

The rise of the Andes promoted rapid diversification in Neotropical *Phlegmariurus* (Lycopodiaceae)

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Received: 11 September 2018

Accepted: 10 October 2018

New Phytologist (2019) **222**: 604–613

doi: 10.1111/nph.15544

Key words: Andes, biodiversity hotspot, clubmosses, diversification, lycophytes, phylogeny.

Summary

- Tropical mountains are disproportionately biodiverse relative to their surface area, but the processes underlying their exceptional diversity require further study. Here, we use comparative phylogenetic methods to examine the impact of the Andean orogeny on the diversification of Neotropical *Phlegmariurus*, a species-rich lycophyte clade.
- We generated a time-calibrated phylogeny of 105 species of Neotropical *Phlegmariurus* and estimated lineage diversification rates. We tested for correlations between lineage diversification rates and species range size, niche breadth, elevational range amplitude, and mean elevation of occurrence. A recently developed macroevolutionary model was used to incorporate geological data and test for an association between diversification rates and the Andean uplift.
- Diversification rates of Neotropical *Phlegmariurus* are negatively correlated with species range size and positively correlated with mean elevation of species occurrence. The rise of the Andes is strongly associated with increased rates of diversification in Neotropical *Phlegmariurus* during the last 10 Myr.
- Our study demonstrates the importance of mountain-building events and geographical isolation of alpine populations as drivers of rapid diversification, even in spore-dispersed plants. This work also highlights the usefulness of combined phylogenetic, geological and ecological datasets, and the promise of comparative environment-dependent diversification models in better understanding the evolutionary origins of biodiversity.

Introduction

Mountains harbor a disproportionate share of Earth's biodiversity (Humboldt & Bonpland, 1807; Hoorn *et al.*, 2013; Antonelli, 2015; Hughes & Atchison, 2015; Lagomarsino *et al.*, 2016; Xing & Ree, 2017). Although they cover approximately one-eighth of Earth's land surface, mountains host approximately one-third of terrestrial species (Spehn *et al.*, 2012) and have supported exceptional species radiations (Hughes & Eastwood, 2006; McGuire *et al.*, 2007; Schwery *et al.*, 2015; Lagomarsino *et al.*, 2016; Xing & Ree, 2017) in lineages across the Tree of Life. Given the exceptional species diversity encountered in the world's mountains, developing a thorough understanding of the factors driving the diversification of biotic lineages in these regions is an important goal of evolutionary biologists. Methodological advances in comparative phylogenetics and historical biogeography in recent years have improved our capability to identify the relative roles of biotic and abiotic factors as drivers of evolutionary radiations (Matzke, 2013; Morlon, 2014), yet our understanding of the timing and mode of diversification in montane systems remains mostly confined to a few groups of organisms, such as lizards (Doan, 2003; Elias *et al.*, 2009), birds

(Chaves *et al.*, 2011; Fjelds  *et al.*, 2012; McGuire *et al.*, 2014), butterflies (Casner & Pyrcz, 2010; Strutzenberger & Fiedler, 2011; Chazot *et al.*, 2016; De-Silva *et al.*, 2016; Nattier *et al.*, 2017) and flowering plants (Hughes & Eastwood, 2006; Antonelli *et al.*, 2009; Lagomarsino *et al.*, 2016; Diazgranados & Barber, 2017; N rck *et al.*, 2018; Pouchon *et al.*, 2018).

Andean South America is among the most important geographical regions in which to study the diversification of montane lineages. The tropical Andes, which span western South America from Venezuela to northern Argentina and Chile, are of particular interest for researchers studying many groups of organisms. This area is the most species-rich region on Earth, with >45 000 plant and 3400 vertebrate species; nearly half of these are found nowhere else on Earth (Myers *et al.*, 2000). The accumulation of this unparalleled diversity is due in large part to major evolutionary radiations that have occurred in a broad array of Andean lineages, including groups of fungi (Leavitt *et al.*, 2012; L cking *et al.*, 2014), animals (Garc a-Moreno *et al.*, 1999; Doan, 2003; Elias *et al.*, 2009; Chaves *et al.*, 2011; De-Silva *et al.*, 2016) and plants (Hughes & Eastwood, 2006; Antonelli *et al.*, 2009; Luebber & Weigend, 2014; Lagomarsino *et al.*, 2016). These

radiations are particularly striking given that most are recent and ongoing, having started during the Pliocene and Pleistocene epochs (Madriñán *et al.*, 2013) in concert with the rapid uplift of the Andes over the past 10 Myr (Gregory-Wodzicki, 2000; Garziona *et al.*, 2008). Even though the timing and geographical pattern of the Andean uplift remain topics of considerable debate, it is evident that the Andean orogeny, along with climatic fluctuations and biotic interactions, has driven some of the fastest diversification rates known (Madriñán *et al.*, 2013; Lagomarsino *et al.*, 2016).

