

The Role of Geography and Ecological Opportunity in the Diversification of Day Geckos (*Phelsuma*)

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Abstract.—We examine the effects of ecological opportunity and geographic area on rates of species accumulation and morphological evolution following archipelago colonization in day geckos (genus *Phelsuma*) in the Indian Ocean. Using a newly generated molecular phylogeny for the genus, we present evidence that these geckos likely originated on Madagascar, whereas colonization of three archipelagos in the Indian Ocean, the Seychelles, Mascarene, and Comoros Islands has produced three independent monophyletic radiations. We find that rates of species accumulation are not elevated following colonization but are roughly equivalent on all three isolated archipelagos and on the larger island of Madagascar. However, rates of species accumulation have slowed through time on Madagascar. Rates of morphological evolution are higher in both the Mascarene and Seychelles archipelagos compared to rates on Madagascar. This negative relationship between rate of morphological evolution and island area suggests that ecological opportunity is an important factor in diversification of day gecko species. [Adaptive radiation; Indian Ocean; molecular phylogeny; speciation. rate of evolution.]

Both geography and ecological opportunity are thought to play a key role in species diversification. Many species groups have diversified extensively upon reaching geographically isolated islands uninhabited by potential competitors (see Grant, 1998, and references therein). For example, in the Hawaiian islands, silverswords (Robichaux et al., 1990), songbirds (Lovette et al., 2002), and *Tetragnatha* spiders (Gillespie et al., 1994; Gillespie, 2004) have all speciated and diversified ecologically to a much greater extent than their closest mainland relatives. In many cases, these lineages have undergone adaptive radiations, in which a single ancestral species diversifies to fill a wide range of ecological niches (Schluter, 2000).

Most considerations of the role of ecological opportunity in diversification have focused on interspecific competition for resources (Grant, 1968; Schluter, 1988, 2000; Barton, 1996). In this framework, rates of diversification should be highest immediately following arrival in a new habitat (Simpson, 1944). After this initial stage, diversification might slow as niche space becomes filled (Schluter, 2000); alternatively, species might continue to diversify along additional axes, like coloration or behavior (Streelman and Danley, 2003).

Theory and empirical data suggest that most speciation is allopatric and initiated by geographic barriers to gene flow (Coyne and Orr, 2004) and often features ecological divergence of populations (reviewed by Rundle and Nosil, 2005). Geographic barriers permit local adaptation and spur phenotypic differentiation among populations and species. If opportunity for diversification depends on geographic area, rates of diversification should be highest on large archipelagos or continents. This model is supported by empirical findings that speciation rate is positively correlated with island area (Losos and Schluter, 2000).

Thus, two models of diversification in island systems make distinct predictions. Ecological opportunity predicts that rates of speciation and morphological evolution will be elevated following colonization of islands unoccupied by competitor species (Baldwin and Sander-son, 1998; Lovette et al., 2002). By contrast, geographic models predict that rates of diversification should be positively correlated with island area. We tested these predictions in an adaptive radiation of day geckos (*Phelsuma*) using morphological data and a molecular phylogeny. *Phelsuma* occur in the Indian Ocean region, including Madagascar, and the Seychelles, Comoros, and Mascarene Islands, where there are 44 recognized extant species and at least five more geographically and morphologically distinct taxa currently classified as subspecies (Vinson, 1976; Kluge, 1987; Austin et al., 2004; Rocha et al., 2007; see Table S1; all supplementary tables are available online at www.systematicbiology.org). These geckos have evolved a striking variety of forms and occupy a broad range of arboreal habitats (Vinson and Vinson, 1969; Vinson, 1976; Thorpe and Crawford, 1979; Evans and Evans, 1980; Crawford and Thorpe, 1981; Gardner, 1986; Radtkey, 1996), with up to six species coexisting in a single habitat.

Three previous studies have examined the molecular systematics of *Phelsuma* (Radtkey, 1996; Austin et al., 2004; Rocha et al., 2007). We expand these studies, presenting a combined phylogenetic analysis for a total of 35 *Phelsuma* taxa from Madagascar and the Seychelles, Comoros, and Mascarene Islands. Day geckos likely originated in Madagascar and subsequently dispersed and radiated in the other island archipelagos (Austin et al., 2004); thus, each island archipelago provides a replicate instance of diversification following colonization. We use a phylogeny in conjunction with morphological measurements to test our hypotheses about the roles of

geographic area and ecological opportunity in diversification of these geckos.

METHODS

Hypotheses

We compared rates of diversification, including both speciation and morphological evolution, for independent radiations of day geckos in four geographic areas: Madagascar, and the Mascarene, Seychelles, and Comoros Islands. We tested two hypotheses: (1) rates of diversification, both in net speciation (=species accumulation) and morphological evolution, are elevated following colonization of isolated archipelagos; and (2) rates of diversification are positively related to island area.

Geographic Setting

Day geckos occur on islands throughout the western Indian Ocean. Here, we focus on species on Madagascar and three island archipelagos (Fig. 1). One group, the Mascarene Islands, lies about 800 km east of Madagascar. The Mascarenes contain three main islands, Mauritius, Réunion, and Rodrigues, and a few smaller offshore islands. These islands are of volcanic origin and have never been connected to Madagascar or any continental fragments (McDougall and Chamalaun, 1969). The second group, the Seychelles, comprises over 100 islands of varying size, some 41 of which are continental fragments formerly connected to Madagascar and India (Rabinovitz et al., 1983). The main islands in the

Seychelles are about 1100 km from the nearest point in northern Madagascar and all have been submerged at various times since their separation from other landmasses (Rabinovitz et al., 1983). Finally, the Comoros comprise four main islands and many smaller islands (excluding Aldabra, which is politically allied with the Comoros but not geographically part of this archipelago) and are separated from Madagascar by approximately 310 km at the closest point. Madagascar has a much larger total land area (~582,000 km²) than the archipelagos, although total land area in the Mascarenes (~4500 km²) is greater than the Comoros (~2200 km²) and much greater than the Seychelles (~230 km²; data from Losos, 1986).

Madagascar includes a wide range of other lizard species, some of which are potential competitors of day geckos; by contrast, day geckos are the most abundant lizards on the three small archipelagos. Thus, although all localities considered here are islands, the small archipelagos potentially present greater ecological opportunity for these species.

