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Research Article



Diversification of the *Pristimantis conspicillatus* group (Anura: Craugastoridae) within distinct neotropical areas throughout the neogene

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Determining the relative importance of dispersal and vicariance events across neotropical regions is a major goal in biogeography. These events are thought to be related to important landscape changes, notably the transition of Amazonia toward its modern hydrological configuration ca. 10 million years ago. We investigated the spatio-temporal context of the diversification of one of the major lineages of *Pristimantis*, a widespread and large genus of direct-developing Neotropical frogs. We gathered a spatially and taxonomically extensive sampling of mitochondrial DNA sequences from 754 *Pristimantis* gr. *conspicillatus* specimens, which led to delimiting 75 Operational Taxonomic Units (OTUs). Complete mitogenomes of 35 of these OTUs were assembled and collated with two nuDNA loci to reconstruct a time-calibrated phylogeny. We identified five major clades that diverged around the Oligocene-Miocene transition and that are largely restricted to distinct Neotropical regions i.e. Western Amazonia (*P. conspicillatus* clade), the Brazilian Shield (*P. fenestratus* clade), the Atlantic Forest (*P. ramagii* clade), the Guiana Shield (*P. vilarsi* clade) and the northern Andes (*P. nicefori* clade). The majority of the diversification events within these clades occurred in-situ from the early Miocene onward. Yet, a few ancient dispersal/vicariance events are inferred to have occurred among trans-Andean forests, the Atlantic Forest, the Brazilian and the Guiana Shields, but almost none in the last 10 Ma. The radical landscape transformations during the Miocene caused by the Andean orogeny and hydrological barriers such as the Pebas System and the subsequent transcontinental configuration of the Amazon drainage is a likely explanation for the isolation of the different clades within the *P. gr. conspicillatus*.

Key words: historical biogeography, miocene, mitogenomics, Pebas, species delimitation

Introduction

Amazonia is thought to be a major source of diversity for the remaining Neotropical regions (e.g. Antonelli et al., 2018a; Musher et al., 2019). However, counterexamples abound, with many Amazonian lineages having

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dispersed from the Andes (e.g. Santos et al., 2009; Antonelli et al., 2009; Mendoza et al., 2015), the Pantepui region (e.g. Marques-Souza et al., 2018; Fouquet et al., 2021) and others dispersed more recently from the Atlantic Forest (e.g. Batalha-Filho et al., 2013; Dal Vechio et al., 2018; Prates et al., 2018). These examples suggest that the role of Amazonia as a source of biodiversity for the rest of the Neotropics veils a far more complex evolutionary history, notably lineage and time-period dependent.

The Andes currently act as a barrier to dispersal, isolating Amazonian populations to that of the Pacific coast moist forests such as the Chocó (trans-Andean Forest). Yet, the Andean uplift was a protracted process that propagated from South to North and was punctuated by several intensive phases, notably around 12 and 4.5 Ma (Boschman, 2021). The consequence of this gradual process is exemplified on the biogeography of some lowland species that display an ancient divergence dating back to the early Neogene. In frogs, for instance, such examples of ancient divergences are found in the genera *Allobates* (Réjaud et al., 2020), *Engystomops* (Funk et al., 2012), *Dendropsophus* (Pirani et al., 2020) and *Pristimantis* (Mendoza et al., 2015), while other examples displaying much more recent divergences have also been documented (see Guarnizo et al., 2015).

The uplift of the Andes also had an indirect role in the patterns of Amazonian diversification, by promoting novel habitats and complex hydrological changes during the Neogene (Hoorn et al., 2010). These changes were spatially heterogeneous, with a relative stability in Eastern Amazonia's cratons, while Western Amazonian landscapes were heavily transformed (Shephard et al., 2010). ~~The hydrology of the nearby lowlands was heavily transformed.~~ The Pebas System, a large mega-wetland, drained to the Caribbean Sea occupied most of Western Amazonia between around 23 and 10 Ma, and then transitioned to the modern transcontinental drainage toward the Atlantic Ocean (Figueiredo et al., 2009; Hoorn et al., 2010; ~~Hoorn et al., 2017; Hoorn et al., 2022~~). Subsequently, during the Pliocene and the Pleistocene, additional hydrological events such as river captures reshaped the Western Amazonian landscape (Albert et al., 2018). Pleistocene climatic fluctuations also have impacted the Eastern cratons of Amazonia (Fouquet et al., 2012a) but also patterns of land cover within the 'dry diagonal' (Cheng et al., 2013), a region currently characterized by a dominance of open vegetation biomes considered a barrier to forest species migration between Amazonia and the Atlantic Forest (Batalha-Filho et al., 2013; Mori et al., 1981). Many genera or even families of vertebrates are endemic to Amazonia or to the Atlantic Forest, and only a few

species groups occur in both. These species groups have likely dispersed during the late Tertiary or Quaternary, favored by recent forest expansion and climatic fluctuations (Ledo & Colli, 2017). However, ancient (>20 Ma) dispersals from Amazonia toward the Atlantic Forest have also been hypothesized, notably in anuran groups (Fouquet et al., 2012b, ~~Fouquet et al., 2012c~~, Réjaud et al., 2020).

Frogs generally have reduced dispersal abilities and strong association with specific microhabitats (Zeisset & Beebe, 2008) leading to small distribution ranges, therefore it is assumed that their diversification has been influenced by historical climatic and landscape changes. This is the case of *Pristimantis* species which are direct-developing frogs that generally require narrow bioclimatic conditions, and occur in terra firme forests across small geographical ranges (Rivera-Correa et al., 2016). The diversification of the frog genus *Pristimantis* (Anura: Craugastoridae) seems to mirror the one of some other frog groups, notably the well-studied dendrobatids (Santos et al., 2009) that started to diversify along the Andes and Western Amazonia (Canedo & Haddad, 2012; Mendoza et al., 2015; Rivera-Correa et al., 2016; Waddell et al., 2018). However, the extant diversity of *Pristimantis* remains under-documented (e.g. Pérez & Ron, 2019; Vacher et al., 2020), and consequently so is its evolutionary history. This genus is the largest among vertebrates, with 588 recognized species (Frost, 2022) distributed throughout the Neotropics and divided into 11 currently defined species groups (Padial et al., 2014). One of them, the *Pristimantis* gr. *conspicillatus*, encompasses 47 currently recognized taxa occurring mainly at low and mid elevation in Amazonia but also in the Andes, the Atlantic Forest, the Dry Diagonal (Cerrado) and the trans-Andean forests (Choco, Central America) (Padial et al., 2014 updated from recent species descriptions: Padial et al., 2016; de Oliveira et al., 2020; Taucce et al., 2020; Acosta-Galvis et al., 2020; Acevedo et al., 2020; Köhler et al., 2022; Roberto et al., 2022 and preliminary results, Supplemental Appendix 1). The species richness of this species group seems particularly high in Western Amazonia notably along the Andean foothills. However, the actual number of species probably remains vastly underestimated, as suggested by recent studies (e.g. Taucce et al., 2020; Vacher et al., 2020). Given that early branching lineages might be missing, phylogenetic relationships remain speculative and so do divergence times, currently indicative of an early diversification predating Neogene and the crown age of genus *Pristimantis* estimated to date back some 29.0 Ma (95% HDP = 21.6–37.3 Ma, Waddell et al., 2018; Mendoza et al., 2015).