The number of focused studies on the diversification of montane Andean lineages has increased substantially over the past decade; however, most work has focused on a select few taxonomic groups. By contrast, the evolutionary histories of other prominent tropical Andean groups, such as ferns (Kreier *et al.*, 2008; McHenry & Barrington, 2014; Sánchez-Baracaldo & Thomas, 2014) and lichens (Lücking *et al.*, 2014) have received little attention; yet others, including lycophytes and bryophytes, remain unstudied within a phylogenetic context. To better understand how the Andean uplift has impacted the diversification of the region's biota, increased focus on understudied groups, especially those that differ in life-history strategies and dispersal ability, is needed. Here, we address this gap in our knowledge by examining the role of the Andean uplift as a driver of diversification in the species-rich lycophyte genus *Phlegmariurus* (Lycopodiaceae).

The Neotropical clade of *Phlegmariurus* is an excellent study system for examining the relationship between the Andean orogeny and species diversification in spore-dispersed vascular plants. This clade comprises an estimated 150 species and includes species that are remarkably diverse both morphologically and ecologically (Øllgaard, 1992; Field *et al.*, 2016). Neotropical *Phlegmariurus* is distributed from Florida and Mexico to Argentina and southeastern Brazil and can be found from sea level to at least 5000 m above sea level (asl), but is most diverse in the northern Andes (Øllgaard, 1995), where most species are either epiphytes in humid montane forests or terrestrial herbs in alpine grasslands. The presence of a large (>60 species), monophyletic group of terrestrial taxa restricted to geologically young alpine habitats of the Andes and adjacent regions (Øllgaard, 1992) suggests that the group may have undergone a recent and rapid burst of diversification, thus providing a useful comparison to angiosperm genera, whose diversification histories may have different principal drivers (Luebert & Weigend, 2014). In addition, this group provides a useful system for examining the impact of propagule size and biotic interactions on diversification patterns in montane systems, as *Phlegmariurus* species are spore-dispersed and do not engage in obvious biotic interactions during reproduction, like most angiosperms. Using a dated phylogeny, species distribution information, and both climate and geological data, we apply comparative phylogenetic models to investigate the evolutionary history of Neotropical *Phlegmariurus* within the context of the Andean orogeny.

Materials and Methods

Taxon sampling, DNA extraction, amplification, and sequencing

We generated sequence data from 105 species of Neotropical *Phlegmariurus*, including members of all known species groups and representing *c.* 70% of known diversity in the clade (Øllgaard, 1992; Testo *et al.*, 2018b); matching those sampled in a recent study on species group delimitation in the genus (Testo *et al.*, 2018b). Total genomic DNA was extracted from silica-dried leaf material or herbarium specimens using a standard cetyltrimethylammonium bromide (CTAB) extraction protocol (Doyle & Doyle, 1987). PCR was performed in 25- μ l mixtures of 12.5 μ l Bullseye Taq mix (MIDSCI, St Louis, MO, USA), 9 μ l water, 1.25 μ l each of 10 mM forward and reverse primers, and 1 μ l of 10–20 ng μ l⁻¹ DNA. We amplified six regions of chloroplast DNA (*rbcL*, *psbA-trnH*, *rps4-trnS*, *trnL*, *trnL-trnF* and *trnP-petG* IGS) following the conditions outlined in Testo *et al.* (2018b). PCR products were purified using shrimp alkaline phosphatase and then diluted to 2 ng μ l⁻¹ before sequencing. We sequenced all PCR products in both forward and reverse directions using BigDye chemistry on an ABI 3730 xl DNA analyzer at Genewiz, South Plainfield, NJ, USA. Sequences were assembled in GENEIOUS 10.0.3 (Biomatters Ltd, Auckland, New Zealand) and were visually inspected and manually edited as needed. Voucher information and GenBank accession numbers are provided in Supporting Information Table S1.

Divergence time analysis

We performed sequence alignment using the MAFFT (Katoh *et al.*, 2002) plugin in GENEIOUS with a gap-open penalty of 1.1–1.4 and an offset value of 0.123. We used JMODELTEST 2 (Darriba *et al.*, 2012) on each marker partition to identify best-fitting substitution models (see Table S2); the concatenated six-marker dataset was used for all subsequent analyses.

We performed divergence-time estimation analyses using BEAST 2.4.5 (Bouckaert *et al.*, 2014) on the Cipres Science Gateway portal (Miller *et al.*, 2010). For all analyses, the matrix was partitioned by marker, and substitution models were assigned to each partition using the results of our model test analysis; trees were linked and rates were left unlinked. As no reliable fossils are available to provide a minimum age estimate of this clade, we used a secondary calibration from a recently published dated phylogeny of the Lycopodiaceae (Testo *et al.*, 2018a) to calibrate the crown age of Neotropical *Phlegmariurus* at 42.7 Myr ago (Ma); the calibration age is similar to that recovered by Bauret *et al.* (2018) in their study of Malagasy *Phlegmariurus*. This calibration was defined with a normal distribution centered on 42.7 Ma and given a standard deviation of 5, which placed the center 95% of probability space for the node age at 39–55 Ma. A birth–death tree prior was selected with a uniform prior range 0–10 for speciation rate and 0–1 for relative extinction rate, with starting values of 1.0 for speciation and 0.5 for relative extinction. We performed two separate Markov chain Monte Carlo (MCMC) runs

of 50 million generations and sampled every 20 000 generations, resulting in 2500 trees per run and 5000 trees in total. The resulting log files were inspected for convergence and adequate sampling using TRACER 1.6 (Drummond & Rambaut, 2007); ESS values all exceeded 500 and the first 20% of trees were discarded as burn-in. A maximum credibility tree was generated from the remaining 4000 trees.