Molecular Laboratory Protocols and Alignment of DNA Sequences

We collected molecular data for 35 *Phelsuma* taxa, which included 28 of 44 named species and seven pairs of subspecies of uncertain taxonomic status. Two pairs represent genetically and morphologically well-differentiated forms that are not sister taxa (*P. madagascarensis grandis* and *P. m. kochi*; *P. guimbeaui guimbeaui* and *P. g. rosagularis*; Austin et al., 2004; Rocha et al., 2007; also

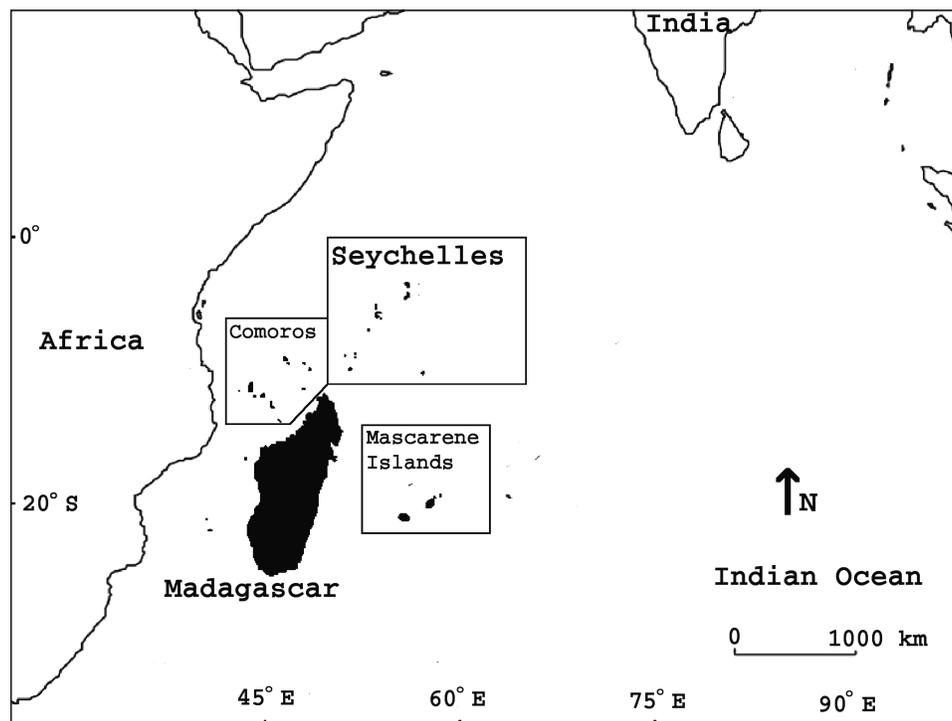


FIGURE 1. Map of Indian Ocean region, with archipelagos highlighted.

see Results); we consider these forms separate species. In a few cases, the taxonomic status of particular subspecies is uncertain; in these cases (*P. sundbergi sundbergi* and *P. sundbergi longinsulae*; *P. ornata ornata* and *P. o. inexpectata*; *P. borbonica borbonica* and *P. borbonica mater*; *P. cepediana A* and *B*; *P. v-nigra anjouanensis*, *P. v-nigra comoraegrandensis*, and *P. v-nigra v-nigra*), we ran all analyses twice, once considering all of these forms separate species ("complete tree," 35 taxa included) and once considering the paired populations conspecific ("pruned tree," 30 taxa included; see Table S1).

We generated new sequences for 17 species (see Table S1) from a 1340-bp segment of the mitochondrial genome including the genes encoding tRNA_{Met}, ND2 (NADH dehydrogenase subunit two), tRNA_{Trp}, tRNA_{Ala}, tRNA_{Asn}, OL (origin of light-strand synthesis), tRNA_{Cys}, tRNA_{Tyr}, and the protein-coding gene *COI* (subunit I of cytochrome *c* oxidase). One sequence was obtained per species. Genomic DNA was extracted from liver or muscle using Qiagen QIAamp tissue kits and various primer combinations (see Table S2). Amplifications of genomic DNA were conducted using a denaturation at 94°C for 35 s, annealing at 53°C for 35 s, and extension at 70°C for 150 s with 4 s per cycle added to the extension for 30 cycles. Negative controls were run for all amplifications. Amplified products were purified on 2.5% Nusieve GTG agarose gels. Cycle-sequencing reactions were run using Promega fmol DNA sequencing system with a denaturing at 95°C for 35 s, annealing at 45°C to 60°C for 35 s, and extension at 70°C for 1 min for 30 cycles. For automatic sequencing, reactions were run on an ABI373 or a BaseStation automatic sequencer. Tissue samples for DNA sequencing were provided by a number of researchers who had collected specimens in the field; GenBank accession numbers are in Table S1.

We analyzed these data in conjunction with two previously collected molecular data sets: Austin et al. (2004), which includes sequences from two mitochondrial genes (12S, 390 to 397 bp; *cytb*, 714 bp) and one nuclear gene (*c-mos*, 374 bp), and Rocha et al. (2007), which includes sequences from these same two mitochondrial genes. For the phylogenetic analysis, one representative sequence was used for each species; species missing from a particular data set were scored as missing data (for justification of this approach, see Wiens et al., 2005).

We also include five outgroups in our analysis, with sequences obtained from the references below or generated anew (see Table S1): *Rhoptropella ocellata* from southern Africa, formerly included in *Phelsuma* (Russell, 1977) but now considered a distinct genus (Austin et al., 2004), and five African gekkonid taxa closely related to day geckos: *Eublepharus turkmenicus*, *Lygodactylus* sp., *Pachydactylus* sp., *Rhoptropus boultoni*, and *Ailuronyx seychellensis* (Austin et al., 2004; Rocha et al., 2007).

We manually aligned all of the new ND2 sequences used in the analyses. Alignment of tRNA genes was based on secondary structural models (Kumazawa and Nishida, 1993; Macey and Verma, 1997). Regions where alignment was ambiguous were excluded from the phylogenetic analyses. We aligned all remaining sequences

(12S, *cytb*, and *c-mos*) using ProAlign (Löytynoja and Milinkovitch, 2003) with the default settings. We adjusted these alignments by hand to maintain the amino acid reading frame and excluded any base pairs with an alignment probability of less than 50%.

Phylogenetic Analyses

For the statistical analyses presented below, we estimated phylogenetic trees using Bayesian Markov chain Monte Carlo (MCMC). We used partitioned Bayesian analysis (Nylander et al., 2004) as implemented in MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) to generate a posterior distribution of phylogenetic trees. We used four alternative data-partitioning schemes: a single model for the whole data set, a model in which each of the four genes used a separate model of evolution, a model in which each codon position and the noncoding regions (12S+ tRNAs) had a separate model, and a model where every codon position in each gene, as well as each noncoding region, had a separate model (see Tables S3 and S4 for details). For each partition, we selected a model of sequence evolution based on the Akaike information criterion (AIC) as implemented in the program MrModelTest (Posada and Crandall, 1998; Nylander, 2002).

