMONG HERBIVOROUS MAMMALS

ABSTRACT

Climatic stability and instability are thought to have opposing effects on speciation and extinction over time. Long-term climatic oscillations select for species with traits that reduce the likelihood of speciation, potentially resulting in low species diversity in regions with historically high levels of climatic instability. Conversely, climatically stable regions suppress extinction by buffering against the loss of populations while promoting speciation through the divergence of populations isolated within refugia. A consequence of this is high species diversity in historically stable regions. However, how species respond to climatic stability (or instability) partly depends on their traits. Here, this study explores the relationship between historical climatic instability and extant species richness of two major groups of herbivorous mammals differing in digestive strategy to explore how an important biological trait influences the effects of long-term climatic change. Though hindgut and foregut-fermenting genera experienced similar levels of climatic instability and do not significantly differ in species diversity, instability was found to have a stronger effect on the richness of foregut-fermenting mammals. Hindgut-fermenting mammals appear to be bounded within a common instability space regardless of their geographic location, suggesting that they can tolerate only a limited range of climatic fluctuations. Furthermore, the effect on richness varied with the particular component of instability, revealing that climate

variables have non-equivalent effects. Lastly, differences between hindgut and foregut-fermenting herbivores in the instability-richness relationship suggest that foregut diversity has not yet reached an equilibrium state.

INTRODUCTION

The historic climate stability hypothesis proposes that climatic stability favors persistence of populations and speciation over time, whereas instability promotes extinction while concomitantly preventing speciation (Dynesius and Jansson 2000, Jansson and Dynesius 2002, Araujo et al. 2008, Abellan and Svenning 2014). One mechanism by which climatic instability depresses speciation is through orbitally forced range dynamics (ORDs) (Jansson 2003). ORDs are major changes in the geographical distributions of species resulting from long-term, cyclical climatic fluctuations (Dynesius and Jansson 2000, Jansson 2003). ORDs select for species that are highly vagile and ecologically generalized (Dynesius and Jansson 2000, Davies et al. 2009, Morueta-Holme et al. 2013), traits that reduce the likelihood of speciation (Birand et al. 2012, Claramunt et al. 2012). As a consequence, biodiversity, measured by alpha diversity or endemism, is expected to be low in regions that experienced historically high levels of climatic instability. Indeed, endemism is reduced in areas of high climatic instability (Fjeldsa et al. 1999, Jansson 2003, Sandel et al. 2011).

In contrast, climatically stable regions serve as refuges for biodiversity during periods of instability (Graham et al. 2010). Refugia prevent extinction by buffering against the loss of populations. Given sufficient time, populations isolated from conspecific population within refugia may diverge to form new species (Ribera and Vogler 2004). An expected outcome of these processes is higher species diversity in climatically stable regions. In fact, there is compelling evidence that alpha diversity and endemism are elevated within stable regions (Fjeldsa et al. 1999, Jansson 2003, Graham et al. 2006, Araujo et al. 2008, Carnaval et al. 2009, Graham et al. 2010, Sandel et al. 2011, Abellan and Svenning 2014, Carnaval et al. 2014). Areas of high endemism also are generally characterized by historically low rates of extinction (Ohlemuller et al. 2008), which is consistent with the buffering effects of refugia. Further evidence for this is the location of the principal biodiversity hotspots within regions of high climatic stability (Fjeldsa and Lovett 1997).

However, the ecology of species influence how they respond to climatic stability (or instability). While vagile species are able to track suitable habitats during periods of climatic variability (Martinez-Meyer et al. 2004, Davis et al. 2005, Tingley et al. 2009, Sandel et al. 2011, Bellard et al. 2012), dispersal-limited species must evolve to persist outside of refugia (Graham et al. 2006, Sandel et al. 2011). Species richness strongly correlates positively with stability in dispersal-limited but not dispersal-capable taxa (Graham et al. 2006, Sandel et al. 2011). That more small-ranged, dispersal-limited species occur in stable regions (Sandel et al. 2011) further indicates that this may be the case. Other traits also may play roles in mediating how species respond to climatic stability, thus affecting the relationship between climate and species diversity.

Herbivorous mammals are a good system to address questions about the effects of climatic instability on species diversity because the types and abundance of herbivores in a regional biota are determined by climate through its controls on primary productivity and habitat structure (Badgley et al. 2008). Herbivorous mammals have two different strategies for processing foods such as leaves that present challenges for maximal nutrient extraction, namely foregut and hindgut-fermentation (FF and HF, respectively). FF has evolved many times during mammal and once in bird evolution, possibly to enable the utilization of patchy high-quality diets (Grajal et al. 1989). In FF animals, cellulolytic bacteria ferment fiber in large, sacculated stomachs and are later digested in the intestine so that microbial proteins are reclaimed (Davies and Oates 1994). HF animals are not as efficient at fermenting cellulose (Alexander 1993, McNab 2002) but have the advantages of being able to ingest foods while fiber is being fermented in the cecum or colon and to directly absorb the easily-digestible parts of cell contents (Janson and Chapman 1999). The two digestive strategies involve trade-offs in the minimum quality of diets, efficiency of digestion, and other aspects (Gilchrist and Mackie 1984) that potentially have far-reaching implications for regional patterns of herbivorous species diversity.

To explore the potential effects of an important biological trait on climatic regulation of species diversity, here the relationship between historical climatic instability and extant species richness of two major groups of herbivorous mammals differing in digestive strategy are examined. First, the effects of different components of climatic instability on the species richness of the two groups are evaluated. Second, the identified effects are compared between the two groups to assess their generality across the herbivorous mammals. Due to differences in habitat productivity and structure related to diet quality, impacts of historical climatic instability on diversity are expected to have differed between the hindgut and foregut-fermenting mammals.

METHODS

Modeling climatic stability from Last Glacial Maximum to present

Data on trophic level and digestive strategy were obtained from Price et al. (2012) and the IUCN Red List (IUCN 2013). Occurrences for each herbivorous species available in the Global Biodiversity Information Facility database (GBIF) (http://www.gbif.org/) were downloaded using functions from the R package RGBIF (Chamberlain et al. 2014). Each species' occurrences were validated by overlaying its distribution and retaining only those coordinates that fell within the delimited range. Distribution data in the form of spatial polygons were downloaded from the IUCN Red List (IUCN 2013) (http://www.iucnredlist.org/technical-documents/spatial-data). Only polygon records of extant or extinct ("Presence" codes 1 and 4-5), native ("Origin" code 1) species that are year-round residents of an area ("Seasonality" code 1) were used to validate the species occurrences. After these procedures, 471 species had five or more unique coordinates (mean ± sd = 76.3 ± 93.7) and were suitable for species distribution modeling (SDM) (Table S4.1). Here, MAXENT V. 3.3.3K (Phillips et al. 2004) was chosen to perform the SDM. MaxEnt outperforms other available algorithms at sample sizes between 5-25 (Hernandez et al. 2006).

Present-day (1950-2000) and historical (Last Glacial Maximum or LGM, ca. 21,000 BP) bioclimatic variables from the WorldClim database (Hijmans et al. 2005) provided environmental data for the SDM (Table 4.1). The LGM data were derived from general circulation model simulations from the Community Climate System Model (Collins 2004). The present-day and historical data sets each have a resolution of 5 arc-minutes (10 km). For each species, the environmental data were cropped with a 100 km (ca. 1°) buffer enclosing the species' total distribution, as defined by the IUCN polygon data (Anderson and Raza 2010, Brown et al. 2014).

The predictive performance of MaxEnt is influenced by the choice of feature types and regularization constants. Therefore, SDM models were calibrated with eight values of regularization multipliers (0.05, 0.25, 0.5, 0.75, 1, 2, 5, 10) (Radosavljevic and Anderson 2013) with “auto features” specified. This parameter determines that all feature types are used when there are at least 80 training samples; that linear, quadratic, and hinge features are used when there are 15-79 samples; that linear and quadratic features are used when there are 10-14 samples; and finally, that only linear features are used when there are fewer than 10 samples. For each species, localities were divided into 10 different subsets and the model was run 10 times using the present-day environmental data. In this 10-fold cross-validation, a different subset of occurrences is used as test cases in each run (Nogues-Bravo 2009). The present-day SDMs were projected back to the LGM data to predict the historical climatic niches of species. Transferring projections through time in this way assumes that species' niches are temporally stable (Nogues-Bravo 2009).

Output was generated in logistic format, with values between 0-1 such that high values indicate higher suitability for a given species. Model performance was assessed using the Area Under the Receiver Operating Characteristic Curve (AUC) value. The AUC discriminates between true positives and true negatives and defines the probability that a SDM will rank presence localities higher than absences (Vorsino et al. 2014). A minimum AUC value of 0.7 is desirable (Swets 1988, Elith et al. 2006). For each species, SDMs with the highest test AUC values greater than 0.7 were retained. Then the models were reclassified using threshold values to convert the distribution predictions to a binary suitable (1) and unsuitable (0) scheme. The "Maximum test sensitivity plus specificity logistic threshold" was used to reclassify the models (Edwards et al. 2012). Cells that fell within the glacial extent at the LGM were reclassified as unsuitable habitat. Climatic stability was estimated from the SDMs by summing the present-day and LGM thresholded models of each species. Raster cells with values of two were suitable during both time periods and are considered "stable" (Graham et al. 2006, Edwards et al. 2012). Raster calculations were performed using functions in the R package RASTER (Hijmans 2014).

Calculating climate anomaly from LGM

Climate anomaly reflects long-term instability in climate (Araujo et al. 2008). Per-species climate anomaly was calculated at each bioclimatic variable by subtracting LGM values from present-day values within the stable cells of the species and averaging the absolute values of the differences (Araujo et al. 2008, Leprieur et al. 2011, Sandel et al. 2011, Gouveia et al. 2013, Abellan and Svenning 2014, Weber et al. 2014). These per-species climate anomalies were averaged across species in each genus to obtain the per-genus climate anomaly. Then the anomaly variables were log-10 transformed to meet the assumptions of parametric statistical tests. Per-genus species richness was obtained from (Wilson and Reeder 2005). Global patterns of species richness within stable areas were visualized by summing the presences of HF or FF species within grid cells of 1° resolution. The thresholded suitability models served as presence data for each species.

Testing and accounting for phylogenetic effects

The phylogenetic structure of the per-genus climate anomalies and species richness were examined with two tests of phylogenetic signal. Both tests measure the extent to which trait correlations reflect species's shared evolutionary history. Pagel's λ statistic (Pagel 1999) is the value by which all internal branches of a phylogeny are transformed to explain the data. Values close to one indicate that the structure of the phylogeny and the Brownian motion model of evolution explain changes in traits well. Blomberg's K statistic (Blomberg et al. 2003) tests whether an observed distribution of traits deviates more ($K < 1$) or less ($K > 1$) from the divergence expected for traits evolving under Brownian motion. A maximum clade credibility phylogeny of mammals (Fritz et al. 2009, Kuhn et al. 2011, Tran 2014) and the *phylosig* function from the R package PHYTOOLS (Revell 2012) was used to perform the tests. Then models of trait evolution were fit to trait data that exhibited significant phylogenetic signal. The models tested were: Brownian motion, Ornstein-Uhlenbeck, early burst, trend, lambda, delta, kappa, drift, and white noise. The *fitContinuous* function from the R package GEIGER (Harmon et al. 2008) was used to fit the models.

