

Key innovations and island colonization as engines of evolutionary diversification: a comparative test with the Australasian diplodactyloid geckos

J. GARCIA-PORTA* & T. J. ORD†

*Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta, Barcelona, Spain

†Evolution and Ecology Research Centre, and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney NSW, Australia

Keywords:

adaptive radiation;
body size disparity;
evolutionary rate;
lizard;
padless;
snakelike phenotype;
toepads.

Abstract

The acquisition of key innovations and the invasion of new areas constitute two major processes that facilitate ecological opportunity and subsequent evolutionary diversification. Using a major lizard radiation as a model, the Australasian diplodactyloid geckos, we explored the effects of two key innovations (adhesive toepads and a snake-like phenotype) and the invasion of new environments (island colonization) in promoting the evolution of phenotypic and species diversity. We found no evidence that toepads had significantly increased evolutionary diversification, which challenges the common assumption that the evolution of toepads has been responsible for the extensive radiation of geckos. In contrast, a snakelike phenotype was associated with increased rates of body size evolution and, to a lesser extent, species diversification. However, the clearest impact on evolutionary diversification has been the colonization of New Zealand and New Caledonia, which were associated with increased rates of both body size evolution and species diversification. This highlights that colonizing new environments can drive adaptive diversification in conjunction or independently of the evolution of a key innovation. Studies wishing to confirm the putative link between a key innovation and subsequent evolutionary diversification must therefore show that it has been the acquisition of an innovation specifically, not the colonization of new areas more generally, that has prompted diversification.

Introduction

A major challenge in evolutionary biology is understanding the main drivers that underlie morphological and species diversity (Wainwright, 2007). Ecological opportunity – access to new or previously inaccessible niches – has been identified as one of the most important drivers of both phenotypic and species diversification (Simpson, 1944; Losos & de Queiroz, 1997; Schluter, 2000; Nosil & Reimchen, 2005; Harmon *et al.*, 2008; Mahler *et al.*, 2010; Yoder *et al.*, 2010). This is because the exploitation of new ecological niches is

often accompanied by phenotypic differentiation among closely related taxa. This can in turn facilitate species diversification if phenotypic differentiation is associated with the appearance of reproductive isolation (Gavrilets & Vose, 2009).

Ecological opportunity can arise from three main sources (Simpson, 1944, 1953): (i) the extinction of ecological competitors that open up previously ‘filled’ niches; (ii) exposure to new environments through dispersal (e. g. island colonization) or changes to existing environments through extrinsic forces that modify the environment (e.g. climate change); and (iii) the evolution of key innovations that allow taxa to use environments or resources in novel ways. These sources of ecological opportunity can appear in concert and interact in complex ways in diversifying groups. Our study examined the latter two sources of ecological opportunity – specifically, the colonization of islands and the

Correspondence: Joan García-Porta, Institute of Evolutionary Biology, CSIC-Universitat Pompeu Fabra, Passeig Marítim de la Barceloneta, 37-49, 08003 Barcelona, Spain. Tel.: +34 93 230 95 00 (ext. 6034); fax: +34 93 230 95 55; e-mail: j.garcia-porta@ibe.upf-csic.es

evolution of two putative key innovations – and explored the extent that these have driven evolutionary diversification in a morphologically diverse and species-rich vertebrate group: the Australasian diplodactyloid geckos.

Island colonization and key innovations can affect evolutionary differentiation in a number of ways. First, we can expect the colonization of islands to result in ecological opportunity if colonizing taxa encounter new or unoccupied ecological niches. Adaptation to these newly available niches can trigger accelerated rates of phenotypic change and can be coupled with accelerated rates of speciation (Losos & Ricklefs, 2009). The Darwin finches of the Galapagos Islands (Grant & Grant, 2011), the explosive speciation of *Drosophila* in Hawaii (Zimmerman, 1970) or the numerous endemic *Anolis* lizard species found across the islands of the Caribbean (Losos, 2009) are classic examples of the sorts of adaptive radiations that can follow island colonization. Nevertheless, island colonization may not always lead to new ecological opportunities or result in accelerated evolutionary differentiation. In fact, reduced rates of evolutionary diversification might be expected if available ecological niches are filled by one or a few generalist species (Roughgarden, 1972), or if the composition of island communities reflects immigration rather than *in situ* island speciation (Whittaker *et al.*, 2010).

Second, key innovations are features that allow taxa to interact with their environment in novel ways and reach previously inaccessible regions of the adaptive landscape (Miller, 1949; Hunter, 1998; de Queiroz, 2002; Losos, 2009). The filling up of these newly accessed niches following the evolution of a key innovation may prompt increased rates of change in other phenotypic characteristics or high species diversification (Galis, 2001). Classic examples of key innovations are the evolution of feathers and wings in dinosaurs (which allowed flight; Hunter, 1998) and the appearance of flowers in plants (which allowed animal pollination; Vamosi & Vamosi, 2010). The concepts of key innovation and adaptive radiation are tightly linked in the literature (see Losos, 2009, 2010 and references therein). However, taxa such as the aardvarks (family Orycteropodidae) or even ourselves, humans, possess various key innovations and exhibit only low morphological and species diversity (Hunter, 1998; Wood & Collard, 1999). Such examples caution that the evolution of key innovations need not always open up the door to greater evolutionary diversification (Fürsich & Jablonski, 1984).

The Australasian diplodactyloid geckos (Vidal & Hedges 2009; Wilson & Swan, 2010) offer a wonderful opportunity to assess the contribution of island colonization and the evolution of key innovations in evolutionary diversification. The almost 200 species described so far in this group (Reptile Database: Uetz, 2010; accessed in February 2013) represent the greatest morphological diversity found in geckos (Oliver &

Sanders, 2009). The group, containing three different families (Diplodactylidae, Carphodactylidae and Pygopodidae), forms an extensive radiation throughout Australia and New Guinea with, and of special relevance to our study, independent colonization of the island archipelagos of New Caledonia and New Zealand. Many – but not all – species possess one of two putative key innovations in the form of adhesive toepads or an elongated, near limbless snakelike phenotype (Hitchmough, 1997; Cogger, 2002; Wilson & Swan, 2010). Toepads are classically believed to have promoted ecological and species diversification in squamate lizards because they allow lizards to adhere to almost any surface (Autumn & Peattie, 2002; Hansen & Autumn, 2005; Huber *et al.*, 2005), greatly expanding the ecological niches available to species. Toepad evolution has consequently been inferred to have culminated in the extensive (and often adaptive) radiations of both the Caribbean *Anolis* lizards and geckos (Losos, 2009). In the case of the *Anolis*, these lizards subdivide more of their habitat than closely related padless genera (Warheit *et al.*, 1999). Such comparisons have led to the belief that the evolution of toepads was probably a critical step in the subsequent adaptive radiation of the *Anolis* lizards and presumably geckos as well (Losos, 2009).

Another candidate key innovation within geckos is a snakelike phenotype. Although most of the Australasian geckos have fully developed limbs, a subset of species (family Pygopodidae) possesses an elongated body with no forelimbs and only small scaly flaps as hindlimbs (hereafter referred as ‘snakelike phenotype’, Shine, 1986). This represents one of the most dramatic transformations in the tetrapod body plan and provides a new way to interact with the environment, enabling (i) more efficient locomotion; (ii) the ability to use narrow spaces like crevices for obtaining food, thermoregulation or shelter; (iii) the ability to burrow in soil or sand; and often, (iv) the ability to ingest prey bigger than themselves (Gans, 1975; Shine, 1986). This involves a combination of profound anatomical transformations that take place at different organismic levels, usually involving an extreme reduction in limbs and girdles, an increase in the vertebral number, visceral rearrangements and significant cranial transformations among others (Gans, 1975). The snakelike phenotype has appeared multiple times independently across the evolutionary history of squamates (Wiens *et al.*, 2006) and is associated with instances of high levels of species diversity, as in the case of the snakes or amphisbaenians.

In this study, we examined how the invasion of new environments associated with island colonization and the evolution of key innovations such as adhesive toepads and a snakelike phenotype have affected – independently or in synergy – the rates of phenotypic evolution and the diversity dynamics in a highly diverse group. We focused on changes in species body

size as a proxy for phenotypic evolution, as it is tightly correlated with a range of physiological and ecological characteristics, including metabolic rate, home range size and many life-history traits (Peters, 1986; Brown *et al.*, 2004). Furthermore, divergence in body size is a common outcome of evolutionary diversification with an adaptive component (Williams, 1972; Diamond, 1986; Richman & Price, 1992) because variance in body size among species tends to reflect the existence of resource partitioning (Moen & Wiens, 2009). In the particular case of Australasian geckos, body size varies extensively among species, from minute species of < 5 cm in snout-vent length to massive geckoes reaching well over 30 cm in snout-vent length (Bauer & Russell, 1986; Bauer *et al.*, 2006). Taken together, the Australasian geckos provide an ideal model to study the role of key innovations and island colonization in shaping the evolution of phenotypic and species diversity.

We began our investigation by developing a robust phylogeny of the whole radiation. Using this phylogeny, we then applied a variety of comparative methods to test whether key innovations and island colonization have been associated with accelerated rates of body size evolution and species diversification in the group.

Materials and methods

Phylogenetic analysis

The sequences of two mitochondrial (16S and ND2) and two nuclear genes (CMOS and RAG-1) were downloaded for all taxa assigned to Diplodactyloidea in GenBank (Benson *et al.*, 2011), plus 21 additional species of geckos outside of this group to calibrate the tree (GenBank was accessed in February 2013). The criterion to select genes was based on maximizing the number of species included in the phylogeny while minimizing the amount of missing species for each gene (with a minimum of 20% of representatives per gene). For each taxon, the longest sequence for each gene was retrieved with the additional requirement that all sequences had to be 200 bp or more for inclusion. After this procedure, our sequence data covered 82% of all currently described Australasian diplodactyloids (<http://reptile-database.reptarium.cz>; accessed February 2013), with an additional 35 undescribed species and nine highly divergent subspecies, resulting in a total of 202 taxa. Each gene was then trimmed and aligned using two procedures: the ribosomal coding 16S was aligned by means of MAFFT version 6 (<http://www.ebi.ac.uk/Tools/msa/mafft/>; Katoh *et al.*, 2002;) and the protein coding genes (ND2, CMOS and RAG-1) were aligned by means of the translation alignment algorithm implemented in the software Geneious (Drummond *et al.*, 2010). In both cases, the gap penalties and gap extension costs were left to default values. Finally, ambiguously aligned regions in the 16S alignment were

excluded by means of Gblocks (Castresana, 2000). The final alignment consisted in a total of 3418 bp distributed in each gene as follows: 16S (227 bp), ND2 (939 bp), CMOS (372 bp) and RAG-1 (1880 bp).

The phylogenetic analysis was conducted by means of the package BEAST version 1.6.2 (Drummond & Rambaut, 2007). The prior for the distribution of branching times was based on a birth–death process. The nucleotide substitution model was set to GTR + G + I, and the variation of nucleotide substitution rates across the tree was assumed to be nonauto-correlated and log-normally distributed. The clock model and the nucleotide substitution models were applied independently to four partitions: 16S, ND2, CMOS and RAG-1, with every codon position considered separately in the protein coding genes.

