Title: Allopatric speciation is more prevalent than parapatric ecological divergence in tropical montane systems (Asteraceae: *Piofontia*)

Short running title: Speciation modes in tropical montane systems

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ABSTRACT

Elucidating how species accumulate in diversity hotspots is an ongoing debate in evolutionary biology. The páramo, in the Northern Andes, has remarkable high indices of plant diversity, endemicity, and diversification rates. A hypothesis for explaining such indices is that allopatric speciation is high in the páramo given its island-like distribution; an alternative hypothesis is that the altitudinal gradients of the Andean topography provides a variety of niches that drive vertical parapatric ecological speciation. A formal test for evaluating the relative roles of allopatric speciation and parapatric ecological divergence has not been carried out. The main aim of our study is to test which kind of speciation is more common in the páramo. We developed a framework incorporating phylogenetics, species' distributions, and a morpho-ecological trait (leaf area) to compare sister species and infer whether allopatry or parapatric ecological divergence caused their speciation. We applied our framework to the species-rich genus *Piofontia* (63 spp.) and found that the majority of speciation events in *Piofontia*, (80%) have been driven by allopatric speciation events, while a smaller fraction (13%) are attributed to parapatric ecological divergence; one event produced inconclusive results (7%). We conclude that páramo autochthonous diversification is primarily driven by allopatric speciation.

INTRODUCTION

Alexander von Humboldt's and Aimé Bonpland's *Tableau Physique des Andes et Pays Voisins* illustrated how plant species are assembled from lowlands to high altitudes in the tropical Andes (von Humboldt and Bonpland 1805). This representation visualized for the first time how diversity changes locally with elevation, setting a seminal starting point for biodiversity studies. Today, 214 years after the first publication of the *Essay on the Geography of Plants* (von Humboldt and Bonpland 1805), scientists have mapped species richness around the globe and have identified numerous hot-spots of biodiversity. Understanding how species accumulation occurred in such hotspots is important for evolutionary biology and biogeography.

Because biodiversity hotspots often coincide with areas of topographic complexity (Barthlott et al. 1996; Myers et al. 2000; Mutke and Barthlott 2005; Jenkins et al. 2013) geographical isolation and ecological opportunity are typically cited to explain species richness. In mountain systems, valleys and canyons act as barriers for organisms (van der Hammen and Cleef 1986; Muños-Ortiz et al. 2015) promoting allopatric speciation (vicariant or peripatric) via geographical isolation; while slopes and ecological gradients can drive parapatric speciation via ecological divergence (Hughes and Atchison 2015; Pyron et al. 2015). Vicariant speciation occurs when a mother species that is distributed broadly is divided into two daughter populations, which speciate via subsequent independent evolution. Glacial and interglacial cycles are often assumed to have caused these vicariant events (van der Hammen and Cleef 1986; Carstens and Knowles 2007). Peripatric speciation occurs when a dispersal event from a source lineage to a new, previously uncolonized, area takes place (founder speciation event). If the newly colonized area is geographically isolated enough, then lineages eventually become

reproductively incompatible with one another, resulting in progenitor and derivative lineage as different species (Coyne and Orr 2004). Parapatric speciation takes place when a continuous population that is distributed along an ecological gradient (e.g. an altitudinal gradient) is subdivided in two or more subpopulations that locally adapt to different niches (e.g. lower vs. higher elevations); the initial subpopulations become independent species by means of ecological differentiation, non-random mating, and the formation of reproductive barriers (Givnish 1997; Schluter 2000; Simpson 1953).

The Páramo, a high-altitude ecosystem found above the timberline in the Northern Andes (the Andes of Ecuador, Colombia, and Venezuela, Luebert and Weigend 2014; Weigend 2002), provides an ideal escenario to test how speciation happens in biodiversity hotspots (Fig. 1). With c. ~3,400 species of vascular plants (Luteyn 1999), of which 60% to 100% are estimated to be endemic (Luteyn 1992; Madriñán et al. 2013), and particularly high diversification rates (Madriñán et al. 2013), the páramo is considered the most species rich ecosystem of the world's tropical montane regions (Sklenář et al. 2014). Unlike other South American high-altitude areas farther south, the páramo is characterized by abundant precipitation, and is therefore defined by both high altitude and humidity. It has been estimated that the páramo originated when the high altitudes (>3,000 m) of the Northern Andes emerged as a result of rapid uplift 2–4 mya (van der Hammen and Cleef 1986; Gregory-Wodzicki 2000). The fragmented coverage of the páramo and its altitudinal gradient (~3000–4500) are hypothesized to have acted as drivers of diversification by promoting both allopatric speciation (vicariant or peripatric) via geographical isolation (van der Hammen and Cleef 1986) and parapatric speciation via ecological divergence (Hughes and Atchison 2015). Despite efforts documenting Andean diversification (Nürk et al. 2015; Uribe-Convers and Tank 2015; Lagomarsino et al. 2016; Pérez-Escobar et al. 2017) a formal test to

quantify the relative prevalence of allopatric versus parapatric ecological speciation of taxa in the region is lacking. To quantify the relative contributions of allopatric and parapatric speciation in the páramo, we propose a comparative framework that combines phylogenetic, geographical, and ecological information. We applied this approach to *Piofontia*, a genus restricted to the páramo and the upper boundary of the cloud forest (Blake 1928; Cuatrecasas 1969; Vargas 2011, 2018; Vargas et al. 2017).

