Into the light: diurnality has evolved multiple times in geckos

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Geckos are the only major lizard group consisting mostly of nocturnal species. Nocturnality is presumed to have evolved early in gecko evolution and geckos possess numerous adaptations to functioning in low light and at low temperatures. However, not all gecko species are nocturnal and most diurnal geckos have their own distinct adaptations to living in warmer, sunlit environments. We reconstructed the evolution of gecko activity patterns using a newly generated time-calibrated phylogeny. Our results provide the first phylogenetic analysis of temporal activity patterns in geckos and confirm an ancient origin of nocturnality at the root of the gecko tree. We identify multiple transitions to diurnality at a variety of evolutionary time scales and transitions back to nocturnality occur in several predominantly diurnal clades. The scenario presented here will be useful in reinterpreting existing hypotheses of how geckos have adapted to varying thermal and light environments. These results can also inform future research of gecko ecology, physiology, morphology and vision as it relates to changes in temporal activity patterns. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**, 896–910.

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INTRODUCTION

Temporal niche partitioning early in a clade's evolutionary history has profound effects on behaviour, ecology, reproduction, physiology and morphology (Duellman & Pianka, 1990; Webb *et al*., 2002; Vitt *et al*., 2003; Vitt & Pianka, 2005). Reconstructing the history of temporal activity patterns can provide insight into the evolution of associated traits and the structuring of ecological communities. Geckos, for example, are the only primarily nocturnal lizard clade; 72% of the 1552 described species are active at night (Table S1). Geckos possess numerous adaptations to low light and low temperatures, suggesting nocturnality evolved early in their evolution. These adaptations include the evolution of vocalization and acoustic communication, olfactory specialization,

enhanced capability for sustained locomotion at low temperatures, shifts in diet and foraging mode, and the absence of the parietal foramen and pineal eye (Ralph, 1975; Gundy & Wurst, 1976; Marcellini, 1977; Pianka & Huey, 1978; Schwenk, 1993; Autumn *et al*., 1999; Vitt & Pianka, 2005; Bauer, 2007; Daza, Bauer & Snively, 2013). Geckos also have acute vision and have many adaptations for seeing in low light including large eyes, pupils capable of an extreme degree of constriction and dilation, retinas without foveae, short visual focal length, multifocal colour vision, and rod-like photoreceptor cells in the retina that lack oil droplets (Underwood, 1951a, 1970; Kröger *et al*., 1999; Röll, 2000b, 2001a; Roth & Kelber, 2004). However, not all gecko species are nocturnal; there are over 430 diurnal species (Table S1). Many of these diurnal lineages have their own adaptations to living in warmer, photopic environments including round pupils, UV-filtering crystalline lens proteins, smaller eyes, partial to complete foveae,

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cone-like photoreceptor cells in the retina and a return to higher energetic costs of locomotion (Walls, 1942; Pianka & Huey, 1978; Autumn, 1999; Röll, 2001a, b; Werner & Seifan, 2006). Geckos are thought to be ancestrally nocturnal and diurnality evolved multiple times (Walls, 1942; Autumn, 1999; Röll, 2001b). However, this hypothesis has never been tested in a phylogenetic framework. We performed comparative analyses using a newly generated gecko phylogeny and examined the evolution of temporal activity patterns to: (1) test the hypothesis of an early origin of nocturnality in geckos; (2) verify repeated subsequent transitions to diurnality; and (3) determine whether the evolution of temporal activity patterns has influenced diversification rates.

MATERIALS AND METHODS

We estimated phylogenetic relationships among 264 gecko species and 16 outgroups including exemplars from 119 of 120 recognized gecko genera (Table S2). We sequenced fragments of five nuclear protein-coding genes: *RAG1* (1074 bp), *RAG2* (366 bp), *C-MOS* (384 bp), *ACM4* (477 bp) and *PDC* (397 bp); and one mitochondrial fragment: the protein-coding *ND2* gene and associated tRNAs (1414 bp). Details concerning primers, PCR, Sanger sequencing and alignment are discussed elsewhere (Gamble *et al.*, 2008; Jackman *et al.*, 2008). Newly generated sequences have been deposited in GenBank (Table S2).

We estimated phylogenetic relationships and divergence times simultaneously in a Bayesian framework using BEAST 1.7.4 (Drummond *et al.*, 2012). Partitioned data were analysed with an uncorrelated relaxed clock and Yule prior on speciation rates (Drummond *et al.*, 2006). The optimal partitioning scheme, determined using Bayesian information criterion (BIC) in PartitionFinder v1.0.1 (Lanfear *et al.*, 2012), had three partitions: one partition consisting of all nuclear gene data; another partition comprising first and second codon positions of the mtDNA dataset plus tRNAs; and a third partition with the third codon position of the mtDNA dataset. The optimal models of sequence evolution, also calculated by PartitionFinder, were GTR + G for all partitions. We ran two replicate Markov Chain Monte Carlo (MCMC) analyses each with 20 million generations retaining every 5000th sample. We used seven calibrations to constrain the minimum ages of nodes in the time tree analyses. The most recent common ancestor (MRCA) of Gekkota, minimum age – (fossil calibration) *Hoburogekko suchanovi*, Aptian–Albian, 112 Mya (Daza, Alifanov & Bauer, 2012; Daza, Bauer & Snively, 2014). MRCA of *Teratoscincus scincus* + *Teratoscincus roborowskii* – (biogeographical calibration) Tien Shan-Pamir uplift in western China,

10 Mya (Tapponnier *et al.*, 1981; Abdrakhmatov *et al.*, 1996; Macey *et al.*, 1999). MRCA of extant *Sphaerodactylus* species – (fossil calibration) *Sphaerodactylus dommeli* and *S. ciguapa*, 15–20 Mya (Kluge, 1995; Iturralde-Vinent & MacPhee, 1996; Daza & Bauer, 2012). MRCA of *Paradelma orientalis* + *Pygopus nigriceps* – (fossil calibration) *Pygopus hortulanus*, 20 Mya (Hutchinson, 1997; Jennings, Pianka & Donnellan, 2003; Lee, Oliver & Hutchinson, 2009). MRCA of Helodermatidae + Anguidae, minimum age – (fossil calibration) *Primaderma nessovi*, 99 Mya (Nydam, 2000). MRCA of Lepidosauria (Squamata + *Sphenodon*), minimum age – (fossil calibration) *Polysphenodon* and *Brachyrhinodon*, 225 Mya (Evans, 2003). Root (Lepidosauria + Archosauria), normal distribution – (secondary calibration) 252–257 Mya (Reisz & Müller, 2004). Output files were checked for convergence using Tracer (Rambaut & Drummond, 2007), and both runs, minus burn-in, were combined to estimate topology and divergence times.

