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The life and adventures of an eight-legged castaway: Colonization and diversification of *Philisca* ghost spiders on Robinson Crusoe Island (Araneae, Anyphaenidae)



Eduardo M. Soto^{a,c,*}, Facundo M. Labarque^{b,c}, F. Sara Ceccarelli^c, Miquel A. Arnedo^d, Jaime Pizarro-Araya^e, Martín J. Ramírez^c

^aDepartamento de Ecología, Genética y Evolución, IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II (C1428 EHA), Buenos Aires, Argentina

^bLaboratório Especial de Coleções Zoológicas (LEZ), Instituto Butantan, Av. Vital Brasil, 1500, 05503-900 São Paulo, SP, Brazil

^cDivision of Arachnology, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Av. Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina

^dDepartament de Biologia Animal & Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av. Diagonal 645, E-8028 Barcelona, Spain

^eLaboratorio de Entomología Ecológica, Depto. de Biología, Facultad de Ciencias, Universidad de La Serena, Casilla 599, La Serena, Chile

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ABSTRACT

Oceanic archipelagoes, by their young origin and isolation, provide privileged settings to study the origin and diversification of species. Here, we study the anyphaenid spider genus *Philisca*, endemic to the Valdivian temperate rainforest, which includes species living both on the mainland as well as on the Robinson Crusoe Island in the Juan Fernández archipelago. Anyphaenids, as many spiders, are potentially good colonizers due their ability for ballooning, an airborne dispersal mediated by strands of silk that are caught in the wind. We use a molecular approach to estimate both the phylogenetic relationships and the timeframe of species diversification of *Philisca*, with the aim to infer its evolutionary history. We further estimate the rates of speciation on both the insular and continental *Philisca* species and score the microhabitat used by each species and their sizes as a proxy to evaluate ecological niche diversification within the island. Most analyses support the monophyly of *Philisca*, with the exclusion of *Philisca tripunctata*. Our results reveal colonization from a single lineage that postdated the origin of the island, followed by rapid (~2 Ma) diversification. The ancestral microhabitat was most likely leaf-dwelling but we identify two independent microhabitat shifts. Our data provides evidence that *Philisca* has undergone an adaptive radiation on the Robinson Crusoe Island.

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1. Introduction

Oceanic archipelagos provide exceptional conditions for studying the evolutionary patterns and processes involved in species radiations (Mayr, 1967; Carson and Templeton, 1984; Arnedo et al., 2001; Garb and Gillespie, 2009; Shaw and Gillespie, 2016). Empty ecological niches available on volcanic oceanic archipelagos (newly emerged from the sea floor, i.e. Darwinian islands) are gradually filled as species migrate from nearby regions and, given sufficient time, eventually diversify into local endemism. The rate

* Corresponding author at: Departamento de Ecología, Genética y Evolución, IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II (C1428 EHA), Buenos Aires, Argentina.

E-mail address: edusoto@ege.fcen.uba.ar (E.M. Soto).

of migration in highly isolated islands is usually low and hence, the newcomers have good chances of successfully establishing due to the lack of competition and eventually evolve into new species adapted to available niches, in what is known as adaptive radiations (Gillespie and Roderick, 2002; Shaw and Gillespie, 2016). The tradeoff between migration, speciation and extinction determines the species diversity and level of endemism of the island biota while the species dispersal ability, the degree of island isolation and habitat diversity affect the species dynamics and the community assembly and evolution (MacArthur and Wilson, 1967; Agnarsson and Kuntner, 2012; Gillespie, 2013; Shaw and Gillespie, 2016). The most common transoceanic dispersal mechanisms are aerial dispersal, oceanic drift (or "rafting") and biological vehicles (Cook and Crisp, 2005; de Queiroz, 2005; Shaw and Gillespie, 2016). With special emphasis on aerial dispersal, early studies have shown the ability of different organisms in colonizing

remote oceanic islands (mainly of volcanic origin) by following oceanic long-distance dispersal events (Muñoz et al., 2004; Gillespie et al., 2008).

Many remote archipelagos are volcanic in origin and sometimes exist in a linear age progression (Shaw and Gillespie, 2016). The Juan Fernández archipelago is of volcanic origin and is a well-known case of Darwinian islands with high levels of endemism (Crawford et al., 1992; Sang et al., 1994; Anderson et al., 2001). The archipelago is located about 668 km west of the coast of Valparaíso (Chile), approximately at 33° S (Fig. 1; Stuessy and Crawford, 1990; Bernardello et al., 2004; Morrone, 2006), and consists of three volcanic islands. The island closest to the continent is Robinson Crusoe, with an area of 47.9 km² that emerged approximately 4 million years ago (Ma) (Stuessy et al., 1984), followed westward by the smallest and oldest Santa Clara Island (2.2 km² and 5 Ma), and finally by the largest and youngest Alejandro Selkirk Island (49.5 km² and 1–2 Myr). Santa Clara Island is arid, highly eroded and was probably once connected to Robinson Crusoe (Stuessy et al., 1984). The archipelago has never been connected to the continent (Baker, 1967; Stuessy et al., 1984). The flora and fauna of the islands are mainly related with the Valdivian temperate rainforest of southern Chile, one of Earth's 25 biodiversity hotspots (Olson et al., 2001; Morrone, 2006; Nahuelhual et al., 2007; Vargas et al., 2011). However, the Vegetation on Robinson Crusoe Island is composed mainly of grasslands, shrublands and forest formations (Greimler et al., 2002), related to the Valdivian coastal formations of southern Chile and has some common characteristics with the subtropical islands communities of the New Zealand region as well as the Hawaiian *Metrosideros*-forest (Mueller-Dombois and Fosberg, 1998). The marine fauna, however, is predominantly of southeastern Polynesian origin (Donald et al., 2005; Burrige et al., 2006), as also are some terrestrial compo-

nents of the fauna, including a family of land snails and various insects (Gressitt, 1956; Kirch et al., 2009).

Spiders are formidable colonizers due to their ability for air-borne dispersal mediated by strands of silk that are caught in the wind, a behavior known as ballooning. Darwin already witnessed (1839) overseas spider ballooning when aboard of *The Beagle*, >100 km off the southern coast of South America (see Foelix, 2011). It has recently been shown that spiders can sail the wind and take off from the water surface, including marine water with turbulences (Hayashi et al., 2015). The ballooning capacity and propensity of spiders varies according to taxa, size and lifestyle (Greenstone et al., 1987; Bell et al., 2005). Additionally, spiders have the capacity to decrease their metabolic rate to withstand starvation during periods of low prey density, characteristics that allow them to establish and survive in new, remote habitats (Gillespie, 2013).