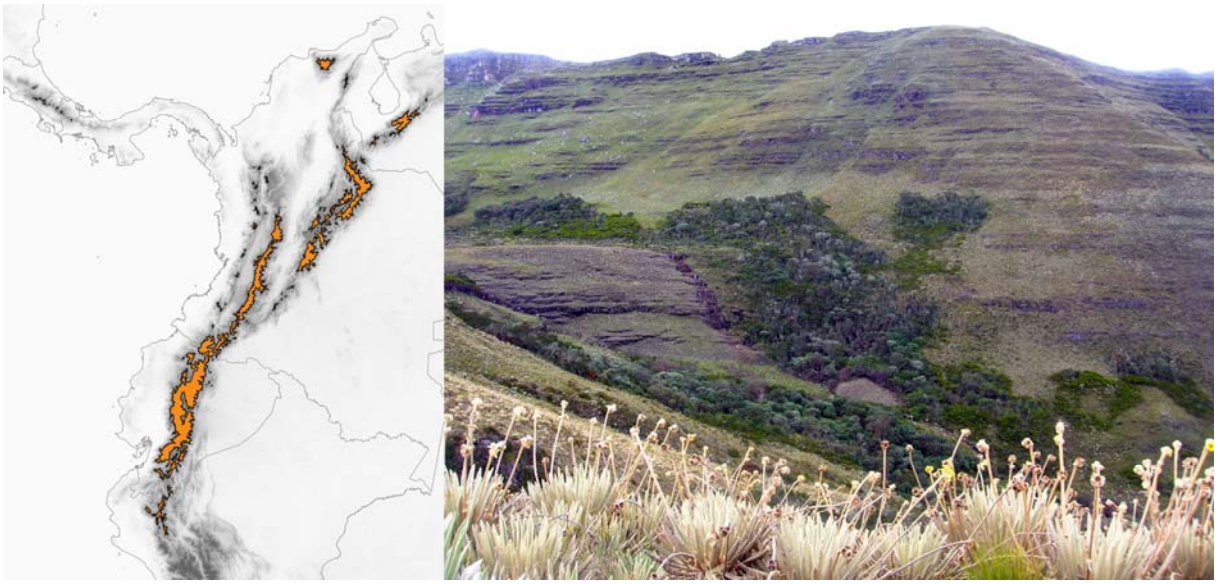

FIGURE 1 Geographical extent of the Páramo ecosystem (left) on the Northern Andes. Páramo la Rusia, Boyacá, Colombia (right); notice the how high Andean forest interdigitates with the Páramo along the creek.

The main aims of our study are to test which kind of speciation, allopatric versus parapatric ecological divergence, is more common island-like systems with high biodiversity. We 1) quantified the relative contribution of allopatric and parapatric ecological speciation in the divergence of sister taxa in *Piofontia*, and 2) complemented our study of recent speciation (sister taxa) with historical biogeographical and comparative phylogenetic analyses to pinpoint the geographical origin of the genus, identify its main center of diversification, and test for significant changes in speciation rates during its evolution.

MATERIALS AND METHODS

R Code, input and control files, and bioregionalization maps are available at https://bitbucket.org/XXXXXXXX/piofontia

FOCAL CLADE

We used *Piofontia* (Asteraceae) because of our recent comprehensive knowledge about its phylogeny (Vargas et al. 2017), distribution, and taxonomy of its species (Cuatrecasas 1969; Vargas 2011; Vargas 2018). Additionally, it is almost entirely restricted to the páramo, although some species dwell in the upper boundary of the cloud forest due to a downslope colonization event (Vargas and Madriñán 2012). The genus contains 63 species distributed in the disjunct mountains of the Talamanca Cordillera (Costa Rica), the Sierra Nevada de Santa Marta (Colombia), as well as the Northern Andes (Cuatrecasas 1969; Vargas 2018). *Piofontia* exhibits a variety of woody habits ranging from decumbent subshrubs only 10 cm tall to small trees 6 m tall. Growth form and leaf area of *Piofontia* species are associated with the habitat they occupy—shrubs and decumbent subshrubs with microphyllous leaves inhabit the open páramo, while small trees with broad leaves reside at lower altitudes in the upper, more humid, edge of Andean forest (Vargas and Madriñán 2012). *Piofontia* was recently segregated from *Diplostephium* (Vargas 2018), a genus with similar morphology and ecology that primarily inhabits the Central Andes.

SISTER SPECIES ANALYSIS OF SPECIATION

To measure the relative contribution of allopatric speciation and parapatric ecological divergence on recent speciation events, we compared the geographical distribution and the leaf

areas of species shown to be sister in the phylogeny of *Piofontia* (Vargas et al. 2017). We used leaf area as a surrogate measure to evaluate ecological divergence between sister species. Leaf area is a functional character that varies with the eco-physiological pressures of a specie's niche (e.g. water availably, irradiance, elevation: Givnish 1987), providing a measurement for ecological niche. When possible, we measured the area of 30 leaves from six different individuals of each species. We scanned the leaves at 600 dpi from herbarium material belonging to ANDES, TEX, and US. Each leaf was outlined using PHOTOSHOP CS4 (Adobe Systems, San Jose, California). We then used the R package MOMOCS (Bonhomme et al. 2014) to calculate the area of each leaf from the images created in the previous step. We performed a Wilcoxon signed-rank tests of the log-transformed leaf areas between sister species using R (R Core Team 2016). It is important to note that this test considers every leaf measurement in each species for the comparison and it is designed to compare non-independent samples.

We scored a sister-species pair as allopatric when they inhabited non-overlapping páramo islands and a sister-species pair as sympatric when their distribution overlapped to some extent at their boundaries on at least one páramo island. Distributional data (see Appendix S1 in Supporting Information) were extracted from a taxonomic treatment (Vargas, in prep.). We interpreted the results in the following fashion (summarized in Fig. 2):