Four calibrations were used to estimate branch lengths in units of time (Fig. S1):

- 1 The minimum age of the root node of Gekkota was set to 99.5 Ma based on the oldest fossil assigned to the crown group of Gekkota, *Hoburogekko suchanovi*, from the Early Cretaceous of Mongolia (Daza *et al.*, 2012) and a soft maximum of 180 Ma. This interval included the age of the oldest fossil of Gekkonomorpha (an undescribed fossil dated around 110 Ma) and the stem Squamatan *Parviraptor sp.*, dating back to 170 Ma (Conrad & Norell, 2006; Daza *et al.*, 2013). The prior was set by means of a gamma distribution ($\alpha = 3$, $\beta = 14$).
- 2 The minimum age for the radiation of *Sphaerodactylus* in the Caribbean was set to 20 Ma based on an amber fossil from the Dominican Republic (Daza & Bauer, 2012). The maximum age of this radiation was set conservatively to a soft maximum of 70 Ma. This was done by means of a gamma distribution ($\alpha = 2$, $\beta = 11$).
- 3 The age of the Tien Shan-Pamir uplift in western China, around 10 Ma, was used to calibrate the split between *Teratoscincus scincus* and the clade formed by *Teratoscincus przewalskii* and *Teratoscincus roborowskii* considering that this split originated via vicariance as a result of this geologic event (Macey *et al.*, 1999). A normal distribution with a mean positioned at 10 Ma and a standard deviation of 1 Ma were chosen to set the calibration prior of this node.
- 4 The minimum age of the clade represented by the *Pygopus* and *Paradelma* (including stem) was set to 20 Ma with a soft maximum of 50 Ma based on the oldest known fossil for this genus (*Pygopus hortulanus* – Hutchinson, 1997; Jennings *et al.*, 2003). A gamma distribution with an offset of 20 Ma was used to set the prior of this calibration point ($\alpha = 2$, $\beta = 6$).

The phylogenetic analysis consisted of two independent Markov Chain Monte Carlo (MCMC) analyses. Each chain was run for 50 000 000 generations with parameters, and trees sampled every 5000 generations. These two independent runs converged on very similar

posterior estimates and were combined using LogCombiner version 1.6.2 (<http://beast.bio.ed.ac.uk/LogCombiner>) after excluding the first 10% of generations in each one. Tracer version 1.5 (Rambaut & Drummond, 2007) was used to confirm convergence and good mixing of each MCMC chain.

To assess the effects of the interactions among the calibration priors, we ran one MCMC chain without sequences for 25 000 000 generations to estimate the distributions of the effective joint priors of our calibration points. We then compared these with the posterior distributions to assess congruence among calibration points (Sanders & Lee, 2007).

Finally, we calculated the summary tree as the maximum clade credibility tree with median node heights using TreeAnnotator version 1.6.2 (<http://beast.bio.ed.ac.uk/TreeAnnotator>), setting the posterior probability limit to 0.5. To incorporate uncertainty in both the topology and branch lengths of our recovered phylogeny in our comparative analyses, we resampled the posterior distribution of the trees generated by BEAST to obtain a set of 1000 trees. These 1000 trees were subsequently used for comparative tests of ancestor state reconstructions and diversification (see the following sections).

Species categories

We grouped species into one of five different categories: 'snakelike' (those taxa that with elongated body and lacking functional limbs; these occurred throughout Australia and New Guinea), 'padless' (those limbed taxa with no adhesive toepads; these were restricted to Australia), 'continental pad-bearing' (those taxa that possessed adhesive toepads and were found throughout the Australian continent), 'New Caledonian pad-bearing' (those taxa that possessed well-developed adhesive toepads and occurred in New Caledonia, abbreviated as NC) and 'New Zealand pad-bearing' (those taxa with well-developed toepads and occurred in New Zealand, abbreviated as NZ; Fig. 1). We distinguished the toepad-bearing categories for the continental and island species to single out the effects of toepads and island colonization (or island colonization plus toepads, in the case of a combined effect of both) on the rate of phenotypic and species diversification. We decided to split island species in New Caledonia and New Zealand given that the gecko radiations were monophyletic on each archipelago and large differences existed between these islands in terms of latitude (being 1700 km from one another), area and physiography (Bauer & Sadlier, 2000; Wallis & Trewick, 2009). New Guinea – represented by a single species (*Lialis jicari*) – was considered as a part of the radiation of Australia. Morphotype assignment of categories (snakelike, padless and pad-bearing) were based on the descriptions

provided by Hitchmough (1997), Bauer & Sadlier (2000), Cogger (2002) and Wilson & Swan (2010).

Body size was measured as the maximum snout-vent length (SVL) reported for a given species. SVL data were compiled from Bauer & Russell (1986), Shea (1991), Bauer & Sadlier (2000), Bauer *et al.* (2006, 2009), Wilson & Swan (2010), Meiri *et al.* (2011), Bauer *et al.* (2012a,b) and the 'Electronic Atlas of the Amphibian & Reptiles of New Zealand' (EAARNZ, available at <http://www.doc.govt.nz/conservation>). All SVL data were log-10 transformed prior to analyses.

Analyses

Ancestral state reconstructions

We reconstructed the ancestral states of our categorical states by means of the function 'make.simmap' in the package 'phytools' version 0.2.80 (Revell, 2011). This function essentially fits a continuous-time reversible Markov model and simulates plausible stochastic character histories along the tree using the most likely model in combination with the states assigned to the tips of the tree (Revell, 2011).

For both the summary tree and the set of 1000 trees, we reconstructed the five categories described in the previous section (i.e. 'snakelike', 'padless', 'continental pad-bearing', 'NC pad-bearing' and 'NZ pad-bearing'). Reconstructions made on the summary tree relied on 100 stochastic character histories, whereas those made on the set of 1000 trees relied on a single stochastic history simulated on each tree. By implementing reconstructions on both the summary tree and the set of 1000 trees resampled from the posterior distribution used to estimate the summary tree, we effectively incorporated uncertainty in both the tree estimation and the character state reconstructions in subsequent comparative analyses.

In addition to these reconstructions, we created a second series using only the summary tree to reconstruct various groupings of these categories (Table S1) to assess whether rates of body size evolution differed or were similar among select categories in follow-up analyses (specifically those of MOTMOT; see next section). For example, all continental categories (snakelike, padless and continental pad-bearing) and island categories (NC pad-bearing and NZ pad-bearing) were grouped together to test whether evolutionary rates of body size evolution differed between continental and island lineages. Another set of reconstructions separated snakelike, padless and pad-bearing lineages (from the continent, NC and NZ) to assess whether evolutionary rates differed more between these lineage types. See Table S1 and the following section for other category groupings. All reconstructions followed the same protocol of simulating 100 stochastic character histories onto the summary tree.

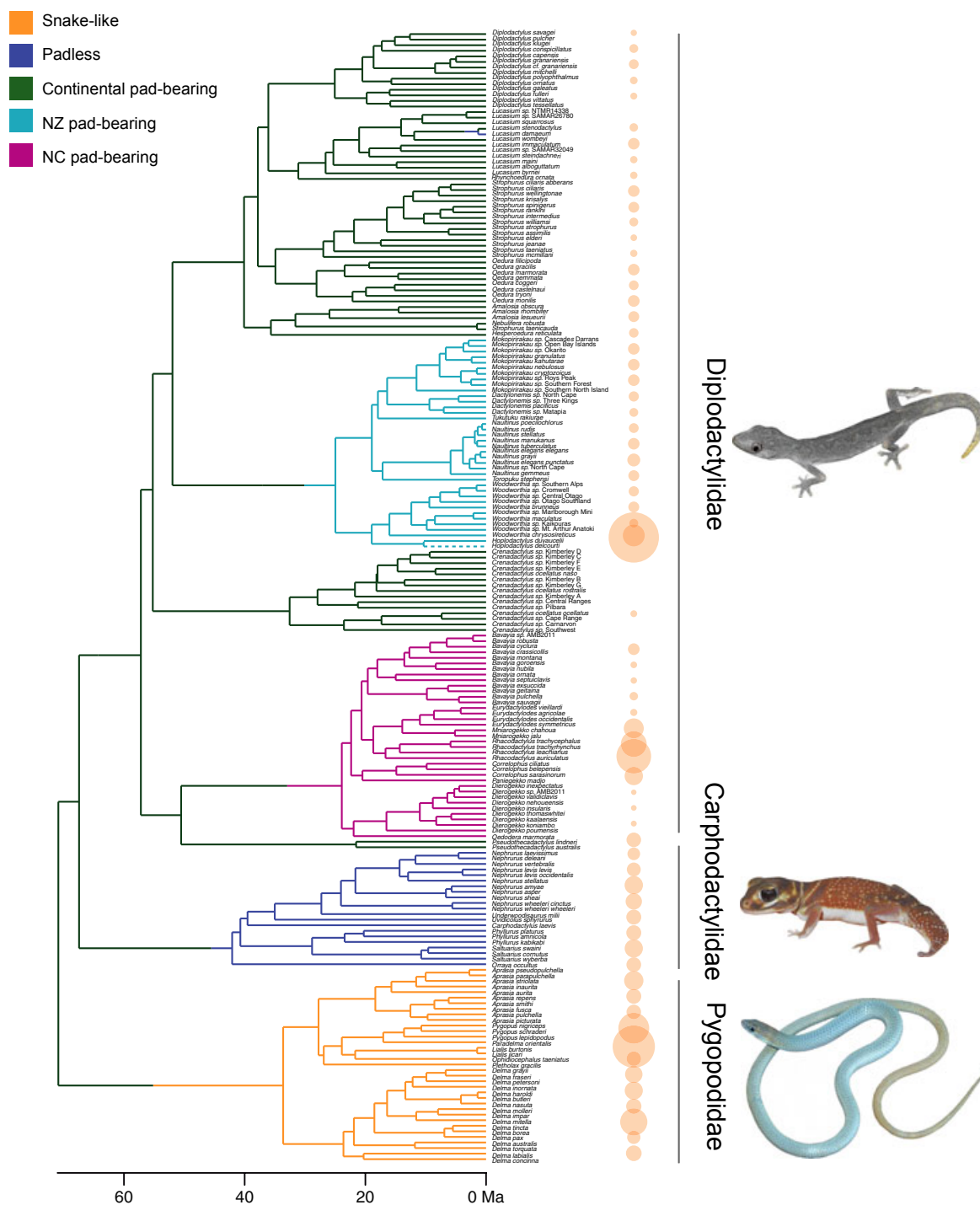


Fig. 1 Time-calibrated tree of the Australian diploidy geckos with the evolutionary transitions among categories reconstructed according to one possible stochastic character history. The shading of the branches correspond to the following: ‘snake-like’ (elongated geckos that lack functional limbs), ‘padless’ species (limbed geckos with no adhesive toepads), ‘continental pad-bearing’ species (geckos that possessed adhesive toepads and occurred on continental Australia), ‘NC pad-bearing’ (geckos that possessed adhesive toepads and occurred in New Caledonia) and ‘NZ pad-bearing’ (geckos with toepads inhabiting New Zealand). The dashed line indicates the hypothetical phylogenetic position of the extinct gecko *Hoplodactylus delectu*. The circles provide a visualization of the body size variation across the phylogeny with diameters proportional to the maximum snout-vent length (SVL) of a given species. Also shown are three representative species for each gecko family covered by the phylogeny.