Because the bioclimatic variables are highly correlated and exhibit phylogenetic signal, a phylogenetic principal components analysis (PCA) of the anomalies was used to produce linearly uncorrelated variables, or principal components (PCs). A scree plot was used to determine the number of PCs to retain for the regression analyses. The cut-off (±0.229) for determining the significance of loadings was determined by taking the square root of the inverse of the total number of variables ($N = 19$).

Comparison of climate anomaly between hindgut and foregut-fermenting mammals

Climate anomaly was compared between the two groups of fermenters using a phylogenetic multivariate analysis of variance (MANOVA). The observed F statistic was compared against a null distribution of the statistic from 1,000 simulations of the anomaly PCs on the phylogeny under a Brownian motion model. The MANOVA was performed in R using the function *aov.phylo*. Then phylogenetic standardized independent contrasts of the per-genus PC scores and species richness data were calculated to obtain statistically independent and identically distributed genus values for these variables.

Modeling relationships between climate anomaly and species richness

The relationship between per-genus species richness and climate anomaly first was explored using the ordinary least squares (OLS) method. The relationship was tested for HF ($N = 113$) and FF ($N = 58$) genera separately. The validity of the OLS model for these data was assessed using several diagnostics. Leverage, or the ability of observations to change the regression slope, was measured with hat values. A hat value measures the contribution of a given observation to its corresponding fitted value, such that observations with larger hat values have greater leverage. Observations that are unusual for species richness given the climate anomalies ("outliers") were determined using Studentized residuals. Observations are likely outliers if $|\text{residuals}| > 2$. Lastly, influence, which is the combined impact of leverage and outlier status, was measured by Cook's

D. Observations with D > 4 exert undue influence in the regression. Heteroscedasticity, or unequal variances of observations, was evaluated using the Breusch-Pagan, Goldfeld-Quandt, and Harrison-McCabe test statistics. OLS is not robust to outliers, which can have significant effects on the fit of the regression line. The fitting and diagnostics of the OLS model were performed in R.

Robust regression (RR) is an alternative to OLS when unusual cases cannot be removed. This method gives less weight to observations that would otherwise influence the regression line. Diagnostics of the OLS model revealed unusual cases in the model for both HF and FF groups. Therefore, robust regression using the M-estimation method with “bisquare” and “optimal” weights for HF and FF groups, respectively, was subsequently used to explore the relationship between per-genus species richness and climate anomaly. The weight functions that generated the highest r^2 values are presented here. The RR model was run using the *lmrob* function from the R package ROBUSTBASE (Rousseeuw et al. 2015). Because the sign of independent contrasts is arbitrarily-determined, the OLS and RR regressions were computed through the origin (Garland et al. 1992).

The generalized least squares (GLS) method is an alternative to OLS when the residuals have unequal variances or are correlated due to space, time, or phylogeny. GLS behaves like the OLS model when errors are uncorrelated and have equal variances. GLS suffers from the pitfall of being vulnerable to unusual cases like OLS. The tests of phylogenetic signal revealed that the per-genus climate anomaly and species richness have significant phylogenetic structure, which was best described by the lambda model of trait evolution. Therefore, the phylogenetic GLS (pGLS) was used to incorporate phylogenetic information in the linear model as the expected covariance between pairs of species (Grafen 1989). The pGLS model was run with the "corPagel" correlation structure specified, in which the off-diagonal elements of the correlation matrix are multiplied by λ. Functions from the R packages APE and NLME (Pinheiro et al. 2014) were used for these last regression models.

RESULTS

Per-genus species richness does not significantly differ between HF and FF herbivores ($F_{1,167}$ = 0.602, $p = 0.439$, phylogenetic $p = 0.883$). Of stable areas globally, parts of North America, Africa, and Australia jointly house the highest species richness of FF ($R_{75\ \mathrm{percentile}} = 0.301$) and HF ($R_{75\ \mathrm{percentile}} = 0.602$) mammals. The highest species richness of HF mammals is concentrated in the following regions: the western U.S.; Central America; northwestern and northeastern South America and southern Paraguay; southern Western, central Eastern, and Southern Africa; parts of New Guinea; and eastern New South Wales in Australia (Figure 4.1). The highest FF species richness is found in stable areas of: the western U.S.; southern Western, northern and central Eastern, and Southern Africa; and eastern New South Wales (Figure 4.1).

Per-genus multivariate climate anomaly exhibits mixed phylogenetic signal in tests of Pagel's λ ($p = 0.003$) and Blomberg's K ($p > 0.05$) statistics (Table 4.2). Both statistics are significantly non-zero in tests of per-genus species richness (Table 4.2). This indicates that phylogenetic structure strongly explains changes in the diversity of herbivorous genera. The anomaly and richness data best fit the lambda model of trait evolution based on the Akaike Information criterion corrected for sample size (Table 4.3).

The first four principal components (PCs) account for approximately 88% of the total explained variance in multivariate climate anomaly (Figure 4.2) and were retained for the regression analyses. PC1 is dominated by strong positive loadings for anomalies in overall total rainfall (BIO12-14, 16-19) and significant negative loadings for anomalies in temperature and rainfall seasonality (BIO4, 15) (Table 4.4, Figure 4.3). PC2 is dominated by strong negative loadings for anomalies in the mean and range of temperature (BIO1-3, 5-11) and significant positive loadings for anomalies in rainfall during the coldest and wettest periods of the year (BIO13, 16, 19) (Table 4.4, Figure 4.3). PC3 has significant positive loadings for anomalies in daily and annual temperature oscillations (BIO2-3, 7) and mean rainfall during the wettest periods of the year (BIO12-13, 15-16) but significant negative loadings for anomalies in rainfall during the driest periods (BIO14, 17) (Table 4.4, Figure 4.3). Lastly, PC4 has significant positive loadings for anomalies in temperature and rainfall seasonality (BIO4, 15) and negative loadings for anomalies in overall temperature (BIO1, 5-6, 8-11) (Table 4.4, Figure 4.3).

Climate anomaly is not significantly different between HF and FF genera ($F_{4,164} = 1.459$, $p = 0.217$, phylogenetic $p = 0.991$) (Figure 4.4). Species that experienced the extremes of climatic instability (i.e., instability limits), defined by their positions in PC space, from both HF and FF groups are listed in Table 4.5. The distributions of FF bovids that are outliers on climate anomaly are mapped in Figure 4.5.

Climate anomaly has no significant effect on the species richness of HF genera when modeled using OLS, RR, or pGLS (Table 4.6). Inspection of leverage, Studentized residuals, and Cook's D from the OLS regression detected likely outliers. However, the lower coefficient of determination of the robust regression model indicates that the data fit the OLS model slightly better ($r_{2,OLS} = 0.024$, $r_{2,RR} = 0.019$) (Table 4.6). Similarly, the OLS model fits the data better than a pGLS model with phylogenetic relationships described by a lambda correlation structure ($AIC_{OLS} = -197.365$, $AIC_{pGLS} = 198.583$) (Table 4.6).

Climate anomaly has a significant effect on the species richness of FF genera when modeled using OLS, RR, and pGLS (Table 4.6). The OLS model fits the data better than the pGLS model ($AIC_{OLS} = -63.489$, $AIC_{pGLS} = 75.823$) (Table 4.6). However, the RR model explains a higher proportion of the variation in species richness than the OLS model ($r_{2,OLS} = 0.262$, $r_{2,RR} = 0.596$) (Table 4.6). In the RR model, genus diversity increases with increasing values on the PC3 axis ($b = 0.453$, $p = <0.001$) but decreases with increasing PC4 values ($b = -0.405$, $p = 0.002$) (Table 4.6, Figure 4.6). This indicates that diversity is higher in genera that experienced greater anomalies in temperature range, overall temperature, and mean rainfall during the wettest periods of the year. Conversely, this result suggests that genera that experienced larger anomalies in rainfall during the driest periods of the year and in temperature and rainfall seasonality have lower diversity.

DISCUSSION

This analysis of climatic instability that species can tolerate, described by climatic anomaly between the LGM and present, and extant species richness of herbivorous mammals revealed marked differences in the effects of historical abiotic perturbations on the diversity of two major groups differing in digestive strategy. Globally, HF and FF genera experienced similar levels of climatic instability and do not significantly differ in richness on average. Yet, instability had a strong effect on the richness of FF genera but not that of HF genera. Furthermore, the effect on richness varied with the particular climatic variable contributing to instability. Greater long-term fluctuations in variables related to intra-annual variation in vegetation availability, specifically precipitation during periods of high water stress (BIO14, 17) and overall seasonality (BIO4, 15), reduce diversity. Conversely, greater fluctuations in temperature (BIO1-3, 5-11) and precipitation during periods of high availability (BIO12-13, 15-16) elevate diversity. Below I discuss what these findings suggest about the impacts of climatic instability on herbivorous mammals.

Effects of climatic instability on species richness are not equivalent across herbivores

The regression analyses consistently indicated that instability strongly controlled the diversity of only FF herbivores. This finding appears to be driven by differences in the extremes of historical climatic fluctuations within stable areas occupied by the two groups. Focusing on the climatic variables that had significant effects (which are captured by PC3-4), HF genera experienced a limited range of instability across multiple continents, whereas variability in instability was large across most continents for FF genera. The most pronounced variability in instability experienced by FF genera occurred in Africa, Iran, and the Indian subcontinent. Bovids (Artiodactyla) occupied the extremes of this variability, while fruit bats (Chiroptera) were restricted to stable environments.

These results show that HF mammals appear to be bounded within a common instability space irrespective of their geographic distributions. In addition, certain lineages experienced climatic fluctuations that dramatically differed from the norm for FF herbivores overall, skewing the instability space of FF mammals. These two patterns hold across all components of instability that explained greater than 88% of the variance in climate anomaly. Two questions arise from these results: (1) what is the significance of the limits on instability of HF genera, and (2) what differentiates the FF genera that are atypical in terms of instability from the rest?

Convergence in the instability profiles of HF genera across a wide latitudinal gradient suggests that there are hard limits on the intensity of climatic fluctuations that these lineages may tolerate. Such limits would exclude HF mammals from areas with instability falling outside the acceptable range. In addition, species richness does not vary with any discernible pattern within the range of instability experienced by HF genera. This accords well with predictions from the intermediate disturbance hypothesis (Connell 1978), in which species diversity is expected to be highest at intermediate levels of disturbance frequency and intensity. Competitive exclusion lowers diversity when disturbance is too little while poor colonizers are selectively removed or excluded from communities experiencing too much disturbance (Connell 1978). Furthermore, similarity of limits across multiple taxonomic groups as different as bats and pikas indicates that tolerance of climatic instability is likely controlled by traits related to HF.