According to de Oliveira et al. (2020), eastern Amazonian species of *Pristimantis* gr. *conspicillatus* mostly originated *in situ*, suggesting limited connectivity between the biogeographical areas, notably within Amazonia. Similarly, recent phylogenetic reconstructions have suggested that the Atlantic Forest species of the *P. gr. conspicillatus* form an ancient clade that could date back to the Paleogene (Trevisan et al., 2020). This also suggests an ancient connectivity between Amazonia and the Atlantic Forest, and mirrors the pattern found in several other Neotropical frog clades (Fouquet et al., 2012b, Fouquet et al., 2012c, Fouquet et al., 2014; Fouquet et al., 2022; Réjaud et al., 2020; Moraes et al., 2022). The higher species richness of the group in Western Amazonia is also suggestive of an intense diversification in this region, although alternatives could be imagined (*ex-situ* diversification in neighboring regions followed by immigration).

We hypothesize that the diversification of the *Pristimantis* gr. *conspicillatus* took place within Western Amazonia, the Brazilian and the Guiana Shields during the Neogene considering the ecology of the species and the barrier formed by the Pebas wetland system, that occupied a large part of Western Amazonia between 23 and 10 Ma (Antonelli et al., 2009; De-Silva et al., 2016). We thus expect to recover distinct clades in different neotropical regions surrounding western Amazonia with crown ages preceding the demise of the Pebas (<10 Ma), and only a few dispersals after that period. The alternative is that widespread clades have diversified via intense dispersals.

We test this hypothesis by exploring the temporality and directionality of the biotic exchanges across neotropical biogeographic areas of occurrence for the *P. gr. conspicillatus*, and at investigating the impact of historical landscape changes on the diversification of the group. We first evaluated species boundaries within the group, then reconstructed a time-calibrated phylogeny and finally inferred spatiotemporal patterns of diversification.

Materials and methods

Species delimitation

We delimited all major mtDNA lineages within the *Pristimantis* gr. *conspicillatus* using a sampling that included 192 tissue samples, obtained through our own fieldwork and loans from collaborators. We chose to sequence a fragment of the 16S rDNA region, because it is a classical marker for Neotropical amphibian taxonomy and systematics and was available for many additional populations (Vacher et al., 2020). Sampling was

complemented with all the available homologous sequences retrieved from GenBank (622 accessions). In total, 754 sequences of 16S were obtained for this study (sequencing protocols can be found in Supplemental Appendix 2 and database details are provided in Supplemental Appendix 3). These samples cover the entire distribution range of the *Pristimantis* gr. *conspicillatus*, and includes 36 out of 44 valid taxa (details about missing taxa are available in Supplemental Appendix 1). DNA sequence alignment was conducted on the MAFFT online server under the E-INS-i option with default parameters, which is designed for sequences with multiple conserved domains and long gaps (Katoh et al., 2019). We used 16 outgroups including *Craugastor*, *Strabomantis*, *Holoaden* and 12 *Pristimantis* from other clades. The final matrix thus comprised 770 terminals and 580 bp.

Three DNA-based single-locus species delimitation approaches were applied on this dataset: (a) a distance-based method, the Automated Barcode Gap Discovery (ABGD; Puillandre et al., 2012; b) a single-threshold coalescent-based method, the Generalized Mixed Yule Coalescent approach (single threshold GMYC; Monaghan et al., 2009; Pons et al., 2006); and (c) a multi-rate coalescent based method, the multi-rate Poisson Tree Processes model approach (mPTP; Kapli et al., 2017). We defined Operational Taxonomic Units (OTUs) using a majority-rule consensus, i.e. a lineage is considered as being an OTU if supported by at least two of these three methods. Details of the species delimitation analyses, incongruences and possible false positives and negatives are provided in Supplemental Appendix 2. The use of only mtDNA for species delimitation generates known pitfalls (Moritz et al., 2004), and thus this method only provides a first hypothesis that requires confirmation based on other lines of evidence such as nuDNA, bioacoustics and morphological data. Nevertheless, most cases of putative species boundaries based on mtDNA that have been tested turned out to be confirmed, representing well differentiated phenotypically and reproductively isolated species for instance in recent contributions in *Pristimantis* (Fouquet et al., 2022; Köhler et al., 2022; Roberto et al., 2022).

Time-calibrated species phylogeny

One representative for each OTU (n = 75, see Results) was selected to obtain a time-calibrated phylogenetic hypothesis. To this end, high-quality mitochondrial genomes were obtained through low-coverage shotgun sequencing for 35 OTU representatives (see Supplemental Appendix 2 for details regarding mitogenomes sequencing, assembling and annotation). OTUs

for which we could not obtain tissue samples ($n=40$) were represented with available mtDNA sequences in GenBank (12S, 16S, ND1, COI and Cytb; see database details in [Supplemental Appendix 4](#)). Twelve of these OTUs were represented by 16S only. We also selected 18 *Pristimantis* terminals belonging to other species groups (*danae*, *unistrigatus*, *lacrimosus*, *devillei*, *myersi*, *ridens*, *rubicundulus*) and 17 additional Brachycephaloidea terminals as outgroups (all 35 outgroups but one have complete mitogenomes, including 30 newly produced). Finally, we gathered TYR and RAG1 nuDNA sequences from GenBank that were available for most outgroups, and at least one terminal of each major lineage was included in our reconstruction ($n=50$ TYR; $n=39$ RAG1) ([Supplemental Appendix 4](#)).