We initially categorized temporal activity as three character states, diurnal, nocturnal or crepuscular/cathemeral with data from the literature (Table S1), hereafter called the three-character dataset. Definitions follow Schmitz & Motani (2010). Some analytical methods, such as the binary-state speciation and extinction (BiSSE) model with a terminally unresolved phylogeny, require binary characters and species categorized as crepuscular/cathemeral were recoded as diurnal or nocturnal based on the time when the preponderance of foraging activity occurs. We called this the binary dataset. Both datasets were used to infer the evolution of temporal activity patterns in geckos.

We analysed both datasets using two methods: Bayesian ancestral state reconstruction and stochastic mapping. A third method, the BiSSE model, was also used to analyse the binary dataset alone. Bayesian ancestral state reconstruction was performed using BayesTraits v2.0 (Pagel, Meade & Barker, 2004). We incorporated phylogenetic uncertainty by analysing a set of 5000 trees drawn from the posterior distribution of trees inferred by the BEAST analyses. Deviations in rates were estimated using the AutoTune function and a hyper prior on all parameters was set to a value between 0 and 1. Analyses were run for 11 million generations, sampled every 1000 generations, and the first 1 million generations discarded as burn-in. We investigated whether a single-rate model (Lewis, 2001) fit either of the datasets better than an asymmetric multi-rate model (Schluter *et al.*, 1997; Pagel, 1999). We also compared alternative root states in both datasets using the 'fossil node' command. Alternative hypotheses were compared using log Bayes Factors (logBF)

with marginal likelihoods calculated via stepping stone sampling and the optimal transition rate model. Each stepping stone analysis used 100 samples with 10 000 iterations per sample.

We counted the number of transitions among states via stochastic mapping with the simmap function in Phytools 0.4-31 (Huelsenbeck, Nielsen & Bollback, 2003; Revell, 2012). We mapped characters onto the maximum clade credibility tree from the BEAST analysis. We used the transition model that best fit the data as estimated by maximum-likelihood (ML) with the ace function in the R package APE 3.1-4 (Paradis, Claude & Strimmer, 2004). Transitions were summarized using the describe.simmap function in Phytools.

We concurrently estimated character transition rates and state-specific extinction and speciation rates using the BiSSE model (Maddison, Midford & Otto, 2007). We converted our phylogeny into a terminally unresolved generic-level tree to accommodate unsampled taxa (FitzJohn, Maddison & Otto, 2009). The phylogeny was pruned to 102 taxa, roughly equivalent to genera, to which we could assign all 1552 described gecko species. There were several instances where multiple genera, whose collective monophyly was strongly supported, were grouped together, as well as several instances where genera were split due to generic paraphyly. We calculated BiSSE model parameters and compared alternative models from the terminally unresolved generic-level tree with both ML and Bayesian methods with Diversitree 0.9-7 (FitzJohn *et al.*, 2009; FitzJohn, 2012). Priors for each parameter used an exponential distribution and estimated ML model parameters were used as a starting point for the Bayesian analyses. Posterior distributions for each model parameter were estimated from a single MCMC chain run for 10 000 generations, with the first 10% discarded as burn-in. Three initial MCMC chains, run for 1000 generations each, converged almost immediately and were consistent with each other and the single 10 000 generation run. Finally, ancestral states were estimated for the terminally unresolved generic-level tree under a BiSSE model using the 'asr-bisse' command in Diversitree.

RESULTS

Phylogenetic relationships and divergence times among gecko families and genera (Fig. 1) were consistent with previous estimates at well-supported nodes (Gamble *et al.*, 2011, 2012; Heinicke *et al.*, 2012). Activity patterns were conserved within most genera and only seven of 120 genera had both diurnal and nocturnal species (Table S1). All ancestral state reconstructions recovered an ancient origin of nocturnality at the root of the gecko tree (Figs). Bayesian hypothesis testing confirmed the robustness of these results and favoured a nocturnal root state in all comparisons (Fig. 2, binary data: nocturnal root = -83.330741, diurnal root = -89.726172, logBF = 12.79; three-character dataset nocturnal root = -128.909312, diurnal root = -135.344277, crepuscular/cathemeral root = -135.909323, logBF nocturnal root vs. diurnal root = 12.87, logBF nocturnal root vs. crepuscular/cathemeral root = 14.00).

Transitions between activity patterns occurred across the phylogeny at a variety of timescales. Comparisons of a 1- to 2-rate model using the binary dataset in a Bayesian framework preferred the 1-rate model (1 rate = -83.305361; 2 rates = -87.187184; logBF = 7.76). A model comparison with ML found no difference between the two models (Table 1). A comparison of the three-character dataset in a Bayesian framework showed a preference for the simpler 1-rate model (1 rate = -128.911706; multiple rates = -142.306639; logBF = 26.79). This contrasts with the ML comparison that found no difference between a single-rate model and a model with all rates different (ARD model, Table 1).

Table 1. Comparison among transition rates models used in the maximum-likelihood ancestral state reconstruction

Model	Binary dataset			Three-character dataset		
	d.f.	ln likelihood	AIC	d.f.	ln likelihood	AIC
ARD	2	-76.193	156.386	6	-117.31	**246.6107**
SYM	n/a	n/a	n/a	3	-122.32	250.6396
ER	1	-76.983	**155.9665**	1	-122.49	246.9797