An alternative explanation for the lack of structure, geographical or otherwise, in the instability and richness of HF genera is that dispersal ability is high in these lineages. When climate fluctuates, highly vagile species can track suitable niches in space and maintain distributional equilibrium with changing climatic conditions (Martinez-Meyer et al. 2004, Davis et al. 2005, Tingley et al. 2009, Sandel et al. 2011, Bellard et al. 2012, Quintero and Wiens 2013). If this was the case, then lineages with poor dispersers should be overrepresented among those at the extremes of HF instability. In addition, highly vagile lineages should cluster together within the bounds of instability. Range sizes of only 4 out of 12 species occupying the instability boundaries for HF are less than the average range size of herbivorous mammals, suggesting that this explanation may play a secondary, if not negligible, role.

In contrast, the limits of instability experienced by FF genera appear to reflect the latitudinal gradient in climatic oscillations. *Aepyceros melampus* and *Neotragus pygmaeus* occupy forested or savannah habitats in Sub-Saharan Africa, while the other bovids occupying the limits of instability occur above the equator in the African Transition Zone, Iran, Pakistan, and India. Therefore, PC3 appears to capture the North-South axis and PC4 the East-West axis for these species, with larger values describing northern and eastern latitudes, respectively. The obliquity of the Earth's axis and the eccentricity of its orbit control Milankovitch oscillations, producing peaks in climatic variability with periods of 21, 41, and 100 thousand years (Jansson 2003). The degree of distributional changes caused by these oscillations, or orbitally-forced range dynamics

(ORDs) (Dynesius and Jansson 2000, Jansson 2003), increases along a latitudinal gradient (Guralnick 2006). This gradient results in smaller ORDs in the tropics and larger ORDs toward the poles (Dynesius and Jansson 2000). The bovids considered here conform to this pattern along the PC3 axis. Because ORDs elevate extinction risk (Dynesius and Jansson 2000), species richness is expected to decrease with increasing magnitude of ORDs at higher latitudes. It is not clear from the results here whether species richness exhibits the expected unimodal distribution along a latitudinal gradient for either FF or HF genera, and this remains to be tested.

Of note is the generally broad extent of instability experienced by FF genera across their geographic distributions, over which many are co-distributed with HF mammals. The strong geographic structure of FF instability space reflects overall spatial differences in climatic fluctuations. Perhaps more interestingly, this suggests that FF mammals are sufficiently adaptable to tolerate a wide range of climatic fluctuations. Biotic responses to climate change involve the ability of species to withstand environmental perturbations (resistance) or to recover from perturbations after they occur (Isaac et al. 2009). Different sets of traits promote one or the other response. For example, species with high physiological or behavioral plasticity, high local abundances, low habitat specialization, and broad distributional ranges are able to withstand climatic fluctuations well (Isaac et al. 2009, Bellard et al. 2012). In addition, static or predictable environments select for species that evolve life strategies which are closely matched with their environments and are not very resilient to changes (Fjeldsa and Lovett 1997). In contrast, heterogenous environments favor species with strategies, such as high dispersal, that evolved to respond to spatiotemporal shifts in resources. It is possible that FF genera evolved during periods of unstable environments. Examination of the predictability of the abiotic environments during which these mammals diversified would provide insight on this issue.

However, the evidence presented here suggests that FF mammals are not insensitive to abiotic perturbations. Many studies have established that changes in herbivorous mammal diversity and abundance reflect transitions in prevailing regional or global climates (Cerling et al. 1997, Badgley et al. 2008, Maguire and Stigall 2009, Figueirido et al. 2012). As one example, African bovid diversity changed in association with a transition from closed and wet environments to closed and dry environments as climate changed during the late Pliocene (Bobe and Eck 2001). In such cases, variation in patterns of extant species richness is better explained by historical stability than contemporary climate (Araujo et al. 2008). When species are poor dispersers, stability is, in fact, the best predictor of species richness (Graham et al. 2006). This corroborates poor dispersal ability having a limited role in explaining the bounded instability experienced by HF mammals, since no effect of instability was observed here for those genera.
(Buckley et al. 2010)

Implications for the historic climate stability hypothesis

The historic climate stability hypothesis is well-supported by past studies (Dynesius and Jansson 2000, Jansson and Dynesius 2002, Araujo et al. 2008, Abellan and Svenning 2014). Mean endemism in a diverse range of vertebrate taxa (mammals, birds, and reptiles) decreases with increasing climatic instability (Fjeldsa et al. 1999, Jansson 2003) or climate change velocity (Sandel et al. 2011). However, no simple relationship between lower instability and higher species richness was observed for herbivorous mammals in this study. The approach taken here disentangled the effects of multiple potential components of climatic instability on richness, revealing that climate variables have non-equivalent effects. The evidence indicates that fluctuations in some climatic variables (temperature, temperature range, and precipitation during the wettest periods) elevate richness while others depress richness (precipitation during the driest periods and seasonality of both temperature and precipitation). Focusing on one variable that had negative effects on richness, seasonality governs the degree of departure from an organism's climatic optimum. Species with flexible adaptations that promote tolerance of unevenly distributed resources are favored in areas with higher seasonality (Gouveia et al. 2013). Though FF herbivores are highly adaptable in general to be able to tolerate a broad range of climatic fluctuations, the negative effect of seasonality on FF richness indicates that these mammals are relatively "inflexible" with regard to spatiotemporal patchiness in resources and conditions.

Several factors may produce spatial variation in patterns of contemporary species richness other than past climate stability, including differences in clade age that result in variation in the time available for diversification, immigration rates, or ecological opportunities as well as the acquisition of key innovations in particular lineages that are geographically localized (Linder et al. 2014). Therefore, exploration of the spatial variation in the effect of climate instability on FF genera warrants further investigation.

The application of species distribution modeling in studies of macroclimate change

This analysis is based on the assumption that species' niches are stable or that species have slow rates of niche evolution. The methods applied here do not model shifts in niche or niche evolution. However, species for which niches cannot be accurately estimated because of niche shifts are expected to be comparatively insensitive to climatic instability. Clades with high rates of niche evolution are potentially more resilient to changes in climate than species with slower niche evolution (Martinez-Meyer et al. 2004, Lavergne et al. 2012, Quintero and Wiens 2013). This analysis also does not incorporate data from extinct species in measures of species richness of genera. If instability had an effect on richness, the extinction of species would be part of the effect that is not captured in the current analysis. Therefore, the analysis is conservative in this manner in its ability to detect the effect of instability, at least a negative effect.

Conclusions

Lastly, differences in the instability-richness relationship between HF and FF herbivores examined here suggest that the species diversity of FF mammals has not yet reached an equilibrium state. Differences in instability at the continental scale for FF mammals provide the strongest evidence for this. Limits on tolerable levels of instability may exist for FF herbivores, as they do for HF mammals, but may not be observed here because of non-equilibrium between the instability and richness of these lineages. Because dispersal can equalize regional variation in species diversity, dispersal limitation is necessary for non-equilibrium differences between regions (Hillebrand et al. 2001).

TABLES

Table 4.1. Description of variables used to calculate multivariate climate anomaly.

For each variable, anomaly was measured as the difference between the Last Glacial Maximum and the present. Climatic data were obtained from the WorldClim database (Hijmans et al. 2005; http://www.worldclim.org/download).

variable	description
BIO1	annual mean temperature
BIO2	mean diurnal range
BIO3	isothermality
BIO4	temperature seasonality
BIO5	maximum temperature of warmest month
BIO6	minimum temperature of coldest month
BIO7	temperature annual range
BIO8	mean temperature of wettest quarter
BIO9	mean temperature of driest quarter
BIO10	mean temperature of warmest quarter
BIO11	mean temperature of coldest quarter
BIO12	annual precipitation
BIO13	precipitation of wettest month
BIO14	precipitation of driest month
BIO15	precipitation seasonality
BIO16	precipitation of wettest quarter
BIO17	precipitation of driest quarter
BIO18	precipitation of warmest quarter
BIO19	precipitation of coldest quarter

Table 4.2. Phylogenetic signal of multivariate climate anomaly and species richness.

Phylogenetic structure of the two traits was estimated using Pagel's λ and Blomberg's *K* statistics. Significance was assessed at $\alpha = 0.05$. Significant *p*-values are indicated by asterisks (*).

variable	**Pagel's λ**	***p***	**Blomberg's *K***	***p***
multivariate climatic anomaly	0.301	0.003*	0.180	0.053
species richness	0.356	0.013*	0.176	0.012*

Table 4.3. Models of trait evolution for multivariate climate anomaly and species richness.

For each trait, nine models of trait evolution were fit to the data: Brown motion, Ornstein-Uhlenbeck, early burst, trend, lambda, kappa, delta, drift, and white noise. Results of these models are given for each trait. The models that best fit the data were selected based on the Akaike Information criterion corrected for small sample size (AICc).

variable	model	log-likelihood	AIC	AICc	ΔAICc	no. parameters
multivariate climatic anomaly	Brownian motion	-78.625	161.250	161.323	67.300	2
	Ornstein-Uhlenbeck	-46.732	99.463	99.609	5.586	3
	early burst	-78.626	163.252	163.397	69.375	3
	trend	-71.960	149.919	150.065	56.042	3
	lambda	-43.939	93.877	94.023	0.000	3
	kappa	-62.995	131.990	132.136	38.113	3
	delta	-66.622	139.244	139.390	45.367	3
	drift	-78.625	163.250	163.396	69.373	3
	white noise	-51.574	107.147	107.219	13.197	2
species richness	Brownian motion	-162.740	329.479	329.552	78.211	2
	Ornstein-Uhlenbeck	-125.354	256.708	256.853	5.512	3
	early burst	-162.741	331.481	331.626	80.286	3
	trend	-155.764	317.528	317.674	66.333	3
	lambda	-122.598	251.195	251.341	0.000	3
	kappa	-145.745	297.491	297.636	46.296	3
	delta	-150.114	306.229	306.374	55.034	3
	drift	-162.740	331.479	331.625	80.284	3
	white noise	-125.657	255.314	255.387	4.046	2

Table 4.4. Scores from phylogenetic principal components analysis (PCA) of climate anomaly.