All coding sequence regions (CDS) and 12S, 16S were extracted from the complete mitogenomes (thus removing D-loop and t-RNAs) and were subsequently aligned with the sequences obtained from GenBank. The alignments were performed gene by gene using the MAFFT7 online server. For rDNA regions, the E-INS-i alignment strategy was used, which is designed for sequences with multiple conserved domain and long gaps, while for the protein-coding genes the G-INS-i strategy was used, recommended for sequences with global homology (Kato et al., 2019). Coding regions were realigned considering reading-frame and concatenated in Geneious V9.1.8.

We selected the best-fit partition scheme and model of evolution for each predefined partition (12S–16S and each codon position of mtDNA and each nuDNA locus) using Modelfinder in IQTREE (Kalyaanamoorthy et al., 2017), with the merging option and with the selection according to the Akaike Information Criterion (AIC).

The time-calibrated tree was reconstructed with BEAST 2.5 (Bouckaert et al., 2014), using a birth-death tree prior to account for extinction processes and incomplete sampling. We parameterized unlinked substitution models according to best model search. Calibration was implemented using an uncorrelated relaxed lognormal clock model of distribution of rate variation among branches for each partition (Drummond et al., 2006). There is no available Craugastoridae fossil evidence, therefore we relied on secondary calibration. We favored secondary calibration over more distant fossil calibration since it would have implied expanding the matrix to distantly related lineages within Hyloidea which would have probably overestimated node ages (Molak & Ho, 2015; Papadopoulou et al., 2010). Three secondary calibration ages were set as uniform priors from Hime et al. (2021), an extensive phylogenomic analysis for anurans: the crown age for Brachycephaloidea excluding

Ceuthomantis (43.0–51.2 Ma), Brachycephaloidea excluding *Ceuthomantis*, *Brachycephalidae* and *Eleutherodactylidae* (39.6–47.8 Ma), the crown age of the clade formed by *Oreobates* + *Phrynopus* and *Pristimantis* (36.4–44.7 Ma).

The Markov Chain Monte Carlo (MCMC) parameters were set with two independent runs of 100 million iterations, recording every 10,000th iteration and discarding the first 15% iterations as burn-in. We combined the log files of the independent runs using LogCombiner 2.5 (Bouckaert et al., 2014) and checked the convergence of our parameters, confirmed by all ESS being above 200. Then, we extracted the maximum clade credibility tree using Tree annotator 2.5 (Bouckaert et al., 2014) resampling 10% of the trees (for a total of 1700 trees).

Biogeographic analysis

Biogeographic inferences were based on a subtree (the full *P. gr. conspicillatus* and two representatives of its sister clade, the *P. gr. danae*) of the time-calibrated phylogeny in the BioGeoBEARS R package (Matzke, 2013). BioGeoBEARS infers ancestral geographic distributions of ancestral species and explores the role of each biogeographic event with a maximum likelihood algorithm. We compared three types of models: (i) a likelihood version of the Dispersal-Vicariance model (DIVALIKE; Ronquist, 1997); (ii) a likelihood version of the BayArea (BBM) model (Landis et al., 2013); and (iii) the Dispersal Extinction Cladogenesis model (DEC; Ree & Smith, 2008). We also compared versions of these models allowing jump dispersal, using the $+J$ parameter, mindful of the debate about the use of this parameter in biogeographical inference (Klaus & Matzke, 2020; Ree & Sanmartín, 2018; Matzke, 2022). We modified the list of geographic ranges in order to forbid state transitions between disjunct areas. Models were compared with the Akaike Information Criterion (AIC).

We considered four non-Amazonian Neotropical areas ([Fig. 2](#)); Atlantic Forest, Dry Diagonal, Andes (considering a ca. 1000 m asl limit with Amazonia), and trans-Andean forests and three regions within Amazonia corresponding to major geological features of the region and to the large biogeographic regions known as Wallace's districts (Hoorn et al., 2010; Wallace, 1854). They include Brazilian Shield, Guiana Shield and Western Amazonia. This results in a total of seven Neotropical areas. It is noteworthy that these subdivisions into West-East-South have been recently confirmed to correspond to major breaks in species composition in birds (Oliveira et al., 2017) and amphibians (Godinho & da Silva, 2018). This partitioning also matches early Neogene East/West and North/South



patterns of diversification (Fouquet et al., 2014; Sheu et al., 2020). Boundaries for the three Amazonian areas correspond to three important modern riverine barriers: the Madeira River, the Negro River and the lower course of the Amazon River. We assigned the different terminals to each of these regions according to their range estimated from the species delimitation. If a OTU was distributed in several regions, we coded the matrix accordingly. We assigned the terminals of the *danae* group to the Andes and Western Amazonia considering all documented species occur in these areas with the exception of one record in the Brazilian Shield.

Results

Species delimitation

The results obtained from the three methods of delimitation were overall congruent, with no hard conflict among partitions i.e. only nested partitioning, ABGD being more conservative with 66 OTUs, while the two other methods, mPTP and GMYC, delimited 72 and 107 OTUs, respectively (Supplemental Appendix 3; Fig. 1). The majority-rule consensus of the three methods yielded 74 OTUs. We further checked the taxonomic identification of these OTUs mostly considering the proximity of our material to type localities since closely related species are generally allopatric but also other taxonomic considerations that are explained in Supplemental Appendix 5). A single OTU was found to lump *Pristimantis giorgii* and *P. moa*, two recently described species that were recovered as distinct OTUs with GMYC (Supplemental Appendix 5). This false negative was avoided following the GMYC delimitation, thus reaching a final number of 75 OTUs. With the exception of *P. koehleri*, all OTUs exhibit small distribution ranges circumscribed to single biogeographic regions. Among these 75 OTUs, 38 were allocated to recognized taxa (out of the 47 ~~currently one~~ for the species group). Closely related OTUs spatially overlap in very rare instances (*P. conspicillatus*, *P. malkini*, *P. condor*; *P. latro*, *P. giorgii*), leading to a strikingly allopatric pattern (Fig. 1). The reevaluation of the species richness and of the species distributions confirmed that the *P. gr. conspicillatus* is heterogeneously distributed with a higher diversity in Western Amazonia (25 OTUs) than in the Brazilian (14 OTUs) and the Guiana Shield (11 OTUs).