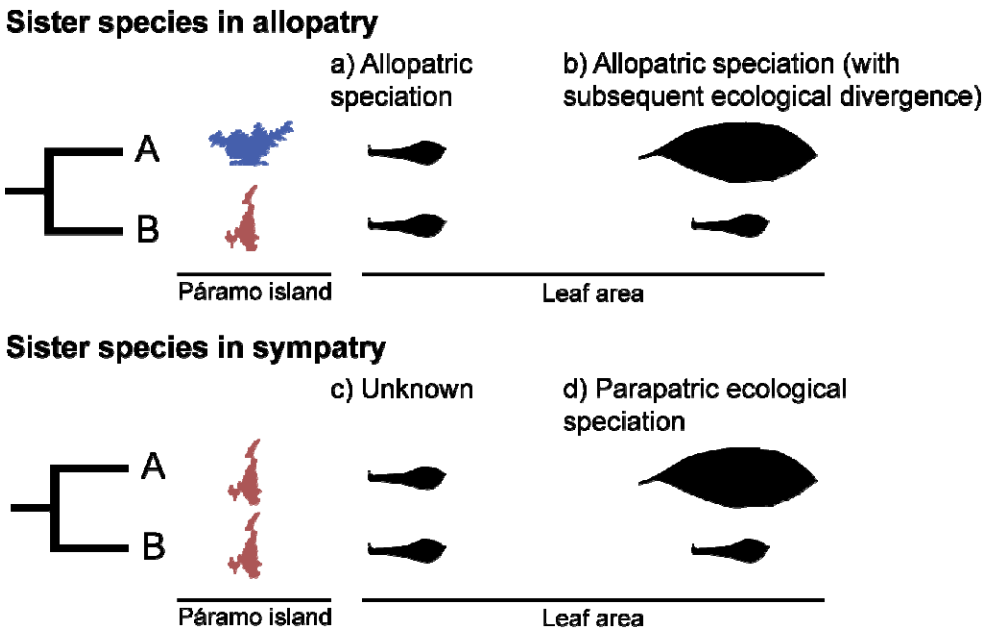

FIGURE 2. Hypothetical scenarios for speciation in sister species. a) Allopatric speciation event in which geographical isolation resulted in two species living in separate páramos islands (indicated by island shape and color) and occupying similar niches (as indicated by similar leaf shapes). b) Allopatric speciation event in which geographical isolation resulted in two species living in separate páramos islands occupying different niches as indicated by different leaf types. c) A speciation event in which the reason for divergence is unknown, sister species inhabit the same island and have similar leaf shapes. d) A parapatric ecological speciation event in which sister species evolved different leaf areas in response to selection to different niches on the same páramo island.

- If a sister-species pair is allopatric and there is no significant differences between their leaf areas, we interpreted this scenario as an event of allopatric speciation driven by geographical isolation, with the reasoning that leaf area had remained similar because either relatively little time had passed since divergence and/or because of niche conservatism. (Fig. 2a; Wiens 2004; Pyron et al. 2015).
- If a sister-species pair is allopatric and their leaf areas are significantly different, we interpreted this scenario as an event of allopatric speciation following geographical isolation (Fig. 2b) in which there was subsequent ecological divergence driven by local adaption (Rundell and Price 2009; Pyron et al. 2015)
- If a sister-species pair is geographically contiguous or slightly overlapping and their leaf

areas are different, we interpreted this scenario as an event of parapatric speciation with ecological divergence (Rundle and Nosil 2005; Rundell and Price 2009) (Fig. 2d).

- If a sister-species pair has overlapping geographical distributions and there is no significant difference between their leaf areas, we interpreted this scenario as inconclusive (Fig. 2c). This pattern could be the result of different processes, e.g., allopatric speciation with no ecological divergence followed by secondary contact (Rundell and Price 2009; Hopkins 2013) or parapatric speciation event driven by ecological divergence in a trait other than leaf area (e.g., Snaydon and Davies 1976; Silvertown et al. 2005).

Our framework assumes that:

1) Leaf area represents a good proxy for the organism's niche, which is likely true in *Piofontia*. Leaf area is a direct measure from the plant, capturing an eco-physiological proxy to what the *Piofontia* species' experiences in its microhabitat. For example, *P. antioquensis* inhabits the upper Andean forest and has an average leaf area of 848.4 mm^2; in contrast *P. phylicoidea*, dwells in the open páramo with plenty of access to sunlight and has an average leaf area of 4.0 mm^2.

2) The phylogeny employed represents the true species tree and contains all taxa. The best hypothesis to date for the species tree in *Piofontia* (Vargas et al. 2017, based on double digest restriction associated DNA data) contains only a subset of documented *Piofontia* species (36 of 63). To account for the potential effects of missing species in our phylogeny, we searched the taxonomic literature for the most morphologically similar species (assuming this is most likely its sister species) of those species not sampled in the phylogeny and compared their

distributional ranges. We provide two sets of results: a) considering only the pairs derived from the phylogeny and b) pairing non-sampled species to their most likely sister species present on the phylogeny based on taxonomic literature (we provide a discussion explaining why this second set of results is likely the most reliable).

3) The páramo developed only in the last 2–4 Ma (van der Hammen and Cleef 1986; Gregory-Wodzicki 2000) and it is therefore reasonable to assume that its carrying capacity for the number of species has not been reached, and therefore extinction rates are low.

4) The modern species ranges are representative of past ranges, a reasonable assumption given the recent divergence of sister taxa pairs.

SPECIATION RATES AND PHYLOGENETIC SIGNAL IN LEAF AREA

We employed BAMM v.2.5 (Rabosky 2014) to calculate rates of speciation and identify shifts of diversification regimes on the *Piofontia* chronogram. BAMM was run with four chains and ten million generations with an effective sample size > 200 (ESS) and a burn-in fraction of 0.25. We used BAMMtools (Rabosky et al. 2014) to draw a phylorate plot visualizing model-averaged diversification rates and regime shifts over the phylogeny, graph diversification rates through time over the phylogeny, and calculate speciation rates.

To test for phylogentic signal reflected in the evolution of the leaf area in *Piofontia*, we averaged log-transformed leaf data and calculated Pagel's (1999) lambda (λ) using the R package PHYTOOLS (Revell 2012). To calculate λ, the observed phylogeny was compared to modified trees in which the internal branches are compressed to various degrees. When $\lambda = 0$ the observed data follow a model in which internal branches are completely collapsed (star phylogeny), meaning that the trait involves independently from the phylogeny. When $\lambda = 1$ the observed data

follow a model in which the internal branches are not modified, meaning that the evolution of the trait is phylogenetically dependent (Harmon 2018; but see Revell et al. 2008).

BIOGEOGRAPHIC ANALYSIS OF *PIOFONTIA* AND ITS GENERIC RELATIVES

To infer the geographical origin of *Piofontia*, we performed an ancestral biogeographic reconstruction of the most recent phylogeny of *Piofontia* and its generic relatives (Vargas et al. 2017). We defined our biogeographic areas based on the regionalization of the neotropics proposed by Morrone (2014). We modified the shape file produced by Löwenberg-Neto (2014) of Morrone's categorization (2014) using QGIS 2.8Wien (QGIS Development Team 2005) to better reflect the altitudinal gradient of South and Central America and make our regions comparable to other studies focused on high Andean biogeography (e.g. Simpson 1974, 1975; Tovar et al. 2013). We edited the areas manually by adding, joining, and extending them using a digital elevation model layer as reference. Areas where focal taxa were sparse or absent were excluded (i.e. regions with lowland rainforest). The regions used in this study and their correspondences (in quotations) to Morrone's (2014) are:

Northern Central America (M). Mountainous and lowland areas of northern Central America (an integration of the "Mexican transition zone" and the "Mesoamerican dominion").

