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Mutualism with Plants Drives Primate Diversification

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Abstract.—Understanding the origin of diversity is a fundamental problem in biology. Evolutionary diversification has been intensely explored during the last years due to the development of molecular tools and the comparative method. However, most studies are conducted using only information from extant species. This approach probably leads to misleading conclusions, especially because of inaccuracy in the estimation of extinction rates. It is critical to integrate the information generated by extant organisms with the information obtained from the fossil record. Unfortunately, this integrative approach has been seldom performed, and thus, our understanding of the factors fueling diversification is still deficient. Ecological interactions are a main factor shaping evolutionary diversification by influencing speciation and extinction rates. Most attention has focused on the effect of antagonistic interactions on evolutionary diversification. In contrast, the role of mutualistic interactions in shaping diversification has been much less explored. In this study, by combining phylogenetic, neontological, and paleontological information, we show that a facultative mutualistic plant–animal interaction emerging from frugivory and seed dispersal has most likely contributed to the diversification of our own lineage, the primates. We compiled diet and seed dispersal ability in 381 extant and 556 extinct primates. Using well-established molecular phylogenies, we demonstrated that mutualistic extant primates had higher speciation rates, lower extinction rates, and thereby higher diversification rates than nonmutualistic ones. Similarly, mutualistic fossil primates had higher geological durations and smaller per capita rates of extinction than nonmutualistic ones. As a mechanism underlying this pattern, we found that mutualistic extinct and extant primates have significantly larger geographic ranges, which promotes diversification by hampering extinction and increasing geographic speciation. All these outcomes together strongly suggest that the establishment of a facultative mutualism with plants has greatly benefited primate evolution and fueled its taxonomic diversification. [Diversification; extinction; fossils; mutualism; primates; seed dispersal; speciation.]

Understanding the origin of diversity is a fundamental problem in biology. Evolutionary diversification, the increase in taxonomic diversity, is a consequence of a decrease in extinction rates and/or an increase in speciation rates. Evolutionary diversification can be prompted by the use of a new resource little used by competing taxa, a phenomenon denominated ecological opportunity (Simpson 1953; Schluter 2000; Losos 2010). Ecological interactions are a main factor affecting diversification by modifying ecological opportunities (McPeek 1996, 2008; Thompson 2004) and influencing both speciation and extinction rates (Schluter 2000; Thompson 2004; Ricklefs 2010). Ecological interactions influence diversification by their intermediate effects on some species-level traits favoring speciation and lessening extinction (Simpson 1953; Schluter 2000). Geographic range is a species property widely associated with high speciation (Gaston 2003), low extinction risk (Jablonski 2005, 2008; Goldberg et al. 2011), and taxon longevity (Kiessling and Aberhan 2007; Crampton et al. 2010) in many disparate fossil and recent organisms.

Ecological interactions may be both antagonistic, such as herbivory, parasitism, predation, or competition, as well as mutualistic, such as pollination or seed dispersal. Antagonistic interactions, especially competition and parasitism, have been widely recognized as diversification drivers through well-known mechanisms like competition-driven adaptive radiation, escape and radiation coevolution, or diversifying coevolution (Thompson 2004; Mckenna et al. 2009; Winkler et al. 2009; Yoder and Nuismer 2010). Theoretical models have shown that mutualistic interactions may also fuel diversification (Grant 1949; Kiester et al. 1984). However, although the role of mutualistic interactions in shaping and driving diversification has been sometimes recognized (Crane et al. 1995; Sargent 2004; Hu et al. 2008; Lengyel et al. 2009), the empirical support is still scarce because different lines of evidence are contradictory (Herrera 1989; Eriksson and Bremer 1992; Kay and Sargent 2009; Yoder and Nuismer 2010).

Evolutionary diversification has been intensely explored during the last years due to the development of molecular tools and the comparative method (Quental and Marshall 2010; Ricklefs 2010). However, most studies are conducted using only information from extant species. This approach probably can lead to misleading conclusions, especially because of inaccuracy in the estimation of extinction rates (Quental and Marshall 2010; see Rabosky (2010) for a discussion on why extinction rates should not be estimated in the absence of fossil data). It is critical to integrate the information generated by extant organisms with the information obtained from the fossil record (Wilkinson et al. 2011). Unfortunately, this integrative approach has been seldom performed, and thus, our understanding of the factors fueling diversification is still deficient. In this study, by combining molecular, neontological, and paleontological information, we explore the importance of mutualism as a driving factor in the diversification of our own lineage, the Primates. Primates represent a very appropriate group to perform this investigation since there is much information on phylogeny, ecology, anatomy, morphology, physiology, behavior, and socioecology of extant and extinct species.