Diversification rate estimation

We estimated lineage diversification rates using BAMM 2.5.0 (Rabosky, 2014), which uses a reversible-jump MCMC to sample a large number of possible diversification regimes from a given time-calibrated phylogeny. Like other lineage diversification models, the BAMM approach has come under criticism (Moore *et al.*, 2016); however, the model appears to perform well when appropriately parameterized for the dataset being analyzed (Rabosky *et al.*, 2017). We acknowledge the limitations of this and other methods of diversification rate estimation and follow the best practices described by the authors of the program. The MCMC was run for 100 million generations and sampled every 40 000 generations. Prior values were selected using the 'setBAMMpriors' function; we accounted for incomplete taxon sampling by providing a sampling file with estimated sampling proportions for each of the eleven species groups in the clade as defined by Testo *et al.* (2018b). Post-run analyses were performed using the 'BAMMTOOLS' (Rabosky *et al.*, 2014) package in R 3.4.2 (R Core Team, 2014). The initial 10% of the MCMC run was discarded as burn-in, and the remaining data were assessed for convergence and ESS values > 200. Net diversification rates were obtained for all taxa in the phylogeny using the 'getTipRates' function; these values represent the posterior distribution of rates at the tip of the tree, as described by Rabosky *et al.* (2015). To compare diversification rates of species groups in the genus, mean clade rates were extracted using the 'getCladeRates' function.

Species distribution data and association with diversification rates

In order to estimate features of species distributions and to estimate niche space, we obtained georeferenced locality data for 4887 collections of Neotropical *Phlegmariurus*. Specimen data were obtained from the GBIF and Tropicos databases and from examination of herbarium material at AAU, COL, FMB, GH, HUA, MEXU, NY, PSO and VT. All collection data were reviewed, and both duplicate collections, and specimens from beyond the known range of a species were visually examined and, if misidentified, deleted. Following deletion of erroneous data, 2974 collections remained, ranging from two for *Phlegmariurus tryoniorum* to 324 for *Phlegmariurus reflexus*. In total, we estimated four features of species distributions and niche occupancy: mean elevation, elevational range, species range size, and niche breadth (Table S3). Mean elevation and elevational range were calculated from values provided on collection labels or estimated using lat/long coordinates and the 'elevation' function in R/RGBIF (Chamberlain & Boettiger, 2018). Range size was estimated by

applying a 5 km buffer around each locality point using the 'gBuffer' function in the R/RGEOS (Bivand *et al.*, 2017), following the methodology of Anacker & Strauss (2014). To calculate niche breadth, we calculated niche models for each species using locality data and climate layers obtained from the CHELSA (Karger *et al.*, 2017) dataset. Highly correlated variables were identified using Pearson's correlation coefficient; all variables with coefficients > 0.6 were removed. The remaining four most predicative bioclimatic variables were then used to estimate niche breadth; these were: annual temperature, annual precipitation, seasonality of temperature and seasonality of precipitation. Niche breadth was calculated using ENMTOOLS (Warren *et al.*, 2010) using Levin's (1968) B metric. The correlations between these variables and species diversification rates were examined with phylogenetically independent contrasts (Felsenstein, 1985) implemented in the R/ape (Paradis *et al.*, 2004); range-size data were log-transformed before analysis to overcome their skewed distribution. We also examined the correlation of each of these niche/distribution variables using the same method. Trait variables were plotted on the phylogeny of Neotropical *Phlegmariurus* using the 'plotTree.wBars' function in PHYTOOLS (Revell, 2012).

Orogeny-dependent diversification

We tested for an association between the uplift of the Andes and diversification rates in Neotropical *Phlegmariurus* by comparing a series of time-dependent diversification models that allow speciation and/or extinction to vary with the paleoelevation of the Andes against constant diversification null models. Paleoelevation data were obtained from the list compiled by Lagomarsino *et al.* (2016), which is based on historical elevation estimates from Garzzone *et al.* (2006, 2008, 2014), Ehlers & Poulsen (2009) and Leier *et al.* (2013). These data are available in Table S4. A smoothing line fitting these data was generated using R/PSPLINE and this line was used to provide the best estimate of Andean paleoelevation at any given time point. A total of eight paleoelevation-dependent diversification models were applied; four with exponential dependency and four with linear dependency. Two null models were also generated: a Yule model and a constant-rate birth–death model. Models were compared and the best-fitting model was selected using the corrected Akaike Information Criterion. These models were implemented in R/RPANDA (Molton *et al.*, 2016) and are based on the environment-dependent birth–death model described by Condamine *et al.* (2013). All models, including parameters and comparison metrics, are provided in Table 1. Results for PICs among trait/niche variables are provided in Table S5.