For each Bayesian analysis, we ran two searches for 10,000,000 generations with four chains each, sampling a tree every 5000 generations to estimate the posterior distribution. In all cases, likelihoods of two independent runs reached the same plateau after 100,000 generations; we discarded the first 1,000,000 generations as "burn-in." Convergence was assessed by the standard deviation of split frequencies, which averaged ~0.01 after 10,000,000 generations in all cases. We compared the fit of each of the four partitioning schemes using Bayes factors (Kass and Raftery, 1995; Brandley et al., 2005). We then selected the simplest partitioning scheme that was supported over other models by 2 ln Bayes factors greater than 10 (Kass and Raftery, 1995). We used the proportion of trees in this distribution that included a particular clade as our measure of support. We also generated a maximum likelihood tree under the GTR+I+ Γ model using GARLI (Zwickl, 2006). We pruned outgroups and made this tree ultrametric using penalized likelihood (Sanderson, 2002) with the smoothing parameter determined by cross validation ($\log[\lambda] = 3.05$). We pruned two species (*Phelsuma andamanensis* from the Andaman islands and *P. parkeri* from Pemba island) and used this tree for all statistical analyses below.

Morphological Data Collection

We collected morphological data from museum specimens for 19 species, a subset of the 30 species in our "pruned" phylogenetic tree chosen for availability of museum specimens (see Table S5). With one exception, only adult males were measured (mean $n = 11.0$, range 1–50; see Table S5 for specimen information). We measured species from all four geographic regions, although our sample of the Comoroan day geckos includes only two

species. For each specimen, we measured 10 characters: snout-vent length (SVL), jaw length, jaw width, distance from the nostril to the eye, diameter of the eye, distance between the eyes, head width, distance from the tip of the snout to the neck, proximal hind-limb length (measured from the insertion of the hind-limb to the knee), and distal hind-limb length (measured on the hind-limb from the knee to the tip of the longest toe). All measurements were log-transformed before analysis. To identify major axes of variation in these data, we performed a principal components analysis (PCA) on the covariance matrix of all variables. We retained all PCA axes from this analysis to represent variation in body size (PC1) and shape (PC2 to PC10).

Testing the Ecological Opportunity Model

The ecological opportunity model predicts that speciation rate is elevated following dispersal to new island archipelagos. Because the day geckos of each archipelago form monophyletic groups (except the Comoros, see below), we tested this hypothesis by comparing species accumulation rates for each archipelago to rates estimated for the genus as a whole. Because our tree is missing multiple taxa, we estimated species accumulation rates using the method of Magallón and Sanderson (2001). Given the number of extant species and age of a clade, this method gives the maximum likelihood estimate for the net species accumulation rate. In each clade, we used the actual number of recognized species of day geckos (see Table S1). Species accumulation rates can be estimated using either the stem-group age or the crown-group age (depending on whether the stem branch leading to a particular clade is included; see Magallón and Sanderson, 2001). Because the location of the root of the *Phelsuma* radiation is uncertain, we used crown-group ages for the rate estimate of the entire clade; for subclades within the tree, such as archipelago radiations, we used both stem- and crown-group ages. These estimates are affected by the rate of background extinction; as suggested by Magallón and Sanderson (2001), we calculated diversification rates under a number of extinction-rate scenarios: where μ = extinction rate and λ = speciation rate, we used $\varepsilon = \mu/\lambda$ ranging from 0 (no extinction) to 0.9 (extinction rate = 90% of speciation rate). To test for differences in diversification rates on archipelagos compared to the genus as a whole, we calculated the probability of obtaining the standing diversity, or greater, for each archipelago given its diversity and age, using the equations given in Magallón and Sanderson (2001). Here, *P*-values less than 0.05 would indicate that a particular archipelago had more species than expected given the diversification rate of the group as a whole.

We also tested for a slowing through time in diversification rate for each group using the gamma statistic of Pybus and Harvey (2000). The original version of the test ignores the stem branch of a clade, instead starting at the node representing the most recent common ancestor of the clade. Because we have stem-branch in-

formation for the archipelago clades, we developed a modified version of the gamma statistic that incorporates this branch length:

$$\gamma = \frac{\left[\frac{1}{n-1} \sum_{i=1}^{n-1} \left(\sum_{k=1}^i k g_k \right) \right] - \frac{\sum_{j=1}^n j g_j}{2}}{\left(\sum_{j=1}^n j g_j \right) \sqrt{\frac{1}{12(n-1)}}}$$

We use the same notation as in Pybus and Harvey (2000), where n is the number of extant species in the clade and g_i is the waiting time to the i th speciation event in the phylogeny, but we start with the waiting time represented by the stem branch, denoted as g_1 . Like the original gamma statistic, this statistic has a standard normal distribution under the null hypothesis of a constant pure-birth process. Negative values indicate a tendency for the species accumulation rate to slow towards the present day (Pybus and Harvey, 2000).

Because unsampled species can bias this test, we used the actual known species richness of each archipelago to correct the null distribution of the gamma statistic for our level of sampling (Pybus and Harvey, 2000). This correction assumes that the number of unsampled species is known and that unsampled species are random with respect to phylogenetic topology for an archipelago, assumptions that we revisit in the discussion section. Our sampling of species is considerably less complete in Madagascar (~50% of species sampled) than in the three archipelagos, where almost all species have been sampled. We accommodated this incomplete sampling by assuming that species missing from the phylogeny were random with respect to the phylogeny and that the total number of species in Madagascar is known. There may, however, be a considerable number of unknown species in Madagascar, especially given recent findings of many undiscovered species in several other Malagasy groups (e.g., Raxworthy et al., 2003, 2007; Steppan et al., 2004).

We also predicted that rates of morphological evolution would increase following colonizations of archipelagos and that archipelago radiations would occupy a substantial proportion of the morphospace of entire radiations. We compared the rate of evolution of morphological characters in each archipelago using Brownie (O'Meara et al., 2006). For each morphological axis, we compared a single-rate Brownian-motion model with a four-rate model where rates of Malagasy, Mascarene, Seychellois, and Comoroan taxa were allowed to differ. We also calculated morphological disparity, calculated as the average squared distance between all pairs of species in a given region, for each archipelago radiation, and compared these disparities to the disparity of the clade as a whole. We then compared these ratios to those expected under Brownian motion using simulations. In the simulations, morphological traits evolved according to an estimate of the evolutionary trait variance-covariance matrix calculated from independent contrasts (Revell et al., 2007).

Testing the Geographic Model

Geographic models of diversification predict that diversification, both in species number and morphology, should be positively associated with area. We tested this model by regressing rates of diversification and morphological evolution on total land area for each island/archipelago (Madagascar, Mascarenes, Seychelles, and Comoros). For diversification, we regressed log-transformed net diversification rate ($\lambda - \mu$) against log area under a range of extinction scenarios ($\epsilon = \mu/\lambda = 0, 0.1, 0.5, \text{ and } 0.9$). For morphological evolution, we excluded the Comoros due to a lack of sampling (see above). Because only three points remained, we calculated the correlation between log rate of evolution (σ^2) and log area for each of the 10 PC axes and noted whether that correlation was positive or negative. We then tested for an excess of positive or negative correlations among all axes using a two-tailed binomial test. All statistical tests were performed in the R statistics package (R Development Core Team, 2007).

