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Phylogenomics of Monitor Lizards and the Role of Competition in Dictating Body Size Disparity

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Abstract.—Organismal interactions drive the accumulation of diversity by influencing species ranges, morphology, and behavior. Interactions vary from agonistic to cooperative and should result in predictable patterns in trait and range evolution. However, despite a conceptual understanding of these processes, they have been difficult to model, particularly on macroevolutionary timescales and across broad geographic spaces. Here, we investigate the influence of biotic interactions on trait evolution and community assembly in monitor lizards (*Varanus*). Monitors are an iconic radiation with a cosmopolitan distribution and the greatest size disparity of any living terrestrial vertebrate genus. Between the colossal Komodo dragon *Varanus komodoensis* and the smallest Australian dwarf goannas, *Varanus* length and mass vary by multiple orders of magnitude. To test the hypothesis that size variation in this genus was driven by character displacement, we extended existing phylogenetic comparative methods which consider lineage interactions to account for dynamic biogeographic history and apply these methods to Australian monitors and marsupial predators. Incorporating both exon-capture molecular and morphological data sets we use a combined evidence approach to estimate the relationships among living and extinct varaniform lizards. Our results suggest that communities of Australian *Varanus* show high functional diversity as a result of continent-wide interspecific competition among monitors but not with faunivorous marsupials. We demonstrate that patterns of trait evolution resulting from character displacement on continental scales are recoverable from comparative data and highlight that these macroevolutionary patterns may develop in parallel across widely distributed sympatric groups. [Character displacement; comparative methods; phylogenetics; trait evolution; *Varanus*.]

Organismal interactions provide an important selective force for evolution (Darwin 1859). On macroevolutionary time scales, interspecific interactions help drive the accumulation and distribution of diversity (Benton 1987). Common antagonistic interactions (e.g. competition) are suggested to facilitate the assembly of communities by encouraging ecological, behavioral, and morphological differentiation through character displacement (Brown and Wilson 1956; Sepkoski Jr 1996). This process has been repeatedly identified in insular adaptive radiations like Darwin's finches, Caribbean anoles, and Lake Victoria cichlids, where young clades have rapidly diverged into many available phenotypes, ecologies, and/or behavioral syndromes (Schluter et al. 1985; Losos 1990; Grant and Grant 2006). While insular systems are instructive, they account for only a fraction of earth's biodiversity, and it has been much more difficult to quantify the influence of competition at continental scales (Drury et al. 2018b). Investigating if insular patterns of competition driving trait evolution can be extrapolated to continental assemblages would provide a greater understanding of the evolution of most of life on earth.

The most obvious axis for differentiation among organisms is absolute size (Peters and Peters 1986).

In animals, body size is often used as a proxy for guild, and because it dramatically affects life-history traits and ecology, it is the most commonly used measurement in macroevolutionary studies (Wilson 1975). Among terrestrial vertebrates, monitor lizards *Varanus* exhibit the greatest variation in body size within a single terrestrial vertebrate genus (Pianka 1995). Extant monitors include island giants like the Komodo dragon *V. komodoensis* (up to 3 m long and 100 kg), and desert dwarves like the short-tailed goanna *V. brevicauda* (0.2 m and 0.016 kg), which vary by orders of magnitude. In fact, while size estimates vary, the recently extinct Australian monitor *Varanus (Megalania) priscus* may have dwarfed even the Komodo dragon, reaching lengths of over 4 m (Wroe 2002; Conrad et al. 2012). Despite a conservative body plan, monitor lizards are ecologically diverse and can be found at home in trees, among rocks, in burrows, and swimming through watercourses and even the open ocean (Pianka 1995). Though there are roughly 80 described monitors, the greatest morphological diversity is concentrated in the 30 or so Australian species (Uetz and Hošek 2019). All Australian monitors are hypothesized to constitute a single radiation that likely dispersed from Sundaland into Sahul (Australopapua), though the timing and

biogeographic history of this group remains uncertain (Vidal et al. 2012). Such incredible diversity in body size begs the question, what has driven it?

Over the years, researchers have suggested that this disparity is the result of habitat partitioning (Collar et al. 2011) or release from competition with carnivorous mammals (Pianka 1995; Sweet and Pianka 2007). However, no one has yet investigated whether variation in monitor body sizes is instead the result of character displacement through competition, either with other *Varanus* or large carnivores with which they may vie for resources. This is likely due to the fact that probabilistic trait evolutionary models largely remain ignorant of such interactions even though they are ubiquitous (Harmon et al. 2019). Only recently have methods for modeling continuous traits attempted to take into account the influence of lineages on one another (Drury et al. 2016; Manceau et al. 2017; Adams and Nason 2018; Quintero and Landis 2019).

In Australia, monitor lizards are not the only radiation of terrestrial vertebrate predators. A similarly diverse codistributed group is the carnivorous and omnivorous marsupial mammals. Dasyuromorphians and peramelemorphians cover a similar breadth in range and body size, inhabiting deserts and closed forests, ranging from the tiny *Ningauia* up to the recently extinct canine-convergent *Thylacine*. Outside of Australia, there is evidence to suggest varanid lizards may compete either directly (through predation) or indirectly (vying for resources) with small-to-moderate sized carnivorans, and this may explain the lack of small monitors west of Wallace's Line (Sweet and Pianka 2007). This presents the question of whether or not Australian monitors and codistributed marsupials have influenced the size evolution of one another, and if this signature may be discernible from comparative data.

In order to address these macroevolutionary questions on the origins and diversity of varanid lizards, it is essential to first construct a reliable time-scaled phylogeny. Relationships among *Varanus* have been reconstructed historically through a number of morphological and molecular methods, but recovered subgeneric relationships have been notoriously inconsistent (Fuller et al. 1998; Ast 2001; Fitch et al. 2006; Conrad et al. 2012; Vidal et al. 2012; Lin and Wiens 2017). We generated a nuclear exon-capture data set and combined it with existing morphological data to build a comprehensive phylogenetic hypothesis for *Varanus* in a combined evidence framework incorporating both fossil and extant taxa. Our phylogenetic estimates are used to reconstruct the global biogeographic history of varaniform lizards, then focus on the evolution of body size among Australian taxa. To address the influence of competition on size evolution, we extend a series of novel comparative phylogenetic models. These include models that integrate continental biogeographic history (not just contemporary distribution), and the possibility of competition with another group of highly diverse Australian carnivores.

MATERIALS AND METHODS

Walkthroughs of the data, code, analyses, and results are available in the [Supplementary Material](#) available on Dryad, on GitHub at www.github.com/IanGBrennan/MonitorPhylogenomics, and from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.tx95x69t8>. Raw sequence reads are available on the NCBI Sequence Read Archive under BioProject ID [SUB7437608].