In order to visualize the accumulation of lineage diversity in Neotropical *Phlegmariurus* through time and compare that rate to patterns of lineage accumulation expected under constant-rate null models, we generated a log-lineage-through-time plot (LTT) for the time-calibrated *Phlegmariurus* phylogeny as well as for two simulated trees of the same age and taxon richness. One simulated tree was generated under a Yule model (birth rate = 1, death rate = 0), and another was generated under a birth–death

Table 1 Comparison of paleoelevation-dependent diversification models implemented in R/RPANDA.

	Models	Mode of dependency	# Parameters	Log L	AICc	Δ AICc	Lambda	Mu
1	λ with elev., no μ	Exponential	2	-298.36	600.84	0.00	0.04	-
2	λ with elev., μ constant	Exponential	3	-298.36	602.96	2.12	0.04	0.00
3	λ with elev., no μ	Linear	2	-299.93	603.98	3.14	0.10	-
4	λ and μ with elev.	Exponential	4	-298.10	604.60	3.75	0.04	0.06
5	λ with elev., μ constant	Linear	3	-299.94	606.12	5.28	0.10	0.00
6	λ constant, μ with elev.	Linear	3	-299.93	606.35	5.51	0.03	0.01
7	λ and μ with elev.	Linear	4	-299.93	608.26	7.42	0.10	0.04
8	λ constant, μ with elev.	Exponential	3	-308.22	622.68	21.84	0.20	0.09
9	λ and μ constant	-	2	-322.75	644.58	43.74	0.09	0.00
10	λ constant, no μ	-	1	-356.57	659.86	59.02	0.07	-

model (birth rate = 1, death rate = 0.5). Simulated trees were generated using the 'LTT' function and all LTT plots were generated using the 'litt.plot' function in the 'APE' package in R (Paradis *et al.*, 2004).

Results

Our phylogeny resolved a mean crown age of 45.8 Ma (95% HPD 41.2–47.7 Ma) for Neotropical *Phlegmariurus*, with most species groups beginning to diversify in the Miocene (Figs 1, S1). Our tree topology and clade ages are similar to those reported by Testo *et al.* (2018a) in a recent dated phylogeny of the Lycopodiaceae. Net diversification tip rates varied from 0.097 events Myr⁻¹ for *P. ericifolius* to 0.308 events Myr⁻¹ for *P. columnaris*; rates were generally lowest in members of the *P. aqualupianus* group and highest in the *P. crassus* group (Tables S6, S7). The fastest diversifying and most species-rich clades in the genus tend to be present at high elevations (Fig. 2); however, there are exceptions to this pattern, such as the monotypic high-elevation *P. lindenii* group. Phylogenetic independent contrasts indicated a significant negative correlation between diversification rates and species range size (Figs 3a, 4a), no significant correlations between diversification rates and both elevational range and niche breadth (Figs 3b–c, 4b–c), and a significant positive correlation between diversification rate and mean elevation (Figs 3d, 4d).

The LTT plots indicate that lineage accumulation in Neotropical *Phlegmariurus* occurred at a slower rate than would be expected under either of the constant-rate simulations (Fig. 5) until the late Miocene (*c.* 10 Ma), when diversity began to rapidly accumulate. The timing of this shift corresponds closely with our paleoelevation estimates (Fig. 5, green dotted line) of the time point at which the Andes reached the approximate elevation of the modern forest/páramo boundary, as well as the crown age of the species-rich alpine *P. crassus* species group (Fig. 5, in red). Our BAMM results also indicate a well-supported shift in net diversification rates corresponding to the stem lineage of the *P. crassus* group (marginal probability = 0.32) or to the stem lineage of the *P. crassus* and *P. reflexus* groups combined (marginal probability = 0.19).

Comparison of ten time-dependent diversification models indicated that the best-fit diversification model included a

positive, exponential association between speciation rates and the paleoelevation of the Andes, with no extinction ($-\log_e L = -298.362$, AICc = 600.84). As shown in Table 1, all paleoelevation-dependent models outperformed both the Yule and birth–death null models.

Discussion

By examining the drivers of diversification in Neotropical *Phlegmariurus*, we partly address this taxonomic unevenness in our knowledge and provide a first step towards understanding the complex evolutionary history of one of the most diverse groups of spore-dispersed vascular plants in the tropical Andes. The evolutionary history of Neotropical *Phlegmariurus* closely mirrors those of other principally Andean groups, with lineage diversification tracking mountain uplift (Doan, 2003; Hughes & Eastwood, 2006; Antonelli *et al.*, 2009). Unlike these studies, which principally discuss diversification within the context of species distributions in the Andes, we explicitly tested for an association between the rise of the Andes and lineage diversification in their study group. We used a paleoenvironment-dependent diversification model developed by Condamine *et al.* (2013), recently used in a study of the radiation of Andean bellflowers (Lagomarsino *et al.*, 2016) to detect such an association in Neotropical *Phlegmariurus*, the presence of which was strongly supported by our analyses (Table 1). The correlation between mountain building and diversification rates in Neotropical *Phlegmariurus* is not surprising given the high species richness at high elevations in the Andes, but this insight is important because it represents one of the few attempts to explicitly test for a relationship between lineage diversification and a paleoenvironmental variable. In the case of Neotropical *Phlegmariurus*, a sustained increase in diversification rates occurred around the late Miocene, coincident with the start of exceptionally rapid uplift in the Andes (Garzzone *et al.*, 2008; Hoorn *et al.*, 2013) and the expansion of montane forests in the region. This burst of diversification matches the timing of an important event in the evolutionary history of Neotropical *Phlegmariurus*: a transition to terrestrial growth in the clade comprising the *P. reflexus* and *P. crassus* species groups (Testo *et al.*, 2018b). Thus, rapid diversification among terrestrial *Phlegmariurus* within the last 10 Myr appears to have been driven by increased ecological opportunity as novel habitats became available, and by