Primates (the mirorder Primatomorpha including closely related orders, Plesiadapiformes and Euprimates) apparently originated during the Cretaceous, around 80–90 Ma (Tavaré et al. 2002; Miller et al. 2005; Steiper and Young 2006; Martin et al. 2007). Since then, primate diversity has been increasing until reaching a maximum diversity in the Holocene (Martin et al. 2007), including at present day around 400 species (Groves 2005). Primate diversification has been associated with increasing in body size (Gittleman and Purvis 1998; Paradis 2005; Freckleton et al. 2008; FitzJohn 2010; Cooper and Purvis 2010; Matthews et al. 2011) and parasite richness (Nunn et al. 2004), although outcomes are inconclusive and contradictory. Primates frequently interact with plants since the diet of most primates is almost exclusively composed of several plant parts (Lambert 2010). These ecological interactions with plants can be antagonistic or mutualistic. The main antagonistic interactions in which primates are involved are folivory, seed predation, and exudativory (Hohmann 2009; Burrows and Nash 2010). Although some lemurs and Platyrrhines may occasionally act as pollinators, the main mutualism in which primates are involved is seed dispersal (Lambert and Garber 1998; Lambert and Chapman 2005). Seed dispersal is considered the most important ecosystem service provided by primates (Chapman and Russo 2006) and has been proposed as a major driver of angiosperm phenotypic evolution and diversification (Tiffney 2004). Fruit consumption and seed dispersal have been even invoked as a factor shaping the adaptive origin and evolution of primates (Sussman 1991; Dominy and Lucas 2001; Soligo and Martin 2006). Body size and vision type (monochromatic, dichromatic, and trichromatic) are the two most frequently invoked organismic traits affecting primate diet and seed dispersal ability (Fleagle 1999; Lucas et al. 2007). An increase in body size is associated with a higher proportion of leaves in the diet, although almost all primates (with the exception of the subfamily Colobinae) regardless of body size can consume fruit for their carbohydrates, along with gums/saps (Lambert 2010). Similarly, the occurrence of trichromatic vision seems to increase the efficiency in the consumption of fruits and leaves (Fleagle 1999; Lucas et al. 2007), although other factors related to sexual selection and predator detection have also been invoked (Surridge et al. 2003).

In this study, we test whether primate diversification was driven by diet or ecological role (mutualistic vs. antagonistic) by calculating their effect on speciation and extinction rates from molecular dated phylogenetic trees (Chatterjee et al. 2009; Fabre et al. 2009). In addition, we reviewed the paleobiological literature and recorded the changes in diet and ecological role through geological time and their effects on species longevity and per capita rate of origination and extinction of primate species (Liow et al. 2008). Finally, we also explored the mechanisms putatively involved in the mutualism-mediated primate diversification by testing how vision type and body size affected geographic range through their intermediate effects on ecological traits (diet and mutualism).

MATERIALS AND METHODS

Extant Primate Diet and Interaction

We reviewed the literature to determine the diet and the ecological role (mutualistic vs. antagonistic) of 381 primate species (see below and supplemental Appendix S1 at http://datadryad.org, doi:10.5061/dryad.kh21qb76). We used the diet categories used by primate biologists: faunivory (including insectivory and meat-eating), folivory, frugivory (consuming any part of the plant's reproductive structures, such as green fruits, fleshy fruits, ripe seeds, unripe seeds, etc.), and exudativory. In addition, we checked the ecological literature and scored the type of items consumed by each species of primates. We considered the following items: fleshy fruits, dry fruits, seeds, flowers, leaves, gum, bark, nectar, fungi, vertebrates, and insects. Finally, we also recorded the primate species that have been observed dispersing seeds (Appendix S1). We considered as mutualistic those primate species where seed dispersal has been accurately detected. Antagonistic primates were those consuming leaves, green fruits, dry fruits, seeds, flowers, bark, gum, fungi, and animals.

Fossil Primate Diet and Interaction

We reviewed the paleontological and paleoanthropological literature to determine the diet and ecological role of as many fossil primate species as possible (see below and Appendix S2). We have used the same diet categories that those used by neontological primatologists to categorize fossil primate diet: faunivory (including insectivory and meat-eating), folivory, frugivory (including frugivory sensu stricto and granivory), and gumnivory. We have added nectarivory since many paleoanthropologists concur that some species belonging to the plesiadapiform family Picrodontidae that lived during the Paleocene were primarily nectarivores (Fleagle 1999). Paleontologists have inferred fossil diet using information coming from different sources, such as body size, dental functional morphology, enamel structure and thickness, mandibular biomechanics, shearing crest analysis, dental microwear, stable isotope analysis, and paleoarchaeology (Ungar 2007; Hublin and Richards 2009). When several sources disagree about the diet of a given primate, we (i) assigned the diet considered by most studies, (ii) used the most recent study, or (iii) repeated our statistical analyses using both diets when they were published at the same time. We did not consider those studies using only body size as an estimator of diet, to avoid any circularity in subsequent analyses including body size (see Structural Equation Modeling section). In total, we compiled information on the presumed diet of 469 primate fossil species (Appendix S2).

Afterward, we categorized each fossil primate as mutualistic (seed disperser) or antagonistic based on the type of diet and the information provided by the different authors. We used a very conservative criterion to minimize any effect of misclassification on our conclusions: we categorized as seed dispersers any species considered by paleontologists to consume ripe fleshy fruits even occasionally, as fallback strategy. Doing so, we ensure that any extinct species behaving as seed dispersers even occasionally and ineffectively will be categorized as mutualistic. This is a conservative approach because it goes up against our main hypothesis of mutualism's positive effect on primate evolution and diversification. So, if we consider as mutualistic some fossil species that in reality behave mostly as antagonists, any detected positive effect of mutualism on primate evolution will appear despite this noise. Nevertheless, in neontological studies, most ecologists consider a given primate as seed disperser independently of the interaction frequency or effectiveness (Lambert and Garber 1998; Lambert and Chapman 2005; Chapman and Russo 2006; Lambert 2010).

Fossil and Extant Primate Body Mass

We obtained data on body mass for 280 extant and 469 extinct primates. This information was obtained from the PanTHERIA database (http://consblog.org/index.php/2009/08/18/pantheria/) (Jones et al. 2009) and The Primata (http://www.theprimata.com/) Web site and completed with data on specific taxa using the literature. Data of fossil primates were obtained from the Paleobiology Database (http://paleodb.org) on 15 November 2010 and completed with data on specific taxa using the literature (http://primatelit.library.wisc.edu).