Rates of body size evolution

We used two complementary approaches to estimate rates of body size evolution across the phylogeny. The first method was implemented by the R package MOTMOT version 1.0.1 (Thomas & Freckleton, 2012) and consisted of first specifying where on the phylogeny each categorical state had evolved. The relative rates of body size evolution among lineages assigned to a given category were then estimated via maximum likelihood (Thomas *et al.*, 2009). We fitted five alternative models each one based on a different category reconstruction (Table S1). Model 1 assumed that rates of body size evolution differed among all of our five categorical groups (snakelike, padless, continental pad-bearing, NC pad-bearing and NZ pad-bearing). Model 2 assumed that continental and island lineages differed in their rates. Model 3 assumed that evolutionary rates differed among the snakelike, continental and island lineages. Model 4 assumed that evolutionary rates differed among the snakelike, padless and pad-bearing lineages. Finally, Model 5 – the null model – assumed that rates of body size evolution were consistent across all lineages. Each model was run twice: once assuming that all categories shared a common phylogenetic mean (notated by ‘a’) and once assuming that categories did not share a common phylogenetic mean (notated by ‘b’). This resulted in a total of ten models (Model 1a, Model 2a, Model 3a, Model 4a, Model 5a, Model 1b, Model 2b, Model 3b, Model 4b and Model 5b).

We evaluated the relative support for each model based on their computed mean second order Akaike’s Information Criterion (AICc) across the 100 ancestor reconstructions on the summary tree (Burnham & Anderson, 2004). We also applied Model 1 (a and b; the most general model) to the set of 1000 trees in which each tree assumed a different stochastic history in the reconstruction of the snakelike, padless, continental pad-bearing, NC pad-bearing and NZ pad-bearing categories. This was done to assess the effect of uncertainties in both the phylogeny and ancestor reconstruction on the computed rates of body size evolution.

The recent extinction of what was the biggest gecko in the world, the New Zealand endemic *Hoplodactylus delcourti*, might have impacted our estimated rates of body size evolution for NZ pad-bearing category. To examine this, we refitted all models described before to the set same set of 100 trees in which *H. delcourti* had been positioned as a sister species of its probable closest relative, *H. duvaucelii* (based on morphological resemblance; Hitchmough, 1997) with a randomly set node height in each tree. We also applied Model 1 (a and b) to the set of 1000 trees in which each tree had *H. delcourti* positioned as sister of *H. duvaucelii* with a random height in each tree. As previously described, each tree

incorporating *H. delcourti* assumed a different stochastic history in the reconstruction of the snakelike, padless, continental pad-bearing, NC pad-bearing and NZ pad-bearing categories.

The second method was implemented by the R package ‘auteur’ version 0.12 (Eastman *et al.*, 2011), which estimated rates of body size evolution along branches of the phylogeny without *a priori* specifying which regions of the tree corresponded with particular categories. That is, there was no prior assumption that evolutionary rates had changed at specific points in the phylogeny (e.g. those lineages reconstructed to have toepads). Within the ‘auteur’ package, we performed a reversible-jump Markov Chain Monte Carlo sampling to estimate the rates of body size evolution along the branches of our summary tree and the 1000 trees subset. Here, rates were computed as a weighted average of posterior rate estimates, where weighting was determined by branch lengths (Eastman *et al.*, 2011). To ensure an optimal mixing of the Markov chain, we first calibrated the proposal width with the summary tree by running three independent chains during 5 000 000 generations. We then ran three independent chains for 20 000 000 generations with a sampling interval of 3000 generations. The posterior estimates of these three runs were subsequently pooled with the first 50% of generations excluded. This analysis allowed us to estimate the posterior rates of body size evolution along branches as well as to localize rate shifts across the branches of the summary tree. To assess whether the results of ‘auteur’ were consistent with the scenario of rate heterogeneity depicted by MOTMOT, we extracted the posterior rate estimates of the branches belonging to each of the five categories (snakelike, padless, continental pad-bearing, NC pad-bearing and NZ pad-bearing). We then plotted their mean rates along with their 95% high posterior density (HPD) to visualize the rate variation among these ‘a posteriori’ defined groups. As described previously for the MOTMOT analyses, to assess the effect of the extinct *H. delcourti*, the analysis on the summary tree was conducted twice, once not including *H. delcourti* and once in which *H. delcourti* had been placed as sister clade to *H. duvaucelii*. For the 1000 trees (in which *H. delcourti* had positioned as sister of *H. duvaucelii* with a random height in each tree), we ran a single chain of 2 000 000 generations per tree with a sampling interval of 1000 generations. Posteriorly, for each tree, we localized which lineages were associated with shifts in rates of body size evolution (only shifts detected in more than 90% of the trees were considered as well supported).

To ensure good mixing and convergence of the Markov chains, all the traces of the summary tree analysis and a subset of the runs for the 1000 trees were analysed by means of the program Tracer version 1.5.

Diversity dynamics

To examine the effect of key innovations and island colonization on species diversification, we applied three approaches. First, we assessed whether snakelike, padless, continental pad-bearing (with the sole exception of *Lucasium damaeum*, which was a padless species in this otherwise toepad-bearing clade) NC pad-bearing and NZ pad-bearing clades differed in their diversity dynamics using the coalescent-based approach described by Morlon *et al.* (2010). This method models the internode distances of a phylogeny assuming that they are distributed according to a standard coalescent approximation (Griffiths & Tavaré, 1994). This has the advantage of modelling species diversity from the present to the past assuming that it can take any value at any point in time. It can also easily accommodate incomplete-sampled phylogenies as the coalescence theory stems from the theory of samples (Morlon *et al.*, 2010). We split our summary tree into five subtrees corresponding to each of the clades of interest. Six models of diversification that differed in their assumed diversity dynamics were then applied separately to each of the five subtrees: Models 1 and 2 assumed that speciation rates were constant through time (a constant birth–death and Yule process, respectively), and the rest of the models assumed that speciation rates varied exponentially through time and differed in the dynamics of the extinction rates: Model 3 assumed a constant extinction rate, Model 4 assumed an extinction rate that varied as a function of the speciation rate, Model 5 assumed an exponential change in extinction rate over time and finally Model 6 assumed no extinction rates (Table S2). The parameters and likelihood of each model were estimated using the R code provided in Morlon *et al.* (2010). The best-supported model was identified as the model with the highest computed Akaike weight (AICw) (see Morlon *et al.*, 2010). This model was then used to interpret the diversification dynamics for a given clade based on its computed parameters estimates.

Second, we compared the rates of diversification among the snakelike, padless, continental pad-bearing, NC pad-bearing and NZ pad-bearing using the ‘Multiple State Speciation Extinction’ (MuSSE) model in the R package Diversitree version 0.9.1 (FitzJohn, 2012). This method estimates the rates of change in a multi-state character and the rates of speciation and extinction associated with each character state given the distribution of observed states along the tips of a tree. This is performed by combining the features of a Markov model of trait evolution (to estimate the rates of transition among characters) and a constant rates birth–death process (to estimate diversification rates in each state character) in the same evolutionary model. We estimated the rates of diversification across the subset of 1000 trees retained from the BEAST posterior, assuming an equal rates model of character evolution.

Finally, we also assessed the among-categories heterogeneity in diversification rates across the subset of 1000 trees by means of a diversity-dependent model (dd), in which the speciation rate was variable through time (varying according to the diversity in a given time) with constant extinction. This was implemented by splitting each of the 1000 trees into five subtrees corresponding to each category and applying the function ‘dd_ML’ (model 1) in the R package DDD version 1.11 (Etienne *et al.*, 2012). For both models, we assessed rate heterogeneity among categories by plotting mean diversification rates and associated 95% confidence intervals computed for each category.

Given that the number of nonsampled species in a phylogeny can produce a bias in the estimates of species diversification (Ricklefs, 2007), all analyses took into account an estimate of the number of species missing from the phylogeny. According to the Reptile Database and the EAARNZ (accessed in February 2013), our sampling coverage for each major group within the Australasian geckos was the following: 85% for the family Pygopodidae, 70% for the family Carphodactylidae, 80% for the continental Diplodactylidae, 88% for the New Zealand Diplodactylidae and the 100% of the described species of New Caledonian Diplodactylidae.

Another source of bias might also occur if the taxonomy within each of the categories was not equally known. For example, if New Caledonia and New Zealand were better taxonomically and phylogenetically studied than species on the Australian continent, this could lead to an underestimation of the real diversity on the continent and subsequently affect its estimated diversification rate. To assess this, we conducted a separate analysis by means of the dd model in which it was assumed that an additional 50% of the total number of currently known species of Pygopodidae, Carphodactylidae and continental Diplodactylidae would be discovered at some point in the future (that is, the current estimated number of species actually represents only two-thirds of the true diversity of the group).

Results

Phylogenetic analysis

We recovered 75% of nodes of the summary tree with a posterior probability (pp) > 0.90 (high to very high support; Fig. S1). The phylogenetic relationships depicted by our summary tree were generally consistent with previous published phylogenies of the Diplodactyloidea (Jennings *et al.*, 2003; Gamble *et al.*, 2008). The only major difference lay in the snakelike Pygopodidae not being recovered as the sister group to Carphodactylidae (see Gamble *et al.*, 2011; although the node in question had low support in our analysis). In addition, the positioning of *Strophurus taenicauda* was

unexpected because it was recovered as the sister species of *Nebulifera robusta*. Although this positioning was consistent with the results of Melville *et al.* (2004; with the same sequence we used in our study), we suspect that this may reflect a mislabelling of the sequence used for *S. taenicauda*. We repeated our analyses with this species removed and found that it had no impact on any of the comparative analyses performed (results not shown). For dating estimates, the medians of the posterior distributions of the calibrated nodes fell within the 95% HPD of the effective priors. This indicated that the priors of the calibration points were largely congruent with one another (Sanders & Lee, 2007).

According to our estimates, the diplodactyloid geckos started to radiate in Eastern Gondwana between 85 and 60 Ma, which is consistent with previous estimates (97–40 Ma – Gamble *et al.*, 2008; 91–53 Ma – Oliver & Sanders, 2009). The mainland–island splits were dated around 50 Ma for both archipelagos (95% HPD = 61–43 Ma for New Zealand and 62–40 Ma for New Caledonia). In both cases, the 95% HPD interval lies after the last contact (90–65 Ma; Neall & Trewick, 2008; Wallis & Trewick, 2009) between Zealandia (the continental fragment containing New Zealand and New Caledonia) and mainland (what was to become Australia, New Guinea and Antarctica; Wallis & Trewick, 2009). The beginning of the radiations in New Zealand and New Caledonia was estimated at 25 Ma (95% HPD = 31–20 Ma; congruent with Nielsen *et al.* 2011) and 24 Ma, respectively (95% HPD = 29–20 Ma; largely congruent with Oliver & Sanders, 2009). This agrees with several lines of evidence suggesting a complete (or almost complete) submersion of Zealandia between 65 and 37 Ma (according to geological evidence from New Caledonia; Espeland & Murienne, 2011) or even until 25 Ma (according to the geological evidence from New Zealand; Trewick *et al.*, 2007) and a subsequent recolonization of these islands by dispersal (Waters & Craw, 2006; Trewick *et al.*, 2007; Espeland & Murienne, 2011). The diversity of the geckos in New Zealand and New Caledonia therefore seem to have originated following at least one dispersal event from the continent to each archipelago and subsequently accumulated via within-island diversification (based on the fact that most of the lineage splits occur within the same island).