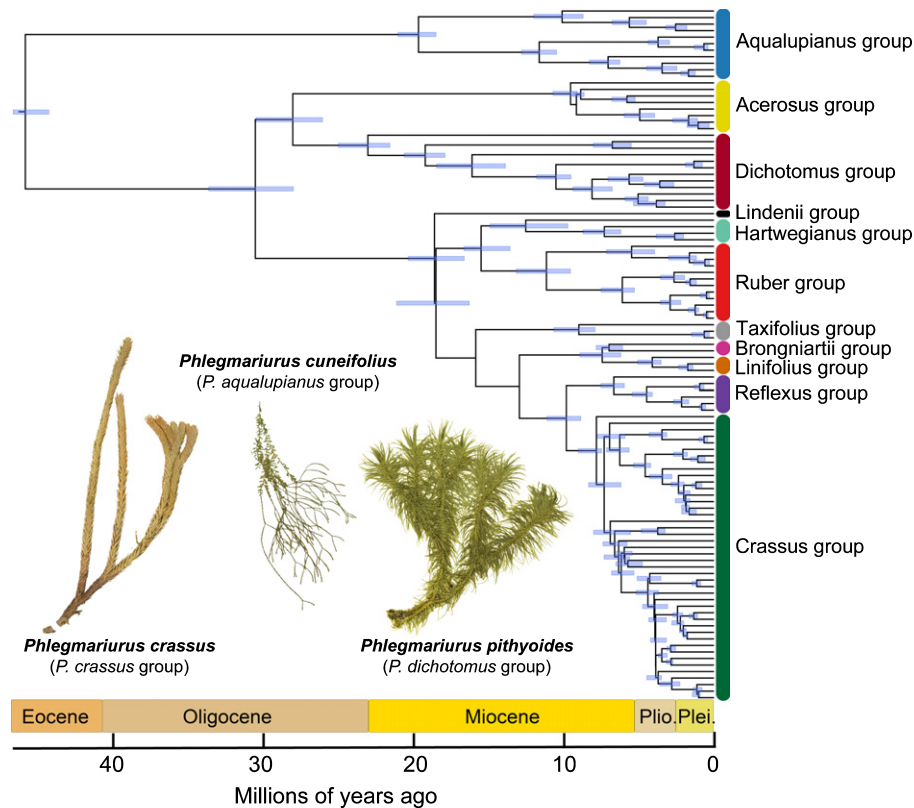


Fig. 1 Dated phylogeny of Neotropical *Phlegmariurus*, showing the timing of diversification of the clade and the relationships of the species groups designated by Testo *et al.* (2018b). Support values are provided for all backbone nodes; support values are Bayesian posterior probabilities. Node bars provided are 95% HPD intervals for mean node ages. Representative taxa from three species groups are shown.

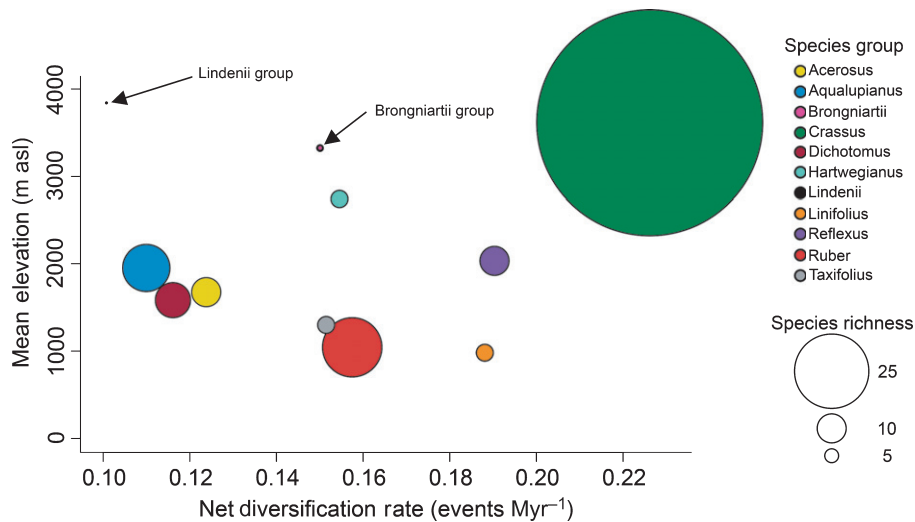


Fig. 2 Elevation and diversity in species groups of Neotropical *Phlegmariurus*. Circles represent species groups in the genus, circle size is relative to group species richness. Species group elevation and net diversification rate values are means obtained from all representatives in the group that were included in this study. asl, above sea level.

the proliferation of discontinuous alpine habitats as the uplift continued.