Talamanca Cordillera (T). Highlands of southern Central America. This area represents the páramos of Costa Rica (part of the "Pacific Dominion" and not considered by Morrone as an independent unit).

Northern Andes (N). Sierra Nevada de Santa Marta and the Andes of Colombia, Venezuela, and Ecuador (an integration and expansion of the "Páramo Province" and the "Cauca Province"). We expanded the combined regions by adding areas above 2,500 m using contours

derived from a digital elevation model. The resulting area incorporated the Serranía del Perijá, the Sierra Nevada de Santa Marta, and the Venezuelan Andes (none considered by Morrone as part of the "Páramo Province"). This region comprises the páramos of South America (Cuatrecasas 1968; Luteyn 1999) and the upper boundary of the high Andean forest beneath them.

Central Andes (*C*). Andes of Peru, Bolivia, northern Chile, and northwestern Argentina. This area comprises the puna, humid puna, and the upper boundary of the high Andean forest found on the eastern slope of the Andes (an expansion of the "South American transition zone"). We expanded this area by including regions over 2,500 m in the same way than we did with the Northern Andes.

Dry Lowlands of Western South America (W). Dry tropical and subtropical areas south to the Amazon rainforest (an integrated area of the "Chacoan and Parana dominions").

The assignment of areas to the tips of non-*Piofontia* and non-*Diplostephium* taxa represented the combined distribution of the entire genus (instead of the sole species sampled); these ranges were inferred from occurrences downloaded from the Global Biodiversity Information Facility portal (http://data.gbif.org) and/or taxonomic revisions (see Appendix S2). The assignment of biogeographic areas to the tips of *Piofontia* and *Diplostephium* species was based on herbarium material from COL, TEX, and US.

We chose BioGeoBEARS (Matzke 2013) to infer the biogeographic history because it implements different models of ancestral range inference, DEC (Dispersal-Extintion-Cladogenesis; Ree and Smith 2008), DIVALIKE (a likelihood version of Dispersal–Vicariance Analysis; Ronquist 1997), and BAYAREAALIKE (a likelihood implementation of the

BAYAREA model; Landis et al. 2013), and it evaluates the addition of the J parameter (Matzke 2014) to each one of the models to account for founder-event speciation (DEC+J, DIVALIKE+J, BAYAREALIKE+J but see Ree and Sanmartín 2018). We pruned the outgroups from the chronogram to carry out the biogeographic analysis, and opted not to use a constrained model (e.g. limiting the presence areas to time windows based on their inferred history) because the paleoaltitudes of the Northern and Central Andes are still debated (Luebert and Weigend 2014).

BIOGEOGRAPHIC ANALYSIS OF *PIOFONTIA* ALONE

To elucidate the biogeographic history of *Piofontia* species and complement our sister species analysis, we performed a second biogeographic analysis at a finer geographical level. We defined the biogeographic areas based on the páramo complexes defined by Londoño, Cleef, and Madriñán (2014) which was restricted to Colombian páramos, and added three complexes to completely cover the distribution of *Piofontia* (and the páramo). Our areas were outlined as follows (areas not included by Londoño et al. (2014) are indicated with a star):

Northern Páramos (N). Páramos of the "Sierra Nevada de Santa Marta" and the "Serranía del Perijá."

Talamanca (T)*. Páramos located in the Talamanca Cordillera of Central America.

Mérida (T)*. Páramos located in the Mérida Cordillera of Venezuela.

Eastern Cordillera (E). Páramos located in Eastern Cordillera of Colombia.

Antioquia (A). Cluster of páramos comprised by areas in the Western and Central Cordilleras of Colombia mostly located in the department of Antioquia, Colombia.

Western Cordillera (W). Páramos located in the Western Cordillera of Colombia with the

exception of those located in the department of Antioquia, Colombia.

Central Cordillera (C). Páramos located in the Central Cordillera of Colombia with the exception of those located in the department of Antioquia, Colombia.

Southern Páramos (S). Páramos located in the Colombian Massif and the Ecuadorian Andes.

We pruned the chronogram of Vargas et al. (2017) to include only *Piofontia* species and used BioGeoBEARS to infer the biogeographic history of the genus evaluating different models. We assigned areas to tips based on a revision of *Piofontia* for Colombia (see Appendix S1).

RESULTS

SPECIATION ANALYSES

Our framework to evaluate speciation modes in *Piofontia* suggests that most recent speciation events were driven by allopatric speciation (Table 1). When only species included in the Vargas et al. (2017) phylogeny are considered (row 1, Table 1; Appendix S3), nine out of 14 sister species pairs (64%) occur allopatrically and have similar leaf areas suggesting divergence by geographical isolation with no evidence of ecological divergence; four species pairs (29%) occur sympatrically and have evidence of ecological divergence in the leaf areas. Only one case presented inconclusive evidence (7%): a sister species pair found in sympatry but with leaf areas that do not present significant differences. When non-sampled species are considered (see Appendix S4) by pairing them to their most likely sampled sister species (row 2, Table 1; Table 2) the contributions of allopatric speciation cases increased to 12 (80%), while the number of cases for parapatric ecological divergence decreased to 2 (13%); the number of inconclusive

cases remains the same, 1 (7%).

TABLE 1 Relative contribution of allopatric speciation and parapatric ecological divergence in *Piofontia* based on sister species comparisons.

Sister sp. pairs based on:	Allopatric isolation	Parapatric ecological divergence	Unknown
Phylogeny of Vargas et al (2017)	9 (64%)	4 (29%)	1 (7%)
Supplementing with missing species	12 (80%)	2 (13%)	1 (7%)

TABLE 2 Sister species comparisons based on the phylogeny of Vargas et al. (2017) and supplemented with non-sampled species (bold).