Principal components (PCs) 1-4 account for ca. 88% of the total explained variance in climate anomaly and were retained for the regression analyses. A cut-off of ±0.229 was used to determine the significance of the loadings on variables. Significant loadings are indicated with asterisks.

anomaly	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19
BIO1	-0.086	-0.650*	-0.151	-0.355*	-0.626	-0.132	0.051	-0.040	-0.015	-0.048	-0.052	0.017	-0.041	-0.009	0.008	-0.014	0.003	-0.003	0.003
BIO2	0.029	-0.839*	0.381*	-0.075	0.291	0.050	0.213	-0.005	0.056	0.041	-0.084	-0.011	0.024	0.003	-0.001	0.000	0.000	0.000	0.000
BIO3	0.047	-0.794*	0.391*	0.018	0.055	0.047	-0.453	0.022	-0.005	-0.002	-0.049	0.001	0.010	0.011	-0.002	-0.001	0.000	0.000	0.000
BIO4	-0.229*	-0.165	0.217	0.274*	-0.418	0.290	0.101	0.724	-0.054	0.014	0.008	0.040	0.019	0.005	-0.003	-0.002	0.000	0.000	0.000
BIO5	-0.132	-0.453*	-0.112	-0.283*	-0.562	-0.216	-0.090	0.020	0.301	0.433	0.163	-0.088	0.025	-0.018	-0.003	0.001	0.000	0.000	0.000
BIO6	-0.085	-0.805*	-0.058	-0.292*	-0.339	0.096	0.072	-0.091	-0.127	-0.147	0.164	-0.081	0.212	0.046	0.004	-0.001	0.000	0.000	0.000
BIO7	0.043	-0.881*	0.346*	-0.046	0.238	0.075	0.046	-0.002	-0.058	-0.034	0.158	0.018	-0.073	-0.021	0.002	0.002	0.000	0.000	0.000
BIO8	-0.090	-0.650*	-0.144	-0.355*	-0.626	-0.132	0.054	-0.047	-0.018	-0.049	-0.053	0.023	-0.040	-0.008	0.005	-0.010	-0.012	0.013	0.000
BIO9	-0.105	-0.644*	-0.139	-0.357*	-0.630	-0.117	0.045	-0.036	-0.005	-0.065	-0.053	0.041	-0.027	0.006	-0.030	0.054	-0.001	-0.002	0.000
BIO10	-0.088	-0.651*	-0.153	-0.355*	-0.625	-0.128	0.053	-0.033	-0.011	-0.049	-0.049	0.021	-0.043	-0.009	0.007	-0.010	0.016	0.005	-0.001
BIO11	-0.082	-0.650*	-0.150	-0.356*	-0.625	-0.134	0.053	-0.047	-0.019	-0.047	-0.052	0.014	-0.040	-0.008	0.010	-0.018	-0.007	-0.013	-0.001
BIO12	0.916*	0.213	0.310*	-0.089	-0.059	-0.044	-0.014	0.000	-0.009	-0.028	-0.008	-0.002	0.038	-0.065	-0.009	-0.002	0.000	0.000	0.000
BIO13	0.846*	0.276*	0.402*	-0.087	-0.054	-0.149	0.027	0.016	0.070	-0.061	0.023	-0.031	-0.025	0.034	-0.020	-0.007	0.000	0.000	0.000
BIO14	0.921*	-0.212	-0.286*	0.137	0.011	0.035	0.001	0.017	-0.031	0.003	-0.013	-0.066	-0.014	-0.002	-0.001	0.001	0.000	0.000	0.000
BIO15	-0.378*	-0.058	0.411*	0.740*	-0.340	0.093	0.045	-0.105	0.001	0.004	-0.001	-0.008	-0.002	-0.001	0.000	0.000	0.000	0.000	0.000
BIO16	0.854*	0.264*	0.404*	-0.082	-0.062	-0.131	-0.010	0.039	0.062	-0.050	0.000	-0.030	-0.006	0.004	0.027	0.008	0.000	0.000	0.000
BIO17	0.929*	-0.204	-0.245*	0.150	0.012	0.040	-0.003	-0.008	0.075	-0.025	0.013	0.061	0.012	0.002	0.001	-0.001	0.000	0.000	0.000
BIO18	0.917*	-0.007	0.139	0.058	-0.002	-0.334	0.022	-0.010	-0.118	0.088	-0.001	0.045	0.008	0.013	0.001	0.000	0.000	0.000	0.000
BIO19	0.795*	0.241*	0.176	-0.219	-0.107	0.461	0.006	-0.053	-0.036	0.052	-0.005	0.016	-0.008	0.010	0.001	0.000	0.000	0.000	0.000

Table 4.5. Species at climatic instability limits of hindgut and foregut-fermenting mammals.

The geographic distributions, range size (m^2), and principal components for which the species are outliers are given.

species	strategy	common name	distribution	range size (m^2)	PC(s)
Aepyceros melampus	foregut	impala	Africa	12.544	3
Eudorcas rufifrons	foregut	red-fronted gazelle	Africa		1 – 4
Nanger dama	foregut	Dama gazelle	Africa	11.476	1 – 4
Neotragus pygmaeus	foregut	royal antelope	Africa	11.661	3
Antilope cervicapra	foregut	blackbuck	India	12.246	1, 4
Gazella bennettii	foregut	chinkara	India, Pakistan, Iran		1 – 4
Macropus irma	foregut	western brush wallaby	Australia		2
Setonix brachyurus	foregut	quokka	Australia	10.258	2
Wallabia bicolor	foregut	swamp wallaby	Australia	12.085	2
Arborimus longicaudus	hindgut	red-tree vole	northwest U.S.	10.733	2
Phenacomys intermedius	hindgut	western heather vole	western North America	11.719	2
Synaptomys borealis	hindgut	northern bog lemming	Canada, Alaska		2
Centurio senex	hindgut	wrinkle-faced bat	Mexico, Central America, northern South America	12.322	3
Dinomys branickii	hindgut	pacarana	South America	12.267	1, 4
Pygoderma bilabiatum	hindgut	Ipanema bat	South America	12.473	3
Desmodillus auricularis	hindgut	cape short-eared gerbil	South Africa	12.293	3
Gerbillus pulvinatus	hindgut	cushioned gerbil	Africa		3
Petromus typicus	hindgut	dassle rat	Africa	11.573	1, 4
Thryonomys swinderianus	hindgut	greater cane rat	Africa	12.880	4
Avahi laniger	hindgut	woolly lemur	Madagascar	10.746	4
Propithecus verreauxi	hindgut	Verreaux's sifaka	Madagascar	10.814	4
Petauroides volans	hindgut	greater glider	Australia	11.803	1
Petropseudes dahli	hindgut	rock possum	Australia	11.301	1

Table 4.6. Regression analyses of climate anomaly and species richness.

For hindgut and foregut-fermenting mammals, three regression models were applied to test the relationship between the group's species diversity and the magnitude of historical climatic change that it experienced from the Last Glacial Maximum. Fit of models was assessed using the correlation coefficient or differences in the Akaike Information Criterion (ΔAIC).

group	method	term	coefficient	std. error	*t*-value	*p*	r^2	AIC	ΔAIC	p_{model}
hindgut	OLS	PC1	-0.088	0.042	-2.107	0.037*	0.024	-197.365	0.000	0.156
		PC2	0.089	0.067	1.329	0.187				
		PC3	0.149	0.106	1.415	0.160				
		PC4	-0.077	0.131	-0.593	0.554				
	RR	PC1	-0.068	0.064	-1.065	0.289	0.019			
		PC2	0.057	0.043	1.318	0.190				
		PC3	0.168	0.098	1.722	0.088				
		PC4	-0.059	0.117	-0.505	0.614				
	pGLS	Intercept	0.933	0.235	3.975	0.000*		198.583	395.948	
		PC1	-0.033	0.040	-0.825	0.411				
		PC2	0.035	0.073	0.475	0.636				
		PC3	0.131	0.100	1.304	0.195				
		PC4	-0.050	0.123	-0.403	0.688				
foregut	OLS	PC1	0.072	0.056	1.282	0.206	0.262	-63.489	0.000	0.001*
		PC2	-0.209	0.097	-2.145	0.037*				
		PC3	0.448	0.106	4.232	<0.001*				
		PC4	-0.215	0.137	-1.567	0.123				
	RR	PC1	0.264	0.140	1.887	0.065	0.596			
		PC2	-0.032	0.198	-0.161	0.872				
		PC3	0.453	0.086	5.268	<0.001*				
		PC4	-0.405	0.127	-3.204	0.002*				
	pGLS	Intercept	0.973	0.020	47.801	0.000*		75.823	139.312	
		PC1	0.131	0.045	2.930	0.005*				
		PC2	-0.071	0.069	-1.024	0.311				
		PC3	0.358	0.090	3.979	0.000*				
		PC4	-0.206	0.119	-1.731	0.090				

Table S4.1. Area under the operator receiving curve (AUC) of MaxEnt models for species analyzed in this study.

For each species, the number of unique geographic coordinates and the regularization multiplier that yielded the highest test AUC are given. Coordinates were obtained from the Global Biodiversity Information Facility database and validated using species distribution data from the IUCN (2013). Details about the species distribution modeling using the MaxEnt algorithm can be found in the main text.

species	no. coord.	reg. mult.	test AUC
Aepyceros melampus	84	0.05	0.923
Ailurus fulgens	5	1	0.798
Alcelaphus buselaphus	75	0.5	0.900
Alces alces	505	0.05	0.958
Alces americanus	95	0.75	0.951
Alouatta caraya	41	0.05	0.960
Alouatta guariba	7	2	0.885
Alouatta palliata	87	0.05	0.851
Alouatta pigra	58	5	0.710
Alticola argentatus	6	0.25	0.965
Ametrida centurio	63	5	0.896
Ammospermophilus harrisii	182	1	0.884
Anisomys imitator	14	5	0.927
Anomalurus derbianus	133	0.25	0.865
Antidorcas marsupialis	45	0.5	0.795
Antilocapra americana	191	0.05	0.861
Antilope cervicapra	11	0.05	0.830
Aotus vociferans	17	0.05	0.828
Aplodontia rufa	206	1	0.914
Arborimus albipes	43	0.25	0.930
Arborimus longicaudus	39	0.05	0.950
Arborimus pomo	46	0.5	0.922
Arctictis binturong	7	2	0.858
Ardops nichollsi	7	1	0.836
Artibeus amplus	25	0.25	0.940
Artibeus anderseni	48	0.05	0.921
Artibeus aztecus	41	2	0.892
Artibeus cinereus	56	0.25	0.979
Artibeus concolor	49	0.5	0.921
Artibeus fimbriatus	22	2	0.941
Artibeus fraterculus	41	2	0.856
Artibeus glaucus	69	0.05	0.895
Artibeus hirsutus	46	0.25	0.925
Artibeus lituratus	75	0.5	0.828
Artibeus obscurus	129	1	0.859
Artibeus toltecus	155	2	0.867
Ateles belzebuth	15	0.05	0.918
Ateles fusciceps	12	0.05	0.766
Ateles geoffroyi	112	0.25	0.801
Avahi laniger	9	0.25	0.922
Baiomys musculus	113	1	0.871
Baiomys taylori	118	2	0.899
Balionycteris maculata	16	0.5	0.828
Bathyergus suillus	10	5	0.908
Bison bison	35	0.05	0.973
Blastocerus dichotomus	28	0.25	0.916
Bos javanicus	17	0.25	0.999
Boselaphus tragocamelus	14	0.05	0.884
Brachylagus idahoensis	58	0.5	0.843