Molecular Data Collection

We assembled an exon-capture data set across 103 *Varanus* specimens representing 61 of 80 currently recognized species. This sampling covers all nine subgenera and major clades of *Varanus*, as well as recognized subspecies, and known divergent populations. We included four additional nonvaranoid anguimorphs (*Elgaria*, *Heloderma*, *Shinisaurus*, and *Xenosaurus*), a skink (*Plestiodon*), and tuatara (*Sphenodon*) as outgroups. Nuclear exons were targeted and sequenced using the Anchored Hybrid Enrichment approach (Lemmon et al. 2012), and resulted in 388 loci (average coverage 350 loci, min = 112, max = 373) totaling ~600 kbp per sample (Supplementary Fig. S7 available on Dryad).

Morphological Sampling

In addition to novel phylogenomic sampling, we included morphological data collected by Conrad et al. (2011). We chose to exclude a number of characters added to this matrix in Conrad et al. (2012) because of extensive missing data and uncertain homology. We filtered the data matrix using an allowance of 50% missing data per character, excluding characters above this threshold, and removed taxa with greater than 70% missing data, as we found these samples to be disruptive in exploratory analyses. We removed invariant characters from the remaining data to conform to assumptions of the MKv model, resulting in a final morphological matrix comprising 303 characters. Disruptive samples—often called “rogues”—are not limited to those with large amounts of missing data. To identify if rogue taxa are causing topological imbalances in our phylogenetic hypotheses, we applied RogueNaRok (Aberer et al. 2012) to initial combined evidence analyses, identified rogues, and removed them for downstream analyses. Morphological sampling includes 55 extant *Varanus*, as well as the extinct *V. priscus*. A number of extant and fossil outgroups are included to sample the closely related groups Helodermatidae (*Heloderma suspectum*), Lanthanotidae (*Lanthanotus borneensis* and *Cherminotus longifrons*), Paleovaranidae (formerly Necrosauridae) (*Paleovaranus (Necrosaurus) cayluxi*, *P. giganteus*, “*Saniwa*” *feisti*) (Georgalis 2017), Shinisauridae (*Shinisaurus crocodilurus*), and uncertain varaniform lizards (*Aiolosaurus oriens*, *Ovoo gurvel*, *Telmasaurus grangeri*, and *Saniwides mongoliensis*).

Phylogenetic Analyses

We reconstructed a partitioned concatenated species tree and individual genealogies for our exon-capture data ($n=388$) under maximum likelihood in IQTREE (Schmidt et al. 2014), allowing the program to assign the best-fitting model of molecular evolution using PartitionFinder, then performed 1000 ultrafast bootstraps (Haeseler et al. 2013). We then estimated the species tree using the shortcut coalescent method ASTRAL III (Zhang et al. 2018), with IQTREE gene trees as input (Fig. 1). We also estimated species trees using the full multispecies coalescent (MSC) and fossilized birth–death MSC (FBD-MSC) models implemented in StarBEAST2 (Ogilvie et al. 2016). Computational limitations under the MSC required that we reduce the input data size, and so we summarized per-locus informativeness using AMAS (Borowiec 2016), then used custom scripts to sort the loci sequentially by (i) missing taxa per alignment, (ii) number of variable sites, and (iii) AT content. We then chose the first three sets of twenty loci (1–20; 21–40; 41–60) as representatives of the most informative and complete loci, and used them to build our phylogeny (Fig. 2, Supplementary Fig. S8a available on Dryad).

Phylogenetic reconstruction under the FBD-MSC allowed us to jointly infer a molecular and morphological species tree, and divergence times using structured node and tip date priors (Supplementary material available on Dryad: “Node Priors and *Varanus* in the Fossil Record”; Supplementary Table S8 available on Dryad). Morphological data were modeled under the Mkv model, a special case of the Mk model (Lewis 2001), and we partitioned morphological characters by differing numbers of states following Gavryushkina et al. (2017). All StarBEAST2 analyses were run for four independent chains under uncorrelated relaxed lognormal (UCLN) and strict molecular clocks for 1 billion generations and sampled each 5×10^5 generations, to assess convergence among runs. To further inspect our prior assumptions we ran all analyses under the priors only and compared against empirical runs. We inspected the MCMC chains for stationarity (ESS > 200) using Tracer v1.7.0 (Rambaut et al. 2018), and discarded the first 10–40% of each run as burn-in as necessary before combining runs. Combined evidence analyses may be biased by difficulties in accurately modeling morphological evolution (Puttick et al. 2017; Luo et al. 2018; Goloboff et al. 2018). In contrast to molecular sites or loci, morphological characters are likely more often correlated (Billet and Bardin 2018), nonhomologous (Baum and Donoghue 2002), or evolving under dramatically different mechanisms (Goloboff et al. 2018), and may disrupt our best efforts at reconstructing phylogeny, divergence times, and rates of evolution. To address this, we also estimated divergence dates using an “extant-only” approach, limiting the sampling to living taxa with molecular data, and used the multispecies coalescent model implemented in StarBEAST2, using the same clock and substitution models, and chain lengths as above.

Fossil taxa are almost always assumed to represent terminal tips that have since gone extinct. To test this assumption, we allowed fossil taxa to be identified as terminal or stem lineages using the *Sampled Ancestors* package implemented in StarBEAST2. Using our prior-only analyses we calculated Bayes factors (BF) for each fossil taxon to test competing hypotheses (ancestor or tip). We used a threshold of $\log(\text{BF}) > 1$ to identify sampled ancestors, $\log(\text{BF}) < -1$ to recognize terminal taxa, and $-1 < \log(\text{BF}) < 1$ taxa were categorized as equivocal.

Biogeographic History

Varanus lizards have been variously hypothesized to have originated in Asia (Keast 1971; Estes 1983; Fuller et al. 1998; Jennings and Pianka 2004; Amer and Kumazawa 2008; Vidal et al. 2012; Conrad et al. 2012), Africa (Holmes et al. 2010), or Gondwana (Schulte et al. 2003), with conclusions largely based on which taxa were included, and the timing of varanid divergence events. We used *BioGeoBEARS* (Matzke 2014) to infer the biogeographic history of varanids and kin, dividing their range into seven major regions: North America, Europe, Sundaland/Wallacea, AustraloPapua, Africa/Arabia, West Asia (Indian subcontinent and surrounds), and East Asia (China, Mongolia, mainland Southeast Asia). As input, we used the maximum clade credibility tree from our combined evidence analyses. Due to the deep evolutionary history of this group, we took plate-tectonic history into account by correcting dispersal probability as a function of distance between areas. We estimated distances between areas and continents through time at 5 myr intervals from 0 to 40 Ma, then 10 myr intervals from 40–100 myr, using latitude and longitude positions from GPlates (Boyden et al. 2011), and calculated pairwise distance matrices using the R package *geosphere* (Hijmans 2016). Additionally, we limited the model-space by providing information about area adjacency. For each time period, we removed unrealistic combinations of ranges (e.g., North America + AustraloPapua), with the aim of recovering more realistic biogeographic scenarios.