Geographic Range Size of Extant Primates

We estimated the geographic range size of the primate species used in our study (excluding *Homo sapiens*) using the maps hosted on the International Union for Conservation of Nature (IUCN) Web site (http://www.iucnredlist.org/). In addition, we use two other complementary sources: the supplementary material provided in Redding et al. (2010) and the resources hosted on the Web site of the Laboratório de Mastozoologia e Manejo de Fauna Sector de Primatas, Departamento de Zoologia, Universidade Federal de Minas Gerais (Brazil) (http://www.icb.ufmg.br/zoo/primatas/bdp_indexgtm.htm), maintained by Prof. Dr Anthony Brome Rylands.

For each extant primate species, we determined the extent of occurrence (EOO) as the area that lies within the outermost geographic limits to the occurrence of the species (Gaston and Fuller 2009). EOO is the standard metric used by IUCN to categorize the threat status of species. In addition, the information provided by the sources did not distinguish between the EOO and the area of occupancy or the area within the EOO where the species actually occurs.

The distribution range of each extant primate species was estimated by downloading the maps for each primate species and afterward quantifying the EOO using the public domain image-processing software ImageJ (http://rsbweb.nih.gov/ij/).

Geographic Range Proxy of Extinct Primates

A proxy of the geographic range size of extinct primates was calculated based on the latitudinal and longitudinal components of the total geographic range. We used the information appearing in the Paleobiology Database (http://paleodb.org) on 15 November 2010. We obtained the spatial location of the primate collection records using primate genera rather than species to overcome problems with geographic singularity and low sample size (Liow et al. 2008). The original data set contains 3611 occurrences of 266 primate genera from the Paleocene to the Holocene. However, we excluded from further analyses those genera having only one occurrence locality, which resulted in 3442 occurrences from 148 genera. To estimate the geographic range size of these taxa, we used the paleogeography (paleolatitudes and paleolongitudes) rather than the recent geographic variables since it offers a more accurate description of the distribution of fossil organisms (Payne and Finnegan 2007). Several approaches have been used to estimate geographic range when there is no information on the exact shape of the distribution area. To avoid any assumption of their distribution shape, we modeled the distribution range of all fossil primates as an ellipse. Thus, we calculated the difference between maximum and minimum paleolatitude and paleolongitude for each primate genera (excluding *Homo*) and considered them as the two main axes of an elliptical geographic range.

Phylogenetic Analyses of Diversification, Ancestral States, and Trait Conservatism in Extant Species

We used 3 different dated phylogenies containing 273 species (Fabre et al. 2009) (Fabre phylogeny), 354 species (Fabre et al. (2009) grafting nonsequenced species on the basis of the taxonomy of Groves 2005) (Groves phylogeny), and 218 species (Chatterjee et al. 2009) (Chatterjee phylogeny). Both Fabre and Chatterjee phylogenies are fully resolved but do not contain all the primate species. In contrast, Groves phylogeny has several polytomies but contains most primate species. These are the two cases of incompletely resolved phylogenies that can be used to infer the effect of a trait on speciation and extinction without complete phylogenetic information (FitzJohn et al. 2009). Fabre's and Chatterjee's trees represent skeleton phylogenies (a fully resolved tree for a random sample of species whose states are fully known), whereas the Groves tree represents a terminally unresolved phylogeny (a tree including all extant species which is fully resolved except for terminal clades that are unresolved and whose character states are known to varying degrees). When character states are fully known, as in our case, the terminally unresolved phylogenies provide higher statistical power to detect differential diversification (FitzJohn et al. 2009).

Using these three phylogenies, we tested mutualism-driven diversification following the binary state speciation and extinction (BiSSE) approach (Maddison et al. 2007) extended for incomplete phylogenies (FitzJohn et al. 2009). This method allows us to estimate mutualism effect on speciation and extinction while taking into account the rates of changes between antagonism and mutualism. The model estimates 6 parameters (speciation rate for antagonism [λ0] and mutualism [λ1], extinction rates for antagonism [μ0] and mutualism [μ1], and rate changes from antagonism to mutualism [q01] and vice versa [q10]). We computed the posterior probability of these parameters under a Bayesian framework after specifying an exponential prior for the 6 parameters.

Diversification driven by diet was tested with the multistate speciation and extinction (MuSSE) model, which is the multiple-character extension to BiSSE. MuSSE allows not only modeling characters with more than two states but also modeling combinations of characters. Therefore, we applied the MuSSE model to study the combined effect of mutualism and diet into diversification rates. This method is only implemented for skeleton trees and therefore could not be used for the Groves phylogeny. To determine whether mutualism affects diversification rate independently of frugivory, we quantified the diversification rate of mutualistic and antagonistic primates in relation to diet (Table S1).

Diversification driven by geographic range was tested with the quantitative state speciation and extinction (QuaSSE) (FitzJohn 2010) model, which is the quantitative-character extension to BiSSE. Only skeleton trees can be used with this method. QuaSSE is a computationally demanding method, and therefore, the likelihood function was used in maximum likelihood and not in Bayesian inference. We compared the likelihood of a model with constant speciation and extinction rates with the models in which the speciation and/or the extinction rates were set to a linear function. Model comparison was assessed with a likelihood ratio test. All the three models (BiSSE, MuSSE, and QuaSSE) were run in the *diversitree* package for R. The likelihoods of the ancestral states of mutualism were calculated using BiSSE in the *diversitree* package.

The evolutionary conservatism of diet and mutualism was determined by estimating the significance of the phylogenetic signal in the 3 primate phylogenies following Maddison and Slatkin (1991). This test estimates whether the minimum number of evolutionary steps in a character on a phylogenetic tree is lower than expected by chance. Whether the steps occurred less than expected by chance was determined under a null model in which data were reshuffled 1000 times across the tips of the phylogeny. These tests were performed with Mesquite 2.74 (http://mesquiteproject.org). In these analyses, we included gumnivores within folivores due to its low sample size.