Time-calibrated species phylogeny

The genus *Pristimantis* was strongly supported as the sister group of a clade formed by *Oreobates*+*Phrynopus*

(Fig. 2). Other major clades within the Brachycephaloidea (Brachycephalidae, Eleutherodactylidae, Craugastoridae and Strabomantidae) were also strongly supported. The inferred phylogenetic tree was well-resolved within *Pristimantis*: only 11 nodes had posterior probability <0.90, most of them corresponding to recent relationships and at least one terminal with incomplete genomic data (Fig. 2). The *P. gr. conspicillatus* was strongly supported as the sister group of the *P. gr. danae*. Together, these two lineages form the sister group of all the other *Pristimantis* lineages included in this study (assigned to *P. gr. unistrigatus*, *P. gr. lacrimosus*, *P. gr. devillei*, *P. gr. myersi*, *P. gr. ridens*, *P. gr. galdi* according to Padial et al., 2014). We inferred the crown age of *Pristimantis* to be 30.6 My old (HDP 95%: 27.6–33.6; Fig. 2), an age concordant with Waddell et al. (2018; M=29 Ma) and the one of the *P. gr. conspicillatus* to be 27.6 My old (HDP 95%: 24.9–30.4; Fig. 2).

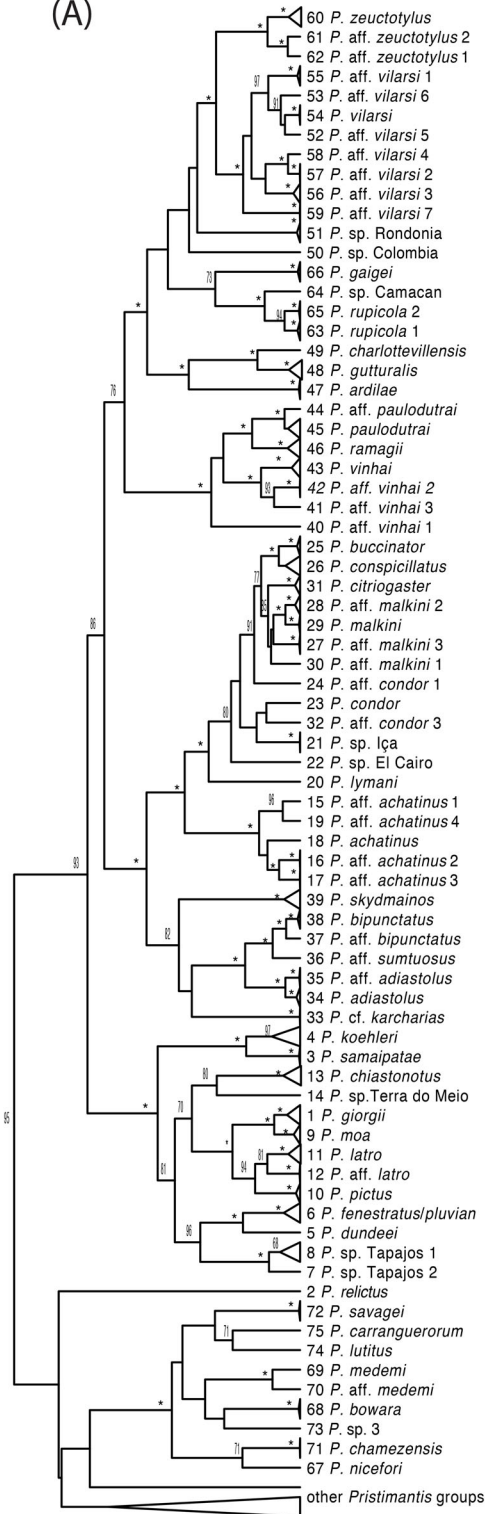
We recovered five major clades within the *P. gr. conspicillatus* that diverged before 23 Ma and are mainly associated to distinct Neotropical regions i.e. the northern Andes (*P. nicefori* clade; 9 OTUs), Western Amazonia (*P. conspicillatus* clade; 25 OTUs), the Brazilian Shield (*P. fenestratus* clade; 13 OTUs), the Guiana Shield (*P. vilarsi* clade; 12 OTUs) and the Atlantic Forest (*P. ramagii* clade; 15 OTUs). Only the *P. ramagii* clade is widespread, with species in the Atlantic Forest, the Guiana Shield (*P. gutturalis*), Trinidad (*P. charlottevillensis*), Western Amazonia (*P. ardila*) and trans-Andean Forests (*P. gaigei*) and the deepest relationships within this clade are poorly supported. The *P. conspicillatus* and *P. fenestratus* clades form a strongly supported group, as well as the *P. vilarsi* and *P. ramagii* clades; while the *P. nicefori* clade forms the sister group of all the other clades of the *P. gr. conspicillatus*. These different clades have diverged around the Oligocene-Miocene transition and each of them diversified from the early Miocene (22.7–17.3 Ma) onward.