Previous spider surveys revealed the existence of two spider genera with high numbers of endemic species in the archipelago: the wandering anyphaenid spider *Philisca* Simon, and the sheet weaver linyphiid spider *Laminacauda* Millidge (Millidge, 1985, 1991; Soto and Ramírez, 2012). The archipelago also presents other endemic species, e.g. *Mecysmauchenius fernandez* Forster and Platnick, and *Selkirkiella alboguttata* Berland, common South American species, e.g. *Chibchea mapuche* Huber, and widespread synanthropic species, e.g. *Dysdera crocata* C. L. Koch (World Spider Catalog, 2016). Here, we focus on the genus *Philisca*, endemic to the Valdivian temperate rainforest. The genus has been recently reviewed (Ramírez, 1993, 2003; Soto and Ramírez, 2012), and its relationships studied using morphological (Ramírez, 2003; Soto and Ramírez, 2012), and molecular data (Labarque et al., 2015). The genus was recovered as the sister group of the remaining members of the tribe Gayennini (Labarque et al., 2015). The phylogenetic placement of the atypical *Philisca tripunctata* (Nicolet) is

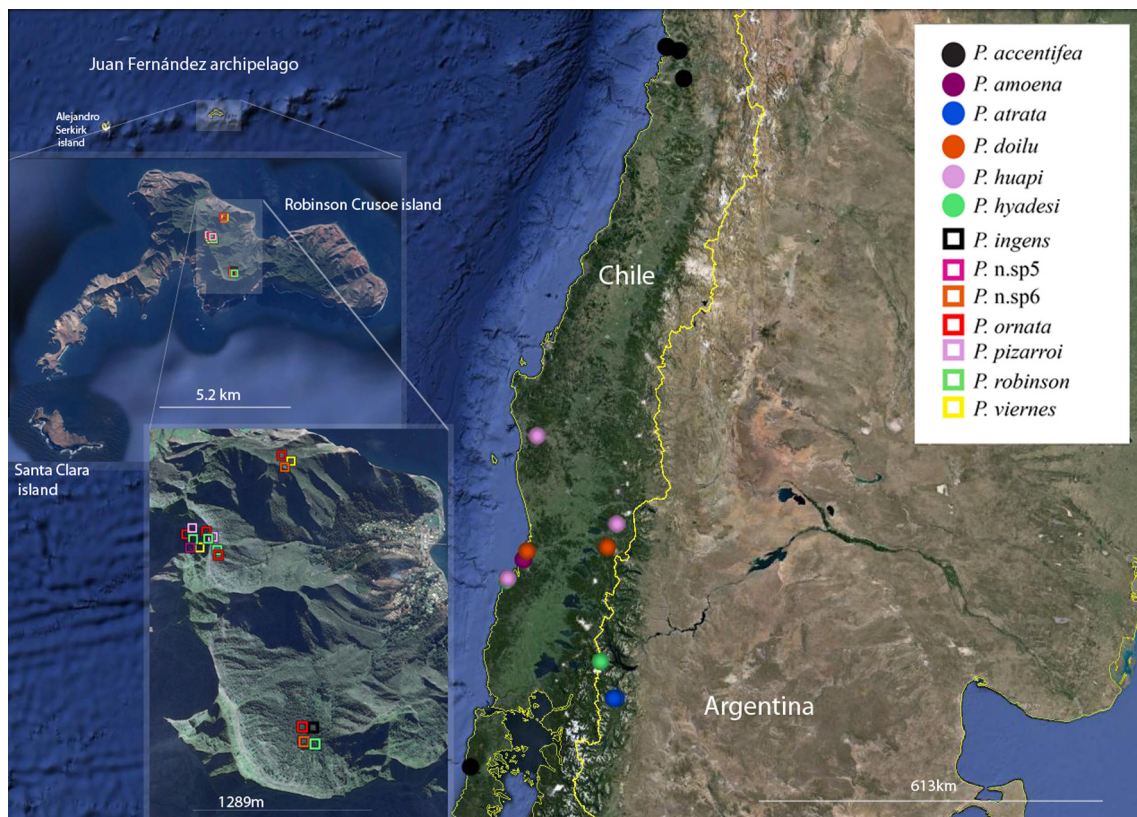


Fig. 1. Maps. Record points of *Philisca* species, continental species (circles) and the endemic species of Robinson Crusoe (squares).

still unclear. While its reduction on the foreleg spination related it with *Philisca*, molecular markers include it with the spinose genera (e.g. *Oxysoma*, *Tasata*, *Phidyle*) (Labarque et al., 2015). Of the 14 species currently listed in *Philisca* (World Spider Catalog, 2016), six are endemic to the Robinson Crusoe Island, and the remaining species are found in southern Chile and adjacent Argentina (Fig. 1). Anyphaenids are known to disperse through ballooning in the northern hemisphere (Dean and Sterling, 1985; Blandenier and Fürst, 1998), and many South American species have been seen conducting the stereotypical ‘tip-toe’ behavior in preparation to ballooning (Ramírez, pers. obs.). The analysis of Soto and Ramírez (2012) was inconclusive regarding the colonization history of *Philisca* in the Robinson Crusoe Island. The optimal morphological phylogenetic tree suggested one event of colonization followed by dispersal back to the continent, while an alternative, slightly suboptimal scenario, showed a single colonization event to the island.

In this study, we focus, in particular, on the endemic *Philisca* species of Robinson Crusoe Island. With the aim to infer the colonization and diversification history of the genus *Philisca*, a molecular data set of four markers (two nuclear and two mitochondrial genes) for species of the subfamilies Anyphaeninae and Amaurobiodinae was obtained. The Amaurobiodinae subfamily includes the tribes Amaurobiodini and Gayennini, including a novel, denser sampling of *Philisca* species. These sequences were subsequently analyzed under Bayesian inference, maximum likelihood, and parsimony to infer the phylogenetic relationships, and subject to node age estimation and maximum likelihood fitting models to provide an evolutionary scenario for their diversification.

