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Global Diversification of Anelosimus Spiders Driven by Long-Distance Overwater **Dispersal and Neogene Climate Oscillations**

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Abstract.--Vicariance and dispersal events, combined with intricate global climatic history, have left an imprint on the spatiotemporal distribution and diversity of many organisms. *Anelosimus* cobweb spiders (Theridiidae), are organisms ranging in behavior from solitary to highly social, with a cosmopolitan distribution in temperate to tropical areas. Their evolutionary history and the discontinuous distribution of species richness suggest that 1) long-distance overwater dispersal and 2) climate change during the Neogene (23–2.6 Ma), may be major factors in explaining their distribution and diversification. Here, we test these hypotheses, and explicitly test if global Miocene/Pliocene climatic cooling in the last 8 Ma affected *Anelosimus* radiation in parallel in South America and Madagascar. To do so, we investigate the phylogeny and spatiotemporal biogeography of *Anelosimus* through a culmination of a 20-year comprehensive global sampling at the species level (69 species, including 84% of the known 75 species worldwide, represented by 268 individuals) using nucleotide data from seven loci (5.5 kb). Our results strongly support the monophyly of *Anelosimus* with an Oligocene (~30 Ma) South American origin. Major clades on other continents originate via multiple, long-distance dispersal events, of solitary or subsocial—but not social—lineages, from the Americas. These intercontinental dispersals were to Africa, Madagascar (twice), and SE Asia/Australasia. The early diversification of *Anelosimus* spiders coincides with a sudden thermal increase in the late Oligocene (\sim 27–25 Ma), though no causal connection can be made. Our results, however, strongly support the hypothesis that global Neogene climatic cooling in the last 8 Ma drove Anelosimus radiation in parallel in South America and Madagascar, offering a rare empirical evidence for diversification of a socially diverse group driven by an interplay between long-distance dispersal and global Neogene climatic changes. [Cobweb spiders; diversification; global biogeography; long-distance dispersal; molecular phylogenetics; neogene climate changes; sociality; vicariance.]

Climatic oscillations are among major abiotic factors underlying patterns of diversity and distribution of biotas (Easterling et al. 2000; Hewitt 2003; Parmesan and Yohe 2003). Such oscillations may cause global changes in habitat cover, such as the relatively recent ($\sim 6-10$ Ma) expansion of grasslands and retraction of forests occurring at both regional and global scales (Pagani et al. 1999; Retallack 2001; Edwards et al. 2010; Fuchs et al. 2015). Many lineages have thrived in such changing environments and undergone evolutionary radiations (Zhang et al. 2013; Fuchs et al. 2015; Agnarsson et al. 2016a; Pozzi 2016). In a changing world, long-distance dispersal may allow taxa to colonize favorable habitats relatively rapidly (Hoffmann and Sgro 2011), and strong dispersal ability, linked to dynamic climate, can facilitate colonization of new landmasses globally.

During climatic fluctuations, certain habitats can act as refugia because they offer the persistence of relatively stable climate conditions at regional scales. For example, tropical rainforests have shrunk and expanded repeatedly through the Earth's history, but persistent pockets of rainforest have likely acted as refugia during such periods (Hewitt 2003). Historically, climatic changes have caused significant habitat changes, both through extension and fragmentation. Such changes, in turn, could have resulted in temporal and spatial shifts in species distribution patterns, leading to isolated populations, facilitating diversification (Hewitt 2003). Vhereas the impact of historical climatic changes on cladogenesis is well documented and understood at regional scales (Goldblatt and Manning 2002; Linder 2003; Daniels et al. 2006; Gouws et al. 2010; Schnitzler et al. 2011; McDonald and Daniels 2012; Ballarin and Li 2017), fewer studies have examined global patterns. Prior studies of animal historical biogeography in relation to climatic fluctuations have focused mainly on recent epochs, especially Pleistocene glaciations, which are often invoked to explain the origin and current distribution of many young taxonomic groups at a local level (Peck 1980; Holsinger 1988; Allegrucci et al. 2011;

SYSTEMATIC BIOLOGY

Niemiller et al. 2013; Bryson et al. 2014). In contrast, the interplay of dispersal and older environmental changes worldwide have been less intensely studied (Leys et al. 2003; Faille et al. 2010, 2014), and often focused on taxa with specialized habitats and dispersal behaviors (Daniels et al. 2006; McDonald and Daniels 2012; Ballarin and Li 2017).

Dispersal by ballooning on silken threads is a wellknown behavior in spiders, especially prominent in families, such as Araneidae, Linyphiidae, Nephilidae, Oxyopidae, Philodromidae, Tetragnathidae, and Theridiidae (Dean and Sterling 1985; Weyman et al. 2002; Bell et al. 2005; Blandenier 2009; Garb and Gillespie 2009; Kuntner and Agnarsson 2011; Hayashi et al. 2015; Lee et al. 2015; Agnarsson et al. 2016a, 2016b). Ballooning confers high dispersal potential on certain spiders. Indeed, in newly created habitats, such as islands emerging from the ocean, spiders are typically among the first organisms to colonize (Meijer 1977; Sugg and Edwards 1998). The length and direction of the passive 'flight' will depend on factors, such as height achieved by the individuals and meteorological conditions, such as trade winds and more temporary weather conditions. Thus, climatic and geologic modifications through time may influence the conditions for long-distance dispersal in spiders.