RESULTS

Sequence Alignment and Model Selection

Seventeen new day gecko sequences representing ~1340 bases of the mitochondrial genome are reported. We unambiguously aligned all base positions in protein-coding genes. There is a gap in the ND2 gene sequences at codon 308 (positions 1352 to 1354) for all *Phelsuma* species but none of the outgroup species (*Eublepharus turkmenicus*, *Pachydactylus* sp., *Lygodactylus* sp., and *Rhoptropella ocellata*). Several unalignable regions in the tRNA genes and origin of light-strand synthesis (O_L) are excluded from the analyses (148 of 1506 aligned sequence positions; see Table S6). For the data from Austin et al. (2004) and Rocha et al. (2007), alignments of the three protein-coding genes are unambiguous, while an additional 110 sites from the 12S sequences are excluded (see Table S6). Thus, a total of 258 of 3013 aligned sites are excluded in the combined analysis. Using the AIC criterion, we selected a complex model of molecular evolution, GTR+I+ Γ , for most, but not all, sequence partitions (see Table S3). These models are used in partitioned Bayesian analyses. A model where each codon position within each gene had a separate partition is strongly supported by Bayes factors over other partitioning schemes (Table 1; see Fig. S1; all supplementary figures are available online at www.systematicbiology.org). Results from this partitioning scheme are used in the analyses described below.

Phylogenetic Relationships

Phylogenetic relationships of *Phelsuma* from the Bayesian analysis are presented in Figure 2; tree files are available on TreeBase (<http://www.treebase.org>, submission SN3882). Monophyly of a group containing all sampled *Phelsuma* receives strong support (Bayesian posterior 100%; Fig. 2a). *Rhoptropella ocellata*, once included within *Phelsuma* (Russell, 1977), does not form a monophyletic group with *Phelsuma* (Fig. 2a). We also recovered

TABLE 1. Bayes factors comparing various partitioning strategies used in phylogenetic analyses. Numbers represent the relative support for the partitioning strategy for each column compared to the strategy in each row, expressed as $2 \ln$ Bayes factors. Bayes factors greater than 10 constitute strong support for the partitioning strategy listed in the column heading (Kass and Raftery, 1995; Brandley et al., 2005).

	Partitioning strategy		
	By gene and codon	By codon	By gene
Single model	2525.3	976.7	1377.7
By gene	1147.6	-401.0	—
By codon	1548.6	—	—

strong support for monophyly of both Mascarene and Seychelles radiations of *Phelsuma* and for the set of Comoroan species excluding *P. comorensis* (Fig. 2a); this latter species likely represents a separate dispersal event, but could also correspond with a single radiation on the Comoros with at least two back invasions of Madagascar. We also recovered fairly deep splits between various forms of *Phelsuma* of uncertain taxonomic status (e.g., *P. ornata inexpectata*/*P. ornata ornata*, *P. madagascarensis madagascarensis*/*P. madagascarensis kochi*, *P. borbonica borbonica*/*P. borbonica mater*, *P. cepediana A* *P. cepediana B*, *P. v-nigra v-nigra* *P. v-nigra comoraegrandis*/*P. v-nigra anjouanensis*; Fig. 2a). Thus, we perform two sets of analyses, one treating each form as separate species ("complete tree") and another treating each taxon pair as a single species ("pruned tree").

Our data were not clock-like (likelihood ratio test $\Delta = 387.3$, $P < 0.001$; Felsenstein, 1988). The ingroup tree from the penalized-likelihood analysis of our maximum-likelihood phylogeny is shown in Figure 2b. This tree differs only slightly from the Bayesian consensus tree in the arrangement of some poorly supported branches (Fig. 2). Because no generally accepted clock calibration exists for all sequences used in this study, placing absolute date estimates on this tree is difficult; however, we note that Austin et al. (2004) obtained an estimate of 5.9 Ma for the root node of the *Phelsuma* radiation using a calibration based on colonization of Reunion by the ancestor of *P. borbonica* at 2.1 Ma. The same calibration on the tree presented here also places the root node of the radiation at 5.9 Ma. However, this date postulates an extremely high rate of sequence divergence in the clade. Some previous studies have suggested that the ND2 gene and surrounding regions used here changes at a rate of 0.0064 changes per site per million years per lineage in a range of lizards and other vertebrates (Macey et al., 1998; Weisrock et al., 2001); if *Phelsuma* are only 7 million years old, their rate would be more than double that estimate.

Diversification Rates

Under the ecological model, we predict that invasion of new geographic regions will spur diversification. Because our results reveal strong support for the monophyly of both the Mascarene and Seychellois radiations of *Phelsuma*, and for all but one species in the Comoros (Fig. 2a), we can analyze independent radiations following colonizations of each of these archipelagos.

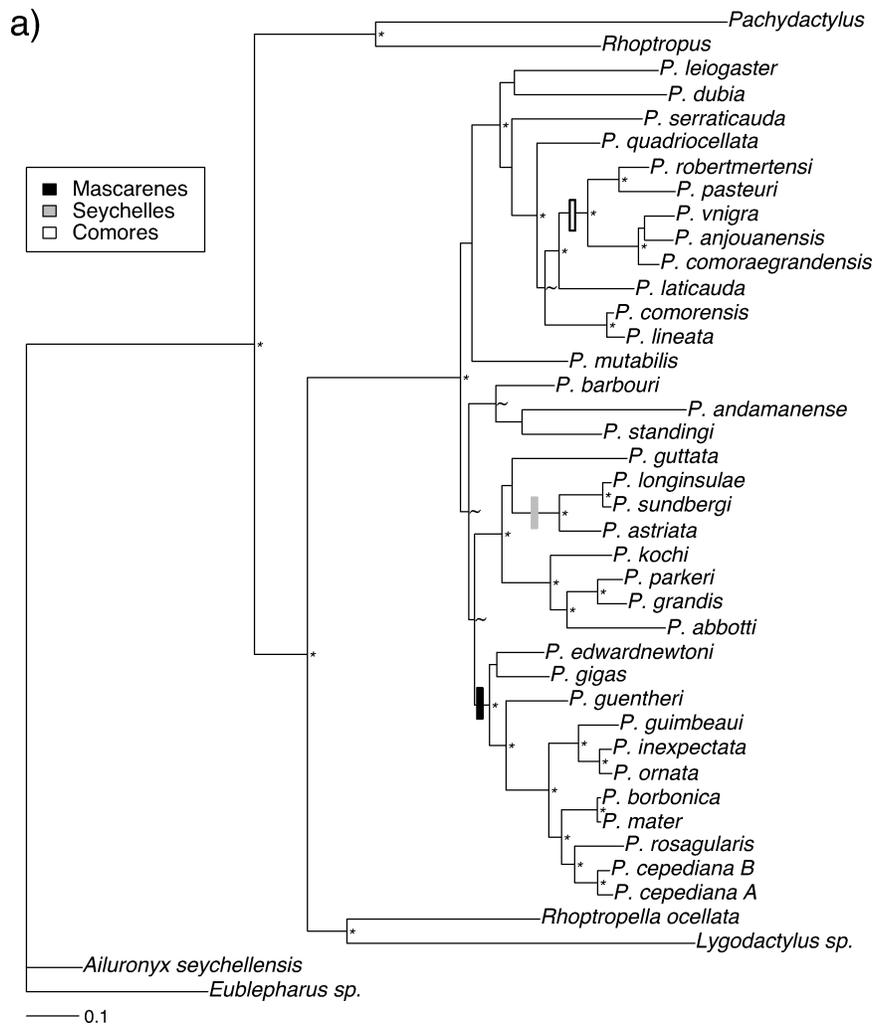


FIGURE 2. Phylogenetic trees of *Phelsuma* relationships from combined analysis of all available molecular data. (a) Bayesian consensus tree. Asterisks above nodes represent Bayesian posterior probabilities greater than 95%. Monophyletic island radiations are indicated with bars. (b) Penalized-likelihood tree including only *Phelsuma* species. (Continued)