species	no. coord.	reg. mult.	test AUC
Bradypus tridactylus	17	0.5	0.881
Bradypus variegatus	136	0.5	0.879
Budorcas taxicolor	7	0.05	0.929
Capra pyrenaica	335	1	0.916
Carollia brevicauda	82	0.75	0.880
Carollia castanea	160	2	0.880
Carollia subrufa	115	1	0.897
Castor canadensis	248	0.75	0.878
Castor fiber	421	0.5	0.968
Cavia aperea	133	0.75	0.927
Centurio senex	213	1	0.868
Cephalophus nigrifrons	12	0.05	0.916
Ceratotherium simum	28	0.5	0.986
Cercopithecus campbelli	24	0.75	0.895
Cervus elaphus	391	2	0.965
Cervus nippon	12	5	0.966
Chaetodipus artus	53	1	0.921
Chaetodipus fallax	89	0.75	0.922
Chaetodipus hispidus	330	0.05	0.830
Chaetodipus pernix	90	0.75	0.945
Chiroderma salvini	122	1	0.884
Chiroderma trinitatum	58	0.05	0.817
Chiroderma villosum	217	0.05	0.836
Chironax melanocephalus	7	0.75	0.899
Choloepus hoffmanni	69	0.25	0.918
Coccymys ruemmleri	8	1	0.931
Coendou bicolor	11	0.05	0.929
Coendou prehensilis	42	0.05	0.719
Coendou rothschildi	7	0.75	0.919
Colobus angolensis	7	2	0.773
Colobus guereza	45	0.75	0.898
Colobus polykomos	13	0.05	0.897
Connochaetes gnou	8	0.05	0.875
Connochaetes taurinus	56	0.5	0.904
Cratogeomys castanops	133	0.5	0.886
Cratogeomys fumosus	20	0.5	0.793
Cratogeomys merriami	33	0.75	0.928
Cryptomys hottentotus	28	0.75	0.935
Ctenomys conoveri	9	0.05	0.893
Ctenomys leucodon	5	1	0.859
Ctenomys maulinus	22	0.25	0.937
Ctenomys opimus	27	0.25	0.881
Ctenomys steinbachi	7	5	0.933
Ctenomys talarum	10	2	0.981
Cuniculus paca	150	0.75	0.830
Cuniculus taczanowskii	15	0.05	0.934
Cynocephalus volans	25	0.25	0.748
Cynomys leucurus	127	0.5	0.861
Cynomys ludovicianus	268	1	0.842
Cynomys parvidens	10	0.25	0.938

species	no. coord.	reg. mult.	test AUC
Cynopterus brachyotis	12	2	0.895
Cynopterus horsfieldii	18	0.25	0.942
Cynopterus sphinx	84	0.05	0.872
Damaliscus lunatus	20	0.5	0.893
Dasyprocta azarae	24	0.25	0.936
Dasyprocta fuliginosa	17	0.25	0.821
Dasyprocta kalinowskii	6	0.05	0.880
Dasyprocta leporina	27	1	0.845
Dasyprocta mexicana	18	0.05	0.912
Dasyprocta punctata	236	0.75	0.867
Dendrohyrax arboreus	33	0.25	0.959
Dendrohyrax dorsalis	33	0.5	0.863
Dendrolagus goodfellowi	8	5	0.909
Dendrolagus inustus	12	2	0.968
Desmodillus auricularis	99	0.75	0.841
Diceros bicornis	52	0.5	0.906
Dinomys branickii	14	1	0.908
Dipodomys californicus	89	1	0.828
Dipodomys deserti	193	0.75	0.912
Dipodomys merriami	142	1	0.894
Dipodomys nelsoni	85	0.75	0.873
Dipodomys nitratoides	50	0.25	0.937
Dipodomys phillipsii	96	0.75	0.874
Dipodomys stephensi	28	0.25	0.935
Dipodomys venustus	27	2	0.890
Dobsonia minor	32	0.75	0.881
Dobsonia moluccensis	74	0.5	0.798
Dobsonia pannietensis	11	0.05	0.886
Dobsonia praedatrix	16	0.05	0.848
Dolichotis patagonum	29	1	0.811
Dolichotis salinicola	11	0.75	0.937
Dorcopsulus vanheurni	16	0.5	0.881
Echimys chrysurus	6	0.25	0.756
Ectophylla alba	10	0.05	0.975
Eidolon helvum	154	0.5	0.863
Elephas maximus	5	0.5	0.793
Eligmodontia typus	35	0.5	0.786
Eliurus webbi	20	0.05	0.967
Enchisthenes hartii	105	1	0.915
Epomophorus crypturus	22	0.25	0.856
Epomophorus gambianus	83	1	0.868
Epomophorus labiatus	76	1	0.912
Epomophorus wahlbergi	133	2	0.891
Epomops buettikoferi	40	0.75	0.901
Equus grevyi	11	0.05	0.988
Equus hemionus	5	10	0.991
Equus zebra	5	2	0.962
Erethizon dorsatum	295	0.75	0.861
Eudorcas thomsonii	7	0.25	0.797

species	no. coord.	reg. mult.	test AUC
Eulemur fulvus	9	0.05	0.822
Funisciurus anerythrus	78	0.25	0.836
Funisciurus isabella	14	2	0.876
Funisciurus pyrropus	95	0.75	0.903
Galago moholi	22	0.5	0.782
Galea musteloides	120	2	0.861
Galea spixii	13	2	0.819
Gazella gazella	47	0.05	0.997
Gazella subgutturosa	22	0.5	0.908
Geomys arenarius	43	0.25	0.981
Geomys attwateri	8	0.05	0.863
Geomys breviceps	24	0.25	0.782
Geomys bursarius	149	1	0.854
Geomys personatus	12	0.05	0.772
Geomys pinetis	119	2	0.861
Gerbillus andersoni	26	2	0.942
Gerbillus pyramidum	88	1	0.928
Giraffa camelopardalis	52	1	0.936
Hapalemur griseus	8	0.05	0.972
Haplonycteris fischeri	56	1	0.862
Harpyionycteris whiteheadi	21	0.5	0.831
Helarctos malayanus	6	5	0.802
Heliophobius argenteocinereus	38	1	0.841
Heliosciurus rufobrachium	171	1	0.900
Heterocephalus glaber	10	1	0.976
Heterohyrax brucei	52	1	0.898
Heteromys australis	20	0.75	0.887
Heteromys desmarestianus	93	1	0.841
Heteromys gaumeri	103	1	0.793
Hippocamelus antisensis	8	5	0.846
Hippotragus equinus	20	0.25	0.855
Hippotragus niger	27	0.05	0.840
Holochilus brasiliensis	47	0.5	0.931
Holochilus chacarius	43	0.5	0.920
Hoplomys gymnurus	18	2	0.823
Hydrochoerus hydrochaeris	53	1	0.792
Hyemoschus aquaticus	11	0.05	0.884
Hylochoerus meinertzhageni	17	0.25	0.962
Hyomys goliath	7	0.25	0.864
Hypsignathus monstrosus	57	1	0.863
Hystrix africaeaustralis	54	1	0.779
Idiurus macrotis	10	0.05	0.858
Indri indri	15	0.05	0.935
Kannabateomys amblyonyx	19	0.75	0.954
Kobus ellipsiprymnus	75	2	0.862
Kobus kob	22	0.05	0.912
Kobus leche	11	0.75	0.945
Kobus vardonii	6	2	0.919
Lagidium peruanum	31	1	0.893

species	**no. coord.**	**reg. mult.**	**test AUC**
Lagostomus maximus	74	0.5	0.808
Lariscus insignis	22	1	0.798
Lasiorhinus latifrons	92	0.5	0.955
Lemmiscus curtatus	199	1	0.906
Lepus alleni	63	0.5	0.888
Lepus americanus	240	1	0.878
Lepus arcticus	26	2	0.876
Lepus californicus	406	0.25	0.826
Lepus callotis	41	0.5	0.868
Lepus microtis	75	0.5	0.951
Lepus othus	56	0.5	0.892
Lepus townsendii	369	0.75	0.849
Liomys pictus	69	2	0.947
Lionycteris spurrelli	39	0.05	0.894
Lissonycteris angolensis	60	0.75	0.918
Litocranius walleri	16	2	0.836
Loxodonta africana	79	0.75	0.876
Macaca mulatta	29	0.25	0.819
Macroglossus minimus	114	0.75	0.856
Macroglossus sobrinus	36	2	0.922
Macropus agilis	284	0.75	0.975
Macropus giganteus	330	0.75	0.928
Macropus parma	138	2	0.923
Macropus parryi	139	0.75	0.975
Macropus robustus	246	0.05	0.925
Macropus rufus	673	0.05	0.920
Madoqua guentheri	6	1	0.879
Madoqua kirkii	24	0.5	0.923
Madoqua saltiana	6	0.05	0.882
Mallomys aroaensis	11	5	0.884
Mallomys istapantap	7	0.75	0.969
Mallomys rothschildi	20	2	0.936
Mammelomys lanosus	12	0.25	0.891
Mammelomys rattoides	10	0.05	0.991
Marmota flaviventris	333	2	0.859
Marmota marmota	187	2	0.964
Mazama americana	14	0.25	0.977
Mazama gouazoubira	33	1	0.899
Megaerops ecaudatus	7	0.05	0.796
Melomys leucogaster	6	0.25	0.980
Melomys lutillus	5	0.25	0.775
Melomys rufescens	64	0.75	0.812
Melonycteris melanops	15	0.05	0.868
Melonycteris woodfordi	7	0.05	0.732
Meriones crassus	118	0.5	0.891
Mesophylla macconnelli	82	0.05	0.838
Microcavia australis	72	0.75	0.829
Microcavia niata	6	1	0.852
Micropteropus pusillus	115	0.75	0.826

species	**no. coord.**	**reg. mult.**	**test AUC**
Microtus chrotorrhinus	71	0.05	0.921
Microtus longicaudus	130	2	0.929
Microtus oregoni	152	0.5	0.885
Microtus pinetorum	160	1	0.861
Microtus richardsoni	159	2	0.915
Microtus townsendii	126	0.75	0.923
Microtus xanthognathus	10	0.25	0.883
Muntiacus atherodes	7	0.05	0.703
Mus spicilegus	7	2	0.966
Nandinia binotata	63	0.5	0.914
Nanger granti	14	0.25	0.765
Nasalis larvatus	9	2	0.778
Neofiber alleni	72	0.25	0.806
Neotoma albigula	101	1	0.824
Neotoma cinerea	380	1	0.885
Neotoma floridana	269	0.5	0.889
Neotoma lepida	136	5	0.869
Neotoma mexicana	264	2	0.919
Neotoma micropus	183	0.75	0.865
Neotoma phenax	36	0.5	0.926
Neotragus batesi	12	0.05	0.971
Neotragus pygmaeus	18	1	0.832
Nesokia indica	25	0.5	0.907
Nesomys audeberti	7	0.05	0.874
Nesomys rufus	5	0.05	0.944
Nyctimene albiventer	74	0.5	0.752
Nyctimene rabori	7	0.75	0.968
Nyctimene robinsoni	43	0.05	0.981
Nyctomys sumichrasti	104	0.75	0.838
Ochotona cansus	8	0.05	0.971
Ochotona collaris	96	1	0.917
Ochotona dauurica	15	0.05	0.906
Ochotona princeps	163	1	0.959
Octodon lunatus	5	0.25	0.945
Octodontomys gliroides	14	0.05	0.967
Odocoileus hemionus	357	2	0.924
Odocoileus virginianus	506	1	0.908
Oecomys bicolor	104	0.75	0.819
Oreamnos americanus	45	0.75	0.895
Oreotragus oreotragus	37	0.75	0.900
Orthogeomys cavator	5	2	0.817
Orthogeomys cherriei	9	0.25	0.829
Orthogeomys grandis	48	0.75	0.851
Orthogeomys hispidus	118	2	0.785
Oryx gazella	28	0.75	0.839
Otomys angoniensis	31	0.25	0.942
Otomys irroratus	40	1	0.901
Ototylomys phyllotis	160	1	0.798
Ourebia ourebi	34	1	0.798