Sister 1	Sister 2	Wilcox test leaf	Distribution	Divergence	Age (Ma)
P. phylicoidea	*P. lacunosa*	0.4722	Allopatric	Geog. isolation	0.16 (0.01–0.58)
P. obtusa	*P. venezuelensis*	1.0000	Allopatric	Geog. isolation	0.22 (0.01–0.81)
P. violacea	*P. cinerascens*	0.2897	Allopatric	Geog. isolation	0.28 (0.01–0.86)
P. rosmarinifolia	***P. cyparissias***	–	Allopatric	Geog. isolation	–
P. floribunda	***P. farallonensis / perijaensis***	–	Allopatric	Geog. isolation	–
P. rhomboidalis	*P. apiculata*	2.50E-09	Sympatric	Ecological	0.59 (0.01–1.54)
P. alveolata	*P. costaricensis*	1.0000	Allopatric	Geog. isolation	0.56 (0.01–1.46)
P. rhododendroides	*P. schultzii*	1.0000	Allopatric	Geog. isolation	0.92 (0.02–2.14)
P. tenuifolia	***P. elliptica***	–	Allopatric	Geog. isolation	–
P. oblongifolia	*P. mutiscuana*	0.4140	Allopatric	Geog. isolation	0.20 (0.01–0.76)
P. sp. nov. ANT	*P. antioquensis*	0.1663	Allopatric	Geog. isolation	0.52 (0.01–1.47)
P. huertasii	***P. julianii***	–	Allopatric	Geog. isolation	1.41 (0.05–3.18)
P. eriophora	***P. chrysotricha***	–	Allopatric	Geog. isolation	–
P. colombiana	*P. glutinosa*	1.20E-11	Sympatric	Ecological	2.97 (0.11–6.17)
P. romeroi	***P. saxatilis***	–	Sympatric	Unknown	–

COMPARATIVE PHYLOGENETIC ANALYSES

Our diversification analysis with BAMM does not suggest significant changes in the diversification rates inside *Piofontia* (posterior probability = 0.91), for which average speciation rate was calculated at 0.91.

Pagel's (1999) lambda (λ) for leaf area calculated using the phylogeny (Vargas et al.

2017) is 0.98, with a P= 2.8e-09 against the null hypothesis of λ=0, suggesting a strong phylogenetic signal of leaf area in the phylogeny of *Piofontia* (Fig. 3). Considering the result that most sister species have similar leaf areas, this λ also supports the presence of strong niche conservatism in *Piofontia*.

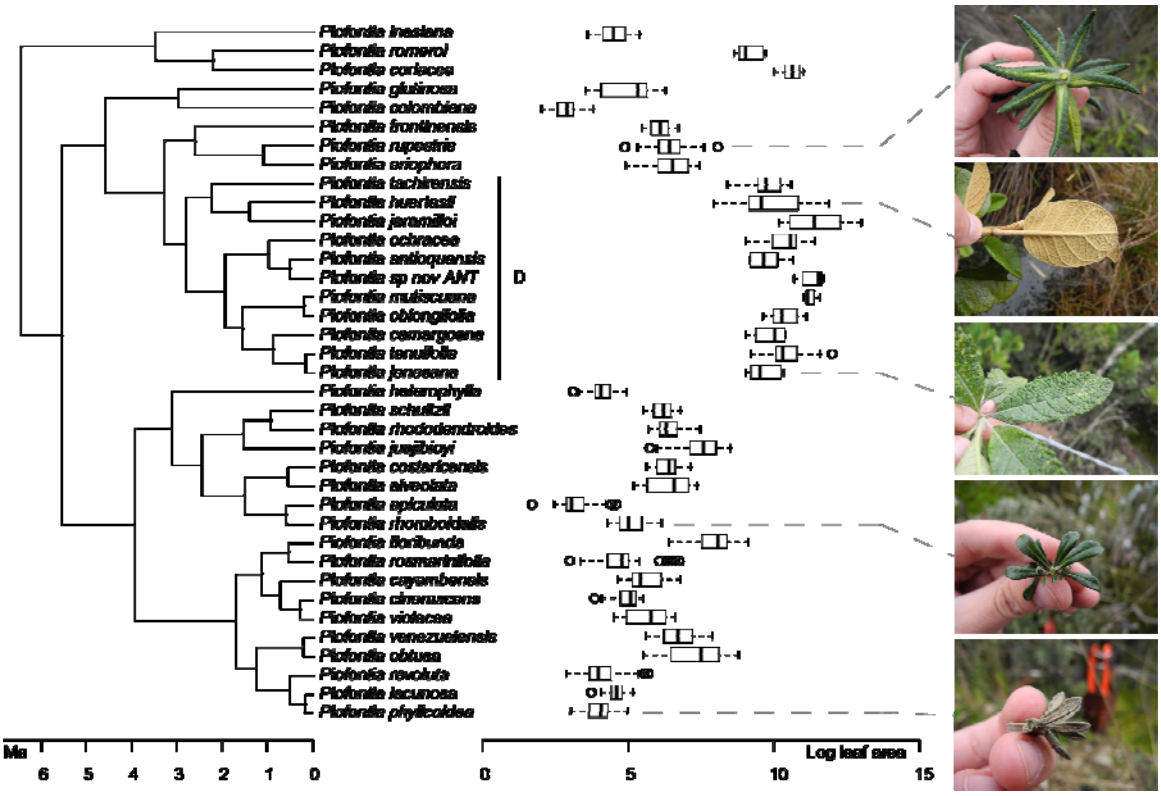

FIGURE 3. *Piofontia* phylogeny (Vargas et al. 2017) with boxplots of the leaf area dataset. Photos on the right correspond to the species indicated by the gray dashed line. The *Denticulata* clade is indicated by the letter D.

BIOGEOGRAPHIC ANALYSES

Among the six models evaluated by BioGeoBEARS using the phylogeny of *Piofontia* and its relatives, DEC performed the best with an AIC of 158.52 followed by DEC+J with an AIC of -160.21 (Table 3). The DEC biogeographic reconstruction suggests that *Piofontia* originated in the Northern Andes and *Diplostephium* originated in the Central Andes (Fig. 4). For

Diplostephium, which is primarily is Central Andean, the analysis also showed that two clades independently colonized the páramo of the Northern Andes (Fig. 4).

The best scoring model in the biogeographic reconstruction for *Piofontia* was the BAYAREALIKE+J with an AICc of 226.78 followed by DEC+J with 232.62 (Table 4). The BAYAREALIKE+J reconstruction (Fig. 5) shows that the Colombian Eastern Cordillera played a major role in the diversification of *Piofontia*. This area, which contains the most species of the genus, was shown to be the ancestral range for most *Piofontia* ancestors (61%). The ancestral range for the node representing the ancestor for all the species is likely the Eastern Cordillera or the Northern Páramos, the latter comprising the Sierra Nevada de Santa Marta and the Serranía del Perijá.