Ancestral area reconstructions

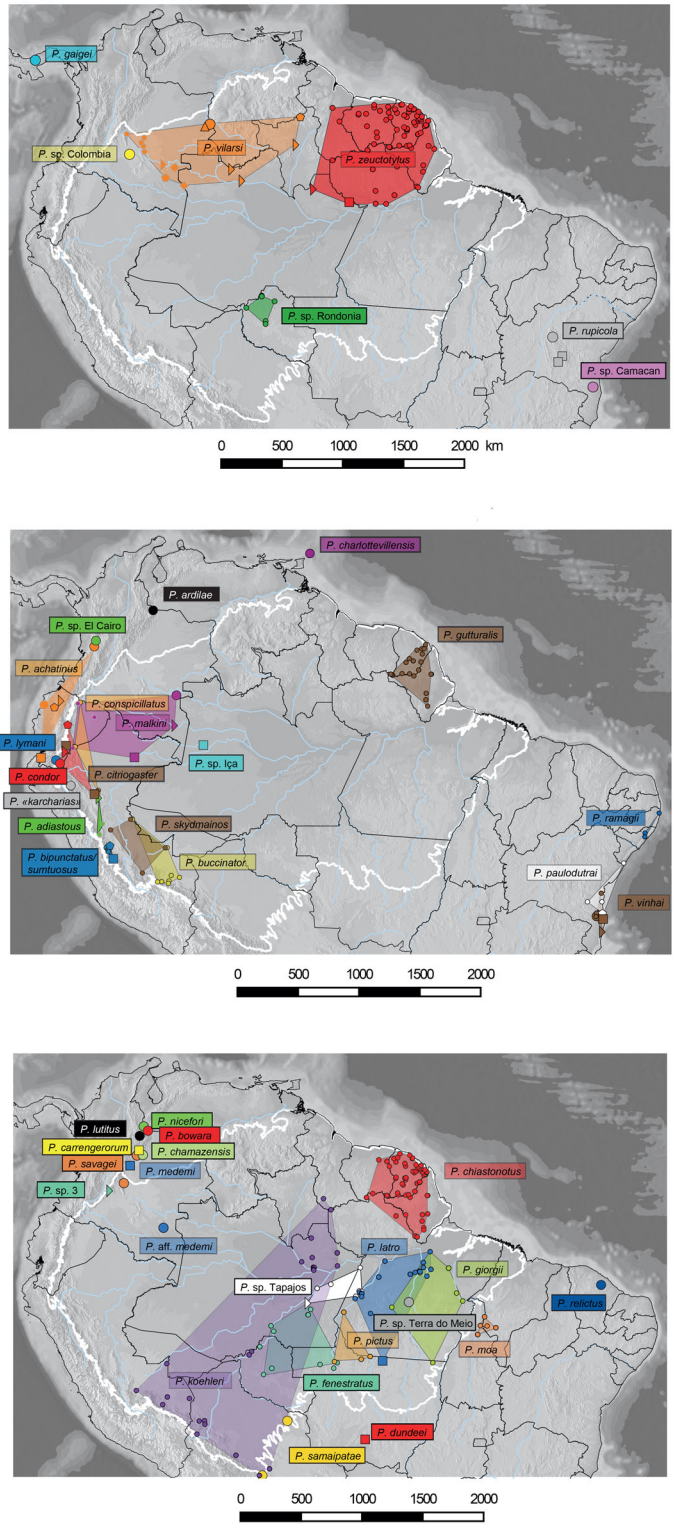
Model comparisons identified DEC+*J* as the model generating the most likely scenario and the DEC as the best model without the *J* parameter (Supplemental Appendix 6). The ancestral range of the most recent common ancestor of the *Pristimantis gr. conspicillatus* is ambiguous (Fig. 3; Supplemental Appendix 7) since it is shared across Amazonia and the Andes in both biogeographic inferences. The *P. nicefori* clade first diverged some 27 Ma from these ancestors apparently in the region that will become the Northern Andes. The four other main clades (*P. conspicillatus*, *P. fenestratus*, *P. ramagii* and

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P. vilarsi) of the *P. gr. conspicillatus* emerged during the Oligocene-Miocene transition some 23 Ma. The *P. conspicillatus* clade diversified starting around 20 Ma in Western Amazonia and its sister group, the *P. fenestratus* clade probably emerged from a dispersal/vicariance event and diversified in the Brazilian Shield as suggested by both DEC and DEC+J models (Fig. 3; Supplemental Appendix 7). The origin of the other clade formed by the *P. vilarsi* clade and the *P. ramagii* clade remains ambiguous since the two models provide contradictory results. It is also the case for the ancestral states of both clades since the DEC+J model favors a Brazilian Shield origin of the *P. vilarsi* clade and an Atlantic Forest origin of the *P. ramagii* clade, while the DEC model favors a Guiana Shield origin of both the *vilarsi* clade and the *P. ramagii* clade. These two clades harbor early divergences corresponding to dispersal-vicariance events complexifying the inferences: (1) Guiana Shield vs Brazilian Shield divergence some 20 Ma for the *vilarsi* clade; (2) Atlantic Forest, Andes, trans-Andean forests and Guiana Shield whose relationships remain ambiguous some 20–23 Ma for the *P. ramagii* clade. It is also noteworthy that diversification within the Atlantic Forest occurred early, with three distinct lineages predating 20 Ma.

Most subsequent dispersal events occurred during the Middle Miocene (10–15 Ma); between the Andes and Western Amazonia in the *P. conspicillatus* and *P. nicefori* clades, as well as between the Brazilian Shield and both the Guiana Shield and the Dry Diagonal. Very few subsequent dispersal events were recovered over the last 10 Ma. All species' distributions are restricted to a single Amazonian area, except *P. koehleri* that stands out as it is distributed in all three of them (Fig. 1). Concomitantly, most diversification events within each clade occurred *in-situ* (Fig. 3).

Discussion

Species diversity in the *Pristimantis conspicillatus* species group

Almost all attempts to investigate how many species actually exist within a particular neotropical amphibian group have uncovered high numbers of candidate species.

Similarly, our exploration of the diversity within the *Pristimantis gr. conspicillatus* highlights that it remains largely undocumented, as already suggested by other studies (Vacher et al., 2020; de Oliveira et al., 2020; Taucce et al., 2020). Considering that we found 75 putative species, this represents a two fold increase in species diversity as compared to the 38 currently recognized taxa that we have included, out of 47 existing nominal species assigned to the group. This rough extrapolation is in line with what has been found in many other co-distributed clades (e.g. *Adelophryne*; Fouquet et al., 2012c; *Allobates* Réjaud et al., 2020; *Bolitoglossa* Jaramillo et al., 2020; *Amazophrynella* Moraes et al., 2022; *Pipa* Fouquet et al., 2022). In the case of *Pristimantis gr. conspicillatus*, this estimation still most likely represents an underestimation of the extent of the unknown diversity since large parts of Amazonia and the Andes remain poorly sampled (Mayer et al., 2019) and given species distributions are circumscribed to narrow areas (at the single exception of *P. koehleri*).