Taxon Duration

The durations of the fossil primates were estimated as the stratigraphic range of the fossil primate genera. We conservatively used as taxonomic resolution for performing this analysis the level of genus because (i) the stratigraphic ranges of species are usually too small and are difficult to include in any statistical test using the fairly coarse stratigraphic resolution we have to use (Strauss and Sadler 1989) and (ii) this approach avoids any error associated with unclear temporal occurrences of rare and cryptic species. In addition, we did not include in these analyses the information on extant genera, to avoid any bias due to the higher knowledge of present fauna.

Data were obtained from the Paleobiology Database (http://paleodb.org) on 15 November 2010. To compare the untruncated taxa duration, we removed from our data set all taxa appearing at localities 0.5 Ma and younger and we excluded all extant and subfossil taxa (Jablonski 2008). Afterward, we calculated an accurate estimate of the temporal duration of each primate genus by calculating the maximum temporal range as

$$R_t = R_0(H+1)/(H-1),$$

where R_t is the estimated theoretical time interval, R_0 is the observed stratigraphic range, and H is the number of stratigraphic levels in which a particular taxon occurs (Kiessling and Aberhan 2007). In our case, since we were working with a global data set, we considered as H the number of collections in the Paleobiology Database containing each taxon.

Per Capita Extinction and Origination Rates

To test whether mutualism was beneficial for primates along its evolutionary history, we studied the per capita rate of origination and extinction of mutualistic and antagonistic primate species in the fossil record using the boundary-crossing methodology (the number of fossil primates with their last or first occurrence, respectively, within a time period relative to the number of boundary-crossing primates surviving into the next time period).

We have followed the procedure of Jablonski (2008) to calculate the per capita extinction (q) and origination (p) rates of boundary-crossers. We tabulated whether a genus was recorded as present or absent during each Cenozoic stage. If a genus was absent during one or more stages but was present in stages before and after those absences, we assumed that it was also present in those time intervals. Per capita extinction and origination rates were calculated for mutualistic and antagonistic genera separately as

$$p = \ln(N_{\mathbf{t}}/N_{\mathbf{bt}})/\Delta t,$$
$$q = \ln(N_{\mathbf{b}}/N_{\mathbf{bt}})/\Delta t,$$

where N_{bt} is the number of taxa crossing both the bottom and the top boundary of a given stage, N_t is the number of taxa crossing only the later boundary, N_b is the number of taxa crossing only the bottom boundary, and Δt is the duration of that given stage in Ma (Strauss and Sadler 1989).

Structural Equation Modeling

We performed a structural equation modeling (SEM) with the extant species in order to test the direct and indirect relationships between the two organismic-level traits (vision type and body size), the ecological traits (diet type and ecological role), and the species-level trait (geographic range) (Fig. S1). Vision type was modeled as 1 = monochromatic vision, 2 = dichromatic vision, and 3 = trichromatic vision. Ecological role was modeled as 0 = antagonism and 1 = mutualism. Diet type was modeled as 0 = faunivory, 1 = gumnivory, 2 = folivory, and 3 = frugivory. We used as variance–covariance matrix the matrix of pairwise covariances between the standardized phylogenetic independent contrasts of all the study traits. The procedure was applied to Fabre and Chatterjee phylogenies. We validated the relationships found in this phylogenetically informed SEM by means of phylogenetic generalized linear models (GLMs). Both standardized independent contrasts and phylogenetic GLMs were performed with library *ape* in R (Paradis and Claude 2002). The likelihoods of the ancestral state of vision type was calculated using MuSSE in the *diversitree* package.

Afterward, we performed an SEM with fossil primates, including the information on geographic range, stratigraphic duration, body mass (in log), diet, and mutualistic role of 264 fossil genera. Diet and mutualism were coded as in previous SEMs. We have also included in these models the age (in Ma) of the fossils to control for differences due to geological time. In both types of SEMs, we performed a saturated model, relating all variables among them, and one confirmatory model where we used the previous information to link variables. To select the best fitting model(s), we performed an information-theoretic approach (Burnham and Anderson 2002) (see Supplementary Information). All analyses were performed with library *sem* in R.

RESULTS AND DISCUSSION

Mutualism-Driven Diversification of Extant Primates

We found that 64% of the extant species are frugivores, 26% are folivores, 7% are faunivores, and 3% are exudativores ($N = 381$ studied species). However, 96% of the primate species at least occasionally consume ripe or unripe fleshy fruits. Our review indicates also that 58% of the primate species disperse seeds of several to many plant species (Appendix S1), behaving as legitimate dispersers for the plants. Seed dispersal was not circumscribed to frugivorous primates since some folivorous species (e.g. *Alouatta*) are effective seed dispersers, whereas some frugivores (e.g., *Cacajao*, *Pithecia*) are antagonistic rather than mutualistic because they consume mostly green fruits and seeds and thus destroy the seeds. Mutualism was strongly phylogenetically conserved (Fig. 1), indicating that close relatives were more similar in seed dispersal ability than expected by chance. In addition, molecular phylogenies showed that ancestral primates were antagonistic (Fabre: proportional likelihood = 0.99; Chatterjee: proportional likelihood = 0.96). The most accepted view on primate origin assumes that this mammalian order arose from a small-body insectivorous ancestor (Soligo and Martin 2006). Our outcome agrees with this idea since it suggests that ancestral primates were not mutualistic but probably ate on insects or leaves.