Neogene events, such as the retreat of the Paratethys Sea and global cooling, likely led to dramatic effects on the global monsoonal circulation by changing atmospheric flow (Clift et al. 2008; Chatterjee et al. 2013; Zhang et al. 2015). Additionally, altered precipitation patterns during the second half of the Miocene led to greater seasonality in some regions (Tang et al. 2015). Molecular evolutionary research supports the roles played by Neogene climatic changes and contemporaneous major geological events in shaping the evolutionary history of numerous organismal communities (Che et al. 2010; Wang et al. 2012; Favre et al. 2015; Jiang et al. 2015). Increasingly, detailed biogeographical analyses are revealing the importance of long-distance dispersal, even in many organisms that have long been thought to be purely vicariant. Once thought of as 'noise'-empty and untestable hypotheses invoked when vicariance failed to explain certain distributions-the field of dispersal biology is now burgeoning (de Queiroz 2005; Gillespie et al. 2012, 2017)

In this article, we revisit the evolution of the cobweb spider genus *Anelosimus* in a new phylogenetic and historical biogeographic framework. *Anelosimus* is a globally distributed lineage that contains species spanning the spectrum from solitary with short-term maternal care of spiderlings (Agnarsson and Zhang 2006) to highly and permanently social species (Vollrath 1986; Avilés 1997; Avilés et al. 2001; Avilés and Guevara 2017; Viera and Agnarsson 2017). *Anelosimus* originated long after the split-up of Gondwana (Penney et al. 2002; Marusik and Penney 2005), likely near the Eocene/Oligocene boundaries (Wunderlich 1988, 2008, 2015; Agnarsson et al. 2016a; Liu et al. 2016). Thus, it is good a candidate for studying dispersal-based biogeography. The genus currently includes 75 described species that inhabit tropical to warm temperate areas (Agnarsson and Kuntner 2005, 2006, 2012a; Agnarsson et al. 2015; World Spider Catalog 2020; Supplementary Table S1 available on Dryad at http://dx.doi.org/10.5061/dryad.sf7m0cg2p). Anelosimus spiders are relatively small (\sim 2–7 mm as adults) and are known to balloon as a means of dispersal (Bell et al. 2005; Blandenier 2009; Blandenier et al. 2013). Our past work has suggested that longdistance dispersal events must have played a key role in the evolution of the cobweb spider genus Anelosimus Simon 1891 (Theridiidae). The presence of Anelosimus on Madagascar, Mayotte, Seychelles (Saaristo 2006), Aldabra (Roberts 1983), and the islands of the Indonesian archipelago indicates successful colonization via overwater dispersal. On the other hand, their absence on more isolated islands such as the Mascarenes (Reunion, Mauritius, and Rodriguez, own data), and the large number of remote Pacific and Atlantic Ocean islands suggests that such events are relatively rare. Curiously, permanently social Anelosimus species are dispersallimited and, while representing multiple independent linages, have all originated in the Americas with no evidence of subsequent overwater dispersal.

Previous Anelosimus phylogenetic work indicated a scattering of American Anelosimus species in three separate clades (Agnarsson and Zhang 2006; Agnarsson et al. 2007, 2012, 2016a). This pattern implies repeated cases of intercontinental dispersal, however, specific biogeographical hypotheses, such as timing and direction of dispersal, have not been unequivocally supported using prior, less taxon-dense, phylogenies. Thus far, the major ambiguities have revolved around 1) whether the two 'smaller' New World clades (the ethicus clade and the rupununi clade) originated there or colonized the Americas from the Old World (Agnarsson and Kuntner 2005), 2) what are the phylogenetic affinities of Australian species, and 3) the unexpected placement in previous phylogenetic hypotheses of the behaviorally unknown species A. luckyi from Papua New Guinea as sister to a clade containing most Anelosimus, with unclear biogeographical implications. We also investigate 4) whether levels of sociality affect dispersal tendencies, and in turn, evolutionary history at the global biogeographic scales. Therefore, to address these questions and to understand major factors in the diversification of the genus, more detailed understanding of the biogeographical history and timing of events required a more complete sampling of Anelosimus species across the globe.

The remarkable differences in diversification patterns of modern *Anelosimus* in the Americas and Madagascar, compared to other global *Anelosimus*, raise interesting questions about the underlying processes. Consistent with the assumed recent history of the genus and its ballooning behavior, we hypothesize that long-distance dispersal and climatic change during the Neogene played a central role in inducing the formation of global lineages. We specifically test, using phylogenetic and climatological data, whether global Neogene climatic

LUO ET AL.-GLOBAL DIVERSIFICATION OF ANELOSIMUS SPIDERS

cooling in the last 8 Ma drove Anelosimus radiation in parallel in South America and Madagascar. First proposed by Agnarsson et al. (2016a), Miocene/Pliocene climate cooling and consequent forest fragmentation in Madagascar, as well as in parts of South America, may have affected the diversification of Anelosimus. These kinds of global tests have so far not been feasible due to the paucity of Anelosimus collections from certain underrepresented regions. Over the last 20 years, the corresponding author has assembled a collection of Anelosimus spiders through extensive global fieldwork, and through collaborators especially in Japan, Brazil, and Europe. By adding numerous new species to the genus (Agnarsson 2005, 2006, 2012a, 2012b: Agnarsson and Kuntner 2005; Agnarsson and Zhang 2006; Agnarsson et al. 2010, 2012, 2016a), and sampling some of the rarest species, this effort has dramatically increased the number of known Anelosimus species and yielded a taxon sampling of 84% of the known 75 species. We present a global molecular phylogeny to test the tempo and mode of Anelosimus diversification and colonization events, based on nuclear and mitochondrial genes, and investigate how the Neogene climate oscillations influenced the evolutionary history of this solitary-social spider genus.