2. Materials and methods

2.1. Molecular data

The molecular data set includes 83 terminals, 50 of which were sequenced for the present study, 30 from Labarque et al. (2015), and three were kindly provided by the ongoing Assembling the Tree of Life (AToL) Phylogeny of Spiders project (W. Wheeler, personal communication). *Philisca* is represented here by 12 nominal species and two putative undescribed species (supplementary Table A). We include a broad geographic sampling of *Philisca* specimens to evaluate their intra- and interspecific molecular variability and to test the monophyly of the species. Fieldwork on Robinson Crusoe Island was conducted on February 2011 by coauthors EMS, JPA, and MJR. Because of weather conditions, samples of *Philisca* were obtained from three forested areas of the island accessible by foot (Fig. 1); two additional sampled areas (Robinson Crusoe village, and the arid area in Punta de Isla in front of Santa Clara) did not result in *Philisca* specimens. *Philisca* specimens were not found in a subsequent expedition to Alejandro Selkirk Island in March 2015 by coauthor MA. Unfortunately, we were unable to obtain suitable material for DNA analysis from *Philisca hahni* Simon and the island endemic *Philisca robusta* Soto & Ramírez. Outgroup terminals included four Anyphaeninae species in four genera and 18 Amaurobiodinae species in 17 genera.

Total DNA was extracted from one to two legs of freshly collected specimens preserved in 100% ethanol. Extraction, amplification and sequencing followed the protocols described in Arnedo et al. (2004). We sequenced partial fragments of the mitochondrial protein-coding cytochrome *c* oxidase subunit I (COI, ~660 bp) and the ribosomal 16S (16S, ~350 bp) and the nuclear ribosomal 28S (28S, ~800 bp) and protein-coding histone 3a (H3a, ~325 pb). Primer sequences and PCR annealing conditions were those reported in Labarque et al. (2015: Table S2).

Sequences were edited, checked for stop codons and managed with the GENEIOUS PRO 4.8.5 software. Voucher numbers, GenBank accession numbers and specimen information are reported in supplementary Table A. The protein coding genes showed no evidence of indel mutations. Automatic multiple alignments for the ribosomal genes were built using the Q-INS-i search strategy in MAFFT 6 (Katoh and Toh, 2010). Gaps were considered as missing data in downstream analyses.

2.2. Phylogenetic analyses

Bayesian analyses were performed using MRBAYES 3.2.1 (Ronquist and Huelsenbeck, 2003), run remotely at CIPRES Science Gateway 3.3 (Miller et al., 2010; <https://www.phylo.org/>). The program JMODELTEST 0.0.1 (Posada, 2008) was used to select the best-fitting model of evolution for each partition using both the Akaike’s information criterion (AIC) and the Bayesian information criterion (BIC) (Posada and Buckley, 2004; Posada, 2008). Ribosomal genes (16S and 28S) were each treated as a different partition. Three different partition schemes were implemented for each of the protein-coding genes (COI and H3a), namely *gene* (each gene a single partition), *3rd codon* (two partitions: 1st + 2nd codons, and 3rd codon) and *codon specific* (one partition to each codon position). The substitution estimates were allowed to vary independently between partitions. For phylogenetic analysis, two independent runs with eight simultaneous Markov chain Monte Carlo (MCMC) chains (one cold and seven heated), each with random starting trees, were conducted simultaneously, sampling every 1000 generations until the standard deviation of the split frequencies of these two runs dropped below 0.01 (10^7 generations). The program TRACER 1.5 (Rambaut and Drummond, 2009) was used to confirm that the Markov chains had converged and that they have reached a stationary distribution by examining the effective sample size values (see below) and to determine the correct number of generations to discard as a burn-in (first 10% of generations). Since preliminary analyses suggested non-monophyly of *Philisca* species, we tested their monophyly in a Bayesian framework by implementing a stepping-stone sampling approach (Xie et al., 2011). Specifically, we ran one chain enforcing the monophyly of *Philisca* (excluding *P. tripunctata*, see below), and a second unconstrained chain for 10 million generations each sampling every 500th generation. Each stepping-stone sampling analysis was set to 50 steps, setting the length of the burn-in equal to the length of each subsequent step in the analyses. The stepping-stone results were evaluated using Bayes factors (BF) calculated as twice the difference in the marginal likelihoods. Acceptance or rejection of each strategy was based on the following cut-off (Kass and Raftery, 1995): $BF \geq 10$ (strong evidence against the competing hypothesis); $10 < BF < 10$ (ambiguous, select least complex strategy); and $BF \leq 10$ (strong evidence for the competing hypothesis). Based on the results obtained, we constrained the taxa belonging to *Philisca* to form a single clade for the final tree reconstructed in MRBAYES 3.2.1.

Maximum-likelihood analysis was performed using the program RAXML 7.3.0 (Stamatakis, 2006; Stamatakis et al., 2008). We used the RAXMLGUI 1.2 (Silvestro and Michalak, 2012) graphical interface to define the partitions and conduct the analyses. Partitioning schemes were implemented as above. The best likelihood tree was obtained out of 100 random iterations, and support was assessed by conducting 1000 nonparametric bootstrap replicates for each analysis. Both independent gene trees and concatenated analyses were run under the different partition schemes.

Parsimony analyses were performed using TNT 1.1 (Goloboff et al., 2008). The data sets were analyzed under implied weights (Goloboff, 1993) with a concavity constant of the weighting func-

tion value $k = 100$ as in Labarque et al. (2015). All tree searches were driven to hit independently 10 times the optimal scoring, using the default values of the ‘New Technologies’ search in TNT with sectorial searches, tree fusing, drift and ratchet, followed by TBR branch swapping. Support values were estimated by jackknifing frequencies; each of the 1000 pseudoreplicates used three random addition sequences plus TBR, followed by TBR collapsing to calculate the consensus.

A group was considered supported when the posterior probabilities were >0.95 for Bayesian analyses, bootstrap proportions >0.75 for Maximum likelihood and jackknifing frequencies >0.75 for Parsimony analyses.