To understand the spatial evolution of *Varanus* in Australia, we used a Bayesian method *rase* (Quintero et al. 2015) which assumes a Brownian motion diffusion process to infer ancestral ranges as point data. We downloaded occurrence records for all continental Australian *Varanus* species from the Atlas of Living Australia (ala.org), curating the data for erroneous records, then trimmed our input tree down to just Australian taxa. We ran *rase* for 10,000 generations, sampling each 10th generation, then discarded the first 10% (100 samples) as burn-in. We inspected the traces of the MCMC chains for stationarity using *coda* (Plummer et al. 2006).

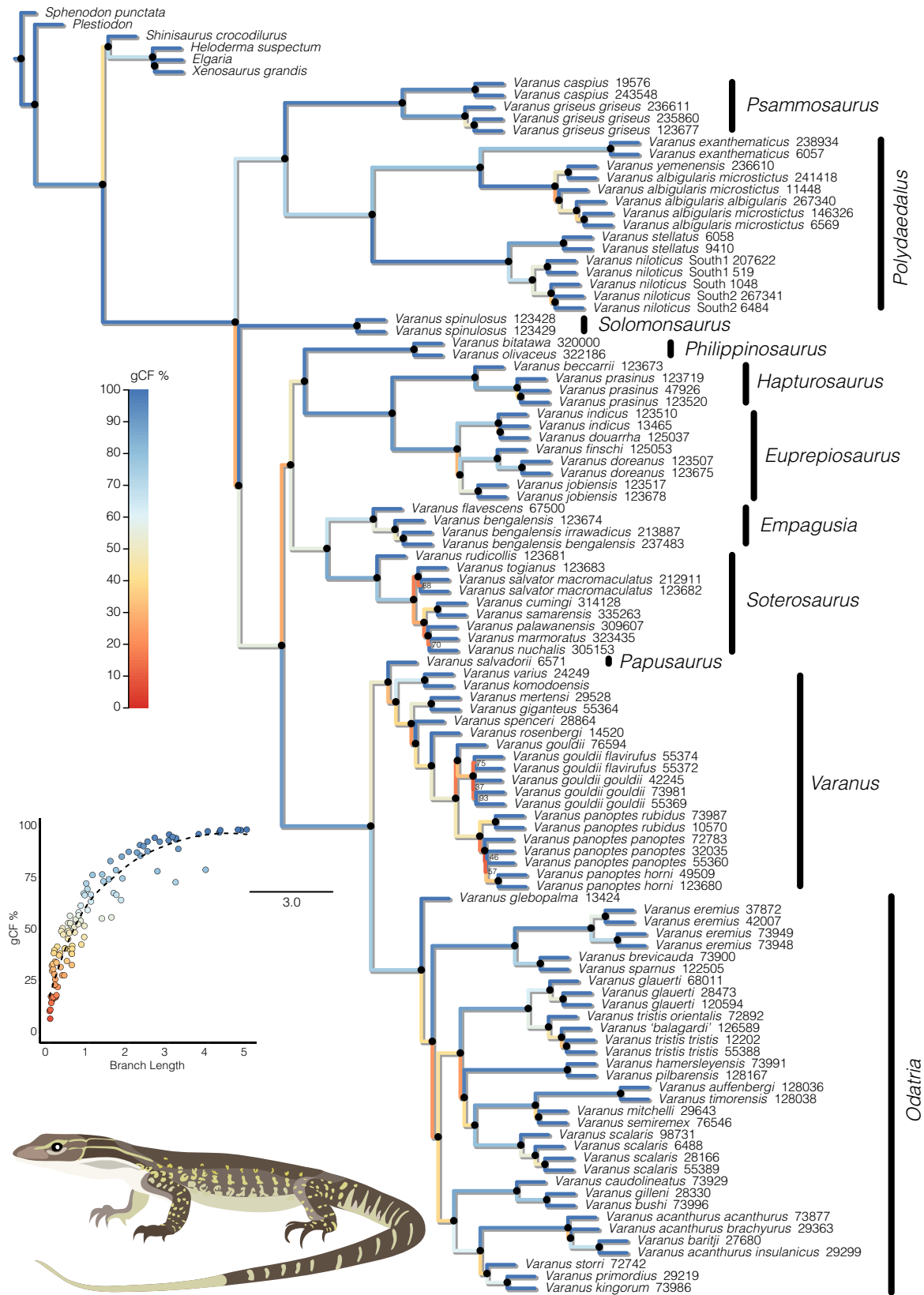


FIGURE 1. The fully sampled species tree estimated with ASTRAL is largely concordant with our total-evidence species tree (Supplementary Fig. S3 available on Dryad). Nodes denoted by ● are supported by local posterior probability values >0.90, all others (<0.90) are considered equivocal and designated by ○ values. Branch colors correspond to gene concordance factors, and represent the percent of gene trees which decisively support the presented bifurcation. Inset plot shows that as expected, gCF values increase with increasing branch lengths, shown in coalescent units. Subgeneric names are listed to the right of each group.