MATERIALS AND METHODS

Sampling and Molecular Data Collection

Spiders were sampled worldwide between 1998 and 2018 and fixed in 95% ethanol. Seven pairs of primers were used to amplify sequences of mitochondrial (COI, 16S) and nuclear (18S, 28S, wingless, ITS2, H3) loci from the collected specimens with annealing temperatures optimized at 44–56 (Supplementary Table S2 available on Dryad). New sequences were submitted to Genbank (Supplementary Table S1 available on Dryad). We then combined these new sequences with previously published sequences from Agnarsson et al. (2007, 2010) and Agnarsson (2012a, 2012b). The total data set contained 268 individuals representing at least 69 species of Anelosimus, 62 described and at least seven as yet undescribed species. Our samples cover the majority of the distribution range of Anelosimus. Twenty-eight taxa from across Theridiidae were used as outgroups. The data matrix is available from the authors and will be submitted to the Dryad database (online at http://datadryad.org/).

Sequence Analyses

We interpreted the chromatographs with Phred and Phrap (Green and Ewing 2002; Green 2009) using the Chromaseq module (Maddison and Maddison 2011a) in Mesquite (Maddison and Maddison 2011b). Quality thresholds were set high: for base trimming to 49 and for calls of ambiguity minimum secondary peak fraction for ambiguity at 0.3. Sequences were checked and edited with SEQUENCHER ver. 4.1.2 (Gene Codes Corporation, Ann Arbor, MI, USA) and BioEdit (Hall 1999), and then aligned in both CLUSTALX (Jeanmougin et al. 1998) under default parameters and MAFFT (http://mafft.cbrc.jp/alignment/server/) using the FFT-NS-i strategy to increase accuracy (Katoh et al. 2005). Gaps resulting from the alignment were treated as missing data. For each gene, we checked possible saturation of substitution types by plotting the number of transitions and transversions versus F84 distance using DAMBE (Xia 2000). The COI, 16S, 18S, 28S, wingless, ITS2, and H3 sequences were concatenated for phylogenetic analyses, divergence time and diversification estimations, and biogeographical reconstruction.

Phylogenetic Analyses

The maximum likelihood and Bayesian inference approaches were used to reconstruct the phylogenetic relationships of 268 sampled Anelosimus individuals. Maximum likelihood analysis was conducted in PhyML 3.0 (Guindon et al. 2010) with a general GTRGAMMA + I substitution model for all genes. Nodal support was evaluated by 1000 bootstrap pseudoreplicates. The subtree pruning and regrafting (SPR) and nearest neighbor interchange (NNI) approach was used in tree improvement (Criscuolo 2011). The maximum likelihood analysis was run in parallel using RAxML-HPC2 on XSEDE (3.2.3) (Zwickl 2006 as implemented on the CIPRES cluster at the San Diego Supercomputing Center (Miller et al. 2010). Bayesian analysis was performed using MrBayes V3.2.1 (Ronquist and Huelsenbeck 2003). The best-fitting substitution model for each codon base or gene partition was selected by jModelTest (Posada 2008) under the Akaike information criterion (Supplementary Table S3 available on Dryad). The Markov chain Monte Carlo (MCMC) simulation was run for 30 million generations using parameters unlinked among partitions and sampled every 1000 generations. Tracer v1.5 (Rambaut and Drummond 2009) was employed to monitor the mixing of the MCMC chains, and the first 25% of sampled trees were discarded as burn-in. The remaining trees were used to compute a 50% majority rule consensus tree.

Divergence Time Estimation

We ran a test including the lost colulus clade (Anelosiminae + Theridiinae, where social origins are concentrated e.g., Agnarsson and Zhang 2006) to determine if a molecular clock model was appropriate based on the harmonic mean (HM) of the likelihood values of the MCMC samples (Newton and Raftery 1994) and a more accurate stepping-stone (SS) sampling method (Xie et al. 2011) in MrBayes V3.2.1. The results suggested that the 91-taxa total data sets did not conform to a strict molecular clock (P < 0.001) and that a relaxed molecular clock method was more suitable for estimating divergence time. Therefore, we estimated

SYSTEMATIC BIOLOGY

divergence times using BEAST ver 1.8.1 under an uncorrelated lognormal relaxed molecular clock model (Drummond and Rambaut 2007). We chose the Yule speciation process as the tree prior. Partitioned strategies (Brandley et al. 2005) were incorporated in BEAST analyses, and each gene was used as a separate partition. For each partition, we employed the corresponding model of evolution for analyses from jModelTest results: GTR + I + G for 16S, 28S, COI and ITS2; GTR + G for 18S and wingless; GTR + I for H3. To obtain reliable results, we concurrently ran five independent MCMC tree searches at the CIPRES web portal (Miller et al. 2010) for 50 million generations and sampled every 1000 generations. Then, five tree-subsets were combined and resampled every 1000 generations using LogCombiner v1.8.0 (in BEAST package) after discarding the initial 10% as burn-in. Finally, the maximum clade credibility tree was calculated using TreeAnnotator v1.8.0 (in the BEAST package) based on 225,000 trees. Tracer ver. 1.5 was used to determine convergence and to measure the effective sample size (ESS). All ESS values were greater than 200.