TABLE 3 Comparison of the different biogeographic models for ancestral range inference evaluated by BioGeoBEARS using the phylogeny of *Piofontia* and its relatives (Vargas et al. 2017).

Model	LnL	Num. params	AIC
DEC	-77.26216	2	158.52432
DEC+J	-77.106813	3	160.213626
DIVALIKE	-79.05914	2	162.11828
DIVALIKE+J	-79.060557	3	164.121114
BAYAREALIKE	-94.815207	2	193.630414
BAYAREALIKE+J	-79.092218	3	164.184436

TABLE 4 Comparison of the different biogeographic models for ancestral range inference evaluated by BioGeoBEARS in the phylogeny of *Piofontia* (Vargas et al. 2017).

Model	LnL	Num. params	AIC
DEC	-115.09205	2	234.184098
DEC+J	-113.31082	3	232.621645
DIVALIKE	-115.63941	2	235.278824
DIVALIKE+J	-115.64036	3	237.280724
BAYAREALIKE	-121.933	2	247.865999
BAYAREALIKE+J	-110.39081	3	226.78162

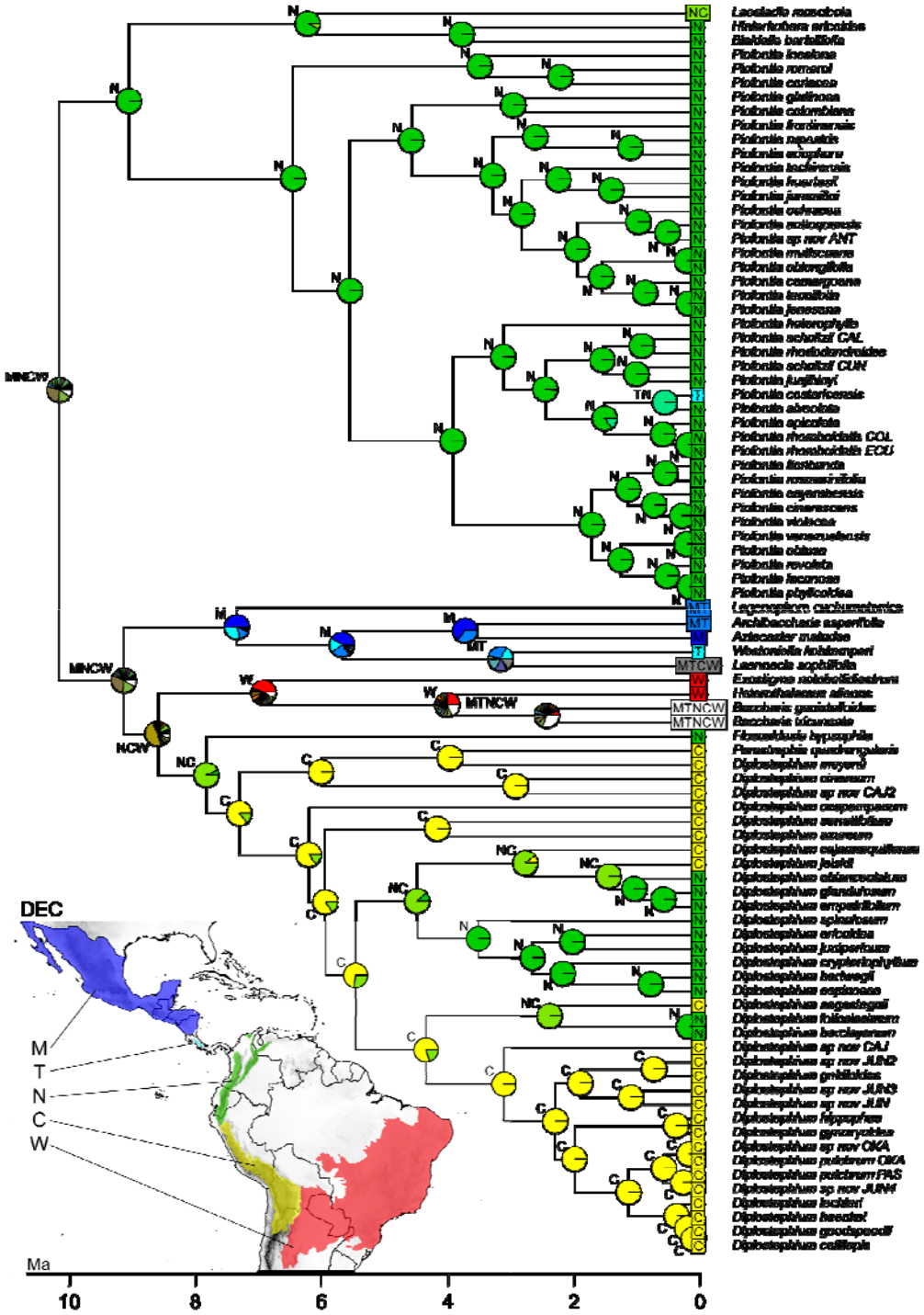

FIGURE 4 DEC ancestral reconstruction based on phylogeny of *Piofontia* and its relatives (Vargas et al. 2017) with percent probabilities of the different ancestral areas shown as pie charts. Letters indicate biogeographic areas considered in the analysis. M: Northern Central America. T: Talamanca Cordillera. N: Northern Andes. C: Central Andes. W: Dry Lowlands of Western South America. Letters above each pie charts indicate the most probably area or area combination for that node.