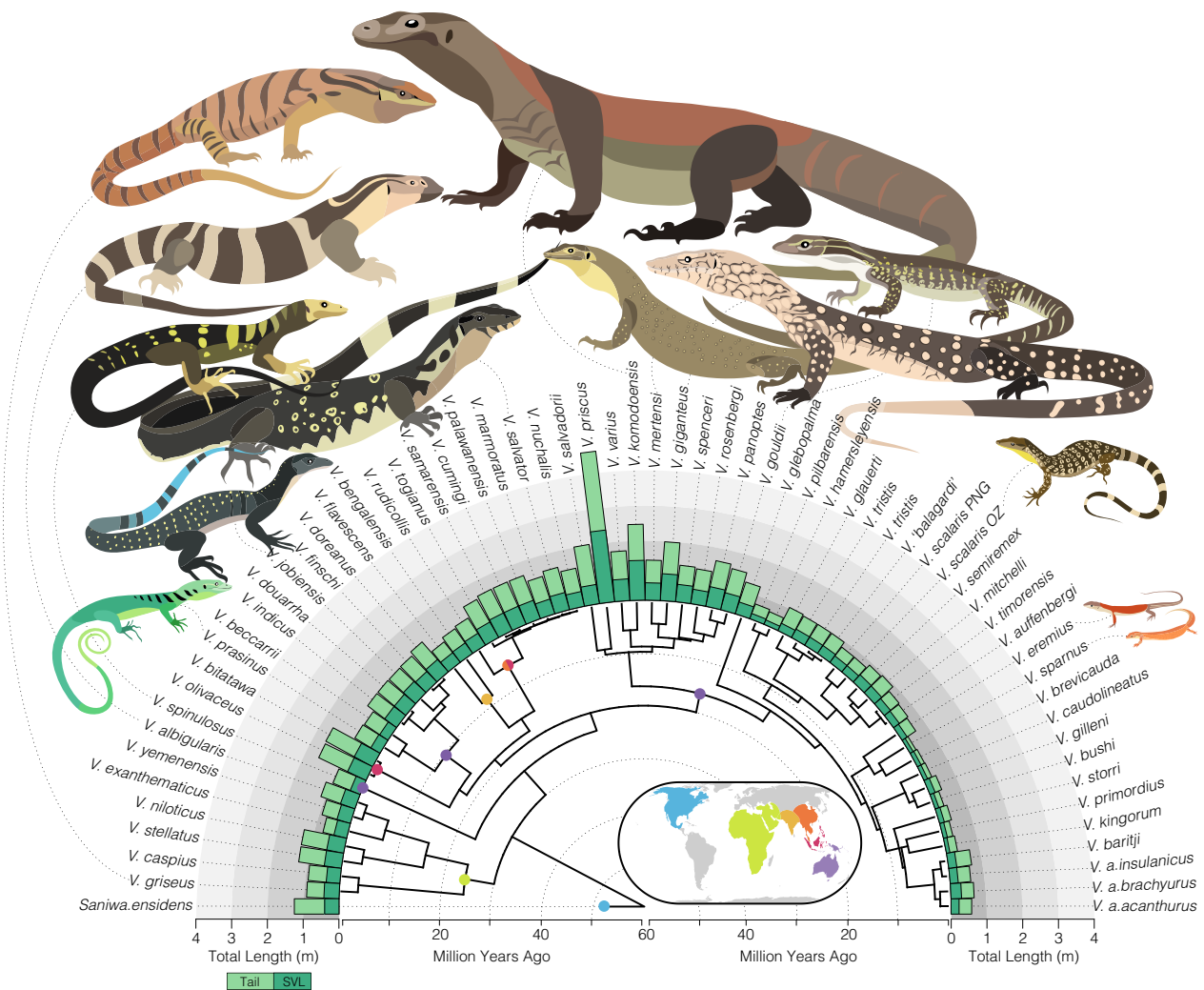


FIGURE 2. Body size among *Varanus* species varies across multiple orders of magnitude. Bar plots at tips of the tree show total length of sampled monitor lizards broken down into snout-vent length (SVL) and tail length. The smallest monitor lizard species *Varanus sparnus* reaches just over 200 mm long from snout to tail tip and may weigh only 20 g, while the largest living species *Varanus komodoensis* can reach well over 2 m long (2000+ mm) and top the scales at 100 kg (100,000 g). By all accounts, the recently extinct *Varanus priscus* was even larger than the Komodo dragon and may have reached over 4 m long (Wroe 2002; Conrad et al. 2012). Inset map shows a rough global distribution of monitor lizards and the extinct relative *Saniwa ensidens*. Colored circles at nodes indicate primary distribution of the major clades of *Varanus* and correspond to distributions on the map (blue—North America; green—Africa and the Middle East; light orange—Indian Subcontinent; dark orange—Indochina and China; red—Sundaland and Wallacea; purple—AustraloPapua).

Signature of Character Displacement

Ecological communities are thought to assemble under opposing processes of habitat filtering and interlineage competition (Webb et al. 2002). Filtering is suggested to select for species with similar phenotypes, resulting in conservatism or convergence, whereas competition is expected to result in greater phenotypic disparity. These expectations can be tested by investigating the functional diversity of communities across the landscape. We divided the Australian continent into half-degree cells and created a site by species matrix using the ALA distribution data for (i) monitor lizards and again for (ii) monitors and

dasyuromorph/peramelemorph marsupials together. We estimated the functional diversity for the two data sets using the package *FD* (Laliberté et al. 2014) and Rao's Quadratic, using body size as the trait of interest. We then estimated functional diversity for each inhabited cell 100 times using a dispersal null metric model which sampled from nearby cells assuming a probability proportional to the inverse of the distance from the focal cell. To compare observed and simulated functional diversities, we calculated standardized effect sizes (SES) for each cell, and a mean SES across the continent with 95% confidence intervals (Fig. 3).

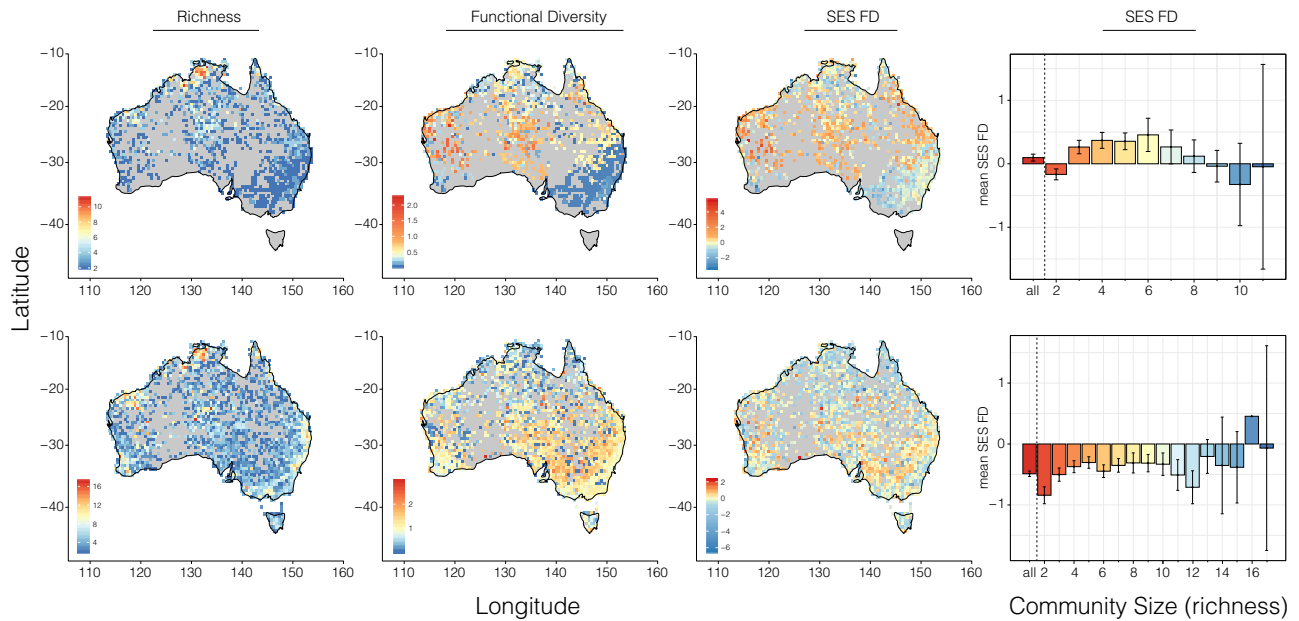


FIGURE 3. Maps of Australia showing patterns of richness (number of species) and functional diversity for monitor lizards (top row) and for monitor lizards and faunivorous marsupials together (bottom row). Values were calculated and plotted for half-degree squares, with warmer colors indicating greater values—but note different scales for each plot. The left plots display species richness across the landscape and center-left plots show absolute values for functional diversity (FD—Rao's Q). Center-right plots show the standardized effect size (SES) of functional diversity when compared to the dispersal-corrected null model, and right plots show how the mean standardized effect sizes vary across communities of varying richness. In communities of moderate richness (3–7 spp), functional diversity is overdispersed in monitor lizards, suggesting character displacement. Functional diversity is almost always underdispersed when considering monitors and marsupials in communities together.