Based on collecting data, field observations and adult body sizes, we scored four classes of microhabitat types as a proxy for ecological niches, namely “foliage”, “logs and barks”, “giant on trunk” and “grass” (see the Results section for further details). These categorical states were assigned to *Philisca* species and closer outgroups, treated as an unordered multistate character and mapped using parsimony or maximum likelihood under the Mk1 model (Lewis, 2001) in MESQUITE 2.74 (Maddison and Maddison, 2010). Trees were visualized and edited with FIGTREE 1.4.0 (Rambaut, 2006–2014) and MESQUITE 2.74. All analyses were rooted in the branch connecting *Anyphaenoides clavipes* (Anyphaeninae) with the remaining taxa. The data sets can be obtained from TREEBASE with the accession number 20045 (available at <http://purl.org/phylo/treebase/phylows/study/TB2:S20045>).

2.3. Lineage age estimation

Age estimates of the most recent common ancestor (MRCA) were obtained using a Bayesian inference framework as implemented in the computer program BEAST 1.7.4 (Drummond et al., 2012). Two independent MCMC chains were run for 5×10^7 generations, with parameters logged every 1000 steps to oversee the convergence of parameter estimates.

We calibrated the molecular clock combining fossil information and prior on the substitution rates. The fossil *Anyphaenoides bulla* from Miocene Dominican amber, dated at 10–20 Myr (Wunderlich, 1988; Penney, 2000) provided a minimum age for the divergence time between Anyphaeninae and Amaurobioidinae (uniform distribution with 15 Ma lower bounds and 500 Ma upper bounds as a proxy to unbound maximum age). Additionally, we define priors for substitution rates for each gene based on the rates estimated by Bidegaray-Batista and Arnedo (2011) for spiders (log-normal distributions with real-space-mean rates: 0.0199 substitutions/site/Myr for COI, 0.0011 substitutions/site/Myr for 28S, 0.0091 substitutions/site/Myr for 16S and 0.0013 substitutions/site/Myr for H3a). The same models of evolution selected for the Bayesian and maximum likelihood analyses were implemented for each gene fragment.

We calculated the harmonic mean of the likelihood values of the trees obtained in BEAST sampled from the stationary posterior distribution (Nylander et al., 2004; Ronquist et al., 2005).

A multispecies coalescent Bayesian analysis was carried out using the *BEAST algorithm (Heled and Drummond, 2010), setting the same parameters and priors as for the dated tree reconstruction and grouping the individuals based on the species they belong to.

The program TRACER 1.5 was used to analyze Bayesian MCMC results and to visualize parameter means and associated 95% highest posterior density (HPD) intervals. Effective sample size (ESS) was monitored to ensure an acceptable amount of mixing (ESS >1000).

2.4. Diversification rates

To investigate diversification rates in *Philisca*, we used the ultrametric species coalescence tree obtained from BEAST with outgroup species removed (excluding also *P. tripunctata*, see below). Diversification rate analyses were carried out using the ‘Laser’ package (Rabosky and Schliep, 2013) for R 3.1.3 (R Development Core Team, 2009). First, diversification rates were estimated under no ($\epsilon = 0$) and high ($\epsilon = 0.9$) extinction rates, assuming almost complete sampling (two missing species). We tested whether the pattern of diversification could be explained best by past decreasing speciation with constant extinction rates (“SPVAR”), increasing extinction with constant speciation (“EXVAR”) or both varying speciation and extinction rates (“BOTHVAR”) (Rabosky and Lovette, 2008) and used the Akaike Information Criterion (AIC) to compare the fit of these models to our data. Additionally, three rate-variable (exponential and linear density dependent models ‘DDX’ and ‘DDL’, and a two-rate Yule model) and two constant rate (‘pure birth’ and ‘birth-death’) diversification models were compared using AIC as a fit to the overall mode of *Philisca* diversification. To visualize the accumulation of species over time, a lineage-through-time plot was drawn using the R package ‘Ape’ (Paradis et al., 2004) and compared to the LTT plots of 10,000 simulated trees generated under Yule model. In addition, the gamma-statistic (Pybus and Harvey, 2000) was calculated to test whether there was a decrease in diversification rates.

We used the BAMM program (Rabosky et al., 2014) to evaluate possible changes in the macroevolutionary rate regimes (e.g., time varying process of speciation, extinction or phenotypic evolution). Four Markov chains were run for 10 million generations, setting the initial lambda and mu priors as chosen by the R package ‘BAMMtools’ 2.0.2 (Rabosky et al., 2014). The maximum shift credibility configuration was identified from the posterior, as well as potential core shifts in diversification rates.

3. Results

Minimal topological incongruence was found for separate and concatenated gene trees, mostly limited to branches of low support (Supplementary Figs. A–L; Fig. 2). Our molecular phylogenetic results mirror the intergeneric relationships within Amaurobioidinae obtained recently with a larger sampling of taxa and a more exhaustive examination of data partitions (Labarque et al., 2015; see Section 4). Therefore, we focus our discussion on the full dataset and the phylogenetic relationships within *Philisca*.

3.1. Phylogenetic analyses and lineage age estimation

The total length of the concatenated aligned data matrix was 2130 sites (657 bp of COI, 327 bp of H3a, 357 bp of 16S and 789 bp of 28S). The preferred models for each partition were as follows: GTR+I+ Γ for the COI and 28S, HKY+I+ Γ for the 16S and H3a, TIM3+I+ Γ , TVM+I and GTR+ Γ for the first, second and third codon positions of COI, respectively, and TIM1, JC and TVMef+ Γ for H3a, respectively. Comparison of the alternative partitioning strategies revealed a preference for the *codon specific* partition in COI and H3a. Bayesian analysis of independent and concatenated genes achieved convergence within 5×10^7 generations (standard deviation of split frequencies <0.01). Two independent analyses of the concatenated matrix yielded one consensus Bayesian tree of score $-\ln L = 15273.29$. Maximum likelihood analysis yielded one single tree of score $-\ln L = 15002.39$ (Supplementary Fig. M). The parsimony analysis under implied weighting produced 100 equally parsimonious trees (distortion 16.71068) (Supplementary Fig. N). The maximum likelihood and parsimony (strict consensus tree) results