Ancestral reconstructions

The maximum likelihood ancestor state reconstructions of the five categories over the summary tree and the subset of 1000 trees generally assigned toepads as ancestral in the Australasian geckos. However, this assignment was not clear-cut with the relative support being low for toepads existing at the root of the phylogeny compared with some other morphotype (the mean scaled likelihood estimate for toepads existing at the root of the phylogeny was 0.55). Reconstructions across

the 1000 trees also revealed that most of the major transitions among morphotypes (snakelike, padless and pad-bearing) occurred between 82 to 38 Ma. There was also an instance of toepad loss during the last 10 Ma in the lineage leading to *Lucasium damaeum* (Fig. 1).

Rate heterogeneity of body size evolution

MOTMOT

Models 3a, 3b and 1a were the best-supported models on the summary tree, with less than four AICc unit-difference between each model (i.e. all three were reasonably plausible scenarios; Table 1). These were the best-supported models regardless of whether the extinct giant gecko, *H. delcourti*, was or was not included in the analysis (see also next paragraph). Model 3 assumed homogeneous rates of body size evolution among padless and continental pad-bearing species, but different evolutionary rates for the snakelike phenotype and island species. The maximum likelihood estimates of the evolutionary rates of this model showed that the snakelike and island lineages had accelerated rates of body size evolution in respect to the padless and continental pad-bearing categories, which exhibit similar rates (Table 1). The other supported model, Model 1a, assumed rate heterogeneity among all categories. However, the estimated rates of body size evolution were consistent with Model 3 in that similar, low evolutionary rates were estimated for padless and continental pad-bearing species, whereas evolutionary rates were over three times higher for the snakelike and island lineages. Inspection of the mean evolutionary rates computed for Model 1a across the 1000 trees and their 95% CI (Fig. 2) again showed no difference between padless and continental pad-bearing lineages, but significant accelerations in body size evolution for the snakelike, New Caledonian and New Zealand clades. That is, the best-supported models based on the summary tree were consistent with the estimated differences in evolutionary rate computed across the set of 1000 trees that incorporated uncertainty in topology and branch lengths.

The effect of including the extinct giant gecko, *H. delcourti*, in the models and in the set of 1000 trees produced an increase in the estimated evolutionary rates for New Zealand species, which subsequently attained levels comparable with those computed for New Caledonia (Table 1, Fig 2).

Auteur

The analysis based on the summary tree revealed that virtually all lineages with accelerated rates of body size evolution (those with posterior rates above the median rate of evolution) were confined to New Caledonia, New Zealand and the snakelike radiation (Fig. 3a). By contrast, low rates of evolution were detected for most of the continental pad-bearing lineages (Fig. 3a). The

Table 1 Models summarizing alternative scenarios of body size diversification across the five defined categories, with their AICc values ranked relative to the best-supported model ($\Delta AICc$). Also, given are parameter values corresponding to the mean relative rate of body size evolution for each category by model fitted. The results are based on 100 plausible ancestral state reconstructions of each model on the summary tree. The grey shades highlight similar supported models (those with $\Delta AICc < 4$). (a) refers to a situation in which *Hoplodactylus delcourti* was excluded from the analysis, in (b) *H. delcourti* has been placed with randomized branch length as the sister species of *H. divinatellii*.

(a)											
Relative rates of body size evolution (excluding <i>H. delcourti</i>)											
Model	Description	Common mean	Snake-like	Padless	Continental pad-bearing	NC pad-bearing	NZ pad-bearing	AICc	$\Delta AICc$		
Model 3a	Snake-like vs. Continental nonsnake-like vs. Islands	Yes	3.10	1	1	4.52	4.52	-308.72	0.00		
Model 1a	Snake-like vs. Padless vs. Continental pad-bearing vs. NC pad-bearing vs. NZ pad-bearing	Yes	3.72	1	1.27	6.59	4.36	-306.38	2.34		
Model 3b	Snake-like vs. Continental nonsnake-like vs. Islands	No	3.04	1	1	4.52	4.52	-305.29	3.43		
Model 1b	Snake-like vs. Padless vs. Continental pad-bearing vs. NC pad-bearing vs. NZ pad-bearing	No	3.73	1	1.27	6.76	4.46	-300.18	8.53		
Model 2a	Continental vs. island	Yes	1	1	1	2.69	2.69	-294.57	14.15		
Model 2b	Continental vs. island	No	1	1	1	2.69	2.69	-292.49	16.23		
Model 4a	Snake-like vs. Padless vs. Pad-bearing	Yes	3.85	1	3.84	3.84	3.84	-281.89	26.83		
Model 4b	Snake-like vs. Padless vs. Pad-bearing	No	3.81	1	3.82	3.82	3.82	-278.80	29.92		
Model 5a	Equal rates	Yes	1	1	1	1	1	-275.14	33.58		
Model 5b	Equal rates	No	1	1	1	1	1	-268.16	40.56		
(b)											
Relative rates of body size evolution (including <i>H. delcourti</i>)											
Model	Description	Common mean	Snake-like	Padless	Continental pad-bearing	NC pad-bearing	NZ pad-bearing	AICc	$\Delta AICc$		
Model 3a	Snake-like vs. Continental nonsnake-like vs. Islands	Yes	2.99	1	1	5.50	5.50	-291.91	0.00		
Model 3b	Snake-like vs. Continental nonsnake-like vs. Islands	No	2.93	1	1	5.50	5.50	-288.47	3.44		
Model 1a	Snake-like vs. Padless vs. Continental pad-bearing vs. NC pad-bearing vs. NZ pad-bearing	Yes	3.14	1	1.07	5.37	6.15	-288.23	3.68		
Model 1b	Snake-like vs. Padless vs. Continental pad-bearing vs. NC pad-bearing vs. NZ pad-bearing	No	3.12	1	1.07	5.44	6.23	-281.75	10.16		
Model 2a	Continental vs. island	Yes	1	1	1	3.35	3.35	-278.71	13.20		
Model 2b	Continental vs. island	No	1	1	1	3.34	3.34	-276.76	15.15		
Model 4a	Snake-like vs. Padless vs. Pad-bearing	Yes	3.29	1	4.04	4.04	4.04	-256.78	35.13		
Model 4b	Snake-like vs. Padless vs. Pad-bearing	No	3.25	1	4.00	4.00	4.00	-253.46	38.45		
Model 5a	Equal rates	Yes	1	1	1	1	1	-249.28	42.64		
Model 5b	Equal rates	No	1	1	1	1	1	-242.24	49.67		

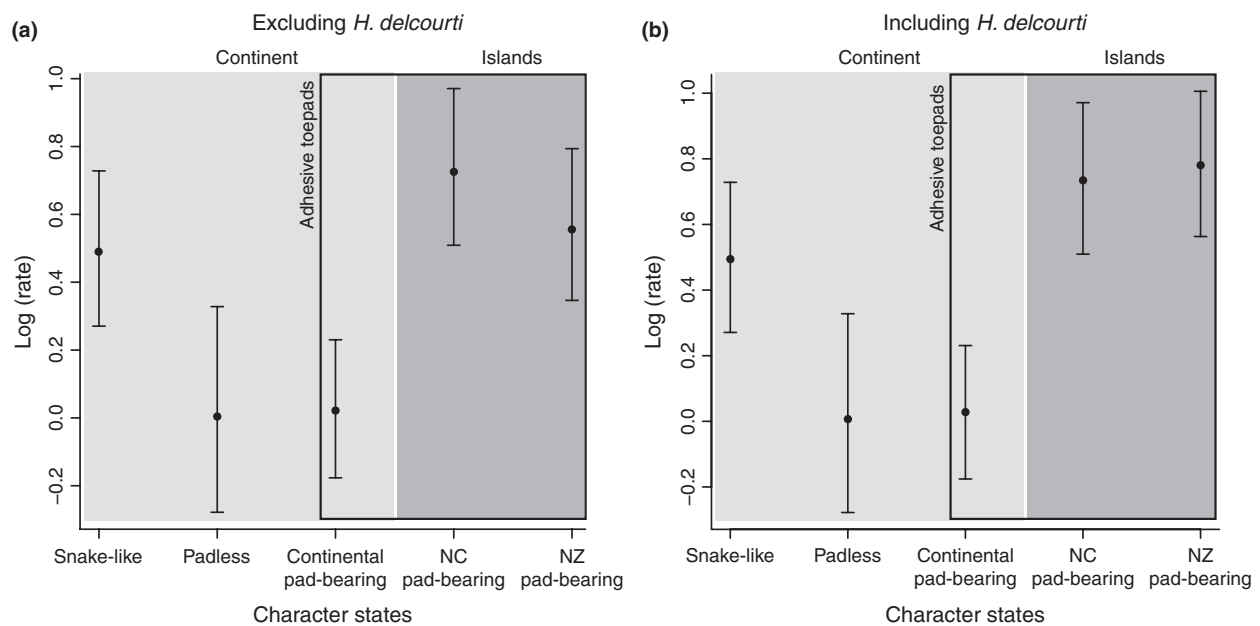


Fig. 2 Plot of the mean relative rates (in a \log_{10} scale) of body size evolution and their associated 95% confidence intervals for each category estimated by Model 1a in which the extinct *Hoplodactylus delcourti* had been excluded (a) or included (b) in the analyses. The light grey rectangle and the darker grey rectangle represent continental and island lineages, respectively. The black frame groups together lineages possessing adhesive toepads. Results are based on a set of 1000 trees that varied in topology and branch lengths.

pattern of rate heterogeneity for those categories found to have accelerated rates of body size evolution was somewhat variable. In the New Caledonian radiation, with the exception of *Dierogekko*, most of the lineages experienced accelerated rates of body size evolution. In contrast, for the New Zealand radiation, high evolutionary rates were limited to select groups with other lineages not deviating from median (background) rates. In New Zealand, those lineages estimated to have experienced accelerated evolutionary rates basically involved all lineages leading to the *Naultinus* radiation (also involving *Toropuku stephensi*) and the lineage leading to *H. duvaucelii* (and to *H. delcourti* when this was included in the analysis, Fig. 3a). Within the snakelike category, high evolutionary rates were generally distributed across all genera.

For the analyses based on the 1000 trees, those shifts associated with high rates of body size evolution recovered in at least 90% of trees were found concentrated within the New Zealand (specifically lineages associated with *Naultinus* and the genus *Hoplodactylus*) and within the New Caledonian radiation, also affecting the split leading to the snakelike clade (Fig. 3a). The mean and 95% HDP intervals of evolutionary rates extracted from posterior rates defined by category depicted a scenario consistent with the MOTMOT results (Fig. 3b), with major increases in the rates of body size evolution found primarily in the snakelike, New Caledonian and New Zealand lineages. Also, consistent with the MOTMOT results was the effect of including the extinct

H. delcourti, which resulted in an increase in the rates of body size evolution detected within the New Zealand clade (Fig. 3b).