We found that all tested phylogenies showed higher speciation rate in mutualistic than in antagonistic primates (0.28 vs. 0.20, 0.27 vs. 0.22, and 0.20 vs. 0.14, respectively, for Fabre, Groves, and Chatterjee phylogenies; see Table 1 for statistical differences). Furthermore, extinction rates were lower in mutualistic than in antagonistic primates (0.11 vs. 0.17, 0.08 vs. 0.19, and 0.05 vs. 0.08; see also Table 1). Consequently, the diversification rates were consistently higher in mutualistic clades than in antagonistic ones (Fig. 2). Diversification rate was also higher in frugivorous primates, but we found that mutualistic primates diversified at higher rate than antagonistic ones both within nonfrugivorous and within frugivorous clades (Table 1). These outcomes suggest that frugivory has favored the diversification of the primates, but they also strongly indicate that diversification speeded up if these frugivorous primates are also seed dispersers.

Mutualism-Driven Diversification of Extinct Primates

We found that 19% fossil species ($N = 469$ species) are classified as faunivores by paleontologists, 27% as folivores, 52% as frugivores (consuming seeds and fleshy and hard fruits), and less than 1% were classified as exudativores and nectarivores. The proportion of species belonging to each diet category significantly differed between extinct and extant species ($\chi^2 = 35.35$, $P < 0.0001$, $N = 964$ spp.; likelihood ratio test), faunivores being overrepresented and frugivores underrepresented in the fossil record. Nevertheless, the proportion of primates with different diet changed through the Cenozoic period ($\chi^2 = 81.94$, df = 3, $N = 285$, $P = 0.0001$, logistic regression; Fig. S2) since faunivores decreased and plant-consuming primates increased from Paleocene to Holocene. Whereas in the Paleocene 44% of the fossil primates were faunivores, 44% were frugivores, and 7% were folivores, during the Holocene only 5% were faunivores, 19% were folivores, and 76% were frugivores. Nevertheless, it seems that primates quickly started to consume plants, frugivory apparently being previous to folivory. The "herbivorous feeding adaptation" hypothesis (Szalay 1968; Szalay and Delson 1979; Silcox et al. 2007) argued that the first primates differentiated from an ancestral stock through feeding adaptations in a burgeoning frugivorous and herbivorous arboreal niche.