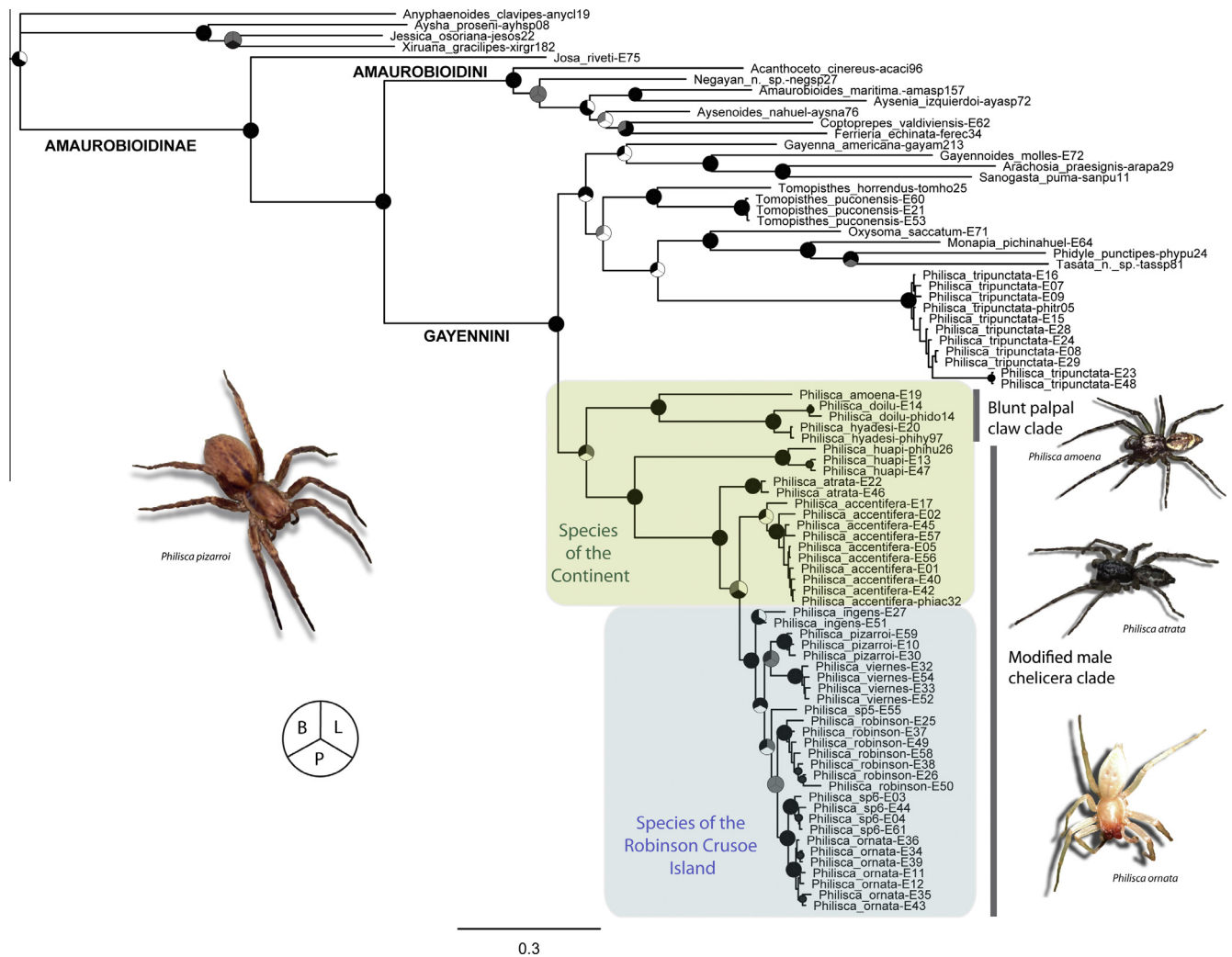


Fig. 2. *Philisca* relationships. Majority rule consensus of the trees sampled by Bayesian Inference of the combined molecular alignment, with the preferred model for each gene fragment. The first 10% of generations were removed as burn-in. The information of the results of the analyses under maximum likelihood and parsimony ($k = 100$) are summarized in the node support. Circles at nodes indicate support levels subdivided by analysis (B, Bayesian; L, maximum likelihood; P, parsimony; see inset). Black indicates posterior probabilities >0.95, bootstrap proportions >0.75 and jackknifing frequencies >0.75; grey indicates that the clade was recovered but with lower support than the previous values; white indicates that the clade was not recovered. Clades discussed in the text and the geographical distributions are highlighted with lateral bars and different colors respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of the concatenated matrix closely mirrored the results of the Bayesian analysis (Fig. 2).

We present in detail the divergence times estimated under the multispecies coalescent Bayesian analysis, since the species tree was subsequently used for the diversification analyses; time estimates from the concatenated analyses yielded consistently older ages, although the confidence intervals overlap with those estimated under the multispecies coalescent. Both estimations are consistent with the main conclusions of a *Philisca* clade originating from a single colonization of the Robinson Crusoe Island (see below). According to our results, the monophyly of *Philisca* was threatened by the exclusion of *P. tripunctata*, a species tentatively placed in the genus, which was supported as the sister group of the Gayennini's spinose genera (e.g., *Oxysoma*, *Monapia*, *Phidyle* and *Tasata*) in the Bayesian analysis (Fig. 2; Supplementary Fig. C), or near *Gayenna americana* in the rest of the analyses (Supplementary Figs. D, M–N). '*Philisca*' *tripunctata* diverged from this group approximately 12.68 million years ago (Ma) (9.6–16.2 Myr 95% HPD interval; Fig. 3). Hereafter we will refer to this species as '*Philisca*' *tripunctata* and exclude it from subsequent *Philisca* analyses. The monophyly of the remaining *Philisca* was recovered

by the Bayesian and maximum likelihood analyses, but only highly supported by the first (Fig. 2). Bayesian stepping-stone sampling analyses yielded $-\ln L$ scores of 15987.33 and 16039.49 for the chain enforcing the monophyly of *Philisca* and the unconstrained chain, respectively. Therefore, the Bayes Factor provides a strong preference for the monophyly of *Philisca* (BF = 52.16). The parsimony analysis did not support the monophyly of *Philisca* but the evidence against its monophyly is faint (Bremer support = 1; jackknifing <50%). *Philisca* originated approximately 15.17 Ma (11.8–19.4). All the analyses recovered the Blunt Palpal Claw Clade and the Modified Male Chelicera Clade (= *ornata* species group) as reciprocally monophyletic with high support (Fig. 2); these two clades diverged approximately 9.37 Ma (5.54–13.66). Within the Modified Male Chelicera Clade, the endemic species of the Robinson Crusoe Island (Figs. 1–3) formed a highly supported monophyletic group. The split of the island species from their continental sister taxa were estimated at 2.21 Ma (1.56–3.06), which postdates the geological origin of the island (4 Ma, Stuessy et al., 1984). The concatenated matrix Bayesian analysis estimated a slightly older divergence at 4.38 Ma (2.8–6.7), still compatible with the emergence of the island. Within the island clade, two supported clusters