The number of parameters (d.f.) for each model is listed. The likelihood scores were produced using two datasets: the binary dataset, with species categorized as diurnal or nocturnal; or the three-character dataset, with species categorized as diurnal, nocturnal or crepuscular/cathemeral. Models were compared using the Akaike Information Criterion (AIC) and AIC scores of the best fitting model for each dataset are in bold type. The following models were compared: all rates different model (ARD); symmetrical rates model (SYM); and equal rates model (ER).
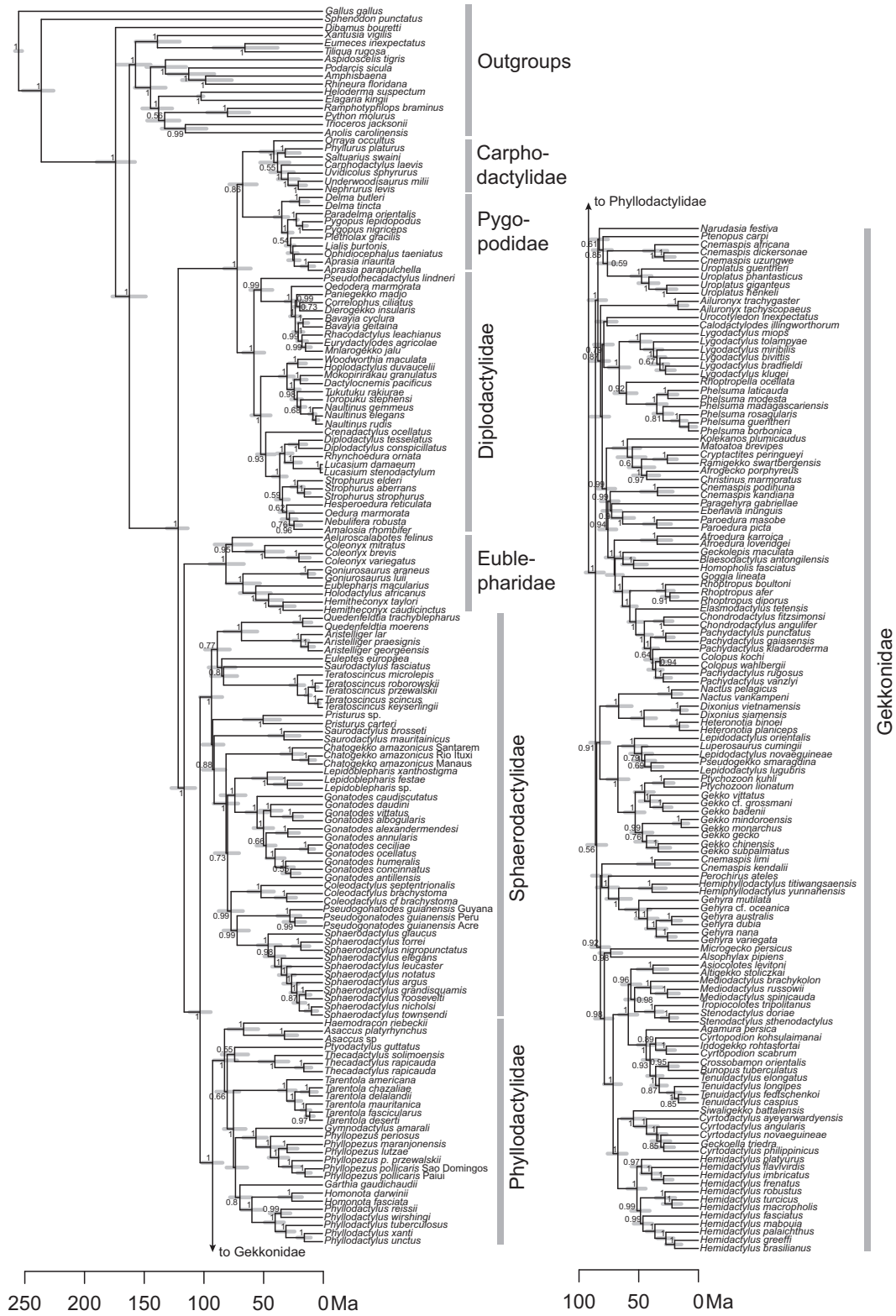
Figure 1. Time-calibrated phylogeny of geckos estimated from a Bayesian analysis of the concatenated nuclear and mitochondrial gene dataset. Nodes with posterior probabilities > 0.50 are labelled. Time scale, in millions of years, is shown at the bottom of the tree. Node bars represent 95% highest posterior density (HPD) interval of divergence times. Gecko families and outgroups are labelled to the right of species names.