Modeling Body Size Evolution with Competition

Only within the past few years have phylogenetic comparative methods (PCMs) begun to account for the interaction of lineages on trait evolution. Conceptual work by Nuismer and Harmon (2015) led to the development of the *Matching Competition* (MC) model by Drury et al. (2016), which infers an interaction parameter (S) dictating attraction towards or repulsion from the mean trait value of interacting lineages. This was extended by Drury et al. (2018b) to incorporate interactions matrices which limited interactions to only codistributed species. We build upon this framework by expanding the biogeographic information to include temporally and spatially dynamic ranges for ancestral taxa (inferred from *rase*, example in Supplementary Fig. S6 available on Dryad). In natural ecosystems, many different organisms compete for the same resources, so accounting for competition only within a single group is perhaps unrealistic. To address this issue, we consider the influence of another broadly distributed group of like-sized carnivores and omnivores, dasyuromorphian and peramelemorphian marsupials, on the size evolution of Australian monitor lizards. To test this hypothesis, we begin by trimming the marsupial phylogeny of Brennan and Keogh (2018) down to just the faunivorous clades, from which we also dropped *Myrmecobius* because of its unusual ecology. We collected body size (mm) information for marsupials from Pantheria (Jones et al. 2009) and monitors from

the literature (Wilson and Swan 2013). Manceau et al. (2017) introduced the *Generalist Matching Mutualism* (GMM) model, a framework that uses two phylogenetic trees to estimate the effect of one clade on the trait evolution of another. This is essentially a two-clade extension of the MC model, which makes the assumption that the evolution of trait values in clade A are the result of interactions *only* with lineages in clade B, and vice versa. The GMM model however makes two very basic assumptions that we expect do not fit our data: (i) interactions between phenotypes are limited to interclade (between trees) matching or competition, meaning there is no influence of intraclade (within tree) interactions and (ii) that all contemporaneous lineages are interacting, regardless of geographic distribution. To address these assumptions, we developed and fit a series of models that expand on the interaction parameter S and incorporate biogeography to provide more realistic models of trait evolution. We present summaries and graphical descriptions of these models in Figure 4 and the Supplementary Fig. S1 available on Dryad. Further, we test if size evolution is instead dictated by nonecological processes, by employing standard models of trait evolution, Brownian Motion *BM* and Ornstein Uhlenbeck *OU*. Using these traditional null models, we can again ask if monitor and dasyuromorphian size has evolved under similar or independent rates using *ratebytree* in *phytools* (Revell 2012), though we also provide implementations of shared *BM* and *OU*

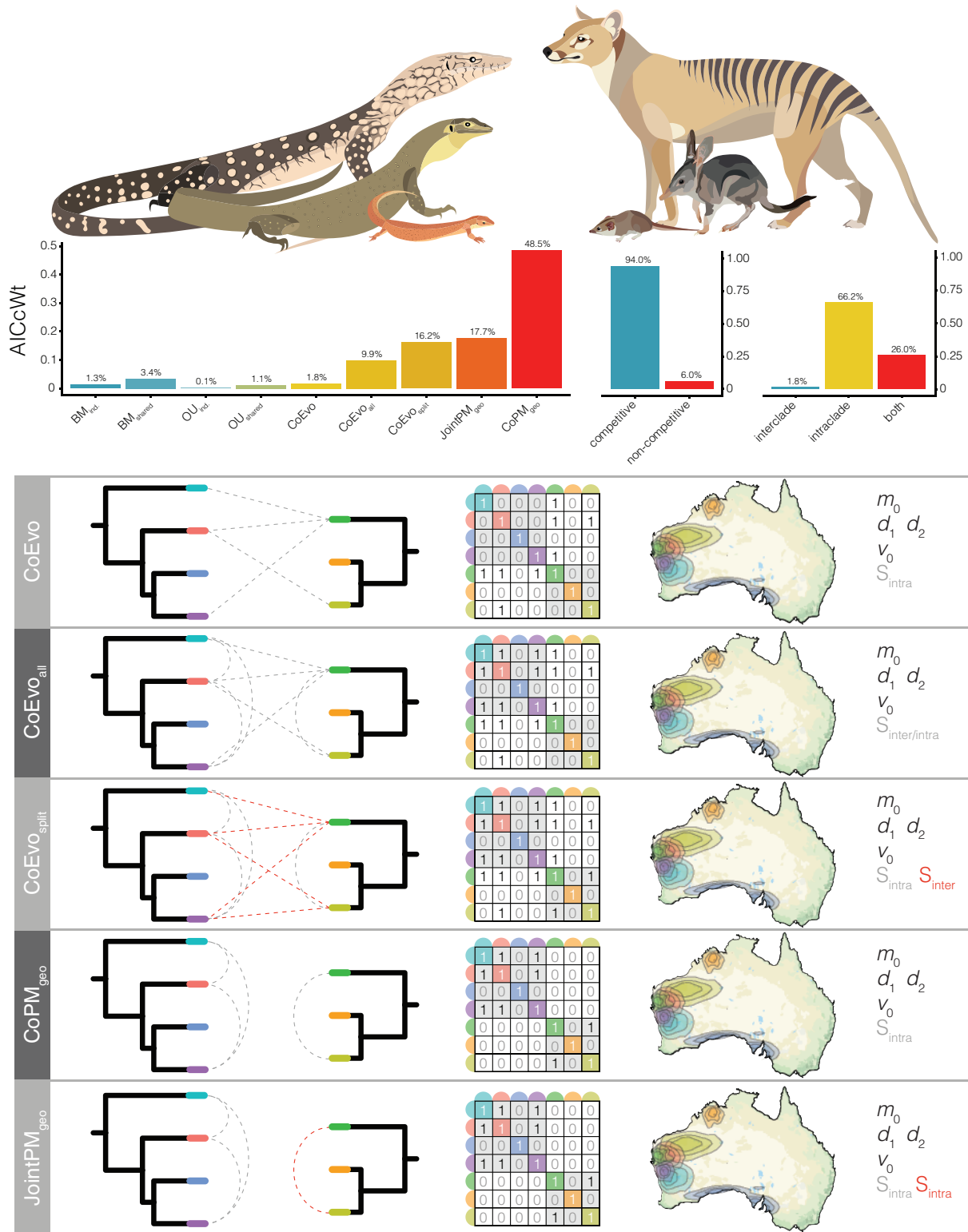


FIGURE 4. Comparative model fitting highlights the importance of incorporating interactions when modeling body size evolution of monitor lizards and faunivorous marsupials. Top, examples of Australian monitor lizards (*Varanus giganteus*, *V. mertensi*, and *V. sparnus*) and marsupials (*Thylacinus cynocephalus*, *Macrotis lagotis*, and *Pseudantechinus bilarni*), drawn roughly to scale. Middle, modeling competition vastly improves model fit, but size evolution appears largely driven by intraclade evolution and not competition between monitors and mammals. Bottom, hypothetical schematic components of biogeographically informed lineage interaction comparative models for two clades. Each model is named at left, followed by a diagram of the two trees with interlineage interactions allowed under the given model designated by dashed lines. If more than one interaction parameter S is estimated, it is denoted by red dashed lines. The contemporary summary of these interactions are presented in the interaction matrix P , and the estimated parameters are listed at far right. Maps show the distribution of the taxa used in these examples, and inform the interaction matrices.