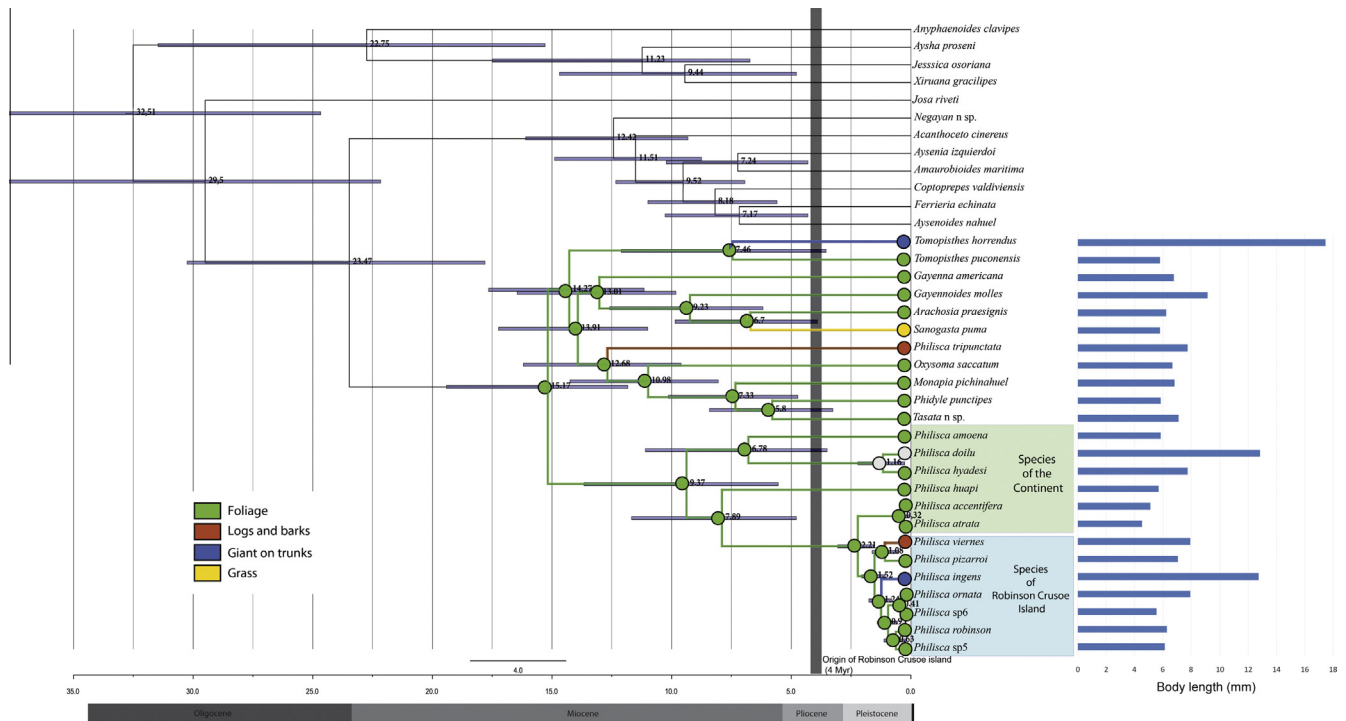


Fig. 3. Lineage age estimation and ecological niche diversification. Chronogram obtained with *BEAST using a fossil calibration point and molecular rates estimated for the four genes. Chronograms with divergence times and 95% HPD intervals, shown as transparent bars and node numbers correspond to the node ages. The time scale and the main geological event are indicated above the x-axis (in million years -Ma). Microhabitat types are color-coded; branches are colored according to the parsimony optimization, pie charts depict likelihood of ancestral states from the Mk1 model. Body lengths (average one male and one female) are depicted with blue bars at the right margin. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of undescribed species were recovered, namely *Philisca* sp.5 and *Philisca* sp.6. Also, most *Philisca* species were recovered as monophyletic and well supported by all the inference methods (Fig. 2), except *Philisca ingens* Berland, that emerged as paraphyletic in the maximum likelihood analysis, and *Philisca accentifera* Simon, that appeared as paraphyletic in the maximum likelihood and parsimony analyses. Our analyses also corroborated the placement of *Tomopisthes puconensis* (Ramírez), formerly described in *Philisca* (see Ramírez, 2003).

3.2. Microhabitat types and ecological niches

As is common in anyphaenids, most *Philisca* species live on the foliage of trees and shrubs, where they build silken retreats in coiled or adjoined leaves (state 0, 'foliage'); *Philisca* species from foliage have contrasting body coloration. Most of the remaining *Philisca* species have dull, brownish, cryptic coloration and make their retreats in dry tree logs or under bark (state 1, 'logs and barks'); *Philisca viernes* Soto & Ramírez and '*Philisca*' *tripunctata* were scored with this state. We distinguished a second niche for two species that, while also living on logs, are twice or three times the size of the other *Philisca* species and thus probably prey on larger items (state 2, 'giant on trunks'); *P. ingens* and *Tomopisthes horrendus* (Nicolet) are the two largest anyphaenid species and were scored as this state. *Philisca doilu* (Ramírez) is a continental species from the Blunt Palpal Claw Clade, with a rather dull coloration and large body size; although it has been collected by canopy fogging, it is probably a trunk rather than foliage dweller, (Soto and Ramírez, 2012) and thus was scored as a missing entry. A third niche, corresponding to grassland-adapted species (state 3, 'grass') was only represented by *Sanogasta puma* Ramírez in this dataset. Parsimony

and maximum likelihood mapping are coincident in inferring that Robinson Crusoe Island was colonized by a foliage species that switched secondarily to logs and barks and giant on trunks states, independently (Fig. 3).