Rate heterogeneity in species diversification

Diversity dynamics

The comparison of the six different diversification models fitted to the subtrees of each category extracted from the summary tree (Table 2) identified Model 6, which assumed a time-decaying speciation rate with no extinction, as the best model for the snakelike, continental pad-bearing and NC pad-bearing clades (in all cases with $AICw > 0.5$, Table 2, Fig. S2). For these three clades, speciation has generally slowed down through time ($\alpha > 0$), but this was estimated to have occurred at different rates within these clades: the New Caledonian radiation appears to have been associated with an early burst of speciation followed by a rapid decay in speciation rate ($\alpha = 0.1$); the continental pad-bearing radiation has experienced a slow decay in speciation ($\alpha = 0.02$); whereas the snakelike radiation has experienced an intermediate pattern of decay ($\alpha = 0.05$). In these clades, none of the two constant rate models (Models 1 and 2) received any substantial support ($AICw < 0.01$; Fig. S2). In padless and the NZ pad-bearing clades, Model 2, which assumed a pure-birth Yule process of diversification (implying diversification has been largely constant through time with no extinction), was highlighted as the best model. Although Model 6

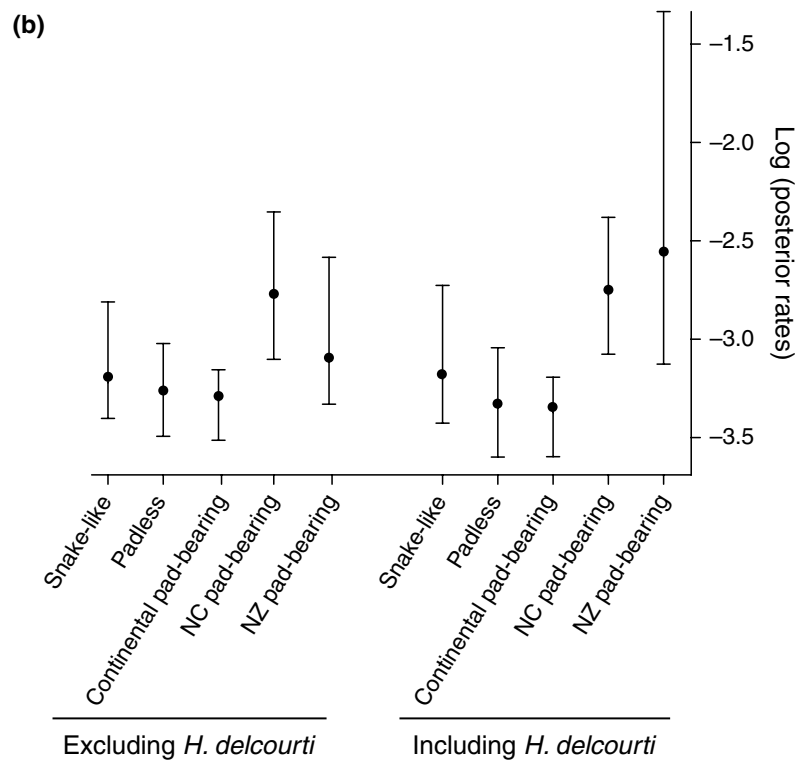
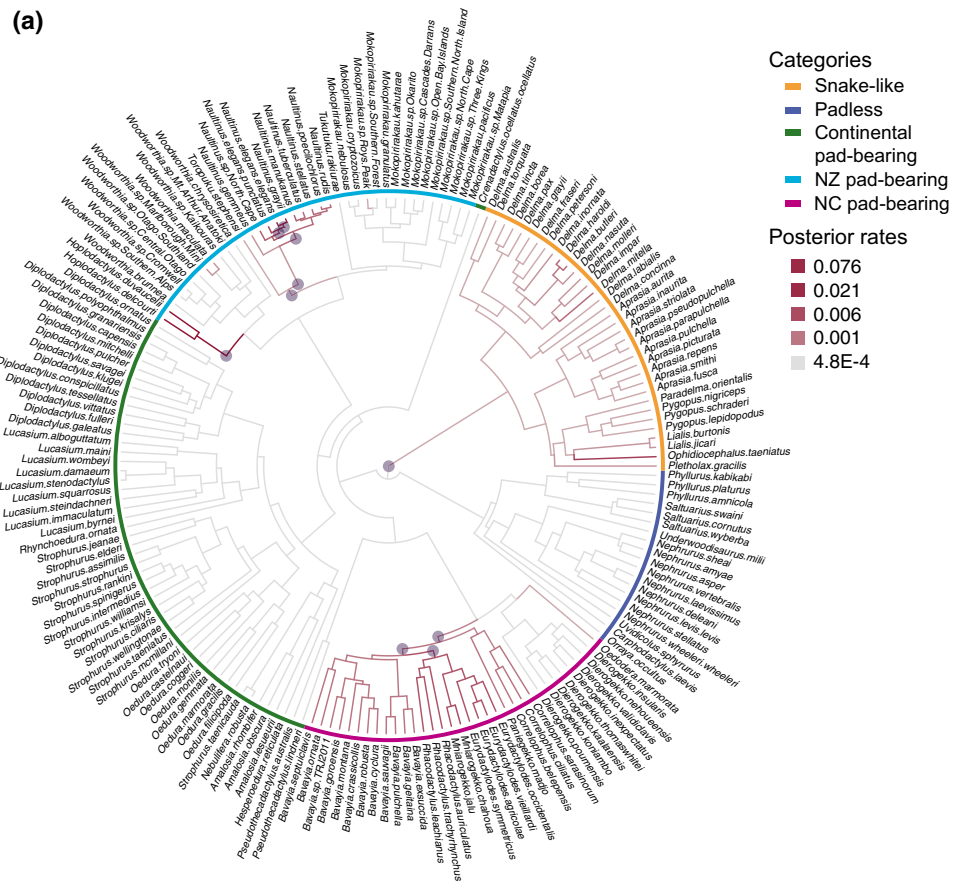


Fig. 3 The top panel (a) shows the summary tree (including *Hoplodactylus delcourti*) with branches shaded to reflect how rates of body size evolution varied across the phylogeny. Background rates (those not deviating from the median rate across the tree) are shaded light grey; those rates greater than median rates are shaded in darker shading proportionally to their computed deviation from the median. Rates corresponding to each shade are indicated in the legend. The circles superimposed onto the phylogeny indicate rate shifts detected in more than 90% of the trees in the 1000 trees sample. The bottom panel (b) provides a plot comparing the posterior densities of the evolutionary rates estimated for the branches assigned to snakelike, padless, continental pad-bearing, NC pad-bearing and NZ pad-bearing. Two sets of analyses were conducted: one without the extinct giant gecko *H. delcourti* (left) and one including *H. delcourti* (posterior rate densities are plotted on a \log_{10} -scale).

Table 2 Parameter estimates and proportion of support (AICw) of the most likely models of diversity dynamics across the five categories. The results are based on the summary tree. Model 6 depicts a scenario of exponential variation in speciation rate and Model 2 corresponds to a Yule process in which speciation rate is constant through time. Here, λ_0 refers to the speciation rates at present day, and α refers to exponential variation in speciation rate.

Category	Best-fit model	AICw	Model properties			Parameter estimates
			Speciation	Extinction	Equation	
Snakelike	Model 6	0.57	Varying	–	$\lambda(t) = \lambda_0 e^{\alpha t}$	$\lambda_0 = 0.043$ $\alpha = 0.053$
Padless	Model 2	0.55	Constant	–	$\lambda(t) = \lambda_0$	$\lambda_0 = 0.062$
Continental pad-bearing	Model 6	0.54	Varying	–	$\lambda(t) = \lambda_0 e^{\alpha t}$	$\lambda_0 = 0.043$ $\alpha = 0.021$
NC pad-bearing	Model 6	0.66	Varying	–	$\lambda(t) = \lambda_0 e^{\alpha t}$	$\lambda_0 = 0.030$ $\alpha = 0.106$
NZ pad-bearing	Model 2	0.43	Constant	–	$\lambda(t) = \lambda_0$	$\lambda_0 = 0.137$

also received some support for the padless and the NZ pad-bearing clades (Fig. S2), the estimated rates of decay for the diversification rates in this model were very low ($\alpha = 0.02$ and $\alpha = 0.01$ for the padless and NZ pad-bearing clades respectively), implying little variation in diversification rates from the onset of the diversification to the present day (again, that diversification has been largely constant through time; see Model 2 above).

The MuSSE model applied to the subset of 1000 trees produced low mean transition rates among categories ($q = 4.2 \cdot 10^{-4}$) and generally lower diversification rates compared with the dd model. Extinction rates were also estimated very differently between the models, with a negligible effect in the MuSSE model but with high rates in some categories according to the dd model (Table S3). Despite these differences, both models produced consistent patterns of rate heterogeneity: both indicated high species diversification rates for the island radiations compared with continental pad-bearing lineages. The snake-like radiation also exhibited some rate acceleration, but the 95% confidence intervals overlapped those of the padless and continental pad-bearing lineages (particularly for the dd model; Fig. 4b). The padless clade showed similar diversification rates to the continental pad-bearing lineages (the MuSSE model; Fig. 4a), or perhaps even higher rates than the continental pad-bearing (the dd model; Fig. 4b), although the broad confidence intervals computed for the padless lineages made it difficult to interpret.

Finally, potential biases in the intensity of taxonomic sampling of islands versus continental communities

were unlikely to have affected our results. When we applied the dd model with the assumption that only two-thirds of the true number of existing species have been described for the Pygopodidae, Carphodactylidae and continental Diplodactylidae, and our results were virtually unchanged (Fig. S3).

Discussion

We examined the effect of the invasion of new environments – island colonization – and the evolution of two key innovations – the acquisition of adhesive toepads or a snakelike phenotype – on evolutionary diversification in a morphologically diverse and species-rich group of lizards, the Australasian diplodactyloid geckos. Our results highlighted colonization of islands and the acquisition of a snakelike phenotype as the primary factors that have prompted accelerated rates of evolutionary diversification in geckos. The evolution of adhesive toepads seems to have had little impact on rates of body size evolution or species diversification, beyond its potential interaction with island colonization (see below).

Island colonization and diversification

Our dating estimates set the probable origin of the gekkotan radiations on New Caledonia and New Zealand soon after the emergence of the archipelagos from their submersion 37–25 Ma (Trewick *et al.*, 2007; Espeland & Muriene, 2011). Rapid colonization of a young

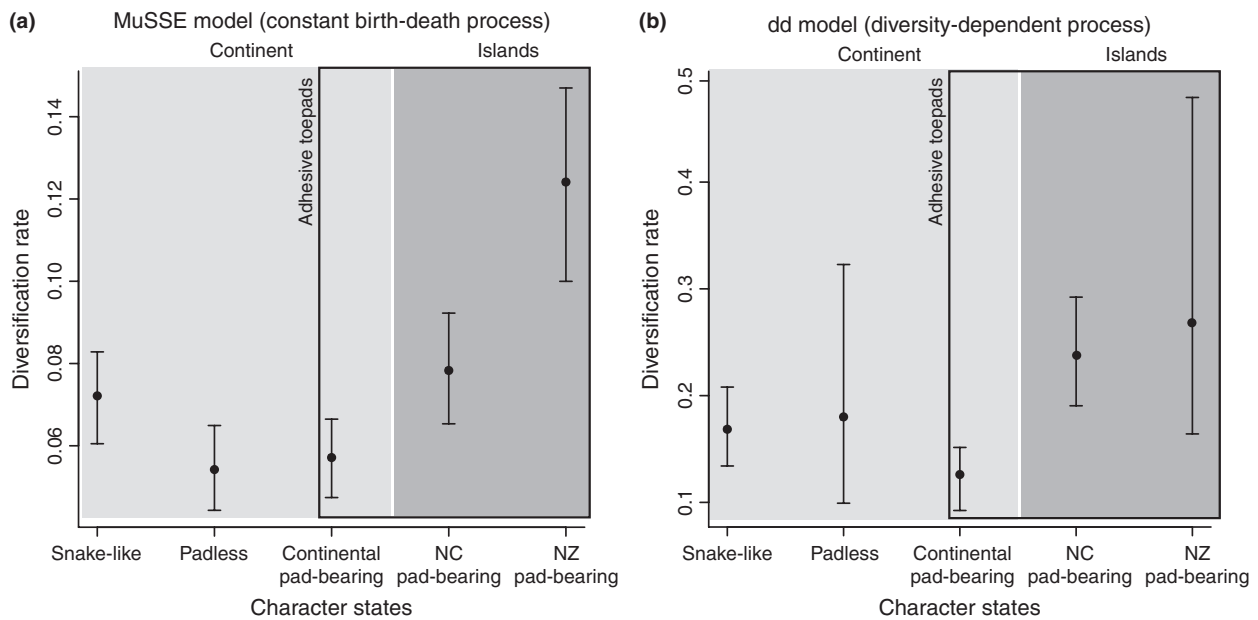


Fig. 4 Net diversification rates (speciation – extinction) and their 95% confidence intervals of each category across the 1000 trees. Results correspond to either data fit (a) with a constant rates birth and death model (bd) using the MuSSE model or (b) with a diversity-dependent model (dd).