Because we rescaled our tree to a total length of one, we report rates as net speciation per lineage per total tree depth. Dividing these rates by the estimated age of the clade (approximately 6 Myr) expresses them in net speciation per lineage per million years. For the entire radiation, estimated net rates of speciation were 3.14 per lineage per total tree depth (Table 2). This corresponds to a rate of 0.53 species accumulated per lineage per million years if the radiation is actually 5.9 Myr old. When six subspecies of uncertain taxonomic status were dropped, the rate estimates are 3.00 per lineage per total tree depth (Table 2). This calculation assumes a pure-birth model. As discussed by Magallón and Sanderson (2001), when models including extinction are considered, estimated net species accumulation is depressed, here by up to 50% (full tree: $\varepsilon = \mu/\lambda = 0.1$, $r = 3.13$; $\varepsilon = 0.5$, $r = 2.87$; $\varepsilon = 0.9$, $r = 1.65$; subspecies excluded, $\varepsilon = 0.1$, $r = 2.99$; $\varepsilon = 0.5$, $r = 2.73$; $\varepsilon = 0.9$, $r = 1.54$). These results correspond to a declining net rate of speciation but, implicitly, increased rates of both speciation and extinction (see Fig. S2). A

lineage-through-time plot for the clade as a whole shows a distinct pattern of a downturn towards the present, suggesting a slowdown in net rates of speciation through time (Fig. 3). This conclusion is supported by a significant

TABLE 2. Estimated net rates of speciation ($\lambda - \mu$) assuming various levels of extinction ($\varepsilon = \mu/\lambda$) for island clades. Rates are expressed in relation to a total tree depth of 1; if absolute, rather than relative rates, are desired, these numbers can be divided by the age of the clade (see text). Daggers represent rate estimates based on stem-group ages for the indicated clades; these are likely more accurate estimates but are possible only for three clades in the tree.

Clade	$\varepsilon = 0$	$\varepsilon = 0.1$	$\varepsilon = 0.5$	$\varepsilon = 0.9$
Whole	3.14	3.13	2.87	1.65
Madagascar	2.56	2.56	2.31	1.20
Mascarenes	2.40	2.39	1.79	0.69
Mascarenes†	1.97	1.97	1.73	0.74
Seychelles	1.48	1.39	0.93	0.25
Seychelles†	1.02	1.02	0.89	0.30
Comoros	3.19	3.04	2.23	0.72
Comoros†	2.93	2.92	2.52	0.93

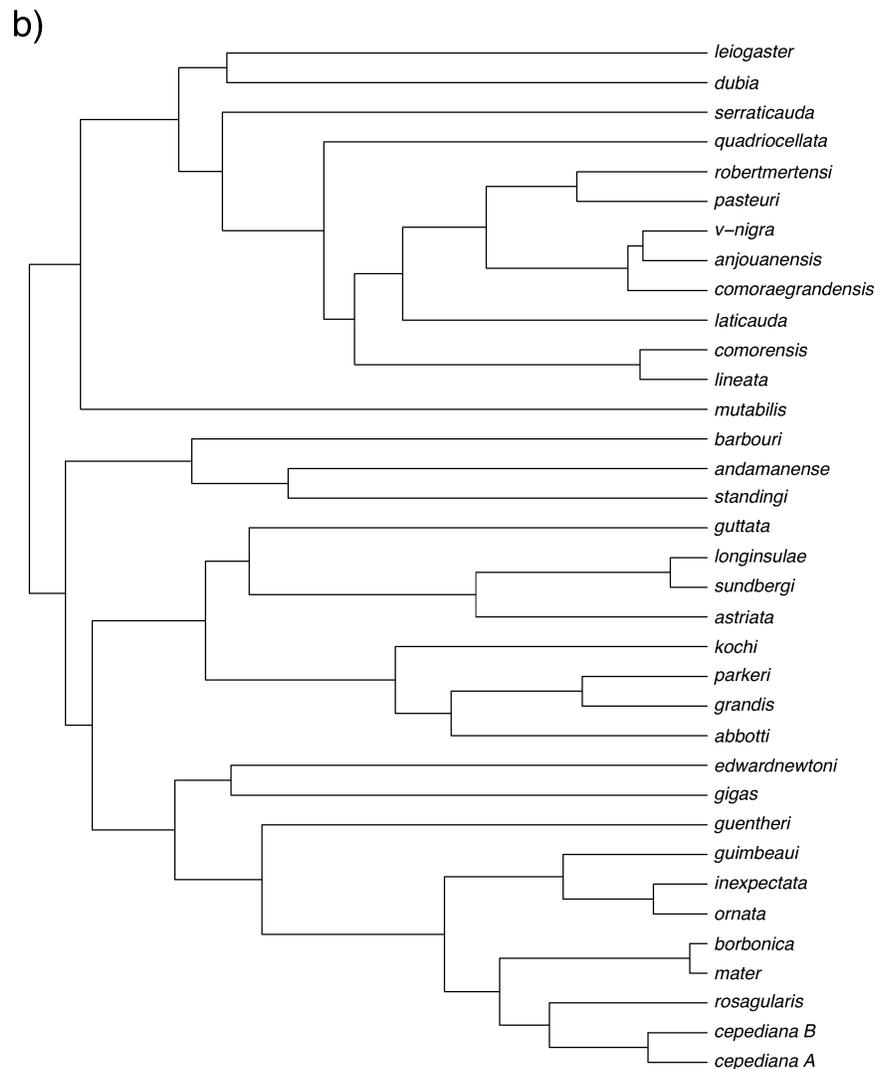


FIGURE 2. Continued.

gamma statistic (full tree: $\gamma = -2.9$, $P = 0.006$; subspecies excluded: $\gamma = -4.3$, $P = 0.001$).