species	no. coord.	reg. mult.	test AUC
Ovibos moschatus	12	0.05	0.822
Ovis ammon	6	0.05	0.730
Ovis canadensis	128	0.75	0.874
Ovis dalli	109	0.5	0.892
Papio cynocephalus	14	0.05	0.810
Papio ursinus	51	0.75	0.766
Pappogeomys bulleri	44	0.25	0.853
Paramelomys mollis	6	5	0.910
Paramelomys platyops	32	0.5	0.827
Paramelomys rubex	33	0.5	0.914
Paranyctimene raptor	54	0.5	0.783
Paraxerus poensis	42	2	0.937
Pecari tajacu	312	0.5	0.842
Pedetes capensis	103	0.75	0.824
Pelea capreolus	9	0.05	0.832
Perognathus fasciatus	112	5	0.852
Perognathus flavescens	233	0.05	0.884
Perognathus longimembris	107	2	0.889
Peromyscus aztecus	62	1	0.924
Peromyscus mexicanus	35	0.75	0.954
Peromyscus pectoralis	104	1	0.898
Peroryctes raffrayana	21	10	0.866
Petaurista leucogenys	8	0.25	0.860
Petauroides volans	141	2	0.972
Petrogale persephone	8	0.25	0.978
Petrogale xanthopus	46	0.75	0.982
Petromus typicus	17	0.25	0.785
Petropseudes dahli	51	0.05	0.955
Phacochoerus africanus	60	0.25	0.853
Phalanger intercastellanus	12	0.05	0.874
Phalanger orientalis	36	1	0.900
Phalanger ornatus	5	0.05	0.876
Phalanger sericeus	18	10	0.919
Phalanger vestitus	16	10	0.915
Phascolarctos cinereus	130	2	0.964
Phenacomys intermedius	63	0.25	0.935
Phyllostomus elongatus	119	1	0.883
Pithecia pithecia	27	0.5	0.767
Platalina genovensium	6	0.05	0.961
Platyrrhinus helleri	205	0.05	0.856
Platyrrhinus vittatus	35	2	0.950
Pogonomys loriae	25	0.25	0.937
Pogonomys macrourus	24	1	0.942
Pogonomys sylvestris	11	0.25	0.944
Potorous longipes	6	0.05	0.938
Presbytis rubicunda	16	0.05	0.819
Procavia capensis	131	1	0.893
Procolobus verus	10	1	0.821
Proechimys guairae	23	2	0.752

species	**no. coord.**	**reg. mult.**	**test AUC**
Proechimys guyannensis	36	0.25	0.832
Propithecus diadema	8	0.05	0.956
Propithecus verreauxi	7	0.75	0.914
Protoxerus stangeri	179	1	0.878
Pseudocheirus peregrinus	277	1	0.962
Pseudochirops albertisii	6	0.75	0.972
Pseudochirops archeri	5	0.25	0.989
Pseudochirops corinnae	15	0.05	0.931
Pseudochirops cupreus	37	0.75	0.933
Pseudochirulus forbesi	8	2	0.770
Pseudochirulus mayeri	21	0.05	0.934
Pseudois nayaur	5	2	0.753
Pseudomys delicatulus	221	0.75	0.967
Pseudomys occidentalis	20	0.5	0.889
Ptenochirus jagori	72	0.5	0.853
Pteropus alecto	153	0.75	0.984
Pteropus conspicillatus	24	1	0.901
Pteropus giganteus	23	0.25	0.853
Pteropus hypomelanus	36	0.25	0.885
Pteropus lylei	6	0.05	0.975
Pteropus poliocephalus	153	2	0.980
Pteropus pumilus	12	0.5	0.844
Pteropus samoensis	6	0.75	0.997
Pteropus scapulatus	257	0.5	0.952
Pteropus tonganus	30	0.25	0.997
Pteropus vampyrus	53	1	0.870
Pudu puda	45	0.25	0.920
Pygeretmus pumilio	15	0.05	0.870
Pygoderma bilabiatum	62	0.25	0.946
Rangifer tarandus	175	0.5	0.981
Raphicerus campestris	90	0.5	0.842
Raphicerus melanotis	6	0.25	0.855
Raphicerus sharpei	18	0.75	0.873
Rattus mordax	11	0.05	0.750
Rattus norvegicus	292	0.5	0.984
Redunca arundinum	30	0.75	0.847
Redunca fulvorufula	20	2	0.915
Redunca redunca	31	5	0.849
Reithrodon auritus	73	1	0.888
Reithrodontomys raviventris	18	0.05	0.942
Rhinophylla fischerae	24	0.25	0.902
Rhinophylla pumilio	106	0.5	0.888
Romerolagus diazi	6	0.5	0.995
Rousettus amplexicaudatus	90	0.75	0.877
Rousettus madagascariensis	9	0.05	0.875
Rupicapra rupicapra	194	5	0.982
Rusa unicolor	19	2	0.773
Sciurus arizonensis	31	0.5	0.956
Sciurus aureogaster	228	2	0.815

species	no. coord.	reg. mult.	test AUC
Sciurus colliaei	80	0.5	0.935
Sciurus deppei	245	2	0.823
Sciurus griseus	313	1	0.928
Sciurus igniventris	38	0.25	0.906
Sciurus nayaritensis	50	0.5	0.917
Sciurus spadiceus	60	0.75	0.811
Sciurus yucatanensis	51	0.75	0.811
Semnopithecus entellus	5	0.05	0.827
Setonix brachyurus	40	2	0.917
Sigmodon alstoni	28	0.25	0.864
Spalacopus cyanus	9	0.05	0.864
Spermophilus columbianus	149	0.75	0.883
Spermophilus mohavensis	35	1	0.917
Spermophilus richardsonii	90	0.75	0.804
Sphaeronycteris toxophyllum	37	0.75	0.779
Sphiggurus mexicanus	19	0.5	0.826
Spilocuscus maculatus	53	1	0.820
Sturnira bidens	25	0.25	0.933
Sturnira bogotensis	9	0.05	0.920
Sturnira erythromos	74	2	0.949
Sturnira ludovici	91	0.75	0.977
Sturnira magna	36	2	0.871
Sturnira mordax	18	0.75	0.899
Sturnira tildae	80	0.5	0.850
Stylodipus telum	6	1	0.738
Syconycteris australis	128	1	0.956
Sylvicapra grimmia	110	2	0.829
Sylvilagus aquaticus	189	0.75	0.890
Sylvilagus audubonii	385	2	0.848
Sylvilagus bachmani	309	5	0.945
Sylvilagus brasiliensis	254	0.75	0.873
Sylvilagus cunicularius	78	0.75	0.874
Sylvilagus floridanus	284	0.75	0.891
Sylvilagus nuttallii	403	0.75	0.843
Sylvilagus palustris	78	0.25	0.898
Sylvilagus transitionalis	11	5	0.852
Synaptomys cooperi	260	0.5	0.850
Syncerus caffer	115	0.25	0.833
Tamias alpinus	25	10	0.957
Tamias dorsalis	199	1	0.893
Tamias obscurus	18	1	0.983
Tamias rufus	44	1	0.888
Tamias sonomae	89	1	0.892
Tapirus bairdii	68	1	0.762
Tapirus pinchaque	8	0.25	0.964
Tarsipes rostratus	245	1	0.927
Tarsius syrichta	21	10	0.758
Thomasomys aureus	35	0.5	0.954
Thomomys bottae	218	2	0.887

species	**no. coord.**	**reg. mult.**	**test AUC**
Thomomys bulbivorus	24	0.25	0.953
Thomomys mazama	45	0.25	0.881
Thomomys monticola	121	2	0.937
Thomomys talpoides	201	1	0.889
Thomomys townsendii	94	1	0.922
Thomomys umbrinus	54	0.75	0.913
Thryonomys swinderianus	81	0.75	0.837
Thylogale stigmatica	103	1	0.981
Trachypithecus johnii	5	1	0.933
Trachypithecus obscurus	6	0.05	0.914
Tragelaphus angasii	10	0.05	0.915
Tragelaphus eurycerus	8	0.05	0.857
Tragelaphus imberbis	14	0.05	0.825
Tragelaphus scriptus	114	0.05	0.806
Tragelaphus spekii	19	2	0.850
Tragelaphus strepsiceros	106	1	0.900
Trichosurus caninus	200	1	0.943
Trichosurus vulpecula	262	0.5	0.969
Uroderma magnirostrum	116	0.75	0.807
Uromys anak	12	5	0.910
Ursus americanus	332	0.05	0.921
Ursus thibetanus	12	5	0.815
Vampyrodes caraccioli	86	0.25	0.880
Varecia variegata	7	0.5	0.887
Vicugna vicugna	14	0.75	0.920
Vombatus ursinus	215	2	0.956
Wallabia bicolor	278	1	0.946
Wyulda squamicaudata	11	1	0.965
Xerus inauris	46	1	0.788

FIGURES

Figure 4.1. Maps of species richness.

The species richness of (a) hindgut-fermenting and (b) foregut-fermenting herbivorous mammals are shown. Values of species richness are on a $\log_{10}$ scale.