We dated the tree using fossil information as specified below, as well as previous estimates of the age of Theridiidae from a phylogenomic study (Garrison et al. 2016; Liu et al. 2016). We constrained four nodes. First, we constrained the age of the Anelosiminae and Theridiinae clade (lost colulus clade). This group of theridiid spiders is the most diverse group found in Dominican amber (15 Ma), providing an estimate of the minimum age. In stark contrast, this group is completely absent from Baltic amber (40 Ma) (Wunderlich 1988, 2008, 2015), and we thus use the absence of the lost colulus clade from Baltic amber as indirect evidence for the maximum age limit of this group. Hence for this node, we implemented a normal prior with a range of 15–40 Ma (median 20, 13–27). Second, we used the minimum ages for Theridion, the type genus of Theridiidae (11.608–38 Ma; Wunderlich 1988, 2008, 2015), and Achaearanea (13.82-20.44 Ma; Wunderlich 1988), as fossil calibration points for the molecular clock analyses. The two calibration points were implemented with a lognormal distribution prior, as a minimum age of the stem of the lineage to which the fossil was assigned (Renner 2005; Donoghue and Benton 2007). Third, we set the age of the Theridiidae stem to be a normally distributed prior with a median age of 100 Ma and range of 92–108 Ma as hypothesized by Bond et al. (2014). This previous estimate of Theridiidae age is further supported by the recent finding of a fossil potentially attributable to stem Theridiidae in 100 Ma amber (Wunderlich 2015).

Diversification Rates and Climate Change

The dynamics of species diversification was inferred based on our dated phylogeny of Theridiidae using Bayesian Analysis of Macroevolutionary Mixtures (BAMM) v.2.3 (Rabosky 2014), which simultaneously accounts for variation in evolutionary rates through time

and among lineages using transdimensional (reversiblejump) Markov chain Monte Carlo (rjMCMC) (Rabosky 2014). Two independent runs were performed with a Markov Chain Monte Carlo (MCMC) run of 50 million generations, sampling parameters every 2000th generation, setting a Poisson rate prior of 1.0 and a global sampling fraction at 0.84 to account for the extant diversity missing from the analysis. Prior distributions were set according to the setBAMMPriors function from the BAMMtools R package (Rabosky et al. 2014). The frequencies of the species in each genus were considered. BAMMtools package for R was used to assess the convergence of chains by estimated sample size and to compare competing rate-shift scenarios via Branchspecific Bayes factors (BFs; Shi and Rabosky 2015). There, we drew 'phylorate' plots (showing rates and rate shifts in diversification and size evolution) to depict the speciation rates across the trees, color-coded by relative values on the trees, showing a single best set of rate shifts with the maximum a posteriori (MAP) probability recovered from a credible shift set, as well as a diversification rate-through-time curve for Anelosimus only.

We used the latter to test the hypothesis that speciation rate correlates with climatic change. We used deepsea temperature fluctuations between 0 and 28 Ma as a proxy for global fluctuation in climate, following figure 2 in Zachos et al. (2001, p. 688). Due to the lack of raw data, we extracted it directly from the figure using an online software WebPlotDigitizer (URL: https://automeris.io/WebPlotDigitizer/). For consistency, we also used WebPlotDigitizer to extract data from the diversification rate-through-time plot. We obtained 56 data points from each plot, sampling every 500,000 years. Following our speculation that the shift toward cooler climates at around 8 Ma had an effect on speciation, we split the data into pre-8 Ma and post-8 Ma subsets. Using R (version 3.4.3, R Core Team 2017), we then calculated Kendall's tau correlation coefficient between deep-sea temperature and speciation rate values for each subset as well as the whole data set.

Biogeographical Reconstruction

Biogeographical history of *Anelosimus* was inferred using parsimony-based statistical dispersal–vicariance (S-DIVA), Bayesian binary MCMC analysis (BBM), and dispersal–extinction–cladogenesis analysis (DEC). These three models were implemented in RASP v3.0 (Yu et al. 2010, 2015) with a maximum of two areas per node. All other parameters were set to default settings. After discarding the first 49,000 trees from 50,000 trimmed fossil-calibration trees obtained from BEAST analysis, we used the remaining 1000 trees for biogeographical reconstruction. The maximum clade credibility (MCC) tree produced in BEAST analysis was used as the input tree. On the basis of the dated chronogram for *Anelosimus*, we pruned the tree to remove outgroups but

LUO ET AL.-GLOBAL DIVERSIFICATION OF ANELOSIMUS SPIDERS

kept the sister group comprised of *Kochiura attrita*. We compiled distributional data for species of *Anelosimus* from the World Spider Catalog (2020) and information from our samples. We defined six geographical areas occupied by *Anelosimus* and its closest relatives, including South Africa, Americas, Madagascar + Comoros, Australasia + SE Asia, Seychelles, and Europe + North Africa/Palearctic.