The strong negative correlation between diversification rates and species size (and negative correlation between range size and mean elevation of species' distributions) highlights

another important feature of this recent diversification: geographic isolation of populations among patchily distributed páramo habitats. Given the complex topography of the Andes and the restriction of alpine habitats to high (generally > 3200 m asl) elevations, páramos are generally small and

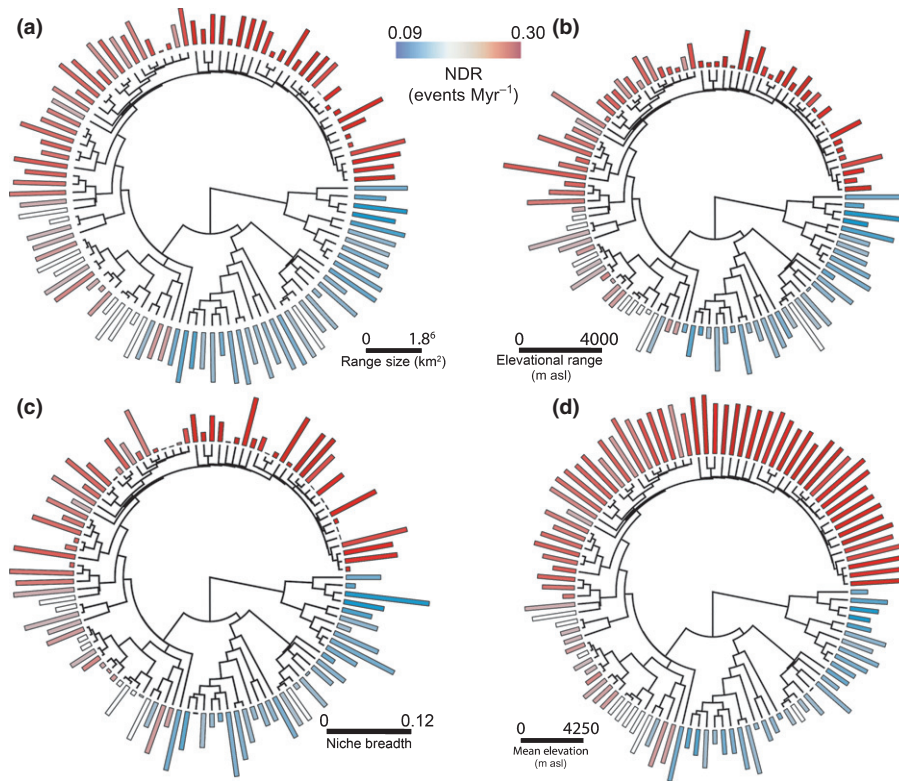


Fig. 3 Phylogeny of Neotropical *Phlegmariurus* with diversification rates and (a) range size, (b) elevational range, (c) niche breadth and (d) mean elevation provided for each species. Bar lengths represent values for given species attributes; bar colors represents species net diversification rate (NDR). asl, above sea level.