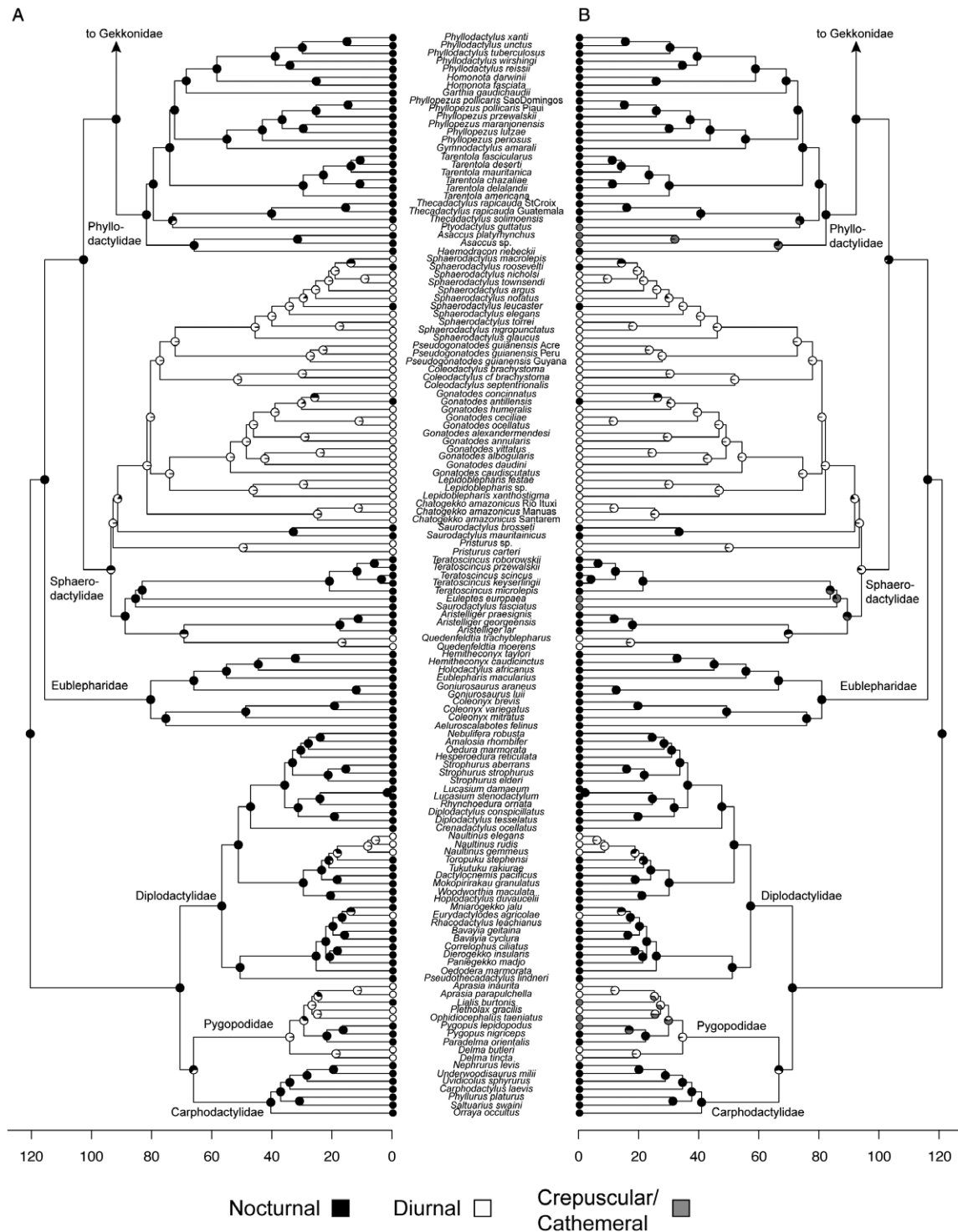
Figure 2. The evolution of temporal niche in geckos. Bayesian ancestral state reconstructions of temporal niche mapped onto a time-calibrated phylogeny of geckos using the one-rate model. Circles at the tips of branches indicate the temporal niche for each included species. Pie charts on internal nodes indicate the posterior probability of that ancestor having a particular temporal niche. A, results using the binary dataset; species are categorized as diurnal (white) or nocturnal (black). B, results with the three-character dataset; species are categorized as diurnal (white), nocturnal (black) or crepuscular/cathemeral (grey).
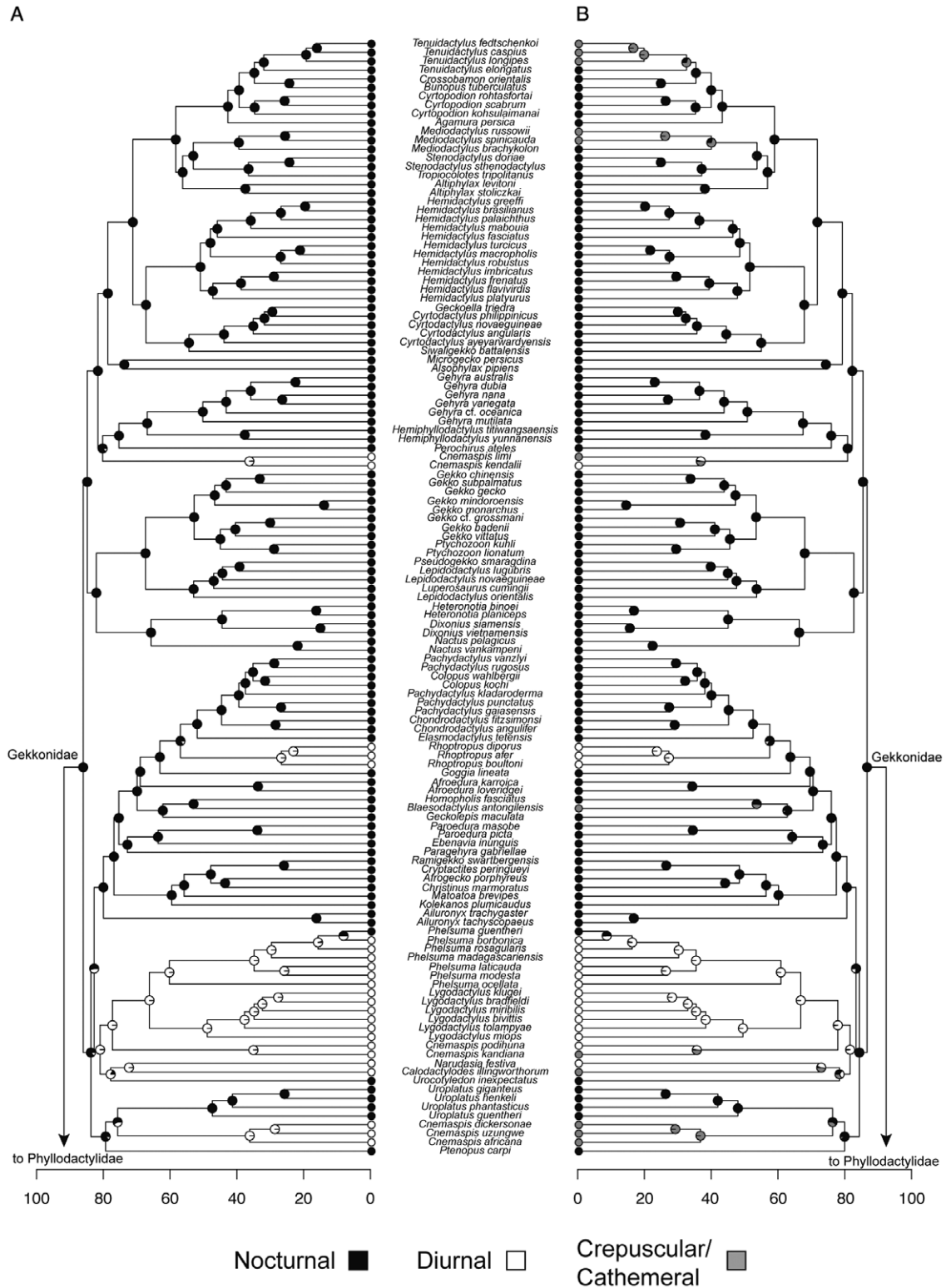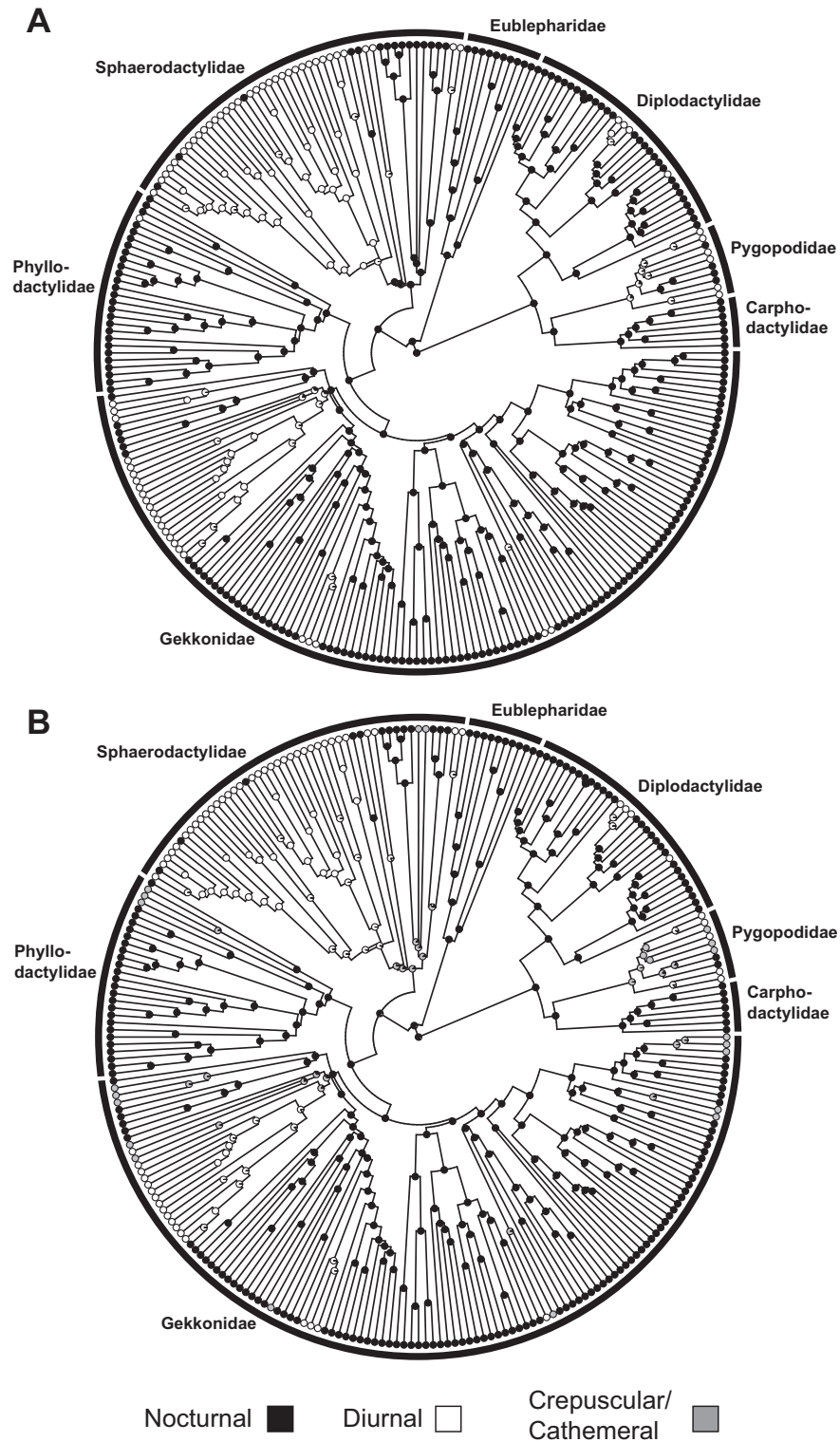
Figure 2. Continued.