RESULTS

Phylogeny of Anelosimus

The concatenated data set was composed of 5499 nucleotides (COI: 1167bp; 16S: 1116bp; H3: 354bp; ITS2: 581bp; Wingless: 385bp; 18S: 1074bp; 28S: 822bp) with 296 terminals. Maximum likelihood and Bayesian analyses infer near identical topologies, differing only in minor tip arrangement within species and among some species of the Madagascar group (Fig. 1). Both phylogenetic analyses support the monophyly of the lost colulus clade (Maximum likelihood bootstrap = 91, Bayesian posterior probability = 81), containing the monophyletic subfamily Anelosiminae (Maximum likelihood bootstrap = 100, Bayesian posterior probability = 100) with two sister genera (Anelosimus and Kochiura), and the monophyletic subfamily Theridiinae (Maximum likelihood bootstrap = 99, Bayesian posterior probability = 100). *Anelosimus* monophyly is strongly supported in all analyses (Maximum likelihood bootstrap = 100, Bayesian posterior probability = 100).

The phylogenies divide Anelosimus into five major groups (Fig. 1). 1) The "rupununi group" (RUG: Agnarsson and Kuntner 2005) includes South African A. nelsoni and two social sister species A. lorenzo and A. rupununi from the Americas. The rupununi group consistently is sister to the remaining Anelosimus species (Fig. 1). 2) The "Australasia + SE Asia group" (AUG; Agnarsson 2012a) is composed of 18 species from Asia and Australia (Fig. 1). This group has two subclades (AUG-1 and AUG-2): AUG-1 is composed of *A. pratchetti* from Australia, A. taiwanicus from Taiwan and Indonesia, and A. crassipes from China, Korea, Japan, and Ryukyu Is.; AUG-2 includes A. agnar from Malaysia, A. bali from Bali, A. chonganicus, A. membraneous and A. sexmaculatus from China, A. eidur, A. pomio, and A. potmosbi from New Guinea, A. exiguous from China, Japan, and Ryukyu Is., A. "hiatus" (manuscript name) and A. "kinabaluensis" (manuscript name) from Borneo, A. iwawakiensis from Korea and Japan, A. kohi from Malaysia and Singapore, A. linda from Malaysia, and A. luckyi from New Guinea. 3) The "cosmopolitan group" (="solitary clade" of Agnarsson 2012b and Agnarsson et al. 2015; COG) includes two subclades (COG-1 and COG-2): COG-1 contains A. vittatus from the Palearctic, A. pulchellus from Europe to Russia, Iran, and North Africa, and A. kohi from southeastern Asia; COG-2 includes A. amelie and A. decaryi from Madagascar and Comoros, A. placens from Seychelles, and A. ethicus, A. misiones, A. nigrescens, A.

pacificus and *A. cf. sumisolena* from the Americas (Fig. 1). 4) The "Madagascar group" (Agnarsson and Kuntner 2005; Agnarsson et al. 2015, 2016a; MAG) contains 15 species from Madagascar (Fig. 1). 5) The "Americas group" ("*eximius* lineage" of Agnarsson and Zhang 2006; AMG) includes 19 species from Americas (Fig. 1). This group has two subclades (AMG-1 and AMG-2): AMG-1 includes social *A. eximius* from Lesser Antilles and Panama to Argentina, 'intermediate-social' *A. dubiosus* and *A. jabaquara* from Brazil, and social *A. domingo* from Colombia to Suriname and Peru (Agnarsson and Zhang 2006); AMG-2 contains species ranging from subsocial to social, found throughout the Americas, including the Caribbean.

Divergence Times

The time-calibrated Bayesian phylogeny (Fig. 2) places the common ancestor of Anelosiminae into Oligocene, around 30 Ma (95% HPD: 34.8-25.5 Ma). The origin of Anelosimus and the initial divergences within the genus were predicted to have occurred about 27.3 Ma (95% HPD: 31.8–23.0 Ma) during Mid-Oligocene, a period of global expansion of grasslands, and regression of tropical broad-leaf forests to the equatorial belt (Pagani et al. 1999; Retallack 2001; Edwards et al. 2010; Stroemberg and McInerney 2011; Fuchs et al. 2015). The rupununi group was derived from a common ancestor around 17 Ma (95% HPD: 22.9–11.2 Ma), from which the group gradually diversified during late Miocene/early Pliocene into the species currently distributed in South America and southern Africa. The Australasia + SE Asia group diverged from around 21 Ma (95% HPD: 24.2-16.8 Ma). Within this species-group, the most recent speciation occurred in Southeast Asia, with local species emerging around 17.6-4.2 Ma during the late Miocene and early Pliocene. The origin of the Cosmopolitan group was in mid-Miocene, and diversification of the species group occurred about 17.7 Ma (95% HPD: 21.2-14.3 Ma), to become distributed worldwide, but slowly diversified about 15.5-0.3 Ma during late Miocene to the present. The origin of the American group and the Madagascar group also dates to mid-Miocene, and the two species groups split around 17.4 Ma (95% HPD: 13.9–21.1 Ma). These groups diversified rapidly during the late Miocene and the Pliocene (after 7.5 Ma).