3.3. Diversification rates

The diversification rates for *Philisca* were estimated at 0.133 lineages/Myr assuming no extinction and 0.054/Myr assuming high rates of extinction. When we compare between a model assuming declining speciation with constant extinction (SPVAR), and a model assuming increasing extinction with constant speciation (EXVAR), the former model better explains the data. This means that overall speciation, rather than extinction, has been defining *Philisca* diversification patterns. Moreover, when comparing three rate-variable (Yule-2-rate and two density-dependent models) and two constant-rate models, the constant-rate Birth-Death model provides the best fit for the data (Table 1). Furthermore, the lineage-through-time plot of *Philisca* does not differ significantly from those of 10,000 pure-birth trees ($\Delta AIC = -0.4156$; $p = 0.999$; Fig. 4a) and the gamma statistic value of 1.471 indicates that the diversification rates have not decreased over time ($p = 0.929$). The BAMM analyses shows an increase in speciation rates for the clade containing *Philisca atrata* Soto and Ramírez, *P. accentifera* and the Robinson Crusoe Island endemics (Fig. 4b), even though no significant core shifts were detected, probably due to the small number of *Philisca* species and thus, the low power of the analysis. When comparing speciation rates through time between all *Philisca* species and the Robinson Crusoe Island endemics (Fig. 4c), it is clear that the overall increase in speciation rates during the last ca. 4 Myr can be attributed to the island endemics.

Table 1
Output for maximum likelihood Δ AIC test statistic from analyses of diversification in *Philisca*.

Model	r1	r2	Model parameters	LnL	AIC	Δ AIC
<i>Rate-constant and variable rate models</i>						
Pure birth	0.1587			−11.2582	24.5163	0.7824
Birth-death	0.0136		0.9581 (a)	−9.8670	23.7339	0
Yule 2-rate	0.1580	0.1621	1.0145 (st)	−9.2321	24.4641	0.7302
DDX	0.1164		−0.533 (x)	−10.7837	25.5674	1.8335
DDL	0.1587		213116 (K)	−11.2582	26.5164	2.7825
<i>Variable speciation/extinction models</i>						
SPVAR			0.3573 (λ), 0.006 (k)	−9.8574	25.7147	1.9808
EXVAR			0.3254 (λ), 17570 (z)	−9.8670	25.7340	2.0001
BOTHVAR			0.3294 (λ), 0.3401 (z)	−9.8120	27.6241	3.8902

r1, r2: initial and final rates, respectively; Model parameters: a = extinction fraction; st = shift time; x = parameter controlling the magnitude of the rate change; K = "carrying capacity" of density-dependent model; λ = initial speciation rate; k = parameter of the exponential change in speciation rate; z = parameter of the exponential change in extinction rate.

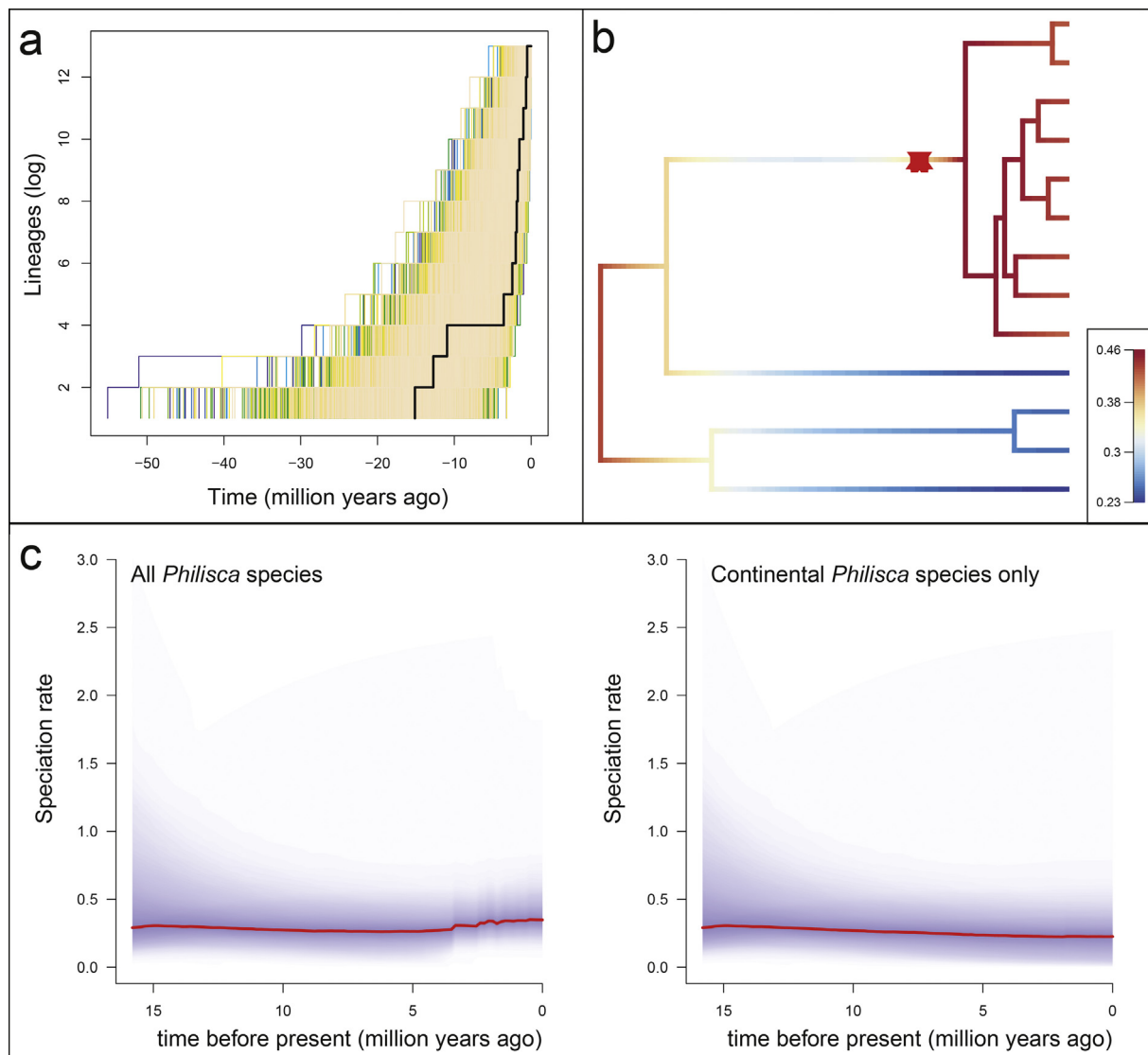


Fig. 4. Diversification rates for *Philisca*. (a) Log-lineage-Through-Time plot of *Philisca* (black line) and 10,000 simulated Yule process trees. (b) Maximum shift credibility configuration on *Philisca* tree with speciation rates color-coded as in the legend. (c) Speciation rate-Through-Time plots for all *Philisca* species (left) versus continental species only (right). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

This is the first study that deals with the evolutionary history of endemic spider species from the Juan Fernández archipelago and

their relatives in the Valdivian temperate forests. Former works on speciation in this archipelago focused on plants (López-Sepúlveda et al., 2015; Takayama et al., 2015), and a study focused on the linyphiid *Lamianacauda* spiders, with >10 endemic species

on the island is underway (G. Hormiga and M. Arnedo, unpublished data).