The Mascarene and Seychelles groups each represent a monophyletic radiation. By contrast, day geckos have likely colonized the Comoros twice, with one invasion producing the radiation of *Phelsuma robertmertensi*, *P. pasteuri*, and the *P. v-nigra* group, and a second invasion producing *P. comorensis* (Fig. 2; Rocha et al., 2007). For the following analyses involving the Comoros, we exclude *Phelsuma comorensis* and thus consider only diversification within the archipelago (we call this clade the Comoroan clade). Separating the phylogeny into Malagasy, Seychelles, Mascarene, and Comoroan radiating clades reveals that the four groups have similar rates of lineage accumulation (Table 2). Madagascar has the highest net rate of speciation over a range of possible extinction values (Table 2). The number of taxa in each of the three groups is not unexpected given their age and the rate in the group as a whole (all $P > 0.05$, using $\varepsilon = 0$ and

$\varepsilon = 0.9$ for both complete and pruned trees; results are unchanged if *Phelsuma nigristrata* is included in the total count for the Comoroan clade). The slowdown in species diversification near the recent is apparent only in the Malagasy clade (Madagascar: $\gamma = -3.9$, 13 of 26 species sampled, $P = 0.001$; Fig. 3). No evidence for net slowing of speciation rates occurs among species from either archipelago (Mascarenes: whole tree $\gamma = -0.2$, $p = 0.4$; pruned tree $\gamma = -1.5$, $p = 0.06$; Seychelles: $\gamma = 0.9$, $p = 0.8$; Comoros: whole tree $\gamma = -0.7$, $P = 0.2$; pruned tree $\gamma = -0.7$, $P = 0.2$). If stem branches are included, there is a significant slowdown in Mascarene taxa excluding subspecies (Mascarenes: whole tree $\gamma = -0.6$, $p = 0.3$; pruned tree $\gamma = -1.9$, $P = 0.03$; Seychelles: $\gamma = 0.3$, $P = 0.6$; Comoros, whole tree $\gamma = -0.9$, $P = 0.2$; pruned tree $\gamma = -1.1$, $P = 0.1$); however, this result must be viewed in light of the multiple tests performed.

Net speciation is not related to geographic area under most extinction rates (Fig. 4). However, there is a positive

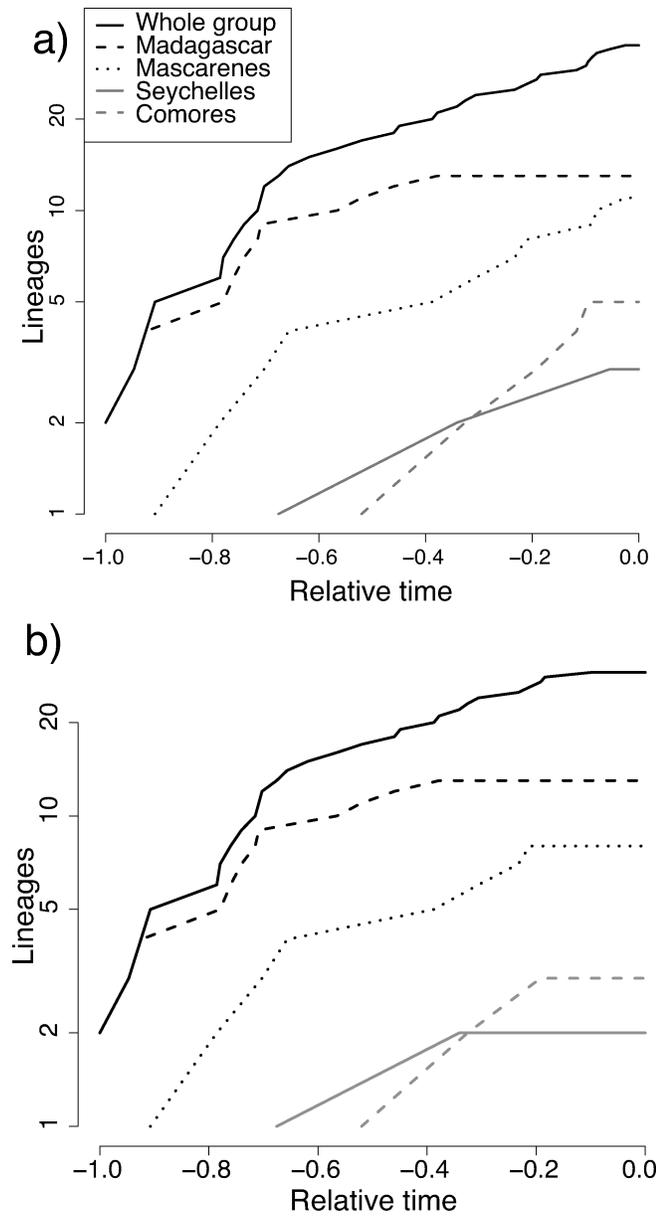


FIGURE 3. Lineage-through-time plots divided by archipelago. (a) Full tree; (b) pruned tree with subspecies of uncertain taxonomic status excluded.

relationship between net rate of speciation and area under the highest extinction scenario (Fig. 4; $\epsilon = 0.9$, $r = 0.97$, $P = 0.03$). Again, this result must be viewed with caution in light of the multiple tests used here and the fact that this result requires a high rate of extinction in the group.

We retained all axes from the principal components analysis on the covariance matrix of morphological measurements. The first axis represents body size and explains 95% of the total morphological variation; other axes represent various aspects of body shape, with the largest of these (PC2) mainly related to eye size, with larger values signifying species with smaller, more separated eyes (Table 3). Morphological disparity of the en-

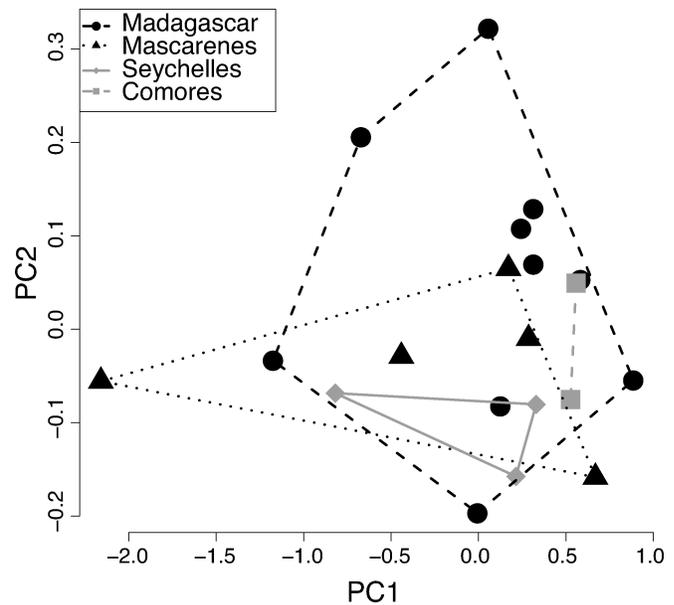


FIGURE 4. Relationship between total land area and (a) net rate of speciation and (b) rate of morphological evolution among archipelagos in the Indian Ocean. In a, different lines represent estimates of net rate of speciation ($\lambda - \mu$) assuming various levels of extinction ($\epsilon = \mu/\lambda$). In b, different lines represent each of the 10 PCA axes derived from the morphological data. Also, in b, the Comoros are excluded due to limited sampling (see text).