Figure 3. The evolution of temporal activity mapped onto a time-calibrated phylogeny of geckos. Circles at the tips of branches indicate the temporal niche for each included species. Circles at internal nodes indicate reconstructions from 1000 stochastic mapping simulations. Gecko families are labelled. A, results with the binary dataset and equal rates (ER) model; species are categorized as diurnal (white) or nocturnal (black). B, results with the three-character dataset and all rates different (ARD) model; species are categorized as diurnal (white), nocturnal (black) or crepuscular/cathemeral (grey).
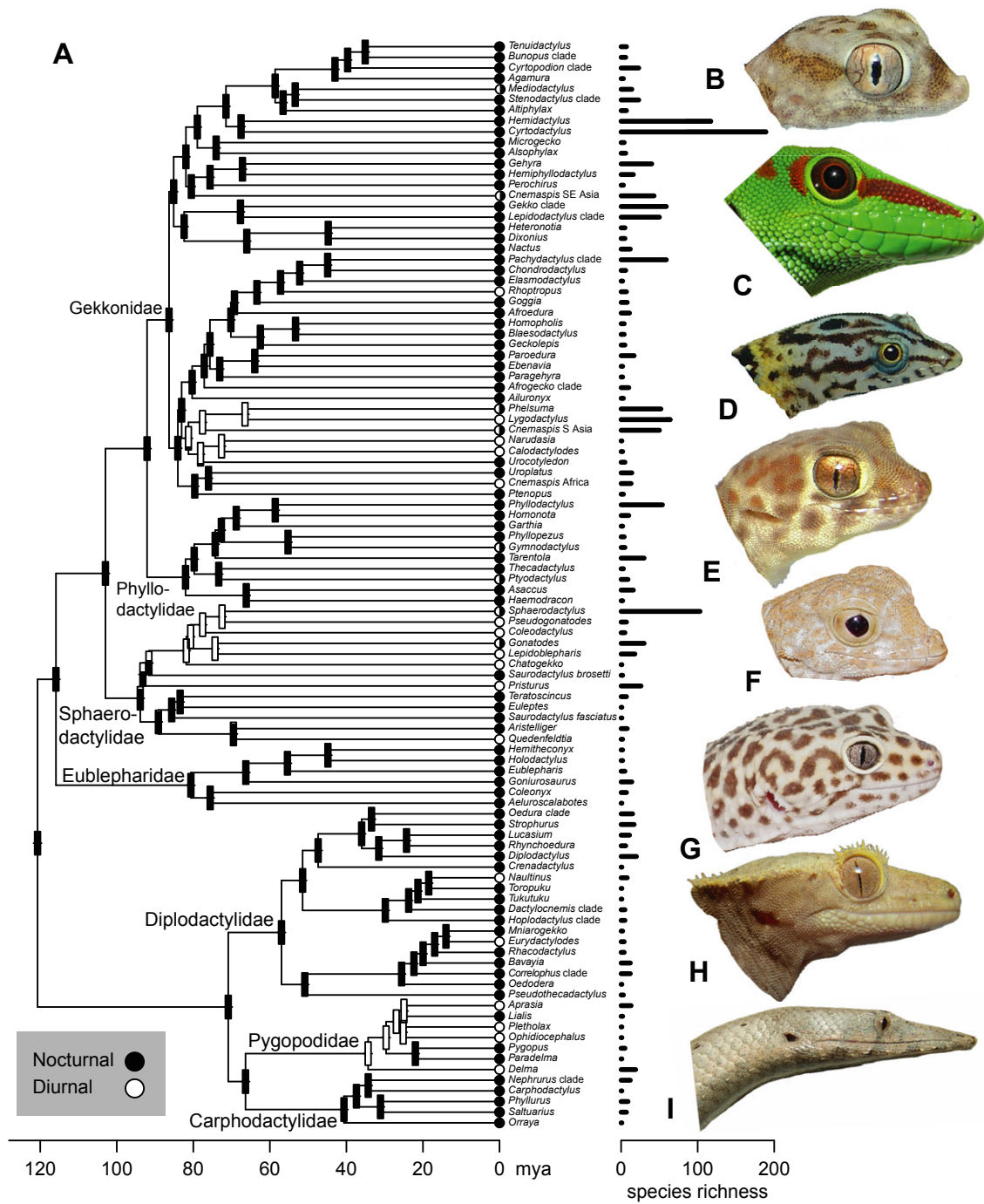
Figure 4. A, ancestral activity patterns inferred using the six-parameter BiSSE model mapped onto a time-calibrated phylogeny of gecko genera. Some genera have been combined for convenience. Circles at the tips of branches indicate temporal activity patterns of species in each genus. Rectangles at internal nodes represent probabilities of ancestral activity patterns inferred using the six-parameter BiSSE model. Time scale, in millions of years, is below the tree. Horizontal lines to the right indicate the number of species in each clade. B–I, representative gecko species showing variation in eye size and pupil shape as it relates to temporal activity. B, Stenodactylus sthenodactylus – nocturnal; C, Phelsuma grandis – diurnal; D, Sphaerodactylus macrolepis – diurnal; E, Teratoscincus roborowskii – nocturnal; F, Pristurus carteri – diurnal; G, Eublepharis macularius – nocturnal; H, Correlophus ciliatus – nocturnal; I, Lialis burtonis – crepuscular/cathemeral.
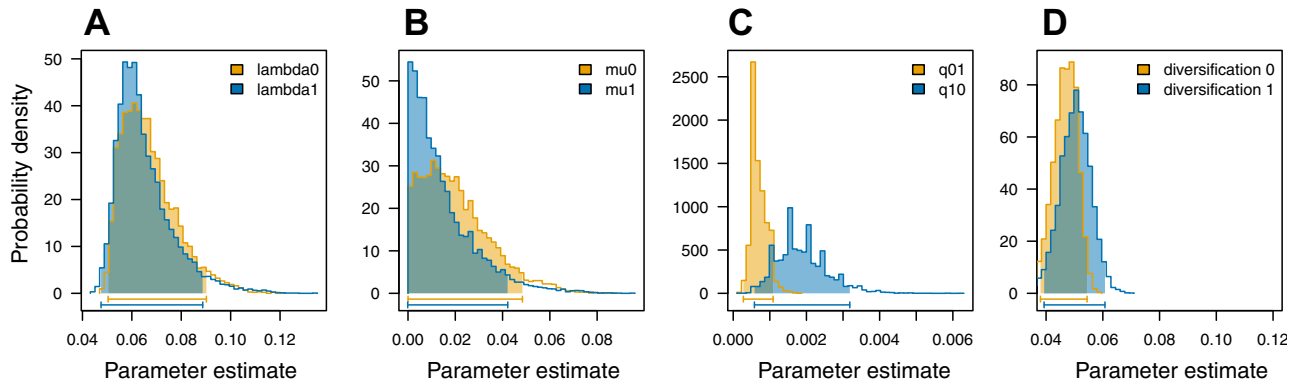
Figure 5. Bayesian parameter estimates inferred using the six-parameter BiSSE model. Zero (0) indicates nocturnality and one (1) indicates diurnality. Estimates of: A, trait-specific speciation rates (lambda); B, trait-specific extinction rates (mu); C, transition rate parameters (q01 = nocturnal to diurnal, q10 = diurnal to nocturnal); D, net diversification rates calculated as the difference between speciation (lambda) and extinction (mu) rates for nocturnal and diurnal genera. The 95% credibility intervals are shaded and indicated by horizontal bars along the x-axis.