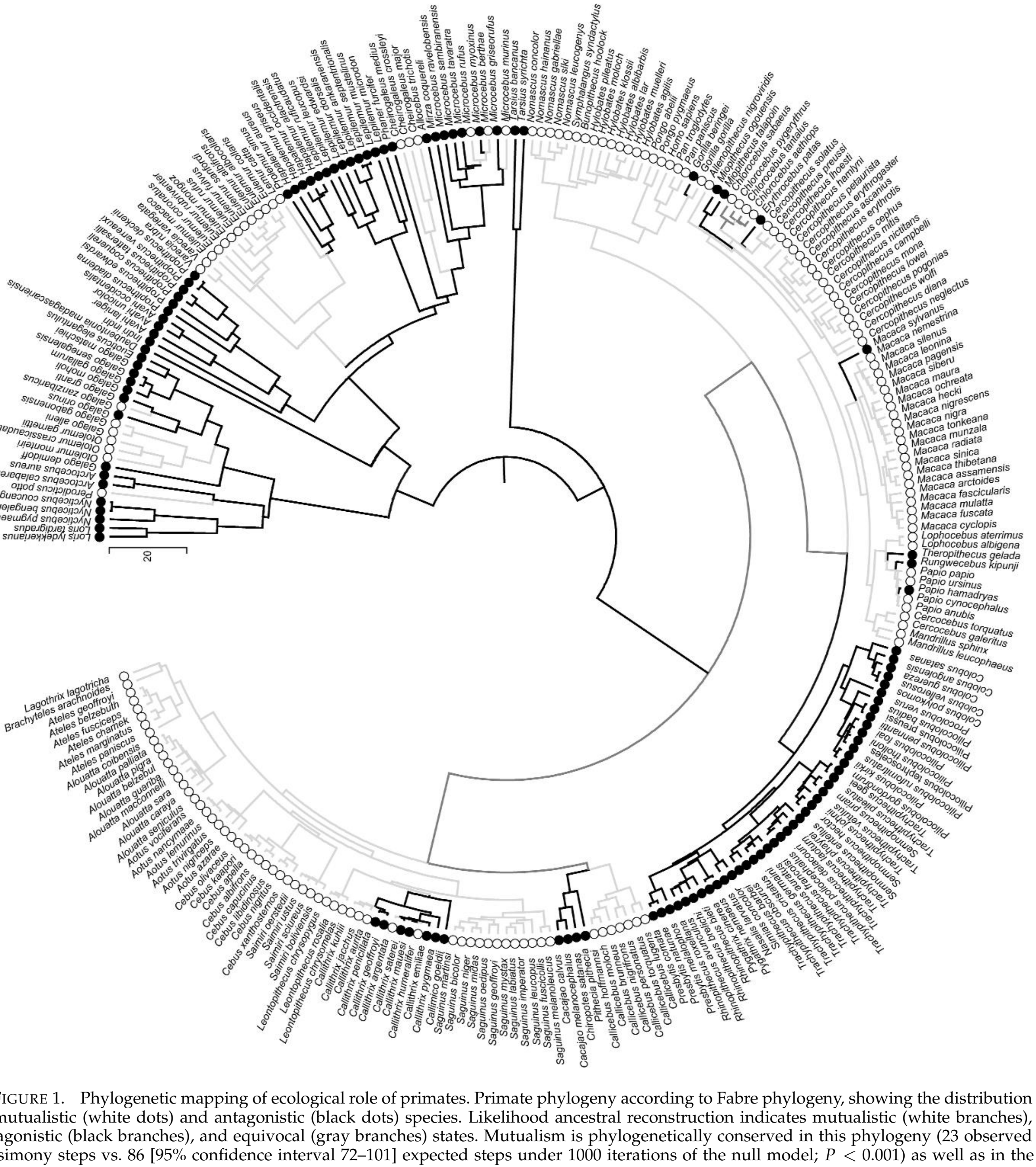

FIGURE 1. Phylogenetic mapping of ecological role of primates. Primate phylogeny according to Fabre phylogeny, showing the distribution of mutualistic (white dots) and antagonistic (black dots) species. Likelihood ancestral reconstruction indicates mutualistic (white branches), antagonistic (black branches), and equivocal (gray branches) states. Mutualism is phylogenetically conserved in this phylogeny (23 observed parsimony steps vs. 86 [95% confidence interval 72–101] expected steps under 1000 iterations of the null model; $P < 0.001$) as well as in the other two—not shown—study phylogenies (Chatterjee phylogeny, 22 observed vs. 65 [54–76] expected steps, $P < 0.001$; Groves phylogeny, 28 observed vs. 126 [111–140] expected steps, $P < 0.001$).

Our results are consistent with this hypothesis since in Paleocene there were already many primates feeding on plants.

We found that the proportion of fossil species potentially being mutualistic was only 39%, a proportion significantly lower than in extant primates ($\chi^2 = 32.47$, $P < 0.0001$, N = 937 spp.; likelihood ratio test). More interesting, the proportion of mutualistic primates increased gradually through the Cenozoic from 33% in the Paleocene to 48% in the Holocene ($\chi^2 = 5.37$, df = 1, $P = 0.02$, logistic regression; Fig. S2). Consequently, paleontological and neontological data agree,

TABLE 1. Effect of diet and ecological role on primate diversification

	Groves phylogeny			Fabre phylogeny			Chatterjee phylogeny		
	λ	μ	r	λ	μ	r	λ	μ	r
Diet									
Faunivore > folivore				0	0	0.729	0.068	0.340	0.100
Faunivore > frugivore				0	0.029	0.009	0.025	0.292	0.008
Folivore > frugivore				0.525	0.856	0.005	0.203	0.420	0.158
Ecological role									
Antagonist > mutualist	0.128	0.908	0	0.068	0.805	0	0.097	0.670	0.010
Diet × ecological role									
Nonfrugivorous antagonistic > nonfrugivorous mutualistic				0.447	0.765	0.187	0.180	0.348	0.410
Nonfrugivorous antagonistic > frugivorous antagonistic				0.477	0.942	0.036	0.272	0.583	0.204
Nonfrugivorous antagonistic > frugivorous mutualistic				0.096	0.868	0	0.096	0.584	0.013
Nonfrugivorous mutualistic > frugivorous antagonistic				0.548	0.643	0.411	0.631	0.689	0.385
Nonfrugivorous mutualistic > frugivorous mutualistic				0.272	0.561	0.271	0.493	0.704	0.257
Frugivorous antagonistic > frugivorous mutualistic				0.166	0.389	0.264	0.330	0.550	0.293

Notes: Outcomes of analyses contrasting speciation (λ), extinction (μ), and diversification (r) rates among diet and ecological role categories using the 3 phylogenies. The effect of ecological role was tested with BiSSE, whereas diet and diet × ecological role were tested with MuSSE. Numbers in the cells indicate the proportion of 1000 Markov chain Monte Carlo runs in which the differences in λ, μ, or r followed the trend specified in each line (λ value in the first line of diet comparisons indicates that none of the 1000 runs showed that faunivores had higher speciation rates than folivores).

both showing a gradual increase in the importance of mutualism through primate history.

Mutualistic primates had similar rates of origination (0.23 ± 0.07 vs. 0.27 ± 0.06, $P = 0.17$, respectively) but smaller rates of extinction than antagonistic ones (0.11 ± 0.08 vs. 0.17 ± 0.06, $P = 0.02$; Table S1). We found that mutualism did affect the longevity of primates (Tables S2 and S3 and Fig. S3). The observed and maximum stratigraphic ranges of mutualistic primates were 5.73 ± 0.40 and 10.77 ± 1.00 myr ($N = 114$), whereas stratigraphic ranges for antagonistic primates were 4.14 ± 0.32 and 7.43 ± 0.88 myr, respectively ($N = 171$). The effect of mutualism on species longevity was evident at any time during the Cenozoic since no interaction between mutualism and geological epoch was found (Tables S2 and S3). Diet affected the observed but not the maximum temporal range (Tables S2 and S3). This weak effect was mostly due to the 3 Paleocene nectarivorous genera from Picrodontidae that occurred only during 3.63 ± 2.5 myr. When comparing only within frugivores, we found that the stratigraphic range of antagonistic primates (3.31 ± 0.65 myr, $N = 48$) was significantly smaller than that of mutualistic ones (5.78 ± 0.43 myr, $N = 111$; $F = 10.05$, $P = 0.002$, one-way analysis of variance; Fig. S3). Again, it seems that paleontological data agree with neontological data since both suggest that mutualism shaped primate diversification by hampering extinction and increasing species longevity and probably speciation.

Causal Models of Mutualism-Driven Diversification

Extinction risk and threat status are negatively associated with broad geographical range in many fossil and extant organisms, including primates (Purvis et al. 2000; Harcourt 2002; Payne and Finnegan 2007; Cardillo et al. 2008; Redding et al. 2010). In addition, a positive relation between geographic range and speciation rate is assumed because, all other factors being equal, broad geographical ranges are more likely to be broken by barriers or to bud off peripheral isolates, than narrow ranges (Maurer 1999; Gaston 2003).