Diversification Rate and Diversity Pattern

We used a time calibrated phylogeny and its topology as the framework for inferring diversification rates (Fig. 3). The best fitting speciation rate model detected two rate shifts in the phylogeny including Anelosiminae outgroups (indicated by red dots in Fig. 3a). The first marks a sudden rise in speciation during the late Oligocene (35.3–33 Ma), which is followed by slight reductions during the late Oligocene and the early

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FIGURE 1. Summary tree based on results of the maximum likelihood as well as the Bayesian analyses of the concatenated mitochondrial (*COI*, 16S) and nuclear (18S, 28S, wingless, ITS2, *H*3) data sets. The numbers at the nodes represent bootstrap support values/posterior probabilities from both likelihood and Bayesian analyses.

group*-eximiu*s group (AMG)

MG-2



FIGURE 2. A dated, fossil calibrated, phylogeny of major Theridiidae taxa estimated in BEAST. Numbers at nodes indicate posterior probabilities. Purple squares are fossil calibration nodes.

Neogene (33–21.4 Ma). The second rate shift occurred relatively recently, 19.7 Ma, at the base of the clade containing American and Malagasy species of *Anelosimus*. This shift is followed by parallel rapid diversification in the two sister clades in the last 8 Ma. Figure 3 shows shifts in climate where blue arrows indicate shifts that have corresponding shifts in diversification rates. The correlation between shifts in climate and diversification rates is most clear following the 8 Ma sudden climate cooling (Fig. 4).

We correlated the *Anelosimus* diversification rate curve (red line in Fig. 3a) with fluctuations in deep-sea temperatures (Fig. 3b) during Miocene and Pliocene (Fig. 4). When taking into account all of the last 28 million years, we found a weak but significant positive correlation, $\tau = 0.29$, P = 0.002. However, when analyzing the pre-8 Ma subset only, we found a small, non-significant positive correlation $\tau = 0.19$, P = 0.093, while for the post-8 Ma subset, the correlation was strongly and significantly negative $\tau = -0.91$, P < 0.001.



FIGURE 3. Diversity analyses of *Anelosimus* spiders. a) Phylorate plot of Theridiidae spiders. Branches are shaded by estimated diversification rates, with diversification being the means of the marginal densities of the rates. Two major rate shifts are indicated by red circles on the nodes. The superimposed red line represents the mean diversification rate-through-time (RTT) curve across *Anelosimus*. The intensity of the shading reflects the relative probability of the inferred diversification with upper and lower 90% Bayesian credibility intervals. b) The major global temperature trends from the Eocene to the present. Blue arrow shows the two shifts that coincide with changes in diversification rates in *Anelosimus*. Modified from Zachos et al. (2001) and Zachos et al. (2008).

Biogeography

A mixture of long-distance dispersal events and in situ allopatric speciation following habitat fragmentation seemed to have shaped the current distribution and diversity of Anelosimus (Fig. 5a and b). The BBM (Fig. 5c) and S-DIVA (Supplementary Appendices and Supplementary Fig. S1 available on Dryad) analyses were generally concordant. The two methods indicated that the most recent common ancestor (MRCA) of extant Anelosimus inhabited South America during the late Oligocene (30 Ma) (Node 1), and probably started to spread worldwide about 27.3 Ma (Node 2). The genus dispersed from South America to South Africa, Australasia/SE Asia, and to Madagascar. After the longdistance dispersals to Australasia/SE Asia, the two major clades (AUG-1 and AUG-2) began diversifying and dispersed to Australia, Japan, and Taiwan, possibly via the Ryukyu Islands (AUG-1), and to eastern Asia possibly

via Indochina (AUG-2). Two major dispersal events were inferred for the Cosmopolitan group, to Eurasia and on to Asia, and to Madagascar. The Madagascar group is reconstructed to have originated via long-distance dispersal event from South America around 17.4–6.5 Ma. North America may have been colonized via Panama, while the occurrence of the genus in the Antilles requires an additional overwater dispersal event. The estimated centers of diversification of the genus covered South America, Southeast Asia and Madagascar (Fig. 5), as suggested by the BBM, S–DIVA and DEC analysis.

DISCUSSION

To understand the origin, age, dispersal history, and other factors contributing to the distribution and diversity of globally distributed lineages, robust phylogenies based on thorough taxonomic sampling



FIGURE 4. Fluctuations in deep-sea temperature and speciation rate for *Anelosimus* 28-0 Ma. For most of the period prior to 8 Ma, both trends are falling, meaning speciation rate and temperatures are decreasing. After 8 Ma, the temperature continues to fall, but the speciation rate starts rising.

(Graybeal 1998; Zwickl and Hillis 2002)—though often hard to come by—are imperative (e.g., Linder et al. 2005; Jansen et al. 2006; Heath et al. 2008; Wickett et al. 2014). However, phylogenies in themselves are only one of the steps necessary for testing hypotheses that relate to historic ecological and biogeographical patterns. Additional tools, such as ancestral area estimation, as well as analyses of diversification rates overlaid with historical climate patterns need to be invoked. These combinations of analytical approaches are particularly useful when considering currently ongoing climatic changes, as they can help us predict future biotic responses, both in ecological time (physiological reactions and taxon range shifts) and in evolutionary time (lineage diversification and extinction).