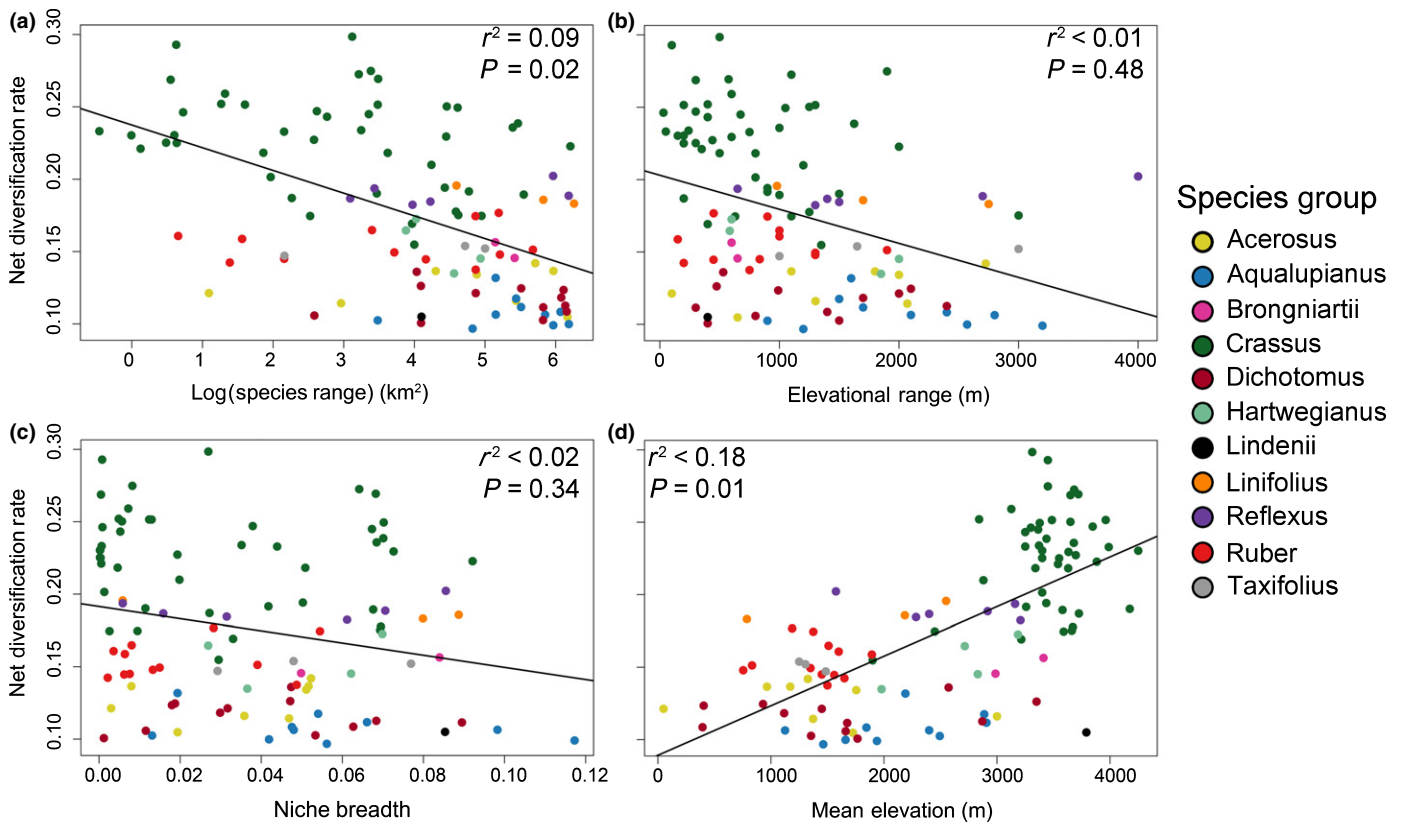


Fig. 4 Association between net diversification rates and (a) range size, (b) elevational range, (c) niche breadth and (d) mean elevation provided for Neotropical *Phlegmariurus* species. R^2 and P -values provided are from phylogenetic independent contrasts.

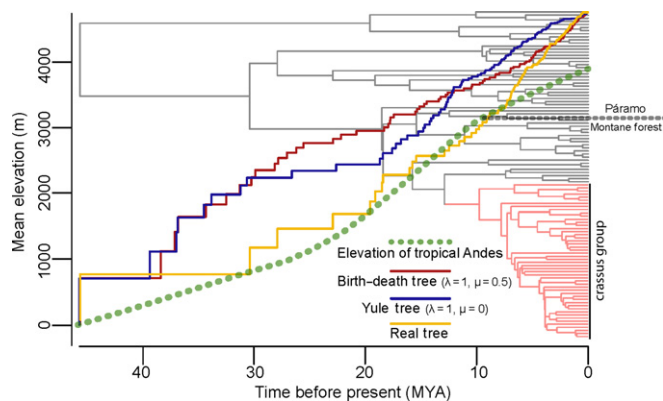


Fig. 5 Diversification dynamics of Neotropical *Phlegmariurus*. The clade highlighted in red on the time-calibrated phylogeny is the *P. crassus* species group. The green dotted line represents the spline of paleoelevation estimates obtained from geological data, as described in the Methods. The red and blue lines are log-lineage-through-time (LTT) plots simulated under birth–death and pure birth (Yule) models of diversification, respectively. The yellow line is a log-LTT plot for the time-calibrated phylogeny of Neotropical *Phlegmariurus* used in this study. The horizontal gray dotted line marks the approximate elevation of treeline in the tropical Andes today. MYA, million yr ago.

scattered on the landscape; thus, they have often been considered habitat islands, surrounded by a ‘sea’ of tropical forest and dry valleys (Vuilleumier, 1971; Diazgranados & Barber, 2017). We interpret the narrow ranges of many páramo-dwelling *Phlegmariurus* as strong evidence that the recent, rapid diversification of the *P. crassus* group has principally proceeded via geographical isolation among these patchily distributed habitat islands. Though the exceptional dispersal potential of spore-bearing plants may seemingly preclude the relatively fine-scale geographical isolation observed here in *Phlegmariurus*, evidence suggests that long-distance colonization events in ferns and lycophytes is likely the exception rather than the norm. For example, experimental studies have indicated that most spores are dispersed within a meter of the parent sporophyte (Conant, 1978; Peck *et al.*, 1990) and that most surveyed species predominately engage in outcrossing in the wild, limiting the possibility of establishment via dispersal of a single spore (Soltis & Soltis, 1990; Haufler *et al.*, 2016; Sessa *et al.*, 2016). Furthermore, recent phylogenetic and taxonomic work has presented compelling evidence of allopatric speciation at relatively small geographical scales in both temperate (Wang *et al.*, 2011; Metzgar *et al.*, 2013) and tropical (Luna-Vega *et al.*, 2012; Ramírez-Barahona & Luna-Vega, 2015; Moran, 2016) taxa. Though further work is needed to generate a robust understanding of the drivers of speciation in tropical ferns and lycophytes, this study and earlier phylogenetic work on some Andean fern genera (Kreier *et al.*, 2008; McHenry & Barrington, 2014; Sánchez-Baracaldo & Thomas, 2014) suggests that speciations in these groups largely follow the same patterns observed in montane flowering plant plants, and that the recently formed and patchily distributed habitats in the tropical Andes appear to be hotbeds of rapid diversification in essentially all groups of organisms that occupy them.