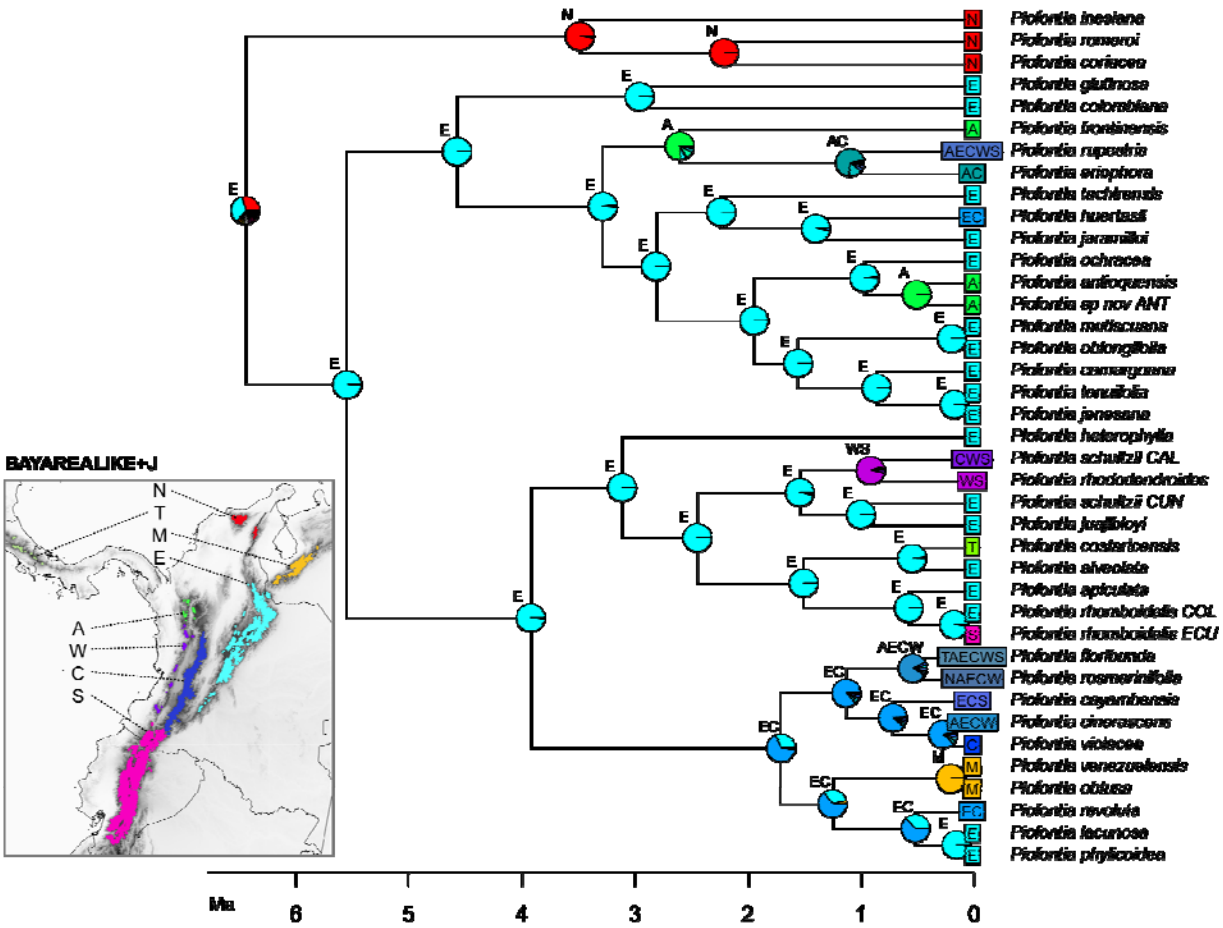

FIGURE 5 BAYAREALIKE+J biogeographical ancestral reconstruction based on the *Piofontia* phylogeny of Vargas et al. (2017) with percent probabilities of the different ancestral areas as pie charts. Letters indicate biogeographic areas considered in the analysis. N: northern páramos. T: Talamanca. M: Mérida. E: Eastern Cordillera. A: Antioquia's páramos. W: Western Cordillera. C: Central Cordillera. S: southern páramos. Letters above each pie charts indicate the most probably area or area combination for that node.

DISCUSSION

In this study, we developed a framework to quantify the relative contributions of allopatric speciation and parapatric speciation ecological divergence for recent speciation events by incorporating phylogenetics, geographic distributions, and a morpho-ecological trait. Our framework was applied to *Piofontia*, a genus of plants restricted to the páramo, which is the most species rich tropical montane ecosystem. Because of the island-like distribution of the páramo and the within-páramo elevation gradient, it has been suggested that allopatric speciation and

parapatric ecological divergence are the main drivers of speciation in the high Andes (van der Hammen and Cleef 1986, Hughes and Atchison 2015). The application of our approach to *Piofontia* revealed that most recent speciation events are allopatric (Table 1). The signal of allopatric speciation between sister species is strong in the two sets of results: using only the sister species of the Vargas et al. (2017) phylogeny (64%) and when non-sampled species are added to the phylogeny (80%). Similarly, the contribution of parapatric ecological divergence to recent speciation events is low (< 30%) in both sets of results: phylogeny only (29%) and non-sampled species added to the phylogeny (13%).

Because 43% species of *Piofontia* were not sampled for its phylogeny (Vargas et al. 2017), we believe that the most reliable estimate for calculating the relative contribution of allopatric speciation vs. parapatric ecological divergence is the phylogeny supplemented with missing sampling (second row, Table 1). Therefore, *we will focus our discussion on the species pairs derived from the phylogeny and supplemented for missing sampling* (second row, Table 1).

ALLOPATRIC VS. PARAPATRIC ECOLOGICAL SPECIATION IN THE PÁRAMO

Our results suggest that most speciation events (12, 80%) in *Piofontia* are driven by allopatric speciation, while only a few are driven by parapatric ecological divergence events (2, 13%). We found no cases of allopatric speciation in which the sister species had undergone subsequent ecological divergence, which was estimated from based on significant differences on leaf areas between species. This lack of ecological divergence suggests a strong signal of niche conservatism in *Piofontia*, as does a Pagel's λ of 0.98 (a value closer to one indicates strong phylogenetic signal in the evolution of leaf area). In the context of the páramo flora, our results are consistent with the idea that páramos are island-like in promoting allopatric speciation,

supporting the idea that allopatric speciation alone can also explain the rapid and high diversification found in other páramo genera where most species seem to be restricted to one or few páramo islands: *Bartsia*, *Espeletia*, *Escallonia*, *Hypericum*, *Jamesonia-Eriosorus*, *Lachemilla*, and *Lupinus*, (Drummond et al. 2012; Zapata 2013; Sánchez-Baracaldo and Thomas 2014; Nürk et al. 2015; Uribe-Convers and Tank 2015; Diazgranados and Barber 2017; Contreras-Ortiz et al. 2018; Morales-Briones et al. 2018).