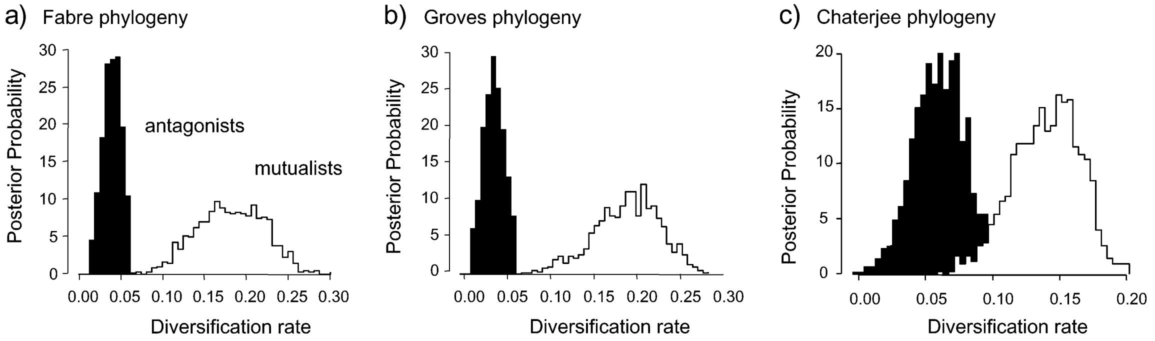

FIGURE 2. Mutualism and taxonomic diversification. The posterior probability distribution of diversification rates of mutualistic (white) and antagonistic (black) primates are calculated on the basis of (a) Fabre phylogeny, (b) Groves phylogeny, and (c) Chatterjee phylogeny. In all cases, mutualistic primates diversify more than antagonistic ones.

TABLE 2. Diversification of primates driven by geographic range

Models	df	LnLik	AIC	χ^2	Probability	Parameters
Fabre phylogeny						
λ constant, μ constant	3	−1213.7	2433.4			
λ linear, μ constant	4	−1211.6	2431.1	4.266	0.0389	$\lambda = 0.206 \pm 0.016x$, $\mu = 0.209$
λ constant, μ linear	4	−1213.2	2434.3	1.094	0.2955	
Chatterjee phylogeny						
λ constant, μ constant	3	−949.32	1904.6			
λ linear, μ constant	4	−947.00	1902.0	4.641	0.0312	$\lambda = 0.073 \pm 0.024x$, $\mu = 0.096$
λ constant, μ linear	4	−947.32	1902.6	3.995	0.0456	0.018

Notes: We contrasted a model in which speciation (λ) or extinction (μ) rate varied linearly with geographic range versus the constant model in which these rates were independent of the geographic range using the QuaSSE approach. Degrees of freedom (df), likelihood (LnLik), and Akaike information criterion (AIC) of each individual model are shown together with the chi-square test and its associate P value of the likelihood ratio test comparing both models. Last column shows the estimate of the speciation and extinction parameters for the best fitted model.

Furthermore, geographic range is also significantly associated with taxon longevity in some organism groups (Kiessling and Aberhan 2007; Crampton et al. 2010). Our phylogenetic analyses indicate that speciation increases with the geographic range whereas extinction is constant (Table 2). This outcome suggests that primates with larger geographic ranges have higher diversification (speciation–extinction) rates.

The SEMs revealed that mutualism directly affected geographic range of extant primates (Fig. 3a,b and Table S4). In fact, mutualistic primates had significantly broader geographic range sizes (767,000 ± 81,000 km^2, $N = 222$ species) than antagonistic ones (498,000 ± 95,000 km^2, $N = 159$ species). It seems, in contrast, that diet affects geographic range only indirectly through its effect on mutualism (Fig. 3a,b and Fig. S4), indicating that being frugivorous does not promote an expansion of the geographic range. Mutualism also affected positively longevity, and through this variable, geographic range of extinct primates (Figs. 3c and Table S5). These causal models suggest that the establishment of a mutualistic relationship between primates and plants produced an increase in their geographic ranges and temporal duration, which subsequently triggered an increase in speciation rate and a decrease in extinction probability. All these factors acting concurrently promoted a higher diversification rate of mutualistic primates over antagonistic ones. Mutualistic primates may have larger geographic ranges due to several nonexclusive reasons. For example, seed-dispersing primates increase the range of their own interacting partners (Chapman and Russo 2006) and consequently their own range. Mutualistic primates may also colonize new habitats by forming new associations with plant species that will not develop strong defenses against this new beneficial consumer.

Two organismic-level traits have been proposed as key innovation driving primates evolution and diversification: body size (Gittleman and Purvis 1998; Paradis 2005; Freckleton et al. 2008; Cooper and Purvis 2010; FitzJohn 2010; Matthews et al. 2011) and trichromatic vision (Dominy and Lucas 2001; Lucas et al. 2007; Jacobs 2009). Primates may be monochromatic (7.3%, $N = 28$ spp.), dichromatic (17.6%, $N = 67$ spp.), or trichromatic, whether routine trichromatic (43.1%, $N = 164$ spp.) or allelic trichromatic (31.8%, $N = 121$ spp.). When mapping vision system onto primate phylogeny, our likelihood reconstruction showed that the ancestral state is dichromatic (Fabre: proportional likelihood = 1.00; Chatterjee: proportional likelihood = 0.99; Fig. S5), as suggested by most evolutionary biologists and primatologists (Lucas et al. 2007). We also found that the type of vision was phylogenetically conserved ($P < 0.0001$). The type of interactions played by primates was significantly associated with their type of vision ($\chi^2 = 22.20$, $P < 0.0001$, likelihood ratio). Thus, 81.9% of mutualistic primates versus 65.4% of antagonistic primates had trichromatic vision. However, according to our SEMs, trichromatic vision affected diet just weakly (Fig. 3a,b).