Additional factors associated with the Andean uplift and habitat availability that were not detected by our analyses almost certainly played roles in the recent diversification of Andean *Phlegmariurus* and deserve further study. Foremost among these was likely the complex history of fluctuating habitat zonation known to have occurred in the Andes in response to cyclical glaciation during the Quaternary (Simpson, 1975; van der Hammen & Cleef, 1986; Hooghiemstra & van der Hammen, 2004). Given the dramatic topography of the high Andes and the rapid turnover of habitats along elevational gradients in the tropics (Janzen, 1967; Colwell *et al.*, 2008), glacial–interglacial cycles would have had profound impacts on habitat connectivity and gene flow among populations of organisms in the high Andes. During periods of glaciation, the lower limits of alpine habitats were depressed, connecting páramos that had previously been isolated and driving compressions of some montane forest habitats of $\leq 55\%$ (Hooghiemstra & van der Hammen, 2004). Forest limits would then expand upwards and páramos would contract elevationally, and again become isolated as glaciers retreated. An important consequence of this cycle of alternating fusion and fragmentation of alpine habitats is that populations would have been in intermittent contact with each other, complicating the history of divergence among then-young evolutionary lineages in, for example, the *P. crassus* species group. Coupled with the slow accumulation of reproductive isolation in peridophytes (Øllgaard, 1985; Hanušová *et al.*, 2014; Rothfels *et al.*, 2015; Sigel, 2016), this fluctuation in habitat connectivity may explain the weak morphological and genetic differentiation observed among páramo-dwelling species of *Phlegmariurus*. Resolving such dynamic, complex evolutionary scenarios is difficult (Hughes *et al.*, 2006, 2013) and requires larger datasets generated from highly variable markers. Using a large nuclear dataset, Vargas *et al.* (2017) demonstrated widespread introgression and hybridization in a rapidly diversifying clade of Andean *Diplostephium* (Asteraceae) that was undetected with chloroplast and mitochondrial datasets; similar patterns were reported in a recent paper on *Lupinus* (Nevado *et al.*, 2018). These patterns of repeated isolation and fusion of populations have been demonstrated previously in rapidly diversifying extra-Andean groups, such as African cichlids (Joyce *et al.*, 2011; Genner & Turner, 2012), North American sedges (Escudero *et al.*, 2014) and Mexican frogs (Streicher *et al.*, 2014). Application of a similar dataset and approaches should prove illuminating for better understanding the dynamics of recent diversification of *Phlegmariurus* and other high Andean groups.

Acknowledgements

We thank Benjamin Øllgaard and Ashley Field for helpful conversations on the Lycopodiaceae, especially Neotropical *Phlegmariurus*. Michael Sundue and Art Gilman provided important insights that contributed to the development of ideas expressed in this work. We thank Laura Lagomarsino for sharing R scripts and paleoelevation data, as well as for helpful discussion. Editor Jana Vamosi, Laura Lagomarsino and two anonymous reviewers provided helpful comments on earlier versions of this


manuscript. This work was supported by a National Science Foundation Doctoral Dissertation Improvement Grant awarded to WLT and DSB (DEB-1601502).

Author contributions

WLT and DSB planned and designed the research; WLT conducted fieldwork, performed lab work, analyzed data; and WLT, ES and DSB wrote the manuscript.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Time-calibrated phylogeny of Neotropical *Phlegmariurus* generated using BEAST 2.4.5, based on six chloroplast markers. Values given at nodes are mean node ages; bars represent 95% HPD ranges of those ages.

Table S1 Voucher information and GenBank accession numbers for 106 Neotropical *Phlegmariurus* species used in this study.

Table S2 Alignment statistics, selected nucleotide substitution models, amplification/sequencing primers, and PCR conditions for chloroplast DNA regions used in this study.

Table S3 Distributional and ecological attributes of Neotropical *Phlegmariurus* species used in this study.

Table S4 Andean paleoelevation estimates based on Garziona *et al.* (2006, 2008, 2014), Ehlers & Poulsen (2009) and Leier *et al.* (2013).

Table S5 Phylogenetic independent contrasts of distributional and ecological attributes of Neotropical *Phlegmariurus* species used in this study.

Table S6 Tip net diversification rates for 106 species of Neotropical *Phlegmariurus* estimated in BMM.

Table S7 Mean speciation, extinction, and net diversification rates of Neotropical *Phlegmariurus* species estimated in BMM, averaged by species group.

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