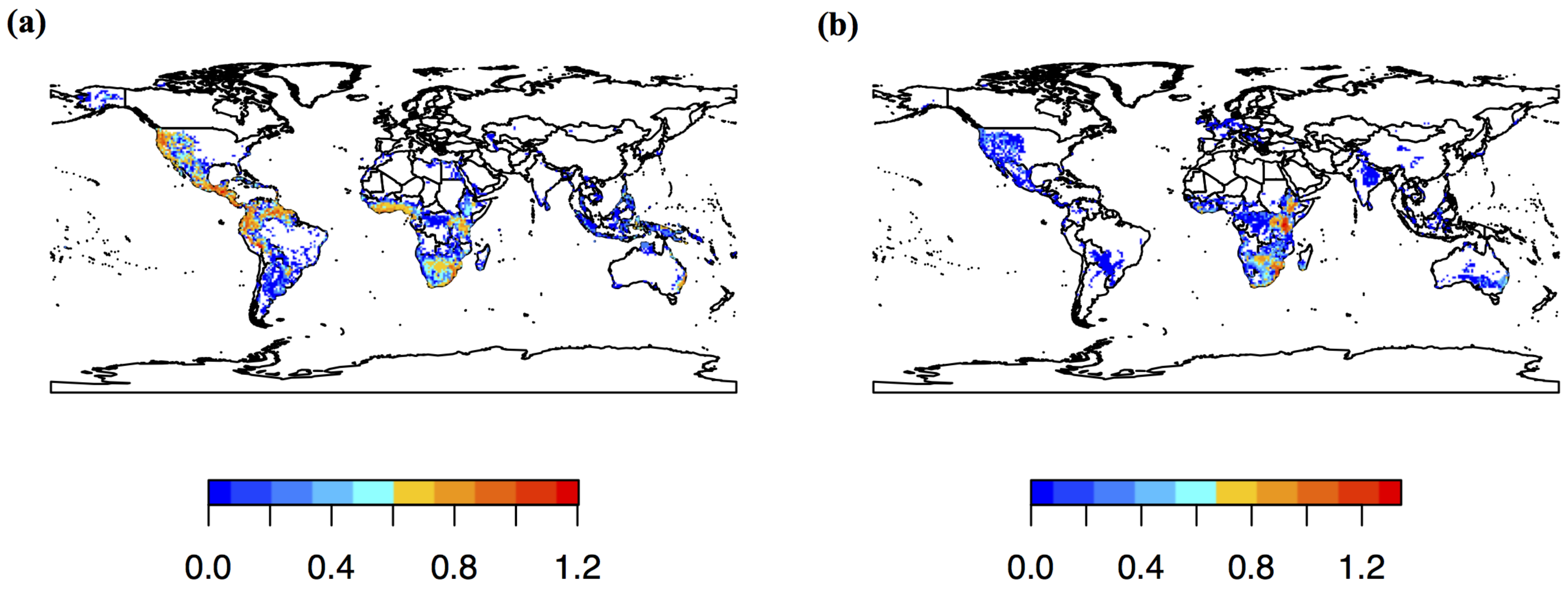


Figure 4.2. Plot of phylogenetic principal components of climate anomaly.

The percent variance explained by each principal component is shown here. The solid line indicates the threshold used to retain the PCs.

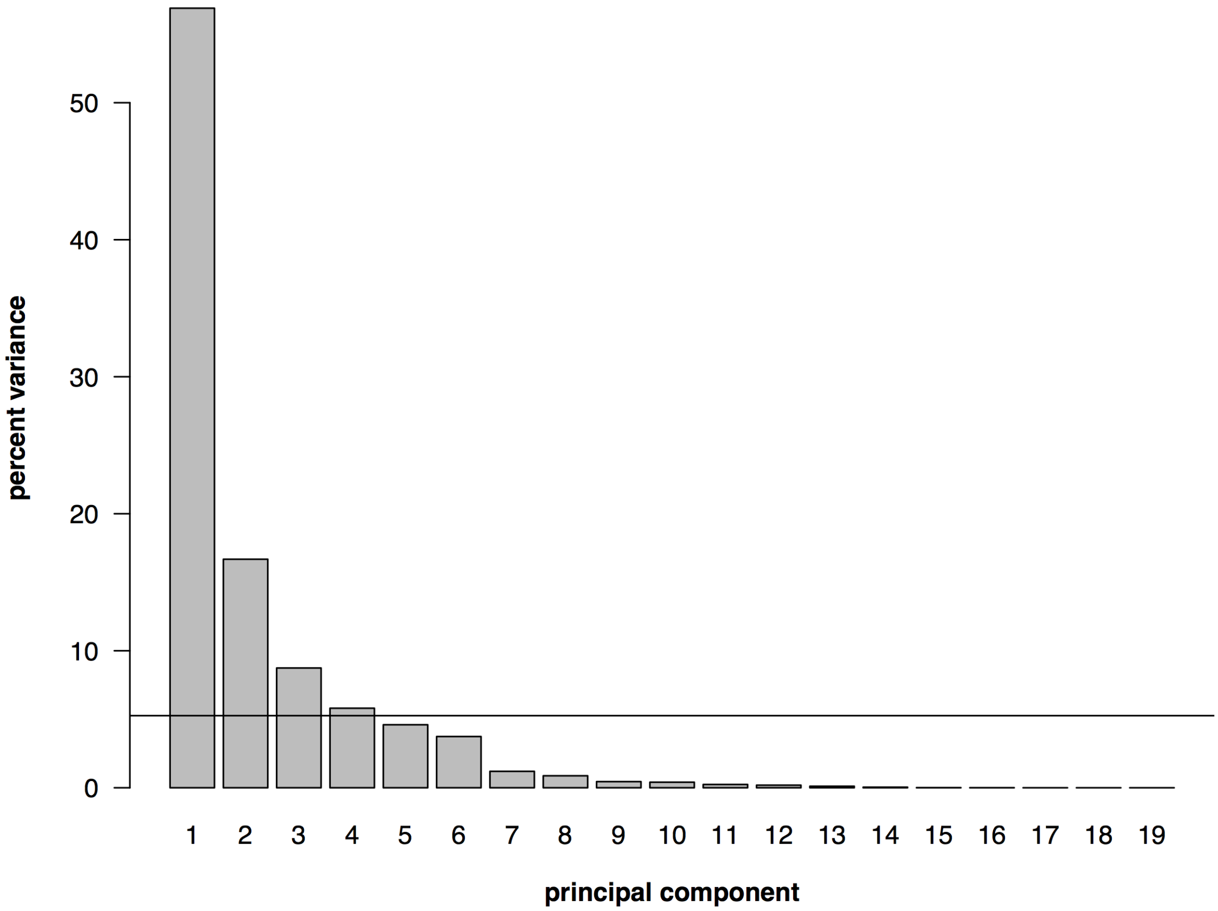


Figure 4.3. Phylogenetic principal components bi-plot.

The vectors describe the contributions of the 19 climate anomalies in principal component space for (a) PCs 1-2 and (b) PCs 3-4. For purposes of visual organization, only the major anomaly variables are displayed in the plots.

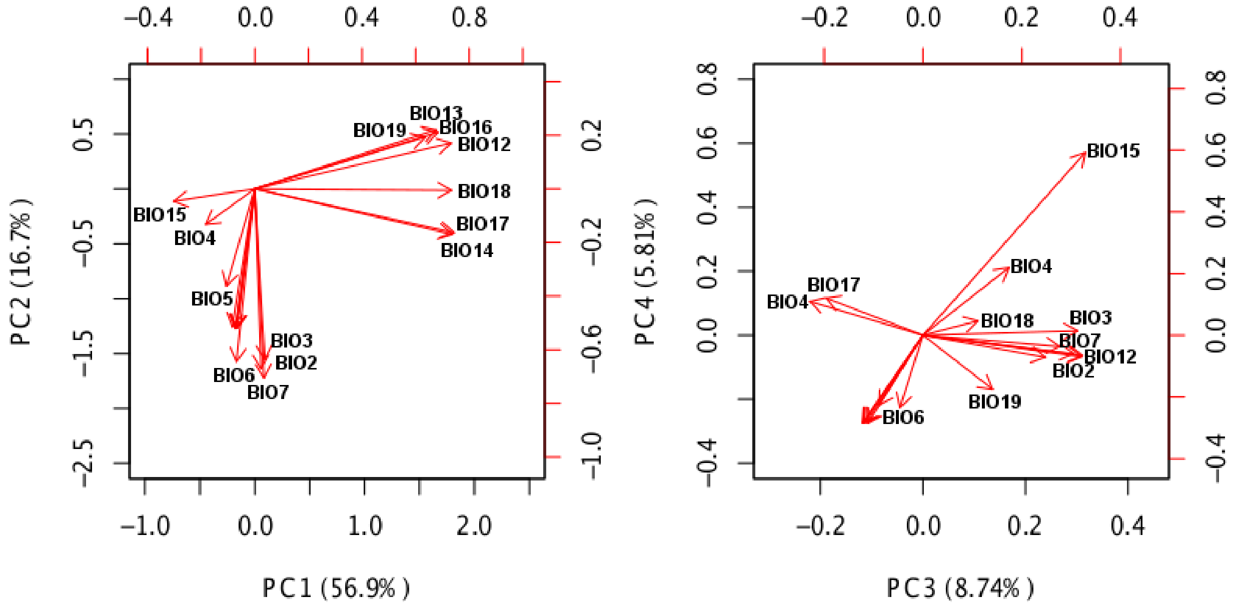


Figure 4.4. Comparisons of climate anomaly and species richness between hindgut and foregut-fermenting mammals. Independent contrasts of the major principal components of climate anomaly and $\log_{10}$-transformed species richness were compared between the two groups. Lower and upper whiskers represent the minimum and maximum data, respectively, within $\log_{10}(1.5)$ of the interquartile range of the data. Neither climate anomaly ($F_{4,164} = 1.459$, $p = 0.217$, phylogenetic $p = 0.991$) nor per-genus species richness ($F_{1,167} = 0.602$, $p = 0.439$, phylogenetic $p = 0.883$) significantly differs between hindgut and foregut-fermenting herbivores.

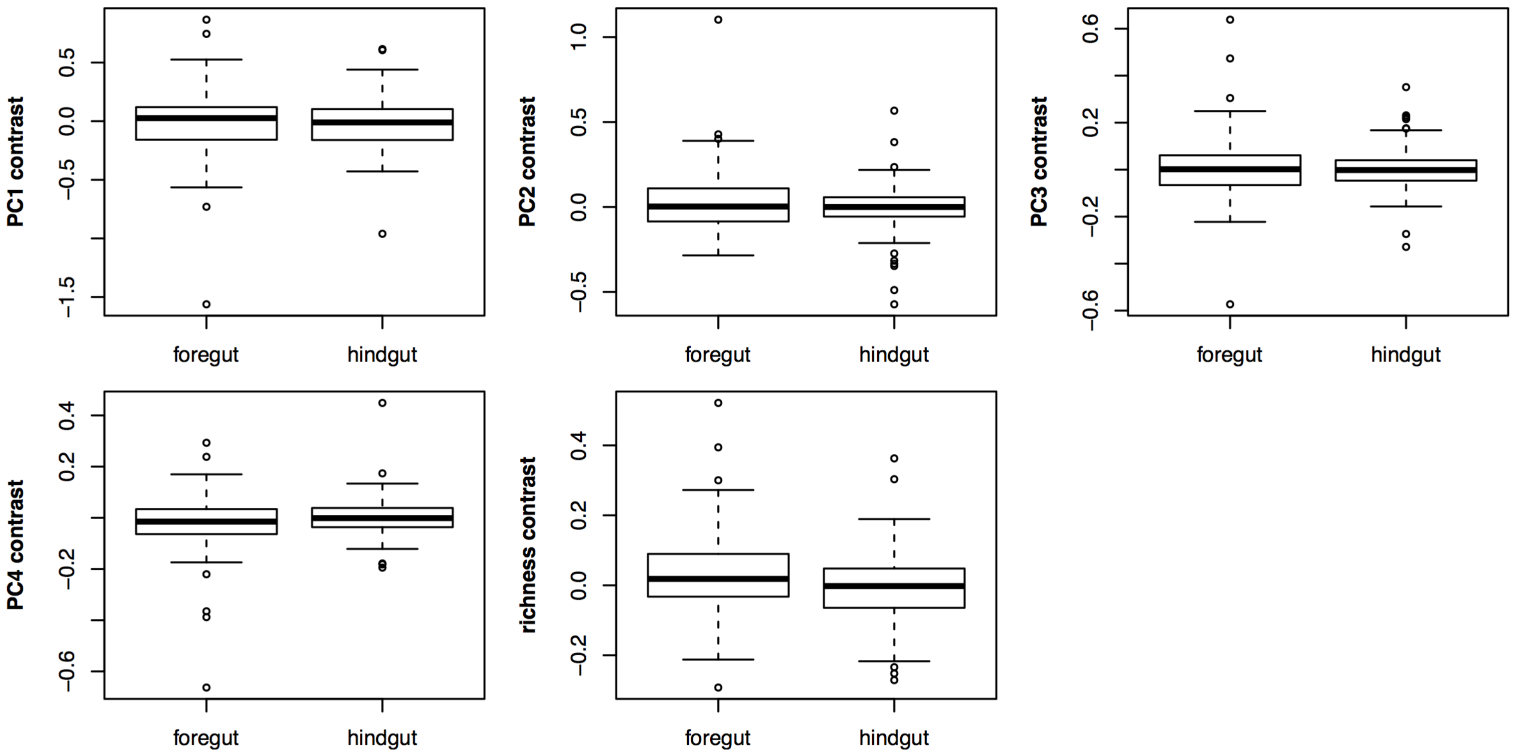


Figure 4.5. Geographic distributions of artiodactyl species at limits of climatic instability.