models in the *RPANDA* (Morlon et al. 2016) framework—*CoBM* and *CoOU*. To compare against an alternative hypothesis of varanid size evolution (Collar et al. 2011) where variation is dictated by habitat use, we also fit a multi-optimality (OUM) model in *OUwie* (Beaulieu et al. 2012).

To incorporate historical and contemporary biogeography, we extended our *rasc* analyses to marsupials with data collected from the ALA. We designed a number of custom scripts and functions to process the spatial data and model objects including extensions of the “CreateGeoObject” of *RPANDA*. Our functions “CreateGeoObject_SP” and “CreateCoEvoGeoObject_SP” produce *RPANDA* GeoObjects that take as input a tree, spatial distribution data in latitude/longitude format, and a postprocessed *rasc* object. Internally, these functions use the packages *sp* and *rgeos* to translate spatial data into spatial polygons representative of species distributions. Then, at each cladogenetic event, we determine the pairwise overlap of all contemporaneous lineages to construct our GeoObject (see Supplementary Fig. S8 available on Dryad). The “CreateCoEvoGeoObject_SP” function has adapted this process for two trees, to be applied to GMM-type models.

Model Behavior and Identifiability

The ability to identify competition and estimate associated parameters using process-based models has been tested extensively previously (Drury et al. 2016, 2018a, 2018b). From this we know that the ability to recover competitive models and estimate the interaction parameter S —when it is the generating process—is strongly linked to the absolute value of S , and to a lesser degree the size of the phylogeny. Parameter estimates and recovery of S can also be highly influenced by the incorporation of stabilizing selection (ψ or α), with the two parameters working agonistically in instances of competition ($-S$), and synergistically in mutualistic circumstances ($+S$). To ensure that we can accurately identify our models and estimate parameter values, we undertook a focused simulation exercise. Following the advice of Manceau et al. (2017), we simulated data directly onto our Australian monitor and marsupial trees under the same models we fit to our empirical data: BM_{shared} , OU_{shared} , $CoEvo$, $CoEvo_{\text{all}}$, $CoEvo_{\text{split}}$, $JointPM_{\text{geo}}$, and $CoPM_{\text{geo}}$. We used the *RPANDA* function “simulateTipData” to simulate body size data under all specified models, keeping the empirical biogeography constant. Specifics of the generating parameter values are noted in the Supplementary Table S3 available on Dryad. We then iteratively fit the models to our simulated data, and compared fit using AICc and plotted AICc weights. To determine the ability to accurately recover parameter values, we then compared estimated to simulated values under each model.

RESULTS

Phylogenetics of Monitor Lizards and Kin

Topologies estimated across maximum likelihood (IQTREE; Schmidt et al. 2014), shortcut coalescent (ASTRAL; Zhang et al. 2018), and Bayesian multispecies coalescent (StarBEAST2; Ogilvie et al. 2016) methods are highly concordant and generally strongly supported (Fig. 1 and Supplementary Figs. S2, S3 available on Dryad). Contentious nodes are limited to some subspecific (*Varanus gouldii* and *V. panoptes*) and interspecific relationships (*V. salvator* complex) which occur across a number of extremely short branches with low gene concordance factors, indicating both low information content and confidence. All analyses support the monophyly of *Varanus* and anguimorphs, and unite the Shinisauridae with the Helodermatidae, Anguillidae, and Xenosauridae along a short internal branch. The Varanidae is sister to this group.

Interestingly, our trees are broadly consistent with the first molecular phylogenies of *Varanus* proposed by Fuller et al. (1998) and Ast (2001) two decades ago. Our results verify the monophyly of African and Arabian monitor lizards, and contrary to other recent studies (Lin and Wiens 2017), support the monophyly of both *Psammosaurus* and *Polydaedalus* subgenera. Our data support a geographically widespread clade comprising Philippines (*Philippinosaurus*) and tree (*Hapturosaurus*) and mangrove monitors (*Euprepiosaurus*), with water monitors (*Soterosaurus*) and species from the Indian subcontinent (*Empagusia*). We return a well resolved clade of Indo-Australopapuan monitors comprising the crocodile monitor (*Papususaurus*), and the subgenera *Varanus* and *Odatria* (the dwarf monitors). Further, we record the first phylogenetic placement of the enigmatic monitor *V. spinulosus* (*Solomonsaurus*) as sister to the Asian and Pacific clade, and confidently place *V. gleboplama* as sister to the rest of *Odatria*.

Dating estimates from our combined evidence and node-calibrated molecular analyses in StarBEAST2 agree on the timing of *Varanus* divergences. They suggest an origin of varanids (split between Varanidae and Lanthanotidae) in the mid-to-late Cretaceous (80–100 ma), and an early-to-mid Oligocene (28–35 ma) origin for the crown divergence of extant *Varanus*. These dates are comparable with recent estimates from the literature (Lin and Wiens 2017; Pyron 2017), and younger than previous estimates (Vidal et al. 2012; Portik and Papenfuss 2012) which used stem varanids to calibrate the crown (Supplementary Fig. S4 available on Dryad). Ten fossil taxa form relatively poorly resolved higher-order relationships, with the Palaeo-Varanidae (formerly Necrosauridae) forming a clade with the Lanthanotidae (*Lanthanotus*, *Cherminotus*), together as sister to the Varanidae (*Varanus*, *Saniwa*). *Varanus priscus*, which is generally considered an extinct relative of the Indo-Australopapuan clade of giant monitors including *V. varius*, *V. komodoensis*, and *V. salvadorii*, is consistently placed in the Australian radiation. Given the existing morphological data, the majority of fossil taxa are

recovered as tips in our analyses (Supplementary Fig. S10 available on Dryad).