Eight OTUs are not closely related to any valid nominal species (see Supplemental Appendix 5), notably one that may correspond to *P. karcharias* (Flores & Rodriguez, 1997), and 29 more are found related to nominal species that were included (see Supplemental Appendix 5). Since we did not examine morphological or acoustic data we cannot rule out the possibility that some of these unnamed OTUs correspond to non-included valid taxa instead (see Supplemental Appendix 5). However, we consider that this remains likely marginal considering the type localities of the missing taxa are almost only located outside of sampled areas notably in isolated Andean areas or Andean foothills (Supplemental Appendix 1). These uncertainties highlight the need for investigation focusing on these subclades integrating acoustic, phenotypic and genomic data to test whether these OTUs actually agree with the general lineage concept of species (De Queiroz, 1998). We are confident that our study will contribute to fostering such extended studies. We briefly refer to additional taxonomic implications of our results in Supplemental Appendix 5.

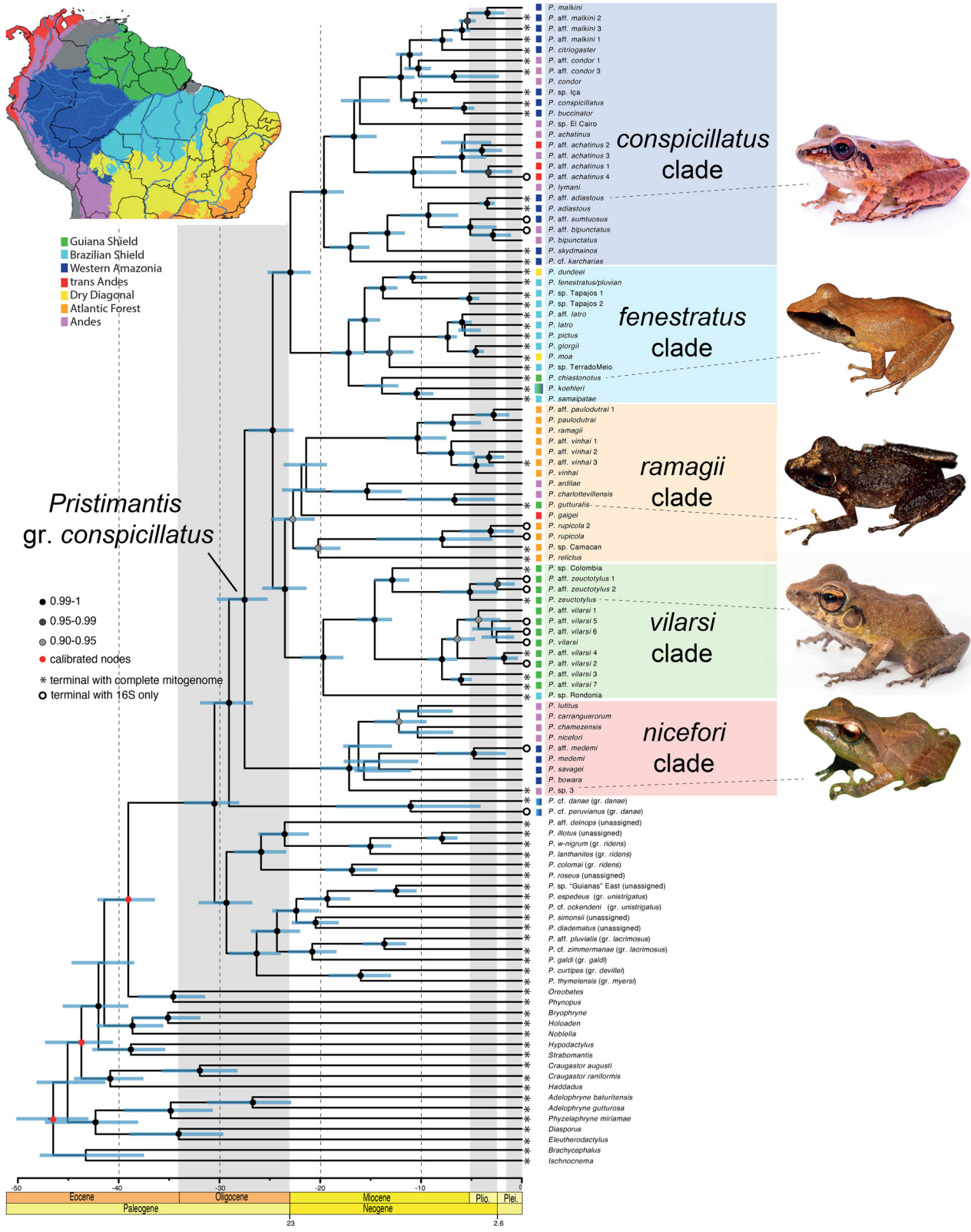
Connectivity among neotropical areas

Because of extinctions, dispersals, vicariances as well as successive landscape changes that reshuffled the spatial distribution of organisms throughout the Cenozoic, our

Fig. 1. DNA-based species delimitation and distribution of resulting OTUs. (A) Maximum clade credibility chronogram inferred in BEAST 2 obtained from the analysis of 754 sequences of 16S (580 bp) of the *Pristimantis gr. conspicillatus*. Posterior probabilities of the nodes are indicated on the left side of the nodes when >0.7 and depicted with * when >0.98. For sake of clarity, terminal branches are collapsed according to the consensus of the DNA-based species delimitation (ABGD, mPTP, GMYC), to which correspond the numbers before the names of the OTUs. (B) Maps of northern South America showing the distribution of the sampled material color-coded as in the tree according to the species delimitation.

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ability to infer the geographic center of diversification of most Neotropical groups generally remains restricted to relatively recent periods i.e. the Plio-Pleistocene period (e.g. for birds: Smith et al., 2014; Silva et al., 2019; Cracraft et al., 2020). Possibly because of their reduced dispersal abilities and their generally strong association with specific microhabitats (Zeisset & Beebee, 2008), amphibians often unraveled much older diversification events (tens of millions of years) than generally found in codistributed groups of birds. The case of the *P. gr. conspicillatus* is unique in this matter since the biogeographic pattern recovered within the group displays a strikingly ancient (early Neogene onward) signal of *in-situ* diversification within each Neotropical region, with only a few subsequent exchanges. Moreover, the distribution and phylogenetic relationships of these lineages suggest that the origin of the entire group is shared between the Andes and Amazonia and predates Neogene. Reinforced by the sister relationship with the *P. danae* group centered on southern Andes and Southwestern Amazonia and the early divergence of the *P. nicefori* clade in the northern Andes, this result points to an origin of the group in the western part of the continent during the late Oligocene. In fact, the whole *Pristimantis* genus is believed to have originated along the Andes during late Oligocene (Waddell et al., 2018).