island typically offers an array of vacant niches and sets the stage for subsequent elevated rates of cladogenesis (Whittaker *et al.*, 2010; Ortí *et al.*, 2012). In accordance with this, our results showed that the gekkotan radiations in New Caledonia and New Zealand have likely experienced accelerated rates of body size evolution and increased rates of species diversification relative to continental Australia. This is consistent with the classic notion that islands offer new ecological opportunities that can spur adaptive evolutionary diversification (Schluter, 2000). This is generally attributed to an ecological release in which species expand their resource or habitat use because of an absence of competitors (Thomas *et al.*, 2009). By contrast, in continental settings, most ecological niches have already been filled and provide fewer opportunities for niche expansion and subsequent adaptive diversification. An example of how island species expand their niches compared with their continental relatives can be found in the genus *Naultinus* in New Zealand. This genus has evolved a diurnal lifestyle (Nielsen *et al.* 2011), whereas all continental limbed geckos are nocturnal. In the case of New Caledonia, some evidence points towards a possible diurnal activity also in the genus *Eurydactyloides* (Bauer & Sadler, 2000). Although diurnality could be considered an innovation in itself, the fact that in these geckos, it only appears after the colonization of New Zealand and New Caledonia likely reflects that both island archipelagos lack the diurnal competitors common in mainland environments (such as the large family of diurnal agamids). In the particular case of

Naultinus, this shift to diurnality has also been associated with an accelerated rate of body size diversification (Fig. 3a) and provides a possible example of how low competitive environments on islands can spur evolutionary diversification.

Furthermore, predation is generally more severe in mainland habitats than on islands (where predators are often absent or less diverse; Millien, 2011), and any release from predation can allow phenotypic change in what were initially prey species. For example, less time is spent hiding from predators on islands, and this has allowed some lizards to expand their diets to include larger, more elusive prey, and this has in turn facilitated extreme body size evolution (Case, 1978; Meiri, 2008). Gigantism has arisen independently after the colonization of both New Zealand and New Caledonia. New Zealand was home to the massive, now extinct gecko *H. delcourti*, which was more than 300% bigger than the mean size of current size of geckos on the island (Bauer & Russell, 1986), and is still home to *H. duvaucelii*, the biggest gecko in New Zealand, which is a 80% larger than the mean body size of all geckos in the archipelago. New Caledonia harbours the world's largest living gecko, *Rhacodactylus leachianus*, with a body size more than 200% bigger than the mean gecko size on the island. Not surprisingly, our analyses detected separate instances of accelerated rates of body size evolution associated with these lineages (Figs 2–3). Despite both island archipelagos exhibiting the highest rates of body size diversification in limbed species, not all within-island lineages were equal in rates of body size

evolution (Fig. 3a). In New Caledonia, although most of the lineages were associated with accelerated amounts of body size diversification, *Dierogecko* was an obvious exception. In New Zealand, virtually only the diurnal *Naultinus* and the giant genus *Hoplodactylus* (*H. duvaucelii* and *H. delcourti*) appeared to have experienced accelerated rates of body size diversification (Fig. 3a). This implies that not all lineages experienced the same degree of (or responded in the same way to) ecological opportunity on the same islands. Some groups for example might have diversified in traits other than body size. In line with this, other well-known lizard radiations on islands such as the *Anolis* have diversified not only in body size, but other phenotypic axes known to be involved, at least, in some stages of the adaptive diversification (Losos, 2009). For example, possible changes in diet could presumably have prompted morphological diversification in other functional characteristics independent of body size, such as head shape (e.g. larger prey items select for larger heads; e.g. Schoener, 1968) or perhaps limb length (more elusive prey might select for longer legs and faster sprint speeds; e.g. Irschick & Losos, 1999). This invites future comparative analyses of diversification in other morphological characteristics in these island clades.

It is also interesting to note how the clades in New Caledonia and New Zealand differed in the dynamics of diversification. In New Caledonia, we detected a strong diversity-dependent pattern of diversification (i.e. diversification that varied as a function of the number of species already in existence at a given time). This was characterized by an early burst of speciation following colonization, which subsequently slowed rapidly to much lower diversification rates towards the present day. This pattern has been detected for several other taxonomic groups on the same archipelago (e.g. flowering plants, diving beetles, spiders and reptiles) including skinks, which constitutes the other major radiation of lizards on the archipelago (Espeland & Murienne, 2011). This type of diversification pattern has often been interpreted as the signature of adaptive radiation following the colonization of new areas (Losos & Ricklefs, 2009). That is, speciation rates are high at the beginning of a radiation as taxa rapidly fill empty niche space, but diversification then slows as ecological opportunity decreases as niches are progressively filled (Rabosky & Lovette, 2008).

In New Zealand, on the other hand, we found that species diversification seems to have been relatively constant through time. This suggests that the New Zealand radiation of geckos might have yet to reach the saturation of its available niches (which should then result in a strong decline in diversification). In line with this, in the Caribbean *Anolis* lizards, species assemblages on big islands present proportionally slower declines in speciation compared with smaller islands. This reflects

that big islands have greater carrying capacities than small islands and therefore take longer to reach niche saturation (Rabosky & Glor, 2010).

Key innovations and diversification

Snakelike phenotype

Our ancestral state reconstructions inferred that the snakelike phenotype evolved early in the gekkotan radiation in Australasia (before 35 Ma) and before the appearance of many of the other limbless reptiles that now inhabit Australia (typhlopids, colubrids, elapids and skinks which likely arrived to the continent in the last 30–25 Ma: Alfaro *et al.*, 2008; Kelly *et al.*, 2009; Skinner *et al.*, 2011; Marin *et al.*, 2012). Therefore, the onset of diversification in the snakelike geckos seems to have taken place in environments that were probably relatively free of other ecologically similar groups. Whereas in many groups the evolution of a snakelike phenotype seems to have been associated with the acquisition of a burrowing lifestyle (Wiens *et al.*, 2006), in Australian pygopodids, the acquisition of this phenotype seems to have predated the evolution of a burrowing lifestyle (Wiens *et al.*, 2006). This implies that the evolution of a snakelike phenotype is likely adaptive in a variety of ecological roles (and not simply a response to the restrictive use of the environment through burrowing). Indeed, the ecological diversity exhibited by Australian Pygopodidae is remarkable compared with the other continental geckos, including the diversity of habitats occupied, feeding strategies adopted and circadian activity (with many diurnal species; Shine, 1986). Consistent with this high ecological diversity, our analyses show that the snakelike geckos have likely experienced high rates of body size diversification and potentially high rates of species diversification as well.

Toepads

Despite being a classic example of a key innovation, and one that has been widely assumed to have facilitated the exemplarily diverse radiation of the geckos, the evolution of toepads appears not have had any impact on rates of body size and species diversification (Figs 2–4; see also Gamble *et al.*, 2012). The failure of a key innovation in driving evolutionary diversification has been reported in a number of other groups as well (Hodges, 1997; Price *et al.*, 2010; Claramunt *et al.*, 2012). This suggests that either the role of key innovations in spurring (potentially adaptive) radiations has been overplayed in the literature or the dependency of key innovations on the particular circumstances of a given taxonomic group has been underappreciated. Although a key innovation might provide the potential for a species to interact with the environment in new ways, this potential may nevertheless be limited by its particular ecological setting (Hodges, 1997; de Queiroz,

2002). For example, the evolution of the pharyngeal jaw in African cichlids is a key innovation that has only led to an adaptive radiation in recently formed, competitor-free rift lakes (Liem, 1973). In Australasian geckos, there are a number of context-related factors that could have similarly limited the impact of toepads on evolutionary diversification rates. One of these factors relates to the fact that most of the gekkotan diversity in continental Australia is associated to arid environments (Powney *et al.*, 2010). In these environments, selection may have constrained body sizes to minimize evaporative water loss (Vucko, 2008) and subsequently limited the potential for body size diversification to occur. This would be the case regardless of whether species occupied a structural-rich environment and possessed toepads that allowed them to exploit such an environment.

Furthermore, toepads might constitute a key innovation in some habitats but not others. Adhesive toepads are classically considered to be a key trait involved in the transition from terrestriality to arboreality (Kluge, 1967; Russell, 1979; King & Horner, 1993). The causal link between the presence of toepads and ecological opportunity has therefore usually been framed in terms of the evolution of arboreality (i.e. adhesive toepads enable animals to move more effectively in an arboreal environment and on a broader range of surfaces more generally – Irschick *et al.*, 2006; Losos, 2009). In a previous study comparing evolutionary diversification between lizard species with and without toepads, Warheit *et al.* (1999) documented significantly greater levels of body size disparity among species of the toepad-bearing *Anolis* genus compared with the closely related padless *Sceloporus* genus. This difference in body size diversity between the two genera was inferred to reflect the evolution of toepads providing greater ecological opportunity through a highly arboreal lifestyle of *Anolis* (Warheit *et al.*, 1999).

In Australia geckos occupy a range of terrestrial, saxicolous and arboreal habitats. Many of the species across this range of habitats possess toepads that appear similar in design (King & Horner, 1993). As an example, species within *Oedura* exhibit similar toepad designs and are arboreal, saxicolous or both (Wilson & Swan, 2010). Although there is a clear mechanistic link between toepads and greater ecological opportunity in arboreal environments (Irschick *et al.*, 2006; Losos, 2009), this link is less obvious in saxicolous or terrestrial environments. The possession of toepads in nonarboreal species might therefore have failed to translate into greater ecological opportunity compared with lineages that lack toepads more generally.

Finally, intrinsic morphological or genetic constraints on the evolution of phenotypic variation, or an inherent lack of 'evolvability' (*sensu* Losos, 2010), have been proposed to explain the low rates of evolutionary diversification following the acquisition of a key inno-

vation in other taxa (Schluter, 2000; Price *et al.*, 2010). Such constraints, for example, have been invoked to explain why innovations in the jaw design of parrotfishes have not been followed by the evolution of greater morphological diversity among species (Price *et al.*, 2010). Although the toepads of anoles and geckos are functionally equivalent, the body designs of the two groups are quite different. In geckos, especially arboreal species, limbs are laterally oriented with respect to the body and form a low angle with the substrate. This keeps their centre of mass close to the substrate (Wang *et al.*, 2011 and references therein) and maximizes the pull-off force during the pad-to-substrate attachment process (Persson, 2007). This type of body design in arboreal geckos may have constrained the extent geckos have been able to adapt to different microhabitats (Losos, 2010). In line with this, the diurnal and arboreal geckos of the genus *Phelsuma* exhibit some habitat partitioning and associated body size segregation (Harmon *et al.*, 2007); however, this is relatively modest compared with the *Anolis* lizards (Losos, 2010). Alternatively, Bergmann & Irschick (2009) propose that the possession of toepads has been associated with constraints on evolutionary change in vertebral number, and these constraints may have subsequently limited evolutionary variation in SVL among species. However, it is clear that great evolutionary diversification has occurred within the Australasian geckos following island colonization. Therefore, a general lack of evolvability in these lizards is not a compelling argument for why the evolution of toepads in geckos has failed to promote accelerated body size evolution or speciation.