tire clade, calculated as average squared pairwise distance (D) in the morphospace defined by the ten PC axes, was 1.12. Because the Comoroan data set includes only two species, one of which is not in the main Comoroan clade considered here, these islands are not included in analyses involving morphological disparity. Within archipelagos, disparity is much greater among Mascarene species ($D = 2.53$) than among species from the Seychelles ($D = 0.82$) or Madagascar ($D = 0.78$; Fig. 5). The ratio of Mascarene disparity to that of the entire clade (2.26) is significantly greater than expected by chance based on Brownian-motion simulations ($P = 0.02$); other regions are not different from simulated data (Madagascar ratio = 0.70, $P = 0.9$; Seychelles ratio = 0.73, $P = 0.6$). These results are based on all PCA axes combined in a single multivariate analysis; when PC1 (body size) is excluded, there are no differences in morphological disparity among island groups (whole clade: 0.06, Mascarene: 0.04, Seychelles: 0.02, Madagascar: 0.08; all $P > 0.05$). Likelihood-based model comparisons of individual PC axes revealed support for a three-rate model for four of ten PC axes, with three still significant after Bonferroni correction (axes 1, 4, and 8; Table 4). In these models, rates of evolution in both the Seychelles and Mascarene islands were much higher than in Madagascar for axes 1 and 4 and higher only in the Seychelles for axis 8 (Table 4). Rates of morphological evolution are negatively correlated with archipelago area for 8 of 10 PC axes (Fig. 4, binomial test, two-tailed $P = 0.02$).

TABLE 3. Principal-component loadings for morphological data.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
SVL	-0.34	0.05	-0.17	0.04	0.29	0.16	0.11	0.02	-0.22	0.83
Jaw length	-0.32	0.04	-0.18	0.14	0.04	-0.11	0.05	-0.60	-0.61	-0.32
Nose to eye	-0.35	-0.12	-0.28	0.09	0.28	0.57	0.16	0.41	0.03	-0.43
Eye diameter	-0.27	-0.76	0.22	0.39	-0.30	0.04	-0.17	-0.06	0.08	0.10
Distance between eyes	-0.31	0.61	0.08	0.42	-0.46	0.15	-0.32	0.11	0.07	0.02
Head width	-0.33	0.14	0.41	0.02	-0.05	-0.09	0.75	-0.16	0.33	-0.04
Snout to neck	-0.32	0.04	-0.17	0.24	0.46	-0.64	-0.23	0.12	0.34	-0.10
Jaw width	-0.31	0.02	0.65	-0.40	0.16	-0.07	-0.27	0.29	-0.35	-0.09
Proximal hind limb	-0.31	-0.01	-0.11	-0.52	-0.02	0.26	-0.34	-0.48	0.46	0.01
Distal hind limb	-0.30	-0.11	-0.42	-0.40	-0.54	-0.35	0.17	0.33	-0.11	0.01
Proportion of original variance	0.95	0.03	0.01	0.008	0.003	0.001	0.001	0.0004	0.0003	0.0002

DISCUSSION

Upon dispersing to new islands, populations experience environments that differ in important ways from those on mainlands, including isolation, small initial population size, distinct environments (Barton, 1996), and simplified community structure (Blumstein, 2002). Here, we report a direct test for increased diversification rates, both in terms of species and morphological disparity, among day geckos in the Indian Ocean region. Our phylogenetic analysis recovers monophyletic Mascarene and Seychellois radiations of *Phelsuma* (Vinson and Vinson, 1969; Radtkey, 1996; Austin et al., 2004). Because these geckos exhibit multiple independent island radiations, we use replicated tests for the effects of island colonization on evolution.

Species Diversification Rates

Geckos did not exhibit elevated net rates of speciation following colonization of isolated archipelagos. Furthermore, there was no relationship between island area and net rates of speciation except under the highest extinction scenario. We found evidence for a slowdown in net rates of speciation among Malagasy *Phelsuma* but not in radiations on the Mascarene, Seychelles, or Comoros Islands. One possible interpretation of these results is that the Madagascar slowdown represents density-dependent cladogenesis, with diversification slowing as communities become saturated (Weir, 2006); in this framework, day geckos in the three archipelagos may not have reached community saturation. In fact, reconstructed net rates of speciation in these three archipelagos are apparently similar to those found early in the radiation

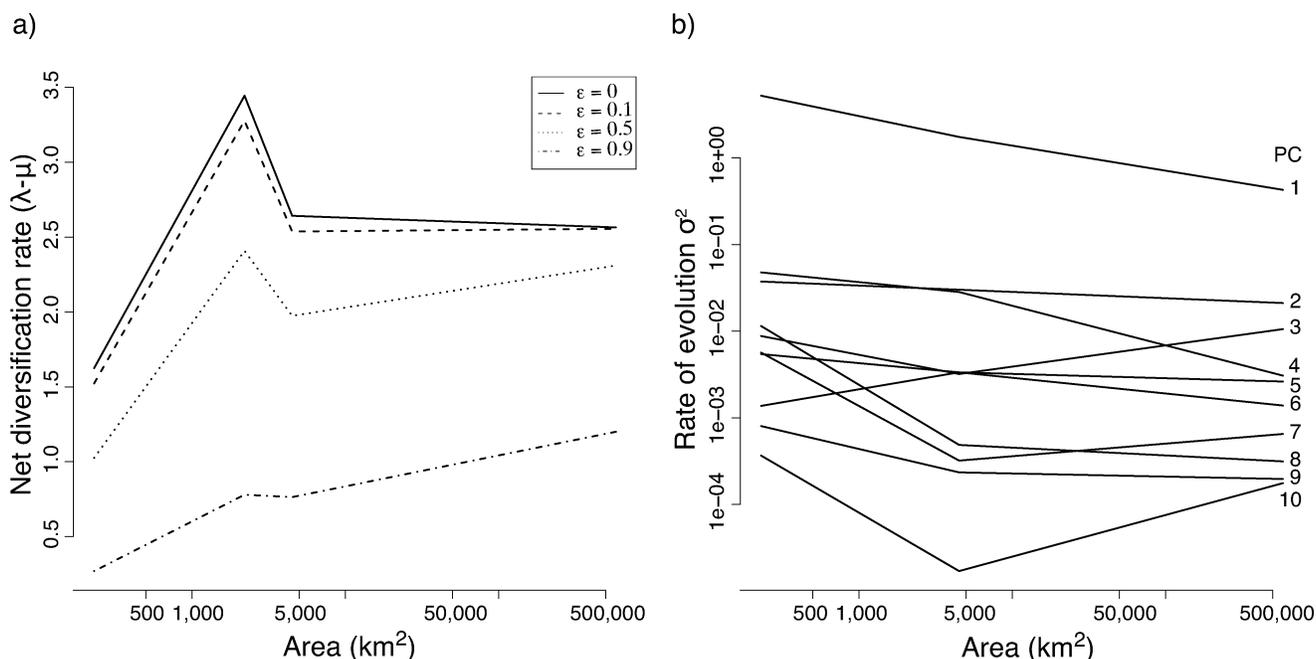


FIGURE 5. Plot of *Phelsuma* species in the morphospace defined by the first two axes of a principal-components analysis of morphological data. PC1 represents size, with smaller values corresponding to larger lizards, whereas PC2 contrasts lizards with small, wide-set eyes (high values of PC2) with species having large, closely spaced eyes (low values).