Table 2. Comparison of full and constrained maximum-likelihood binary-state speciation and extinction (BiSSE) models

Model	lambda0	lambda1	mu0	mu1	q01	q10	d.f.	ln Likelihood	AIC	ΔAIC
Full model	0.07095	0.07984	0.02537	0.03588	0.00074	0.00160	6	–818.60	1649.2	4.0
Equal lambda	0.06690	–	0.01963	0.02040	0.00068	0.00163	5	–818.62	1647.2	2.0
Equal mu	0.06918	0.06870	0.02270	–	0.00068	0.00165	5	–818.61	1647.2	2.0
Equal q	0.06514	0.08886	0.01763	0.04681	0.00098	–	5	–819.49	1649.0	3.8
Equal lambda & mu	0.06919	–	0.02286	–	0.00068	0.00168	4	–818.62	1645.2	0.0
Equal lambda & q	0.07384	–	0.02827	0.03081	0.00090	–	4	–820.09	1648.2	3.0
Equal mu & q	0.06816	0.06633	0.02088	–	0.00087	–	4	–820.15	1648.3	3.1
Equal lambda, mu, & q	0.06971	–	0.02355	–	0.00088	–	3	–820.36	1646.7	1.5

Trait 0 is nocturnal and trait 1 is diurnal. Lambda, trait-specific speciation rates; mu, trait-specific extinction rates; q, transition rate. Constrained models are compared using the Akaike Information Criterion (AIC).

Stochastic mapping of binary data with a single-rate model counted 20 transitions between nocturnal and diurnal activity patterns (median = 20, min. = 18, max. = 28). More transitions from nocturnality to diurnality were counted (median = 12, min. = 10, max. = 19) than the reverse, that is from diurnality to nocturnality (median = 7, min = 4, max = 13). Stochastic mapping with the three-character dataset with the ARD model counted 40 transitions among activity patterns (median = 10, min. = 31, max. = 53). Most transitions were from nocturnal to crepuscular/cathemeral (median = 13, min. = 9, max. = 22) or from crepuscular/cathemeral to diurnal (median = 12, min. = 6, max. = 18). There were fewer transitions from nocturnal to diurnal (median = 3, min. = 0, max. = 7), from diurnal to nocturnal (median = 5, min. = 4, max. = 12), and from crepuscular/cathemeral to nocturnal (median = 6, min. = 1, max. = 15). There were no transitions counted from diurnal to crepuscular/cathemeral. These estimates should be considered a minimum count, as only 17% of described gecko species were included in our stochastic mapping analysis and some recent transitions, particularly within *Cnemaspis* and *Sphaerodactylus*, were not included.

BiSSE analysis indicated no influence of temporal activity patterns on speciation or extinction rates (Fig. 5). We found the model constraining equal speciation and extinction rates to have the best Akaike information criterion score, whereas the full, six-parameter model had the poorest model fit (Table 2), a result also supported by the broad overlap in posterior distributions of speciation and extinction parameters (Fig. 5).