Concluding remarks

Our study shows how the influence of two key innovations and two independent island colonization can produce different outcomes in terms of body size evolution and species diversification. Island colonization has played the most prominent role in the evolutionary diversification of Australasian geckos, followed by the evolution of a snakelike phenotype. The evolution of adhesive toepads, however, appears not to have impacted diversification rates directly, although it is conceivable that island colonization promoted evolutionary diversification in geckos only because colonizing species possessed toepads. That is, although there was no evidence that toepads in themselves lead to changes in body size or species diversification, they might have facilitated the radiation of the groups that colonized islands. In this regard, untangling the interaction of toepad evolution and island colonization was not possible for the New Caledonia and New Zealand archipelagoes because both island radiations originated from toepad-bearing ancestors.

Nonetheless, for this very reason, our study offers an important cautionary note: the invasion of new environments (such as islands) needs to be incorporated in studies that explore the effects of key innovations on evolutionary diversification because it may not be the innovation specifically, but the invasion of a new environment more generally, that has driven diversification. Most studies usually address whether an innovation is coupled with shifts in the evolutionary diversification of a given group without considering other possible causal agents (Weber & Agrawal, 2012). In our case, had we pooled mainland and island species into the same category, 'geckos with toepads', the island effect would have inflated estimated rates of evolution and we might have inferred a link between the evolution of a key innovation and subsequent diversification (see for instance Model 4 in Table 1). Relaxing the assumption of where on the phylogeny evolutionary rate shifts are expected to have occurred can help circumvent this problem. This could be carried out using methods like 'auteur' that proved crucial in our study for detecting patterns of evolutionary diversification inconsistent with the key innovation hypothesis. These types of analyses can in turn prompt further investigation of the possible cause of unexpected evolutionary patterns and identify the more probable origin of evolutionary diversification.

Acknowledgments

We are very grateful to Victor Soria-Carrasco and Javier Igea for their advice on perl and R scripting, Rampal Etienne for help with the package DDD, and Gavin Thomas and two anonymous reviewers who provided constructive comments that greatly improved this manuscript. Many thanks also to Brian Bush and Stewart Macdonald for providing the pictures shown in Fig. 1. Our study was only possible because of the morphological and molecular data collected by many researchers over many years. JGP is recipient of a predoctoral research fellowship (JAE) from the CSIC. All data compiled by our study have been archived in the Dryad Digital Repository (doi:10.5061/dryad.56vf1).

References

- Alfaro, M.E., Karns, D.R., Voris, H.K., Brock, C.D. & Stuart, B.L. 2008. Phylogeny, evolutionary history, and biogeography of oriental–Australian rear-fanged water snakes (Colubroidea: Homalopsidae) inferred from mitochondrial and nuclear DNA sequences. *Mol. Phylogenet. Evol.* **46**: 576–593.
- Autumn, K. & Peattie, A.M. 2002. Mechanisms of adhesion in geckos. *Integr. Comp. Biol.* **42**: 1081–1090.
- Bauer, A.M. & Russell, A.P. 1986. *Hoplodactylus delcourti* n. sp. (Reptilia: Gekkonidae), the largest known gecko. *N. Z. J. Zool.* **13**: 141–148.
- Bauer, A.M. & Sadlier, R.A. 2000. *The Herpetofauna of New Caledonia. Contributions to Herpetology*, **17**; Society for Study Amphibians and Reptiles, Ithaca, New York.
- Bauer, A.M., Jackman, T., Sadlier, R.A. & Whitaker, A.H. 2006. A revision of the *Bavayia validiclavus* group (Squamata: Gekkota: Diplodactylidae), a clade of New Caledonian geckos exhibiting microendemism. *Proc. Calif. Acad. Sci.* **57**: 503–547.
- Bauer, A.M., Jackman, T., Sadlier, R.A. & Whitaker, A.H. 2009. Review and phylogeny of the New Caledonian diplodactylid gekkotan genus *Eurydactyloides* Wermuth, 1965, with the description of a new species. *Annls. Mus. Hist. Nat. Paris* **198**: 13–36.
- Bauer, A.M., Jackman, T.R., Sadlier, R.A. & Whitaker, A.H. 2012a. Revision of the giant geckos of New Caledonia (Reptilia: Diplodactylidae: *Rhacodactylus*). *Zootaxa* **3404**: 1–52.
- Bauer, A.M., Sadlier, R.A., Jackman, T.R. & Shea, G. 2012b. A new member of the *Bavayia cyclura* species group (Reptilia: Squamata: Diplodactylidae) from the southern ranges of New Caledonia. *Pac. Sci.* **66**: 239–247.
- Benson, D.A., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J. & Wheeler, D.L. 2011. GenBank. *Nucleic Acids Res.* **33**: D32–D37.
- Bergmann, P.J. & Irschick, D.J. 2009. Alternate pathways of body shape evolution translate into common patterns of locomotor evolution in two clades of lizards. *Evolution* **64**: 1569–1582.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. 2004. Toward a metabolic theory of ecology. *Ecology* **85**: 1771–1789.
- Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* **33**: 261–304.
- Case, T.J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* **59**: 1–18.
- Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol. Biol. Evol.* **17**: 540–552.
- Claramunt, S., Derryberry, E.P., Brumfield, R.T. & Remsen, J. 2012. Ecological opportunity and diversification in a continental radiation of birds: climbing adaptations and cladogenesis in the Furnariidae. *Am. Nat.* **179**: 649–666.
- Cogger, H. 2002. *Reptiles and Amphibians of Australia*. Reed Books, Chatswood, NSW.
- Conrad, J.L. & Norell, M.A. 2006. High-resolution x-ray computed tomography of an early cretaceous gekkonomorph (Squamata) from Öösh (Övörkhanga; Mongolia). *Hist. Biol.* **18**: 405–431.
- Daza, J.D. & Bauer, A.M. 2012. A new amber-embedded sphaerodactyl Gecko from hispaniola, with comments on morphological synapomorphies of the Sphaerodactylidae. *Breviora* **529**: 1–28.
- Daza, J.D., Alifanov, V.R. & Bauer, A.M. 2012. A redescription and phylogenetic reinterpretation of the fossil lizard *Hoburogekko suchanovi* Alifanov, 1989 (Squamata, Gekkota), from the early cretaceous of Mongolia. *J. Vert. Paleontol.* **32**: 1303–1312.
- Daza, J.D., Bauer, A.M. & Snively, E. 2013. *Gobekko cretacicus* (Reptilia: Squamata) and its bearing on the interpretation of gekkotan affinities. *Zool. J. Linn. Soc.* **167**: 430–448.
- Diamond, J. 1986. Evolution of ecological segregation in the New Guinea montane avifauna. In: *Community Ecology* (J.

- Diamond, T.J. Case, (eds), pp. 98–125. Cambridge, MA, HarperCollin.
- Drummond, A.J. & Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **7**: 214.
- Drummond, A., Ashton, B., Buxton, S., Cheung, M., Heled, J., Kearse, M. *et al.* 2010. Geneious version 5.0. Geneious, Auckland, New Zealand.
- Eastman, J.M., Alfaro, M.E., Joyce, P., Hipp, A.L. & Harmon, L.J. 2011. A novel comparative method for identifying shifts in the rate of character evolution on trees. *Evolution* **65**: 3578–3589.
- Espeland, M. & Muriene, J. 2011. Diversity dynamics in New Caledonia: towards the end of the museum model? *BMC Evol. Biol.* **11**: 254.
- Etienne, R.S., Haegeman, B., Stadler, T., Aze, T., Pearson, P.N., Purvis, A. *et al.* 2012. Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc. Biol. Sci.* **279**: 1300–1309.
- FitzJohn, R.G. 2012. Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol. Evol.* **3**: 1084–1092.
- Fürsich, F.T. & Jablonski, D. 1984. Late Triassic naticid drill-holes: carnivorous gastropods gain a major adaptation but fail to radiate. *Science* **224**: 7880.
- Galis, F. 2001. Key innovations and radiations. In: *The Character Concept in Evolutionary Biology* (G.P. Wagner, ed.), pp. 581–605. Academic Press, San Diego.
- Gamble, T., Bauer, A.M., Greenbaum, E. & Jackman, T.R. 2008. Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. *J. Biogeogr.* **35**: 88–104.
- Gamble, T., Bauer, A.M., Colli, G.R., Greenbaum, E., Jackman, T.R., Vitt, L.J. *et al.* 2011. Coming to America: multiple origins of new world geckos. *J. Evol. Biol.* **24**: 231–244.
- Gamble, T., Greenbaum, E., Jackman, T.R., Russell, A.P. & Bauer, A.M. 2012. Repeated origin and loss of adhesive toepads in geckos. *PLoS One* **7**: e39429.
- Gans, C. 1975. Tetrapod limblessness: evolution and functional corollaries. *Am. Zool.* **15**: 455–467.
- Gavrilets, S. & Vose, A. 2009. Dynamic patterns of adaptive radiation: evolution of mating preferences. In: *Speciation and Patterns of Diversity* (R. K. Butlin, J. R. Bridle & D. Schluter, eds), pp. 102–126. Cambridge University Press, Cambridge, UK.
- Grant, P.R. & Grant, B.R. 2011. *How and Why Species Multiply: the Radiation of Darwin's Finches*. Princeton University Press, Princeton, NJ. 272 pp.
- Griffiths, R.C. & Tavaré, S. 1994. Sampling theory for neutral alleles in a varying environment. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **344**: 403–410.
- Hansen, W. & Autumn, K. 2005. Evidence for self-cleaning in gecko setae. *Proc. Natl. Acad. Sci. USA* **102**: 385–389.
- Harmon, L.J., Harmon, L.L. & Jones, C.G. 2007. Competition and community structure in diurnal arboreal geckos (genus *Phelsuma*) in the Indian Ocean. *Oikos* **116**: 1863–1878.
- Harmon, L.J., Melville, J., Larson, A. & Losos, J.B. 2008. The role of geography and ecological opportunity in the diversification of day geckos (*Phelsuma*). *Syst. Biol.* **57**: 562–573.
- Hitchmough, R. 1997. A systematic review of the New Zealand Gekkonidae. Unpublished PhD thesis, Victoria University of Wellington, Wellington.
- Hodges, S.A. 1997. Floral nectar spurs and diversification. *Int. J. Plant Sci.* **158**: 81–88.
- Huber, G., Mantz, H., Spolenak, R., Mecke, K., Jacobs, K., Gorb, S.N. *et al.* 2005. Evidence for capillarity contributions to gecko adhesion from single spatula nanomechanical measurements. *Proc. Natl. Acad. Sci. USA* **102**: 16293.
- Hunter, J.P. 1998. Key innovations and the ecology of macroevolution. *Trends Ecol. Evol.* **13**: 31–36.
- Hutchinson, M.N. 1997. The first fossil pygopod (Squamata, Gekkota), and a review of mandibular variation in living species. *Mem. Queensl. Muse.* **41**: 355–366.
- Irschick, D.J. & Losos, J.B. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *Am. Nat.* **154**: 293–305.
- Irschick, D.J., Herrel, A. & Vanhooydonck, B. 2006. Whole-organism studies of adhesion in pad-bearing lizards: creative evolutionary solutions to functional problems. *J. Comp. Physiol. A. Neuroethol. Sens. Neural. Behav. Physiol.* **192**: 1169–1177.
- Jennings, W.B., Pianka, E.R. & Donnellan, S. 2003. Systematics of the lizard family pygopodidae with implications for the diversification of Australian temperate biotas. *Syst. Biol.* **52**: 757–780.
- Katoh, K., Misawa, K., Kuma, K. & Miyata, T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res.* **30**: 3059–3066.
- Kelly, C.M., Barker, N.P., Villet, M.H. & Broadley, D.G. 2009. Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. *Cladistics* **25**: 38–63.
- King, M. & Horner, P. 1993. Family Gekkonidae. In: *Fauna of Australia. Vol. 2A Amphibia and Reptilia* (C.J. Glasby, G.J.B. Ross & P.L. Beesley, eds), pp. 221–233. Australian Government Publishing Service, Canberra.
- Kluge, A.G. 1967. Higher taxonomic categories of gekkonid lizards and their evolution. Bulletin of the AMNH. v. 135, article 1.
- Liem, K.F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Syst. Biol.* **22**: 425–441.
- Losos, J.B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, CA., 512 pp.
- Losos, J.B. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. American society of naturalists E. O. Wilson award address. *Am. Nat.* **175**: 623–639.
- Losos, J.B. & de Queiroz, K.D. 1997. Evolutionary consequences of ecological release in Caribbean Anolis lizards. *Biol. J. Linn. Soc.* **61**: 459–483.
- Losos, J.B. & Ricklefs, R.E. 2009. Adaptation and diversification on islands. *Nature* **457**: 830–836.
- Macey, J.R., Wang, Y., Ananjeva, N.B., Larson, A. & Papenfuss, T.J. 1999. Vicariant patterns of fragmentation among gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: a molecular phylogenetic perspective and an area cladogram for Central Asia. *Mol. Phylogenet. Evol.* **12**: 320–332.
- Mahler, D.L., Revell, L.J., Glor, R.E. & Losos, J.B. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of greater Antillean anoles. *Evolution* **64**: 2731–2745.
- Marin, J., Donnellan, S.C., Blair Hedges, S., Doughty, P., Hutchinson, M.N., Cruaud, C. *et al.* 2012. Tracing the history