The five main clades in the group had already diverged at the Paleogene-Neogene (Oligocene-Miocene) transition, some 23 Ma and each of these clades seem to have a distinct spatial origin across the Neotropics. This period corresponds to a global cooling event and dramatic landscape changes in the western part of the continent with large-scale marine incursions (Pozo System) and subsequent presence of large lacustrine systems in Western Amazonia (Hoorn et al., 2010), isolating the Andes and their foothills from the rest of the continent (Bicudo et al., 2019). These changes have been followed by the set-up of the Pebas System which lasted until approximately 9 Ma (Hoorn et al., 2017; Albert et al., 2018) and may have isolated the ancestors of each of these groups that subsequently diversified mainly within each region such as the *P. vilarsi* clade in the Guiana Shield and the *P. fenestratus* clade in the Brazilian Shield. Nevertheless, because of uncertainties regarding ancient paleo-topologic reconstructions

(Bicudo et al., 2019) and dates recovered from time-calibrated phylogenies, it is important to remain cautious on putative causality.

However, the spatial origin of one of these groups, the *Pristimantis ramagii* clade, suggested as being located in the Atlantic Forest by the DEC+J model, actually remains largely uncertain because relationships among early diverging (20–23 Ma) are poorly supported and because these lineages occur in four distinct biogeographic areas. It is therefore possible that Atlantic Forest lineages may in fact form a clade, and given (1) the ancestral distribution of the group is centered on the western part of continent, (2) the sister group of the *ramagii* clade is centered on the Brazilian and the Guiana Shield (*P. vilarsi* clade), (3) a similar ca. 23 Ma dispersal from the Guiana Shield and Amazonia have been found in *Allobates* (Réjaud et al., 2020); *Adelophryne* (Fouquet et al., 2012c), Cophomantini (Duellman et al., 2016); *Adenomera* (Fouquet et al., 2014); *Pipa* (Fouquet et al., 2022) and *Chiasmocleis* (de Sá et al., 2019), and (4) the early divergence of *P. gagei* in trans-Andean Forest and *P. ardilae* + *P. charlottevillensis* from the northern Andes suggest an early diversification in the northern part of the continent, we find more likely that the entire clade ~~find its origin in this area~~ and subsequently dispersed to the Atlantic Forest via the Guiana and/or Brazilian Shields (Fig. 3). In any cases, our results imply that a dispersal route, suggested several times already for frogs (e.g. *Adelophryne*, Fouquet et al., 2012b; *Adenomera*, Fouquet et al., 2014; *Allobates*, Réjaud et al., 2020; *Pipa*, Fouquet et al., 2022) and other vertebrates (Ledo & Colli, 2017), may have existed between Amazonia and the Atlantic Forest at this period (Early Miocene) which is characterized by higher temperature (Zachos et al., 2001). The spatial and temporal similarity of this Amazonia/Atlantic Forest dispersal pattern with the one of *Adelophryne* is particularly remarkable; further similarities are found in the position of a Western Amazonian related group (*Phyzelaphryne* and *P. conspicillatus* clade, respectively); as well as an early divergence within the Atlantic Forest and within the Guiana Shield with similar time frames. Both groups share similar ecological features as they are direct-developing leaf litter frogs; and thus, a possible parallel history of isolation and dispersal (Fouquet et al., 2012b).

Fig. 2. Maximum clade credibility chronogram inferred in BEAST 2 based on concatenated mitogenomic and nuDNA. Nodes with maximum posterior probability are indicated with black dots under the branches and lower support with distinct shaded gray. Calibrated nodes are indicated with a red circle. Node bars indicate the 95% highest posterior distribution of node dates. Squares on the tips of the trees indicate the geographical distribution of extant species sampled in the phylogeny and the corresponding regions are coloured accordingly on the top left map (Llanos, Marajo Island and southern pacific coast being let gray).