4.1. *Philisca* relationships and morphological implications

The molecular phylogenetic analyses provided in this work corroborate Labarque et al.'s (2015) main conclusions about the relationship among higher taxa, e.g. the monophyly of the subfamily Amaurobioidinae and the tribes Amaurobioidini and Gayennini, and the genus *Josa* as sister group of both tribes. After the addition of sequences from the majority of *Philisca* species we clarified the relationships within the Modified Male Chelicera Clade; of prime importance is the clustering of all the endemic species of the Robinson Crusoe Island in a monophyletic group, thus compatible with colonization by a single lineage. The *Philisca* species from Robinson Crusoe are remarkably similar in genitalic morphology (Soto and Ramírez, 2012), thus sequence data is important to help distinguish species; after this analysis we found two supported clusters corresponding to putative undescribed species from the island that we will study in the near future. We also confirm here that, according to the sequence data, '*Philisca* *tripunctata* is unlikely a member of *Philisca*, but probably the sister group of the spinose genera of Gayennini (*Oxysoma*, *Monapia*, *Phidyle*, and *Tasata*); we prefer to defer a taxonomic change after sequences of the type species *Philisca hahni* are available.

4.2. *Philisca* adaptive radiation and ecological niche diversification

The genus *Philisca* provides an excellent model for testing evolutionary scenarios, especially by analyzing its patterns of colonization and diversification on the Robinson Crusoe Island. Adaptive radiations are defined by a rapid ecological/phenotypic diversification following colonization of a new region with empty ecological niches (Schluter, 1996, 2000; Schluter et al., 1997; Rainey and Travisano, 1998). Our results indicate that *Philisca* colonized the Robinson Crusoe Island from the mainland approximately 2 Ma. Colonization was followed by rapid species diversification that, at least in two cases, involved ecological shifts. One of them, *P. viernes* is abundant in cryptic habitats such as the interior of dry, rotten tree logs and under their barks, occasionally in suspended leaf litter of ferns, while the other, *P. ingens* is a nocturnal hunter which sits on well-exposed tree trunks, and hides in tree logs or under barks during the day. *Philisca robusta*, also an endemic insular species, has an unusual morphology, with a stocky constitution and powerful chelicerae; it may occupy an unusual niche as well, but we lack any natural history information on this atypical insular species. Most species coexist in the same localities (Fig. 1), which in combination with the shift in microhabitat use suggest that diversification has been for the most part adaptive (Rundell and Price, 2009). Moreover, the radiation seems to have happened rapidly, as indicated by the fact that half of the genus diversity was generated in last 10% of the genus geological time span, in the comparatively minuscule geographical area of Robinson Crusoe. The statistical tests, however, failed to detect significant shifts in diversification rates, probably as a result of the low number of species. Since the accelerated speciation rates were detected for the Robinson Crusoe Island endemics plus two closely related continental species (*P. accentifera* and *P. atrata*), this can be taken as an indication that the trend predated the colonization of the island. Alternatively, this can be explained by a methodological bias: since the island became available for colonization only 2 million years ago, the split between continental and insular species is by force very young, and thus the branch between island and continental species very short; under this circumstance, the BAMM method is likely to include the continental species as part of the highly diversifying group. The comparative distributional ranges

also favor the interpretation that continental and island species have very different evolutionary dynamics. While each continental species *Philisca atrata* and *P. accentifera* occupy comparatively immense geographical ranges of nearly 2300 km in latitudinal span (Soto and Ramírez, 2012; Fig. 38), they did not produce a comparable diversity in species and morphological variation as occurred in a small and rather homogeneous oceanic island, of only 16.4 km in its larger width. Considering the previous studies of spiders from volcanic islands (*Tetragnatha* and *Orsonwelles* on the Hawaiian archipelago, *Dysdera* on the Canary islands, *Pholcus* in the Macaronesian archipelago, and *Hogna* on the Galapagos islands; Gillespie et al., 1994; Arnedo et al., 2001; Hormiga et al., 2003; Dimitrov et al., 2008; De Busschere et al., 2010; Gillespie, 2013), the rapid diversification of seven *Philisca* species in the small island of Robinson Crusoe may be among the fastest rates documented for spiders.

A further interesting question is what traits, if any, have favored an adaptive radiation of *Philisca* species in Robinson Crusoe Island, in addition to the availability of empty ecological niches. Identifying the traits that favor adaptive radiations in certain groups over others is complicated (Ackerly et al., 2006; Gavrillets and Losos, 2009), and often involves combination of life-history traits and ecological conditions. Considering that the known distinctive characters of the Modified Cheliceral Clade are sexual structures (Soto and Ramírez, 2012), reproductive behavior is a warranted candidate in the quest for those traits.

5. Conclusions

Our results of the evolutionary history of *Philisca* species clarified the relationships between them, in particular within the Modified Male Chelicera Clade; and revealed that a single *Philisca* lineage colonized the Robinson Crusoe Island and subsequently underwent rapid (~2 Myr) diversification. Moreover, we provide evidence that *Philisca* has undergone an adaptive radiation on the Robinson Crusoe Island involved ecological shifts. The ancestral microhabitat was most likely leaf-dwelling but we identify two independent microhabitat shifts; one of them, *P. viernes* is abundant in tree logs and under barks, while the other, *P. ingens* sits on well-exposed tree trunks, and hides in tree logs or under barks during the day.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2016.10.017>.

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