TABLE 4. Maximum likelihood estimates of evolutionary rates of morphological PC axes for single- and four-rate models with different rates for each archipelago and results of likelihood-ratio tests comparing the fit of these two models. 2Δ represents two times the likelihood ratio comparing the two models; P is calculated under a χ^2 distribution with 3 *df*.

Axis	Single rate	Four-rate model				2Δ	P
		Madagascar	Mascarenes	Seychelles	Comoros		
PC1	0.89	0.37	1.25	2.63	0.0004	19.2	<0.001
PC2	0.02	0.02	0.02	0.02	0.007	0.8	0.85
PC3	0.005	0.008	0.002	0.005	0.0003	6.0	0.11
PC4	0.01	0.003	0.02	0.02	0.000002	23.7	<0.001
PC5	0.002	0.002	0.002	0.003	0.0003	2.2	0.53
PC6	0.001	0.001	0.002	0.0007	0.0003	3.0	0.39
PC7	0.0008	0.0005	0.0005	0.003	0.0008	7.4	0.06
PC8	0.001	0.0002	0.0003	0.005	0.00003	21.9	<0.001
PC9	0.0002	0.0002	0.00002	0.0004	0.00003	3.2	0.36
PC10	0.0001	0.0001	0.00001	0.0002	0.00001	10.1	0.02

of Malagasy *Phelsuma* (Fig. 3) before the net slowdown of species accumulation rates near the recent. Further evidence for the idea that archipelagos are not saturated is the smaller numbers of sympatric species on archipelagos and the separate dispersal of an additional species, *P. comoroensis*, into the Comoros. It is possible that these archipelagos represent different “snapshots” of the stages of radiation in this group, with Seychellois and Mascarene radiations representing early, rapid stages of microhabitat partitioning among species, with the Malagasy radiation having moved into a slower stage of diversification associated with ecologically saturated communities (Streelman and Danley, 2003). Further sampling of day gecko species, especially in the Comoros and Madagascar, could be used to test this idea. One caveat to these conclusions is that the three archipelago radiations are smaller than the Malagasy radiation and thus provide less statistical power for rejecting a model of constant net rates of speciation.

In *Anolis* lizards in the Caribbean, there is an effect of island area on speciation, such that speciation events are concentrated on islands with large area (Losos and Schluter, 2000). Although our data do not show elevated rates of speciation on larger islands, the absolute number of speciation events is still related to archipelago area, being greatest on Madagascar, followed by the Mascarenes (six to nine reconstructed speciation events, depending on taxonomy), the Comoros (one to four) and then the Seychelles (one to two).

The oldest known exposed lava sites on both the Mascarenes (7.8 Ma; MacDougall and Chamalaun, 1969) and Comoros (8.7 Ma; Nougier et al., 1986), which represent minimum island-age estimates, are considerably older than our reconstructed dates for colonization by day geckos, suggesting a delay between island formation and colonization or, perhaps, extinction of earlier colonists. This pattern is also seen in some bird taxa that have diversified in the region (Groombridge et al., 2002, 2004; Warren et al., 2003, 2005; but see Shapiro et al., 2002). However, as we note above, there is considerable uncertainty in our dating methodology; further work is required to describe the actual time scale for diversification in these geckos. Despite this uncertainty, the age of the

Malagasy day gecko clade is clearly very young relative to the island’s separation from Africa, ~165 to 140 Ma; this pattern is shared with many other endemic groups on Madagascar, and it suggests that many groups have evolved after relatively recent oceanic dispersal events (Yoder and Nowak, 2006).

Disparity and Rates of Morphological Evolution

We found elevated rates of morphological evolution in both body size and shape on two of three archipelagos (Table 4). For the third group, the Comoroan radiation, rate estimates are compromised by limited sampling. We suggest that this pattern might reflect ecological opportunity. Islands with low species richness and simplified community structure may provide enhanced opportunities for ecological diversification. Alternatively, the increased rates of morphological evolution may reflect the relatively young age of archipelago radiations; perhaps evolution proceeds quickly early when groups have recently arrived in a new place, and slows with time. If this is true, then the day geckos on Madagascar likely experienced a similar phase of rapid evolution early in their history.

Despite their younger age, morphological disparity among species in two of the three radiations on archipelagos was greater than that among species in Madagascar. This may reflect the absence (or very low species richness) of many potentially competing groups, such as chameleons, on the archipelagos. Some species in Mauritius, in particular *Phelsuma guentheri*, occur outside the region of morphospace spanned by Malagasy taxa. Furthermore, the two extinct giants *P. edwardnewtonii* and *P. gigas*, for which we do not have morphological measurements, are also much larger than any known Malagasy species of *Phelsuma*. The lower morphological disparity in Madagascar may also be related to its geographic size. Madagascar may accommodate multiple allopatric species that are ecologically and morphologically very similar, a phenomenon less likely on smaller islands. Because our measure of disparity is an average distance between all pairs of species in morphospace, morphologically similar allopatric forms would decrease total

disparity. Many species in Madagascar occur allopatrically (Losos, 1986; Henkel and Schmidt, 2000; Raxworthy et al., 2007), whereas a significant proportion of species occurring on the archipelagos can coexist at a particular locality: up to five species in the Comoros (Henkel and Schmidt, 2000), three in Mauritius (Harmon et al., 2007), and two in Seychelles (Radtkey, 1996).

In the analyses presented here, we used the total area of an archipelago as a predictor of rates of species diversification and morphological evolution. However, these locations differ in their distribution of island size. Madagascar is mainly composed of a single very large island, the Mascarenes are formed almost entirely by three large islands, whereas the Seychelles and Comoros are archipelagos that include many small islands. These differences may have an impact on diversification; for example, on archipelagos, there is more opportunity to generate new species through allopatric separation among island populations. The Indian Ocean basin does not provide sufficient replication to address this question. More complex island systems, such as those in the southwestern Pacific Ocean, may provide an opportunity to investigate the difference between single islands and archipelagos.

Monophyletic radiations of taxa on island archipelagos provide a unique opportunity to study replicated instances of evolution in similar environments (Losos et al., 1998). Although there are no significant differences in species accumulation rates among four areas, a decreasing rate of lineage accumulation occurs only in the largest island of Madagascar. At the same time, there are of increased rates of morphological evolution on smaller islands with fewer ecological competitors.

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