DISCUSSION

We confirmed the long-held hypothesis that nocturnality evolved early in gecko evolutionary history (Walls, 1942). Furthermore, we identified multiple

transitions to diurnality at a variety of evolutionary time scales. Several transitions occurred deep in the phylogeny, including ancestors to the Pygopodidae, the New World sphaerodactyl geckos and the *Phelsuma* plus *Lygodactylus* clade. More recent transitions occurred in *Rhoptropus*, within New Zealand and New Caledonian diplodactylids (*Naultinus* and *Eurydactylodes*), and within *Gymnodactylus*, *Ptyodactylus* and *Mediodactylus*. Both Asian *Cnemaspis* clades seem to include multiple transitions, although additional taxonomic sampling is needed to confirm this. We also identified several well-supported reversions to nocturnality within otherwise diurnal clades, including *Sphaerodactylus*, *Gonatodes*, *Phelsuma* and the Pygopodidae.

Results of the ancestral state reconstructions were mostly concordant across datasets and methodologies. However, phylogenetic uncertainty and differences among datasets contributed to ambiguity in the reconstructions at some nodes. The MRCA of the Sphaerodactylidae, for example, was either: nocturnal, as estimated from BiSSE and stochastic mapping using the binary dataset; diurnal or crepuscular/cathemeral, as estimated by Bayestraits and stochastic mapping analyses of the three-character dataset; or equivocal as estimated by the Bayestraits analysis of the binary dataset. How this node is reconstructed determines whether *Quedenfeldtia*, *Pristurus* and New World sphaerodactylini are independently derived diurnal lineages or the nocturnal sphaerodactyl geckos such as *Teratoscincus*, *Aristelliger* and *Euleptes* are reversals to nocturnality from a diurnal ancestor. Further work that better resolves the phylogeny plus examination of independent evidence for activity pattern evolution and visual morphology will be necessary to resolve reconstructions at these ambiguous parts of the tree.

The comparative phylogenetic hypothesis presented here will be useful for interpreting or reinterpreting adaptations to different thermal and light environments in geckos. For example, rod-like visual cells that lack oil droplets are characteristic of nocturnal geckos, whereas most diurnal lizards, including many diurnal geckos, have cone-like visual cells with oil droplets (Walls, 1942; Underwood, 1951b; Röll, 2000b; Bowmaker, 2008). The small oil droplets found in visual cells are thought to filter light and aid in spectral tuning (Bowmaker & Knowles, 1977). Cone-like visual cells with oil droplets have evolved independently in diurnal geckos across the phylogeny and are present in *Gonatodes*, *Phelsuma*, *Quedenfeldtia* and *Pristurus* (Underwood, 1951b; Röll, 2000a). There are several exceptions to this trend, and the diurnal Pygopodidae, *Sphaerodactylus*, *Rhoptropus*, *Naultinus* and *Lygodactylus* all lack oil droplets and

have visual cells more typical of nocturnal geckos (Underwood, 1951b, 1957; Röll, 2000b). Further insight into visual adaptations to diurnality comes from examining the composition and amount of certain lens proteins called lens crystallins (Röll, 2001b). *Sphaerodactylus* and *Narudasia* have lens crystallin composition similar to nocturnal geckos (Röll, 2001b). However, many other diurnal genera have recruited the CRBPI protein to bind with 3,4-didehydroretinol (vitamin A$_2$) to filter harmful ultraviolet light (Werten, Roll, van Aalten & de Jong, 2000). The presence of CRBPI in the lens is unique to *Lygodactylus*, *Phelsuma*, *Pristurus*, *Gonatodes*, *Quedenfeldtia* and African *Cnemaspis*, and is not found in the lenses of any other vertebrates (Röll, Amons & deJong, 1996; Röll & Schwemer, 1999; Röll, 2001b). The presence and amount of other lens crystallins also varies among different diurnal gecko lineages (Röll, 2001b). Understanding the curious phylogenetic distribution of oil droplets and lens crystallins will require detailed examination of a gecko species' visual environment, including intensity and wavelengths of light. However, it is clear that visual adaptations to diurnality are repeatedly gained across the phylogeny. Furthermore, it does not seem that the age of a diurnal lineage corresponds to the acquisition of vision-related adaptations. Some older diurnal lineages exhibit apparently plesiomorphic traits, whereas some young diurnal lineages exhibit a large number of derived visual adaptations to diurnality. Reinterpreting these and other traits, in light of the comparative phylogenetic hypothesis presented here, will provide a better understanding of the evolution and function of visual adaptations in geckos.

Our results indicate frequent shifts in temporal activity patterns in geckos at a variety of evolutionary timescales. Determining what factors initiate shifts in individual clades is beyond the scope of the current paper, but there are, very broadly, three possible causes: climate, predators and competition. Some shifts in activity pattern may be related to thermoregulation and evading extreme temperatures and desiccation. For example, geckos in the genus *Sphaerodactylus* appear to overheat easily (Allen & Powell, 2014) and several species that inhabit hot, xeric habitats are nocturnal, including: *S. leucaster*, *S. thompsoni* and *S. ladae* in southern Hispaniola; *S. roosevelti* in south-west Puerto Rico; and *S. inaguae* from the Bahamas (Schwartz & Henderson, 1991; Rivero, 1998; Scantlebury et al., 2011). Similarly, some gecko species living at high altitudes, such as *Mediodactylus amictopholis*, are thought to have shifted to diurnal activity to facilitate thermoregulation in colder climates (Szczerbak & Golubev, 1996). However, there are numerous counter examples

of both nocturnal and diurnal gecko species inhabiting extreme environments. *Pristurus* and *Rhoptropus*, for instance, are diurnal genera that can be active at extremely high temperatures in arid environments (Arnold, 1993; Nagy, Seely & Buffenstein, 1993; Autumn, 1999) whereas *Homonota darwnii* and *Alsophylax pipiens* live in cold climates at extreme latitudes and remain nocturnal (Szczerbak & Golubev, 1996; Aguilar & Cruz, 2010; Weeks & Espinoza, 2013). Furthermore, nocturnal geckos seem quite capable of regulating body temperature while hidden in retreats during the day (Huey *et al.*, 1989; Downes & Shine, 1998; Kearney & Predavec, 2000; Aguilar & Cruz, 2010) or through occasional daytime basking (Werner, 1969; Pianka & Huey, 1978; Werner & Whitaker, 1978; Gibson *et al.*, 2015) and thus switching to diurnality solely for thermoregulatory purposes may be uncommon overall.

Predation could also instigate changes in temporal activity patterns in geckos and such shifts are well documented in other vertebrate species (Halle, 1993; Rydell & Speakman, 1995; Fraser *et al.*, 2004; McCauley *et al.*, 2012). Most predator-induced niche shifts in geckos involve the alteration of the spatial niche (Hoare *et al.*, 2007; Pike *et al.*, 2010). However, Bauer (2013) hypothesized that geckos may transition to a more conspicuous, diurnal lifestyle in environments where predators are less abundant or absent, such as on islands. Lack of predators is thought to be responsible for dramatic changes in phenotype and behaviour in many island species, such as the evolution of flightlessness in birds (Darwin, 1859; Whittaker & Fernández-Palacios, 2007). Thus, it is reasonable that similar selective pressures could alter temporal activity in geckos.