Biogeography and Community Assembly

Global biogeographic analysis of *Varanus* and allies suggests an origin of varaniform lizards in East Asia, with dispersals west across Laurasia into Europe, and east into North America. The origin of the genus *Varanus* is equivocal (Supplementary Fig. S11 available on Dryad), but likely followed a similar pattern, with independent clades dispersing west through the Middle East and into Africa and Europe, and south and east through Southeast Asia, Sundaland, and into Indo-Australia. After reaching the western and eastern extents of their range, both the African and Australopapuan clades appear to have begun dispersals back towards their origins. This has resulted in *V. yemenensis* extending across the Red Sea into the Arabian Peninsula, and *V. komodoensis* and members of the *V. scalaris* complex reaching back into Wallacea. A DEC model incorporating dispersal probability as a function of distance is strongly preferred (AIC = 170.66, $x = -0.682$) over the traditional DEC model (AIC = 186.04, Δ AIC = 15.38).

Biogeographic reconstruction of Australian *Varanus* reveals an origin spread across much of northern and central Australia (Fig. 3). Considering northern Australia was the most likely colonization point for monitors, it makes sense that our analyses of community structure highlight this area as the center of greatest species richness for *Varanus*, with up to 11 species recorded in some half-degree grid cells. Taken together with dasyuromorph and peramelemorph marsupials, we again see high richness in the Top End, but also note species richness hotspots in the Central Deserts and the Pilbara regions. These regions are functionally diverse for monitors as well, but much less so for communities of marsupials and monitors analyzed jointly. Overall, we find support for overdispersion in trait values in the monitor-only data set. Across Australia functional diversity of most communities is greater than expected under our null model (mean SES across all cells for monitors = 0.07 ± 0.05). Functional diversity is greatest in monitor communities of moderate-to-high (3–7 spp.) richness (mean SES = 0.45 ± 0.13), and lower than we would expect under our null model in communities of only two species (mean SES = -0.16 ± 0.08) (Supplementary Table S9 available on Dryad). In contrast, communities of monitors and marsupials together have estimates of functional diversity consistently lower than expected under the null model (mean SES across all cells = 1.2 ± 0.26) (Supplementary Table S10 available on Dryad).

Modeling Body Size Evolution

We extend a coevolutionary comparative method framework (Manceau et al. 2017) to incorporate historical biogeography and estimate the influence of lineage

interactions on trait evolution. Comparison of traditional models of trait evolution (Brownian Motion, Ornstein Uhlenbeck) with those that incorporate interactions among lineages decisively favors interactive models (AICc weight 94%) (Fig. 4, Supplementary Fig. S12 available on Dryad). These models can be broadly divided into those which estimate the interaction parameter S from occurrences (1) within clades (S_{intra}), (2) between clades (S_{inter}), or (3) both. We find greatest support for models that estimate interactions only within clades (Fig. 4). Support for the best-fitting model CoPM_{geo} —which fits only a single S_{intra} parameter for both trees—suggests that the strength of intracade interactions cannot be differentiated between the two groups. Across fitted models that estimate S_{intra} , we inferred negative values of S , supporting competitive interactions in both monitors and marsupials, $S_{\text{intra}} = -0.043 \pm 0.005$.

Support for the CoPM_{geo} model also comes indirectly from parameter estimates of the $\text{CoEvo}_{\text{split}}$ model. In fitting the $\text{CoEvo}_{\text{split}}$ model, which estimates separate inter- and intracade interaction parameters ($S_{\text{inter}}, S_{\text{intra}}$), we estimate a weak positive S_{inter} parameter of 0.0043. This parameter estimate is small enough to likely be biologically meaningless, and with $S_{\text{inter}} \approx 0$ the $\text{CoEvo}_{\text{split}}$ model collapses to CoPM_{geo} (see Supplementary material—Nested Models available on Dryad). This suggests that interclade interactions between marsupials and varanids are indistinguishable from these data.

Results of our model identifiability exercise indicate that all proposed models can be recovered under realistic circumstances (Supplementary Fig. S13 available on Dryad). Because a number of these are nested forms of one variety or another, when simulated values of S (as S_1 or S_2) approach 0, some models may be incorrectly conflated. Consistent with previous assessment (Drury et al. 2016), we also find that the accuracy of estimated S is directly related to the absolute value of S , with greater values of S being more precisely recovered (Supplementary Fig. S14 available on Dryad).

DISCUSSION

Competitive interactions are expected to impact diversity by influencing species ranges, and influence phenotypic and behavioral evolution through character displacement (Brown and Wilson 1956; Benton 1987). Over time, this development of spatial and functional diversity shapes local communities and continental assemblages, and is central to our understanding of global biodiversity. In Australia, a number of codistributed endemic radiations display extreme morphological disparity, including the monitor lizards *Varanus*. In analyzing patterns of *Varanus* size evolution, we provide a compelling case for considering biogeographic history and competition in phylogenetic comparative methods (PCMs) of trait evolution.

Phylogenetic Relationships and Origins

Relationships among anguimorph lizard groups have been contentious, particularly with regard to the placement of fossil taxa (Conrad 2008; Conrad et al. 2011; Pyron 2017). Our reanalysis of these morphological data in concert with novel phylogenomic data are largely consistent with previous assessments, however we provide new insights into the phylogenetics of living members of *Varanus*. One of the most intriguing results from our data is the phylogenetic placement of *V. spinulosus*. Although it is not wholly unexpected (Ziegler et al. 2007a, 2007b; Bucklitsch et al. 2016), it is not affiliated with the subgenus *Varanus* (Sweet and Pianka 2007) or with *Euprepiosaurus* (Harvey and Barker 1998). Instead, we place *V. spinulosus* alone on a long branch between the African and Asian monitors, and corroborate the previous erection of a unique subgenus *Solomonsaurus* (Bucklitsch et al. 2016). The phylogenetic position of *V. spinulosus* is remarkable given that it is a Solomon Islands endemic, meaning it likely made a considerable over-water dispersal or island hopped to the Solomons only shortly after their formation ~30 Ma (Hall 2002). This corroborates the intriguing observation that relatively young Melanesian islands have long been sources for ancient endemic diversity (Pulvers and Colgan 2007; Heads 2010; Oliver et al. 2017, 2018, 2020). It also suggests at least three independent dispersals of *Varanus* across Wallace's line, and a convoluted history of movement throughout the Indo-Australian region.

Our phylogeny of *Varanus* also highlights the adaptive capacity of these amazing lizards (Fig. 2, Supplementary Fig. S5 available on Dryad). For example, the perentie *V. giganteus* is the largest extant Australian lizard, reaching well over 2 m long, while remaining extremely thin. Its sister species *V. mertensi* in contrast, is a heavy bodied semiaquatic lizard built for the watercourses of northern Australia. Together, these species are sister to a group of sturdy terrestrial wanderers, the sand goannas *V. gouldii*, *V. panoptes*, *V. rosenbergi*, and *V. spenceri*. In roughly 5 myr, these monitors diverged broadly both ecologically and morphologically, and spread across Australia's landscape. In the process of diversifying, monitor lizards have also converged repeatedly on ecological niches and body plans. There are at least four different origins of amphibious monitors (*V. salvator*, *V. mertensi*, *V. mitchelli*, *V. niloticus* groups), and four or more origins of arboreal species (*V. prasinus*, *V. gilleni*, *V. salvadorii*, *V. olivaceus*, *V. dumerilii* groups), emphasizing the ability of monitors to fill available niches.