We have here presented a study that uses phylogenies (Figs. 1 and 2), ancestral area estimations (Fig. 5), and diversification rates in a lineage of spiders (Figs. 3 and 4), genus *Anelosimus*, to test the links of these variables with historic data on climate and ecology (Fig. 4). A comprehensive, global Anelosimus phylogeny has only now become available, through our decades long accumulation of specimens that now amounts to 84% species coverage yielding a well-supported phylogeny. We used this new time calibrated phylogeny to interrogate the diversification rates within the genus, its geographic origin, as well as to reconstruct its biogeographic history. Specifically, we test the hypothesis proposed by Agnarsson et al. (2016a), predicting a link between diversification rates and climate change in the last 8 my. These biogeographic and diversification histories suggest that the evolution of this lineage was strongly affected by intercontinental dispersal on the one hand, and historic climatic shifts on the other, while at the intercontinental level, we find no evidence for vicariance. Instead, we find that long-distance overwater dispersal, and barrier formation due to climate change rather than geological change, are the major events that have affected the biogeography of these spiders. These findings mirror other studies highlighting the critical role of longdistance dispersal in biogeography (de Queiroz 2005; Yoder and Nowak 2006; Schaefer et al. 2009; Agnarsson and Kuntner 2012; Gillespie et al. 2012, 2017; 2014; Vicent et al. 2017). Furthermore, we hypothesize that the levels of sociality—a varying factor in *Anelosimus* biology—are linked with the propensity of species to disperse long distances, and thus to give rise to new radiations on previously unoccupied landmasses.

Biogeography of Anelosimus

The new species level phylogeny overcomes some of the major limitations of earlier studies on the genus Anelosimus (Agnarsson and Kuntner 2005, 2006; Agnarsson et al. 2007, 2010, 2012a, 2015), especially with its increased global taxonomic coverage and improved resolution at deeper nodes (Fig. 1). The phylogeny corroborates the monophyly of Anelosimus, Anelosiminae, the lost colulus clade, and the scattering of American Anelosimus species in three clades (Agnarsson and Kuntner 2005, 2006; Agnarsson et al. 2007, 2010, 2012a, 2015). It also supports previously well-supported clades or groups and their placements (e.g., Agnarsson et al. 2015), such as the *eximius* lineage (the Americas group), the Madagascar group, and the Cosmopolitan group (also dubbed the "solitary clade"). Finally, it resolves the, previously surprising, position of the Australian A. pratchetti that now falls within the Australasia + SE Asian clade as would be the expected biogeographical pattern. Thus, the Anelosimus tree of life has stabilized, and the current phylogeny should serve to improve classification, illuminate phenotypic and behavioral evolution, and reconstruct the global biogeographical history of the genus.

Based initially on morphological data, Agnarsson and Zhang (2006) suggested that *Anelosimus* may have originated in the Old World, with three different

9



FIGURE 5. Biogeography of *Anelosimus* and probable global dispersion routes. a) Potential dispersion routes (arrows) and major diversification areas (sunburst) of the Americas, Madagascar, Australasia + SE Asia and original groups. b) Potential dispersion routes (arrows) and major diversification areas (sunburst) of the cosmopolitan group. c) Reconstruction of the historical biogeography using Bayesian binary MCMC analysis (BBM) in RASP v3.0. Colors of pie wedges at each node represent geographical areas inferred to have been occupied by ancestral taxa.

Anelosimus clades being found in the New World. This scenario could be congruent with a Gondwanan origin, in the absence of time calibration. In contrast, the sparse available fossil evidence is more consistent with a much more recent origin of the genus (Agnarsson 2004;

Marusik and Penney 2005; Dunlop et al. 2019). Our large molecular data set enabled a new test of these alternative scenarios to reach dramatically different biogeographical conclusions. While we confirm that the American *Anelosimus* species scatter in the three separate groups

LUO ET AL.-GLOBAL DIVERSIFICATION OF ANELOSIMUS SPIDERS

(rupununi group, COG, and AMG), ancestral area reconstruction and divergence time estimates suggest that *Anelosimus* originated in the Americas in the late Oligocene (Fig. 2). Long-distance dispersal from the Americas is implicated as the major factor shaping its global distribution (Fig. 5). We hypothesize multiple transoceanic dispersal events, and that climatic cooling played a major role in the diversification of the genus in the Neogene. Long-distance dispersal events occurred from Americas to Australasia/SE Asia twice, and three independent long-distance dispersal events occurred

independent long-distance dispersal events occurred from Americas to Africa, to the continent once, and to Madagascar twice. Further long-distance dispersal events are implied due to the presence of *Anelosimus* on multiple islands in the Caribbean, Indonesia, and in Australia.

All occurrences of Anelosimus outside the New World require LDD hypotheses (Fig. 5), given that these reconstructed colonization events are relatively recent and all the continents must have been close to their current placement. Particularly striking is the LDD events taking place between Americas and Madagascar twice (Fig. 5), which contrasts with the most common pattern of Cenozoic colonization of Madagascar from mainland Africa, seen in a broad variety of organisms from plants, arthropods, amphibians, and mammals (Yoder and Nowak 2006; Weyeneth et al. 2008; Raselimanana et al. 2009; Schaefer et al. 2009; Agnarsson and Kuntner 2012). However, similar patterns have been found in other groups capable of passive dispersal in the upper air jet stream, such as ferns and other spiders, as well as in some flying arthropods (Agnarsson and Kuntner 2012; Sundue et al. 2014; Bauret et al. 2017; Vicent et al. 2017). These noticeable biogeographical parallels to other jet stream dispersing groups, beg for comparative studies across very different organisms sharing dispersal modes.