Shifts in temporal activity patterns may also be related to competition avoidance and the exploitation of underutilized resources. Temporal resource partitioning helps competitors coexist by avoiding direct confrontation or reducing resource overlap (MacArthur & Levins, 1967; Schoener, 1974). For example, the early shift to nocturnality in ancient geckos has been attributed to avoiding competition with diurnal lizards and exploiting the relatively open nocturnal niche (Vitt *et al.*, 2003; Vitt & Pianka, 2005). The lack of competition with other diurnal lizards, mostly iguanians, is frequently cited as promoting transitions back to diurnality in geckos (Vitt *et al.*, 2003; Vitt & Pianka, 2005; Garcia-Porta & Ord, 2013). Indeed, many diurnal geckos occur in regions with a paucity of iguanian species. The success of *Phelsuma* and *Lygodactylus* in Madagascar has been attributed to the lack of arboreal iguanians, with the exception of the extremely specialized chameleons (Vitt *et al.*, 2003). Similarly, diurnality in the diplodactylid genera *Naultinus* and *Eurydactylodes* may have been

a shift into empty niche space in the absence of diurnal, arboreal agamids in New Zealand and New Caledonia (Garcia-Porta & Ord, 2013). On the other hand, many diurnal geckos co-occur with iguanians, which requires some explanation. One possibility is that diurnal competitors recently dispersed into the area. For example, the southern African *Rhoptropus* are sympatric with several agamid species (Branch, 1998). However, diurnality evolved in *Rhoptropus* sometime prior to 25–30 Mya (Fig. 3), which predates diversification of agamids in the region 15–20 Mya (Leaché *et al.*, 2014). It is also possible that diurnal gecko lineages evolved in an area lacking iguanians and subsequently dispersed into habitats occupied by diurnal, non-gekkotan lizards. Two *Lygodactylus* species co-occur with numerous diurnal, arboreal iguanians in the arid Chaco and Cerrado regions of South America (Peters, Donoso-Barros & Orejas-Miranda, 1986). South America was already teaming with iguanians by the time *Lygodactylus* dispersed to South America from Africa in the early Miocene (Báez & de Gasparini, 1979; Gamble *et al.*, 2011; Townsend *et al.*, 2011; Albino & Brizuela, 2014). However, it should be noted that direct competition is probably minimal between the miniature South American *Lygodactylus* and co-distributed iguanians due to extreme differences in size (Vitt, 1995). Furthermore, competition does not have to be with other lizards. Competitive exclusion from the species-rich, Neotropical treefrogs has been proposed as a possible explanation for the paucity of nocturnal, arboreal geckos in the Western Hemisphere (Duellman & Pianka, 1990); three-fifths of New World gecko species are primarily terrestrial and diurnal members of the Sphaerodactylidae (Gamble *et al.*, 2011).

Determining the relative importance of climate, predators and competition to individual transitions in gekkotan temporal activity will require further research. Historical approaches that utilize phylogenetic data and incorporate the evolution of ecologically relevant traits to investigate the organization of ecological communities will be particularly useful in this regard (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009). Because temporal niche shifts between diurnality and nocturnality are relatively rare among animals (Schoener, 1974) the large number of transitions observed in geckos will prove quite useful for testing hypotheses of temporal niche partitioning and ecological community assembly over a variety of evolutionary timescales.

It is reasonable to assume that changes in temporal activity in geckos could be associated with increased diversification rates in diurnal lineages. The occupation of a new adaptive zone can lead to ecological release promoting diversification and adaptive

radiation (Simpson, 1944; Schluter, 2000; Harmon *et al.*, 2008). However, we found no association between changes in temporal niche and speciation and extinction rates with our BiSSE analysis. This lack of a relationship could be due to several factors. First, the invasion of a new adaptive zone need not automatically lead to adaptive radiation (Losos, 2010; Yoder *et al.*, 2010). For example, genetic constraints could limit the evolution of ancillary phenotypic traits necessary for subsequent diversification (Schluter, 1996). This could include the evolution of eye lens crystallins to filter harmful UV light or physiological adaptations to increased daytime temperatures (Autumn, 1999; Röll, 2001b). Second, geckos as a whole may be 'prone to radiating', *sensu* Losos (2010). There are numerous species-rich gecko clades, some of which are diurnal and others that are nocturnal (Fig. 4). Any increase in diversification rate experienced by a diurnal lineage due to ecological opportunity may not be significantly greater than the high diversification rates exhibited by many nocturnal gecko lineages. Investigating the factors that promote diversification in geckos will require additional data, as many traits may be linked to increased diversification in geckos (Harmon *et al.*, 2008; Gamble *et al.*, 2012; Garcia-Porta & Ord, 2013), as well as the development of robust methods that can more accurately identify the correlates of diversification (Maddison & FitzJohn, 2015).

CONCLUSIONS

Temporal niche partitioning among species can have a strong phylogenetic basis and geckos overall exhibit significant phylogenetic conservation of physiological and behavioural traits related to temporal activity patterns (Autumn *et al.*, 1999; Vitt *et al.*, 2003; Vitt & Pianka, 2005). However, multiple shifts in temporal activity have occurred across the gekkotan phylogeny and parsing out the causes and consequences of such transitions will provide important insights into many aspects of gecko biology (Dial & Grismer, 1992; Autumn, 1999; Autumn *et al.*, 1999). The comparative phylogenetic framework presented here will be useful for interpreting, or reinterpreting, adaptations to varying thermal and light environments in geckos (Autumn, 1999; Röll, 2001b; Werner & Seifan, 2006). Furthermore, replicate transitions to diurnality in geckos provide an exceptional opportunity to further study the evolution of suites of complex traits and determine whether convergent traits associated with diurnality follow predictable evolutionary patterns.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Activity patterns of 120 gecko genera representing 1552 species. *Cnemaspis* is separated into three clades. Definitions: Nocturnal – most activity and foraging occurs at night; Diurnal – most activity and foraging occurs during the day; Cathemeral/Crepuscular – most activity and foraging occurs at twilight and/or during both day and night.
Table S2. Details of material examined.

SHARED DATA

GenBank numbers are listed in the supplementary material. Trees, diurnality data and sequence alignments deposited in the Dryad repository (Gamble *et al.*, 2015).