- and biogeography of the Australian blindsnake radiation. *J. Biogeogr.* **40**: 928–937.
- Meiri, S. 2008. Evolution and ecology of lizard body sizes. *Glob. Ecol. Biogeogr.* **17**: 724–734.
- Meiri, S., Raia, P. & Phillimore, A.B. 2011. Slaying dragons: limited evidence for unusual body size evolution on islands. *J. Biogeogr.* **38**: 89–100.
- Melville, J., James, A., Schulte, I. & Larson, A. 2004. A molecular study of phylogenetic relationships and evolution of antipredator strategies in Australian *Diplodactylus* geckos, subgenus *Strophurus*. *Biol. J. Linn. Soc.* **82**: 123–138.
- Miller, A.H. 1949. Some ecologic and morphologic considerations in the evolution of higher taxonomic categories. In: *Ornithologie als Biologische Wissenschaft* (E. Mayr, E. Schüz, eds), pp. 84–88. Carl Winter, Heidelberg.
- Millien, V. 2011. Mammals evolve faster on smaller islands. *Evolution* **65**: 1935–1944.
- Moen, D.S. & Wiens, J.J. 2009. Phylogenetic evidence for competitively driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: Osteopilus). *Evolution* **63**: 195–214.
- Morlon, H., Potts, M.D. & Plotkin, J.B. 2010. Inferring the dynamics of diversification: a coalescent approach. *PLoS Biol.* **8**: e1000493.
- Neall, V.E. & Trewick, S.A. 2008. The age and origin of the Pacific Islands: a geological overview. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **363**: 3293–3308.
- Nielsen, S.V., Bauer, A.M., Jackman, T.R., Hitchmough, R.A. & Daugherty, C.H. 2011. New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. *Mol. Phylogenet. Evol.* **59**: 1–22.
- Nosil, P. & Reimchen, T. 2005. Ecological opportunity and levels of morphological variance within freshwater stickleback populations. *Biol. J. Linn. Soc.* **86**: 297–308.
- Oliver, P.M. & Sanders, K.L. 2009. Molecular evidence for Gondwanan origins of multiple lineages within a diverse Australasian gecko radiation. *J. Biogeogr.* **36**: 2044–2055.
- Orti, G., Stein, A.M., Marceniuk, A.P. & Alexander Pyron, R. 2012. Apparent signal of competition limiting diversification after ecological transitions from marine to freshwater habitats. *Ecol. Lett.* **15**: 822–830.
- Persson, B. 2007. Biological adhesion for locomotion on rough surfaces: basic principles and a theorist's view. *MRS Bull.* **32**: 486–490.
- Peters, R.H. 1986. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Powney, G.D., Grenyer, R., Orme, C.D.L., Owens, I.P.F. & Meiri, S. 2010. Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Glob. Ecol. Biogeogr.* **19**: 386–396.
- Price, S.A., Wainwright, P.C., Bellwood, D.R., Kazancioglu, E., Collar, D.C. & Near, T.J. 2010. Functional innovations and morphological diversification in parrotfish. *Evolution* **64**: 3057–3068.
- de Queiroz, A. 2002. Contingent predictability in evolution: key traits and diversification. *Syst. Biol.* **51**: 917–929.
- Rabosky, D.L. & Glor, R.E. 2010. Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proc. Natl. Acad. Sci. USA* **107**: 22178–22183.
- Rabosky, D.L. & Lovette, I.J. 2008. Density-dependent diversification in North American wood warblers. *Proc. Biol. Sci.* **275**: 2363–2371.
- Rambaut, A. & Drummond, A. 2007. Tracer v1. 4. pp. <http://beast.bio.ed.ac.uk/Tracer>.
- Revell, L.J. 2011. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.
- Richman, A.D. & Price, T. 1992. Evolution of ecological differences in the old world leaf warblers. *Nature* **355**: 817–821.
- Ricklefs, R.E. 2007. Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* **22**: 601–610.
- Roughgarden, J. 1972. Evolution of niche width. *Am. Nat.* **106**: 683–718.
- Russell, A.P. 1979. Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. *Copeia*. **1**: 1–21.
- Sanders, K.L. & Lee, M.S.Y. 2007. Evaluating molecular clock calibrations using Bayesian analyses with soft and hard bounds. *Biol. Lett.* **3**: 275–279.
- Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, USA.
- Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704–726.
- Shea, G. 1991. Revisionary notes on the genus *delma* (Squamata: Pygopodidae) in South Australia and the Northern Territory. *Rec. S. Aust. Mus.* **25**: 71–90.
- Shine, R. 1986. Evolutionary advantages of limblessness: evidence from the pygopodid lizards. *Copeia* **2**: 525–529.
- Simpson, G.G. 1944. *Tempo and Mode in Evolution*. Columbia University Press, New York.
- Simpson, G.G. 1953. *The Major Features of Evolution*. Columbia University Press, New York.
- Skinner, A., Hugall, A.F. & Hutchinson, M.N. 2011. Lygosomine phylogeny and the origins of Australian scincid lizards. *J. Biogeogr.* **38**: 1044–1058.
- Thomas, G.H. & Freckleton, R.P. 2012. MOTMOT: models of trait macroevolution on trees. *Methods Ecol. Evol.* **3**: 145–151.
- Thomas, G.H., Meiri, S. & Phillimore, A.B. 2009. Body size diversification in anolis: novel environment and island effects. *Evolution* **63**: 2017–2030.
- Trewick, S.A., Paterson, A.M. & Campbell, H.J. 2007. Guest editorial: hello New Zealand. *J. Biogeogr.* **34**: 1–6.
- Uetz, P. 2010. The Reptile Database. <http://www.reptile-database.org>. Accessed January 2013.
- Vamosi, J.C. & Vamosi, S.M. 2010. Key innovations within a geographical context in flowering plants: towards resolving Darwin's abominable mystery. *Ecol. Lett.* **13**: 1270–1279.
- Vidal, N. & Hedges, S.B. 2009. The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *C. R. Biol.* **332**: 129–139.
- Vucko, M. 2008. The dynamics of water loss on the skin of Australian carphodactylinae and diplodactylinae geckos. Masters (Research) thesis. James Cook University.
- Wainwright, P.C. 2007. Functional versus morphological diversity in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* **38**: 381–401.
- Wallis, G.P. & Trewick, S.A. 2009. New Zealand phylogeography: evolution on a small continent. *Mol. Ecol.* **18**: 3548–3580.
- Wang, Z.Y., Wang, J.T., Ji, A.H., Zhang, Y.Y. & Dai, Z.D. 2011. Behavior and dynamics of gecko's locomotion: the effects of moving directions on a vertical surface. *Chin. Sci. Bull.* **56**: 573–583.
- Warheit, K.I., Forman, J.D., Losos, J.B. & Miles, D.B. 1999. Morphological diversification and adaptive radiation: a comparison of two diverse lizard clades. *Evolution* **53**: 1226–1234.

- Waters, J.M. & Craw, D. 2006. Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Syst. Biol.* **55**: 351–356.
- Weber, M.G. & Agrawal, A.A. 2012. Phylogeny, ecology, and the coupling of comparative and experimental approaches. *Trends Ecol. Evol.* **27**: 394–403.
- Whittaker, R.J., Triantis, K.A. & Ladle, R.J. 2010. A general dynamic theory of oceanic island biogeography: extending the MacArthur–Wilson theory to accommodate the rise and fall of volcanic islands. In: *The Theory of Island Biogeography Revisited* (J.B. Losos & R.E. Ricklefs, eds), pp. 88–115. Princeton University Press, Princeton, NJ.
- Wiens, J.J., Brandley, M.C. & Reeder, T.W. 2006. Why does a trait evolve multiple times within a clade? Repeated evolution of snake-like body form in squamate reptiles. *Evolution* **60**: 123–141.
- Williams, E.E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evol. Biol.* **6**: 47–89.
- Wilson, S. & Swan, G. 2010. *Complete Guide to Reptiles of Australia*. Reed New Holland, Sydney.
- Wood, B. & Collard, M. 1999. The changing face of genus *Homo*. *Evol. Anthropol.* **8**: 195–207.
- Yoder, J., Clancey, E., Des Roches, S., Eastman, J., Gentry, L., Godsoe, W. *et al.* 2010. Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol.* **23**: 1581–1596.
- Zimmerman, E.C. 1970. Adaptive radiation in Hawaii with special reference to insects. *Biotropica* **2**: 32–38.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Time-calibrated tree showing the radiation of the Australasian diplodactyloid geckos plus 20 species incorporated to place most of the calibration points.

Figure S2 Barplots representing the relative support for six models of diversity dynamics for each category.

Figure S3 Net diversification rates (speciation – extinction) and their 95% confidence intervals of each category across the 1000 trees corresponding to data fit with a diversity-dependent model (dd), assuming that an additional 50% of the currently known species of Pygopodidae, Carphodactylidae and continental Diplodactylidae could be described at some point in the future.

Data deposited at Dryad: doi:10.5061/dryad.56vf1

Received 7 November 2012; revised 12 July 2013; accepted 4 September 2013