Distributions of foregut-fermenting bovids that are outliers on climate anomaly (a) PC3 and (b) PC4 are shown. The solid lines in panel (a) delineate the latitudinal extent of the tropics.

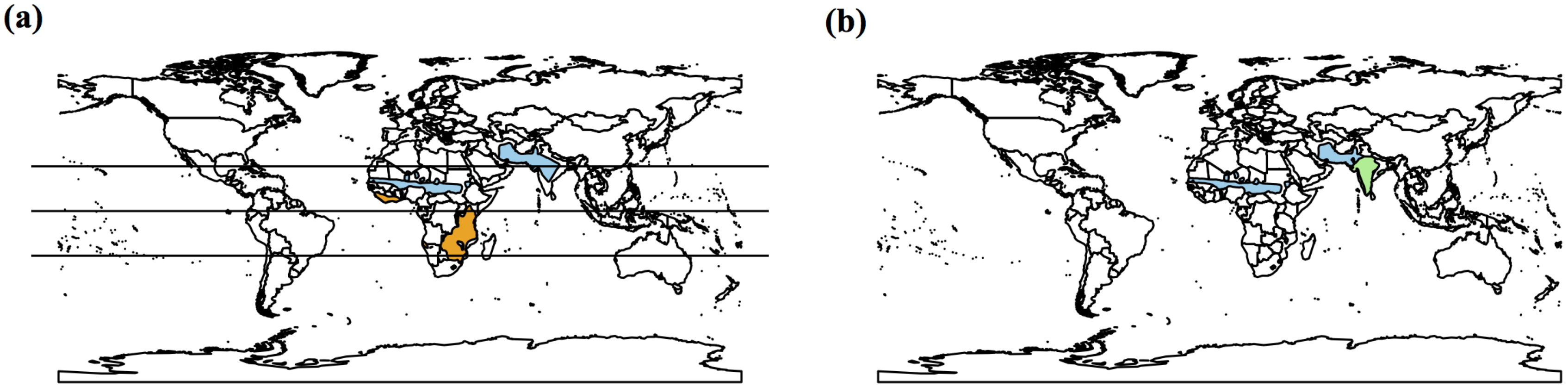
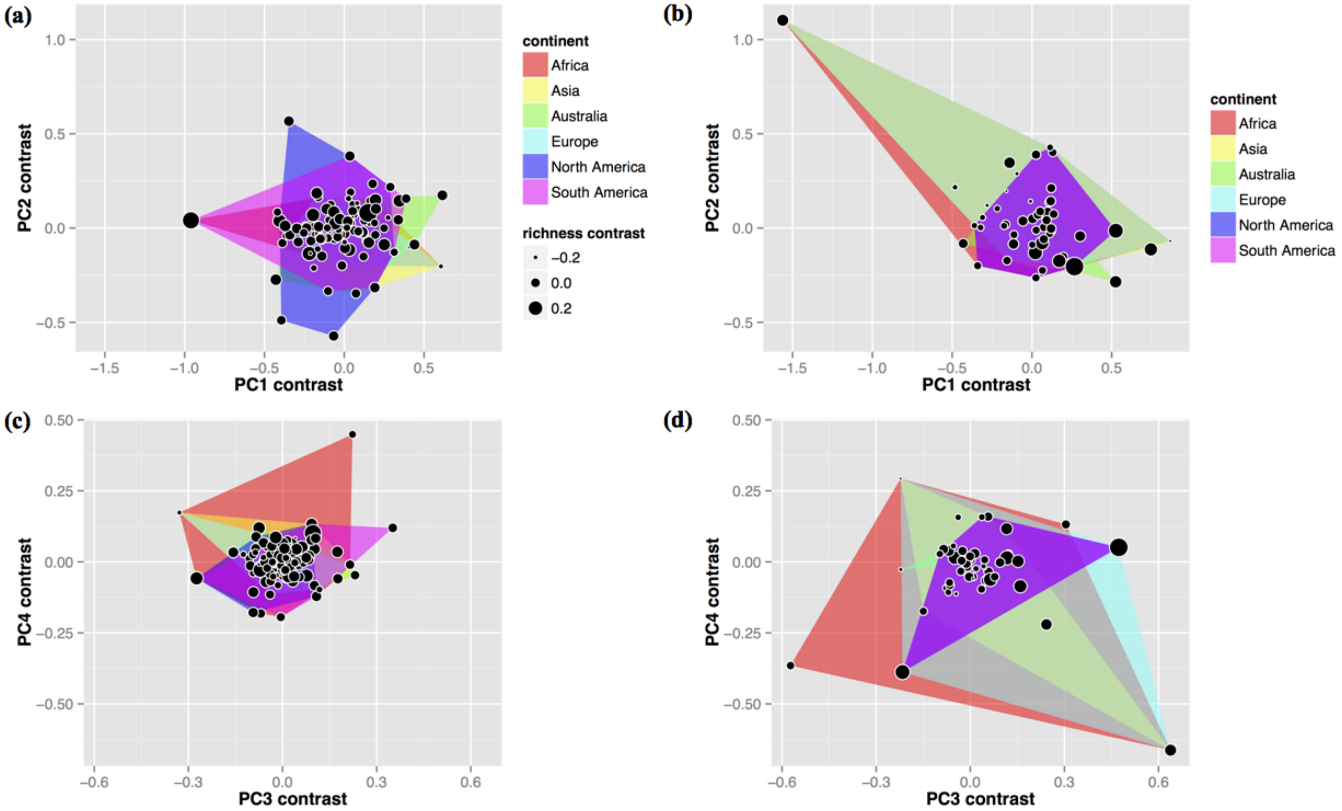


Figure 4.6. Climatic instability space of herbivorous mammals.

Instability described by (a-b) PCs 1-2 and (c-d) PCs 3-4 for hindgut and foregut-fermenting mammals across their continental distributions are shown, respectively. The colored polygons define the instability that taxa on each continent experienced, such that areas that overlap delineate instability found across multiple continents. The size of each point indicates the genus richness of the corresponding phylogenetic node.



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CHAPTER V

CONCLUSION

Current understanding of the effects of biotic and abiotic controls on diversity proposes a complete disjunction in the temporal and spatial scales of these two classes of factors. In the multilevel mixed model (Benton 2009), biotic factors such as interspecific competition predominately govern diversity dynamics over short to intermediate timescales and small to intermediate geographical scales. Conversely, abiotic factors such as changes in climate appreciate in importance while the influence of interspecific interactions wanes over intermediate to longer temporal and larger geographical scales (Benton 2009).

The current framework presents a generalized, and therefore necessarily simplistic, model of the effects of biotic and abiotic factors on diversity. The generalizability of this model across the clades comprising the tree of life is questionable given the multitude of differences observed between clades. Clade-level differences in biological traits and ecological environments are expected to have especially large impacts on the temporal and spatial scales at which biotic and abiotic factors operate. The current multilevel mixed model does not incorporate the effects of such clade-specific differences. In this dissertation, I compared diversification outcomes between groups of herbivorous mammals differing in digestive strategy at multiple taxonomic (Chapters II-IV), temporal (Chapters II, IV), and spatial (Chapters II, IV) scales to evaluate the scales at which biotic and abiotic factors predominate while explicitly considering the biological and ecological contexts of clades.

For genera of herbivorous mammals, this dissertation showed that both biotic and abiotic factors were important controls on species richness over short timescales and intermediate geographical scales (Chapter IV). Similarly, the influences of both biotic and abiotic factors were detected at long timescales and large geographical scales for two subfamilies of herbivorous primates (Chapter II). These two findings amend the current multilevel mixed model by extending the temporal and spatial axes delimiting the effects of biotic and abiotic factors. Only at intermediate temporal and geographical scales is the multilevel mixed model supported for the herbivorous mammals. Consistent with the multilevel mixed model, evidence from this dissertation strongly indicates that abiotic factors had a prominent role on the speciation of herbivorous families at intermediate temporal and geographical scales (Chapter III).

Regardless of which class of factors more strongly controlled diversity, this dissertation also showed that the effects, whether individual or joint, of biotic and abiotic factors are not homogenous across the herbivorous mammals. In particular, the strength of biotic and/or abiotic effects was found to differ between the foregut and hindgut-fermenting mammals at short timescales and intermediate geographical scales (Chapter IV) as well as at intermediate temporal and geographical scales (Chapter III). Therefore, not only do the spatiotemporal effects of biotic and abiotic factors deviate from proposals of the current framework, the effects of these factors themselves appear to be sensitive to biological and ecological differences within and among clades. Overall, this dissertation provides compelling evidence that the effects of biotic and abiotic factors on diversity, and their dependence on temporal and geographical scales, are unlikely to be fully captured by the generalized framework of the multilevel mixed model and will need to be assessed individually on a clade by clade basis, informed by specialist knowledge of the biology and ecology of clades, in order to intelligently advance the understanding of important controls on biodiversity in the future.

Macroevolutionary studies attempt to uncover general rules regulating diversification across the tree of life. This dissertation reveals that general rules, ranging from the early burst model to the multilevel mixed model, are not applicable across all taxonomic and spatiotemporal levels. Even at the same scales, the sensitivity of diversification dynamics to differences in species-specific biological and ecological traits likely will generate deviations that challenge generalized rules. Together, the findings in this dissertation indicate that the most important long-term contribution of macroevolution lies not with the discovery of all-encompassing general rules, but in the careful investigation of the rules of diversification for individual clades with an explicit consideration of why clades differ and how such differences affect their trajectories and outcomes. The clade-specific rules in totality will better reflect the complexity that is inherent in the tree of life.

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