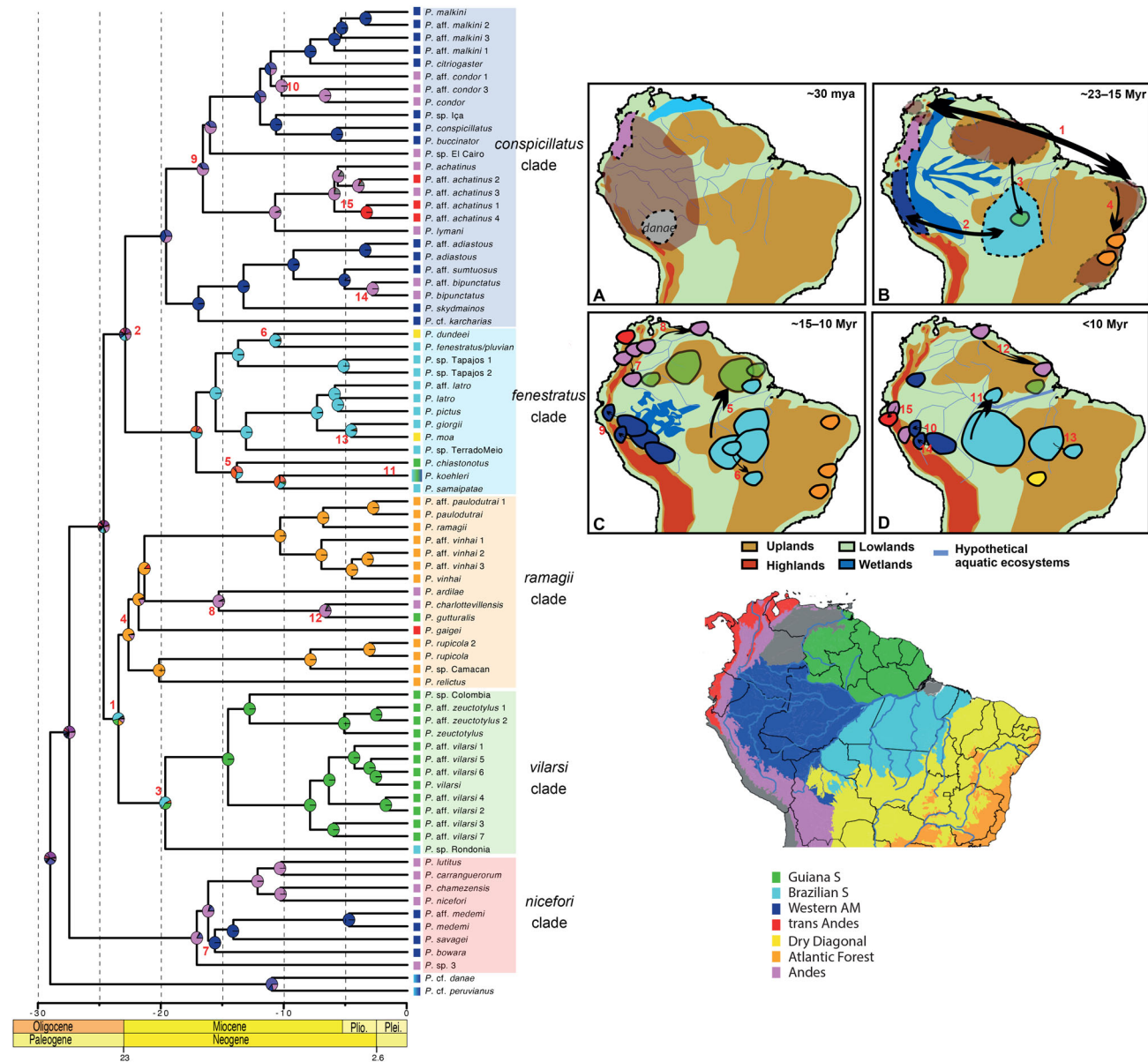


Fig. 3. Ancestral area reconstruction of the *Pristimantis conspicillatus* group using BioGeoBears assuming a DEC + J model for the seven Neotropical biogeographic areas. Squares on the tips of the trees indicate the geographical distribution of extant species sampled in the phylogeny. Pie charts on nodes show the most likely reconstructions of ancestral areas, the size of each slice being proportional to the maximum likelihood. Colors corresponding to the different geographical distributions are depicted in Fig. 2. Hypothetical scenario of dispersal/vicariance depicting 15 events.

The origin of the *Pristimantis conspicillatus* clade is supported in Western Amazonia by both biogeographic models (DEC, DEC + J). However, its subsequent diversification, as well as the one of the *P. nicefori* clade, is characterized by multiple exchanges with the adjacent Andean highlands (three independent dispersals from western Amazonia to Andes for the former, and one dispersal from the Andes to Western Amazon for the second), which secondarily led to trans-Andean dispersals in the *P. conspicillatus* clade (two dispersals from

Andes to Trans-Andean forest). Exchanges between the Andes and Amazonia have previously been identified as an important process in the diversification of *Pristimantis* (Mendoza *et al.*, 2015; Waddell *et al.*, 2018), but also of Dendrobatoidea (Santos *et al.*, 2009), Centrolenidae (Castroviejo-Fisher *et al.*, 2014) and *Bolitoglossa* (Jaramillo *et al.*, 2020). The Andean orogeny induced important climatic changes in this area, notably by altering the moisture transports and precipitations (Insel *et al.*, 2010). These climatic changes

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coupled with an elevational gradient created a mosaic of new environments, a context highly favorable to speciation (Fjelds  et al., 2012; Weir & Price, 2011). Additionally, the complex topography with partially isolated valleys provided high potential for speciation by geographic isolation (Mu oz-Ortiz et al., 2015). We acknowledge that our analyses cannot identify the diversification drivers of the *P. gr. conspicillatus* within the Andean foothills, we notably cannot disentangle between geographic isolation and ecological adaptation (Wiens & Graham, 2005). However, OTUs occurring in the foothills display small distribution ranges that are not overlapping among closely related species (Fig. 1) suggesting a pattern of speciation by geographic isolation. Guayasamin et al. (2017) hypothesized that the low vagility as well as the high mutation rate of *Pristimantis* species could explain why geographic isolation is such an important diversification driver for this genus. The limited proportion of sympatric/ecological speciation in amphibians is similarly observed as an overall niche conservatism (Rolland et al., 2018) which is particularly striking in the *P. gr. conspicillatus*.

There are probably many unsampled species in the *Pristimantis conspicillatus* clade and the effect of such bias hampers many further interpretations. Nevertheless, this clade remained tightly linked to the western part of the continent. Its sister group, the *P. fenestratus* clade, is conversely tightly linked to the eastern part of Amazonia, a situation that is spatially and temporally concordant (ca. 20 Ma) with many other groups such as *Allobates* (R jaud et al., 2020), *Amazophrynella* (Moraes et al., 2022) and *Pipa* (Fouquet et al., 2022). A distribution gap between the Madeira River and the westernmost part of Amazonia is also recovered by our reevaluation of the species range, a situation strikingly similar to the one found in *Amazophrynella* (Moraes et al., 2022). The current diversity within the part of Western Amazonian lowlands previously occupied by the Pebas system mainly originated in the last 10 Ma possibly from dispersals from Andean foothills (Fig. 3). Altogether, this suggests that the Pebas system did prevent dispersals during a period ranging between its formation and the beginning of its conversion to forest ecosystems (23–10 Ma; Hoorn et al., 2010) that might only have been recently suitable for *Pristimantis gr. conspicillatus* species. Several dispersal events predating 10 Ma are recovered between the Guiana and the Brazilian Shield (*P. chiastonotus* and *P. sp.* Rondonia) but none subsequently. It suggests that at some point in the last 10 Ma, the hydrological transformations leading to the formation of a transcontinental Amazon River system prevented exchanges that were previously possible between the Guiana Shield and the Brazilian

Shield for the *Pristimantis gr. conspicillatus* (Albert et al., 2018).

Conclusion

We recovered five major clades that formed before 20 Ma and diversified mostly within distinct biogeographical areas throughout the Neogene. Most of the group diversity accumulated in Western Amazonia and the Andean foothills appear to have played a central role in the diversification. The profound geomorphological changes due to the Andean orogeny induced an alteration of climatic conditions and landscape, setting a favorable context to speciation in the foothills. Conversely, the Pebas system seems to have prevented dispersal across main Amazonian regions as well as diversification in the floodplain until today.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental material

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