A number of phylogenetic questions evade our sampling, and largely concern the population genetics of known species complexes. These include the *V. acanthurus*, *V. doreanus*, *V. griseus*, *V. indicus*, *V. jobiensis*, *V. prasinus*, *V. salvator*, *V. scalaris*, and *V. tristis* groups, of which most have recognized subspecies, very closely related species, or are paraphyletic in our data (Fig. 1). Some of these taxa have experienced dramatic taxonomic growth in recent years as a result of more extensive sampling, and are sure to present exciting

phylogeographic and systematic stories when the right data and sampling are paired together.

Overall, we suggest a more recent timeline for the diversification of modern varanid lizards when compared to other phylogenetic studies, with a crown age in the early-to-mid Oligocene. This timing suggests *Varanus* potentially dispersed into the Indo-Australian region shortly after the collision of the Australian and Asian plates. If this is true, the connection of Sahul to Sundaland likely facilitated the dispersal of monitor lizards across an Indonesian island bridge, and extensive overwater dispersals seem less probable. Similarly, this proximity has also allowed small Australopapuan *Varanus* like the *V. scalaris* complex, as well as the largest extant monitor *V. komodoensis* to disperse back into the Indonesian archipelago (at least Wallacea). This pattern is consistent with the adaptive radiation of Australopapuan elapid snakes (Keogh 1998) and pythons (Reynolds et al. 2014; Esquerre et al. 2019), from Asian origins, and may underlie a more common diversification trend.

Competition, Character Displacement, and Size Evolution

Despite a relatively conservative body form, *Varanus* lizards have diverged into a number of ecological niches and an astonishing array of body sizes. These include highly cryptozoic pygmy monitors like *V. primordius*, slender canopy dwellers like *V. prasinus*, the stout-bodied semiaquatic *V. mertensi* and *V. salvator* complex, and monstrous apex predators like the Komodo dragon *V. komodoensis* and extinct *V. priscus*. Across their range, monitors have also converged ecomorphologically with a number of mammalian predators, potentially putting them in direct competition for resources (Sweet and Pianka 2007). Competition is expected to influence interacting lineages by driving similar organisms apart in geographic space (exclusion), or in phenotypic or behavioral traits (character displacement) (Brown and Wilson 1956). In Australia, the diversity of varanids is matched by that of carnivorous marsupials, which vary from tenacious shrew-sized ningaus (*Ningau*) up to the recently extinct wolf-like *Thylacine*.

By modeling the evolution of body size of Australian monitors and dasyuromorph and peramelemorph marsupials using lineage interaction-informed PCMs, we find strong support for the accumulation of size disparity as a result of character displacement independently and in parallel in these two groups. This is corroborated by greater than expected functional diversity of monitor assemblages (over dispersion). However, we do not find evidence of competition between marsupials and monitors and instead size evolution appears to have been dictated instead by within-clade character displacement. This may seem counterintuitive, considering carnivorous marsupials and monitors largely overlap in diet and size, with small animals eating large invertebrates and small lizards, and larger animals taking larger vertebrate

prey (James et al. 1992). But, marsupial predators and monitors differ in one very basic way, which is their activity period. Both are active foragers, covering wide tracks of land in search of food, but while monitors are almost exclusively diurnal, often roaming during the hottest part of the day, nearly all faunivorous marsupials are nocturnal. This temporal separation may explain a lack of competition and their continued coexistence. Data from other continents lend some support to this hypothesis. Across Africa, the Indian subcontinent, and throughout Southeast Asia, monitor lizards compete with other diurnal carnivorans, such as herpestids (mongooses), viverrids (civets), canids (dogs), mustelids (weasels), and felids (cats). Throughout these regions, *Varanus* have not diversified to the same extent as in Australia. The possibility of competitive release upon reaching the Australian continent provides a plausible explanation for the diversification of dwarf monitor species (Sweet and Pianka 2007).

While monitor lizards and marsupial predators appear to have diversified without outwardly influencing each other's trait evolution, both groups appear to have diverged according to character displacement occurring *within* their respective radiations. This suggests that community assembly processes may result in the same observable macroevolutionary patterns across different sympatric groups. Character displacement has long been associated with trait divergence, and was principally described on shallow scales from observable interactions among extant lineages (Vaurie 1951; Brown and Wilson 1956). The practice of extrapolating this idea to fit evolution on geological timescales fits the concept of a micro-to-macro evolutionary spectrum that is dictated by the same processes. The concept of competition as an impetus for evolution however, has been difficult to show explicitly from the fossil or phylogenetic record, and has been criticized for an unnecessarily "progressive" view of the process of evolution (Benton 1987). With the recent development of more appropriate process-generating models, we are now capable of better testing the influence of lineage interactions on evolutionary outcomes (Drury et al. 2016, 2018b; Manceau et al. 2017; Quintero and Landis 2019). In the case of monitor lizards, the exaggerated disparity in body sizes of Australian species is best described by an evolutionary model which accounts for competition among taxa in both space and time. This finding is further supported by evidence of overdispersion in body size variation within monitor communities, suggesting niche partitioning by body size is prevalent across the continent.

CONCLUSION

Monitors are an exceptional radiation of lizards capable of traversing sandy deserts and open ocean, living in the canopy and below ground. Here we present a comprehensive phylogenomic hypothesis of

Varanus, and place them among related varaniform and anguimorph lizards. In agreement with previous research, we find that varanids likely originated in Eurasia in the late Cretaceous or early Paleocene, but have long been spread across Europe, North America, and Africa, with their greatest richness in Indo-Australia. We also present a set of interaction-informed geographically explicit comparative models that help us propose an explanation for the extreme size disparity of living *Varanus*. We suggest that the diversity of sizes of Australian monitors may be the result of a combination of competitive release from carnivorans and character displacement among other monitor species. Because organisms evolve in natural communities—and not in ecology-free vacuums—we stress the importance of incorporating macroecological processes into macroevolutionary models. Our methodology involves a stepwise process of estimating ancestral ranges in continuous space (Quintero et al. 2015), then using this to inform interaction matrices in comparative models of trait evolution (Drury et al. 2018b). This framework also provides the opportunity to test the influence of taxa from more than one phylogeny on the evolution of a trait of interest (Manceau et al. 2017), with the goal of better understanding how communities develop and evolve. While our stepwise framework is limited by the unidirectionality of influence (species distributions may dictate trait evolution, but not vice versa), already methods are being developed to jointly infer these processes (Quintero and Landis 2019), as the evolutionary community works to provide a more holistic view of speciation, biogeography, and trait evolution.

SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.tx95x69t8>.

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