Body mass positively affected diet (folivorous primates being significantly larger than frugivorous primates, and these two groups larger than gumnivores and faunivores; see also Tables S6 and S7) and mutualism (bigger primates were mutualists) in extant species (Fig. 3a,b). Body mass also positively related with diet of fossil primates (bigger primates were more frugivorous) and their longevity (bigger primates had greater stratigraphic ranges) (Fig. 3c), suggesting that increasing body mass may be positive for primates. Cope's rule postulates that lineages tend to evolve toward larger body size over time due to selective advantage of being larger (Hone and Benton 2005; Clauset and Erwin 2008). In fact, fossil primate body size seems to increase over evolutionary times from Paleocene to Holocene (0.786 ± 0.002, $t = 19.52$, $P < 0.0001$, log–log linear regression; Fig. S6).

CONCLUSION

This study shows that a facultative mutualism, seed dispersal, has probably contributed to diversification in primates, and this process is mostly mediated by the broadening of mutualists' geographic ranges. A main implication of this study is that any habitat loss and fragmentation process leading to a reduction in the

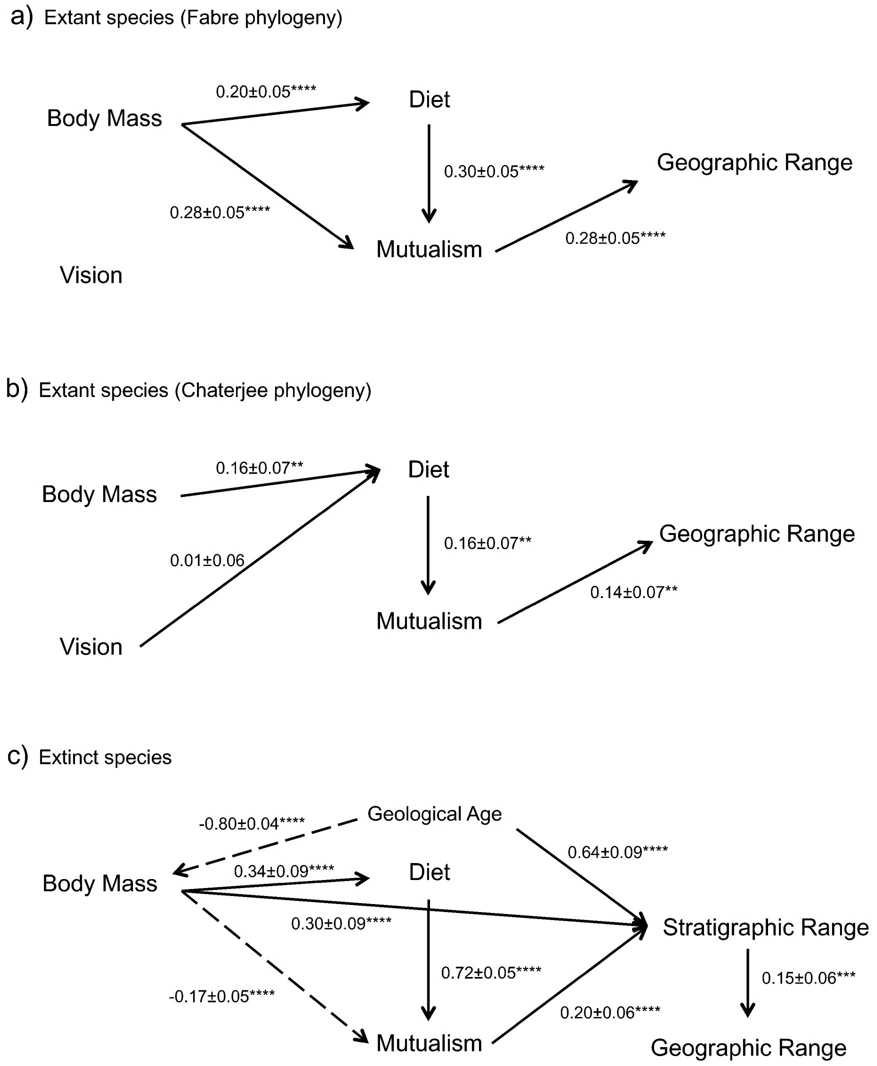

FIGURE 3. Linking organismic traits, ecological interactions, and macroecological processes. a) Best SEM ($\chi^2 = 10.04$, df $= 9$, $P = 0.347$; see Table S6 for model selection process) using data from extant primates and Fabre phylogeny as variance–covariance matrix ($N = 354$ spp.). Figures close to each significant arrow refer to the magnitude and the standard error of the path coefficients relating these two variables (**$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$). b) Best model ($\chi^2 = 11.47$, df $= 8$, $P = 0.176$) using data from extant primates and Chatterjee phylogeny as variance–covariance matrix ($N = 218$ spp.). c) Best model ($\chi^2 = 9.99$, df $= 7$, $P = 0.189$; see Table S7 for model selection process) using fossil primates ($N = 264$ genera).

geographic range of mutualistic primates (and other organisms) will jeopardize not just current biodiversity but also future biodiversity by collapsing their diversification. Conserving present-day ecological interactions will help to preserve future biodiversity.

SUPPLEMENTARY MATERIAL

Supplementary material, including data files and online-only appendices, can be found at http://datadryad.org, doi:10.5061/dryad.kh21qb76.

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