All LDD *Anelosimus* events are most easily explained by ballooning, as it is a common of aerial dispersal in spiders, as opposed to simply being blown off by winds. It is noteworthy that this may help cast light on confinement of the social species to the Americas. Corcobado et al. (2012) hypothesized that dispersal tendencies and abilities decrease with degree of sociality, concluding that in more social species "bridging (and not ballooning) seems to be the main mode used by Anelosimus in both natal and breeding dispersal' Along these lines, long-distance overwater dispersal should occur in solitary and subsocial—but not social— Anelosimus lineages and species, consistent with the pattern we observe. The absence of overwater dispersal in truly social species, if true, suggests a decisive impact that a behavioral syndrome (levels of sociality) can afflict on historical biogeographic patterns. This appears to be a rare pattern in nature. Dispersal strategies may differ between social and nonsocial species, for example in birds (Hatchwell 2009) and many other animals, and may depend on social interactions, for example where individuals may be forced to disperse from familiar conspecifics (Isbell and VanVuren 1996). However, there

is little available evidence for social structure impacting global biogeographic patterns, as suggested in our study. In some eusocial insects where sociality directly impacts dispersal ability, such as in societies where reproductive females are flightless (Peeters and Ito 2001), impact on global biogeographical patterns would not be unexpected, but is rarely discussed. A rare example is discussed in Groom and Rehan (2018) who find clear biogeographical patterns in the distribution of sociality in bees, with multiple dispersal of social species from Africa to temperate zones where the species/radiations become secondarily solitary. However, the absence of dispersal in social lineages limiting their distribution to one continent, as we hypothesize in our linage, is unusual.

Diversity of Anelosimus and Neogene Climate Oscillations

Climatic fluctuations have resulted in significant habitat changes causing temporal and spatial shifts in species distribution patterns, promoting isolation and speciation (Hewitt 2003; Parmesan and Yohe 2003; Hoffmann and Sgro 2011; Jiang et al. 2015). We suggest that climate changes are one of the main biogeographical driving forces underlying major patterns of diversification of Anelosimus (Figs. 3 and 4). The origin of Anelosimus spiders coincides with sudden thermal increase in late Oligocene (~27-25 Ma). However, we cannot suggest any causal factors. On the other hand, climate could explain why most Anelosimus species occur in Madagascar (17 species), South America (23 species), and Southeast Asia (15 species). The complex geography and climate of these regions have been linked to these areas being biodiversity hotspots in general (Rohli and Vega 2011; Favre et al. 2015). More specifically, our results corroborate the hypothesis that climate cooling affected speciation in parallel in the slopes of the Andes, and in the eastern mountain rainforests of Madagascar during the late Miocene/early Pliocene. Looking at the interplay between temperature and diversification, before the Miocene cooling event, we see no significant correlation (Figs. 3 and 4). However—in support of the hypothesis proposed by Agnarsson et al. (2016a)—at around 8 Ma, the diversification trend shifts upwards and the relationship with temperature becomes significantly negative (Fig. 4). This strongly implies that South American and Malagasy Anelosimus diversified concurrently with climate cooling and associated fragmentation of forest as they gave way to the expanding grasslands. Similar patterns have been observed in other spiders (Ballarin and Li 2017), beetles (Faille et al. 2014), freshwater crabs (Daniels et al. 2006), lizards (Raselimanana et al. 2009), birds (Fuchs et al. 2015), bats (Shi and Rabosky 2015), primates (Pozzi 2016), and plants (Schnitzler et al. 2011). Such evidence from multiple unrelated lineages that differ dramatically in their ecology and dispersal mode and ability offers strong evidence for direct impact of climate change on diversification patterns.

SYSTEMATIC BIOLOGY

Concluding Remarks

Our analyses establish a link between the global climate patterns in the Neogene and major patterns of dispersal and diversification in *Anelosimus*. We propose a "long-distance dispersal under climatic changes" diversification scenario in this group of ballooning spiders, and specifically suggest that the Neogene climate change was the key factor in their *in situ* radiation in South America and Madagascar.

Understanding of how past climatic and ecological patterns correlate with diversification history could help predict response to future major climatic events, such as ongoing unprecedented rates in global climate and habitat changes. For example, given that only subsocial and solitary species of *Anelosimus* have made intercontinental shifts, while social species have not, and this reflects intrinsic biological abilities that relate to aerial dispersal, it may be foreseen that the ongoing global changes in climate and habitat availability will affect the social lineages more than the more mobile subsocial and solitary ones. We hypothesize that the American, social *Anelosimus* spiders are more prone to extinction in the near future than are their congeners in the Old World that show lesser levels of social biology.

Now more than ever, the toolkits at our disposal allow us to integrate phylogenies with genomics, biogeographic reconstructions, ecological simulations, life histories, and behavioral syndromes. *Anelosimus* is a test case but the combination of approaches we used here can be applied to other organisms in order to arrive at reasonable models of lineage diversification and extinction patterns in the future.

SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.sf7m0cg2p.

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LUO ET AL.—GLOBAL DIVERSIFICATION OF ANELOSIMUS SPIDERS

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LUO ET AL.-GLOBAL DIVERSIFICATION OF ANELOSIMUS SPIDERS

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