Although our results suggest a minor role (13%) of parapatric ecological divergence (Table 1), our analysis focused on sister species that likely diverged recently and does not consider more ancient divergent events. When we look at the distribution of leaf area on the phylogeny we observe that taxa in clade D (*Piofontia* series *Denticulata*) have significantly larger leaves suited to dwelling in the upper limit of Andean forest (Fig. 3), Wilcox $P < 2.2e\text{-}16$ for both *P*. ser. *Denticulata* vs. its sister clade, and *P*. ser. *Denticulata* vs *Piofontia*'s most species-rich clade (the clade originating with the most common ancestor of *P. heterophylla* and *P. phylicoidea*). This suggests that an event of ecological shift, from microphyllous to macrophyllous leaves, took place ca. 3 Ma in the origin of the *Denticulata* clade leading to the evolution least 20 species (32% of the total). We hypothesize that the downslope colonization event by the *Denticulata* clade was of parapatric ecological nature because we always see ecological divergence associated parapatry in *Piofontia* sister species (Table 1). Regardless of the reason for ecological divergence (after allopatric speciation or during parapatric ecological divergence), ecological divergence may boost allopatric speciation by allowing a lineage to colonize a new niche and rapidly speciate in it by means of allopatric speciation on an island-like system—we propose this as the *Booster Diversification Hypothesis*. In the specific case of *Piofontia*, the evolution of larger leaves, which happened in one single event ca. 3 Ma, allowed a

lineage to colonize a lower vegetational belt and speciate (Vargas and Madriñán 2012). A similar pattern is found in Andean *Senecio*, where a single forest and a páramo clade each have been documented (Dušková et al. 2017). In the context of adaptive radiations, the *Booster Diversification Hypothesis* implies that ecological shifts happen a few times at deep nodes on the phylogeny, instead of multiple times towards the tips of the phylogeny. *Espeletia*, also a páramo endemic which crown origin is estimated at 2.5 Ma, shows a peak in morphological differentiation relatively deep in its phylogeny, at 1.5 Ma. The *Booster* hypothesis predicts that a *Piofontia* tree with large leaves and a *Piofontia* sub-shrub with small leaves inhabiting the same island páramo are highly unlikely to be sister, and instead are more likely to be distantly related; a trend observed in *Piofontia* where most sister species (80%) are found inhabiting non-overlapping páramo islands. Other potential diversification boosters are genome duplication events (Morales-Briones et al. 2018) and pollination shifts (Lagomarsino et al. 2016).

ALTERNATIVE HYPOTHESES AND FURTHER CONSIDERATIONS

The role of parapatric ecological divergence may be underestimated in this study because we only measured leaf area as an ecological proxy. Ecological traits independent from leaf area can confer the ability to colonize different páramo niches (e.g. Cortés et al. 2018), such as underground eco-physiological adaptations to soils with different water saturation, or physiological adaptations at the anatomical and cellular level. Studying alternative physio-ecological variables in sister species comparisons could shed light other types of ecological divergence, and perhaps increase the number of events in which ecological divergence played a role in speciation of our system.

Our framework is unable to distinguish between vicariant and peripatric speciation.

Testing which kind of allopatric speciation is challenging in island systems—typically peripatric speciation predicts that the founder species will be distributed in a significantly smaller area than the source lineage (Coyne and Orr 2004; Anaker and Strauss 2014; Grossenbancher et al. 2014; Skeels and Cardillo 2019), but geographically restricted patches (e.g. páramos) can confound testing for significant differences in the distributions. However, it is possible that the two kinds of speciation leave different genetic signals in the resulting lineages: similar genetic diversity in sister species after a vicariant event, and significantly different genetic diversity in daughter species resulting from peripatric speciation. Selection of the BAYAREALIKE+J as the best model for the fine-grained biogeographic analysis in *Piofontia* supports the idea that founder speciation events (peripatric speciation), modeled by the J parameter, are important for the speciation of *Piofontia* in the páramos.

Our sister-species framework assumes that speciation is a bifurcating process in which every speciation event produces two species. In the context of vicariant speciation in the páramo, a glacial-interglacial event could result in the fragmentation of one previously continually distributed population, into more than two daughter proto-species; the complex topography of the Colombian Eastern Cordillera provides a probable location for this process to occur (Fig 1, Fig 7-10 in van der Hammen and Cleef 1986). Hypothetically, parapatric speciation can also violate a bifurcating speciation model because a widely distributed population could be the source for multiple independent parapatric ecological divergent events (e.g. in different mountains), making the widely distributed population paraphyletic and leaving a signal incompatible with a bifurcating speciation model.

How does the result of allopatric speciation driving diversification align with recent finds of pervasive hybridization-introgression in páramo plants (Vargas et al. 2017; Morales-Briones

et al. 2018; Pouchon et al. 2018)? High gene flow indices can be explained by the three non-exclusive scenarios. First, under allopatric speciation, recent geographically isolated populations (protospecies) should be reproductively compatible for the time that it takes to reproductive barriers to develop. During that time window, gene transfer between these proto-species is likely to occur and imprint a signal of introgression among sister species. Second, it is possible that, given geographic isolation, the biological pressure to enforce reproductive barriers is relaxed, making geographically isolated proto-species reproductively compatible for a long period of time; this would allow hybridization post-morphological differentiation—that is, hybridization after the time point when they are morphologically different and therefore considered by taxonomists as different species. Third, considering the small geographical ranges and likely low population numbers of most *Piofontia* species, it is possible that introgression has a positive effect by increasing genetic variability and counteracting genetic drift —making gene flow adaptive. Testing these hypotheses with phylogeographic approaches would help to elucidate the role of hybridization in the evolution of páramo plants.

Finally, it has been suggested that hybridization can cause speciation because it has the potential of producing genotypes pre-adapted to un-exploited niches (Anderson and Stebbins 1954; Seehausen 2004); this hypothesis predicts a signal of ecological divergence between the hybrid and its parental species. Taking into account that we only observed two cases of parapatric ecological divergence in sister species, our results suggest that hybrid speciation does not play a major role in the diversification of *Piofontia*.

SPATIOTEMPORAL PATTERNS IN THE DIVERSIFICATION OF *PIOFONTIA*

Our biogeographic reconstruction of *Piofontia* and its allies (Fig. 4) shows that *Piofontia*

originated in the Northern Andes 6.46 Ma, predating the estimated origin of the páramo 2–4 Ma (van der Hammen and Cleef 1986; Gregory-Wodzicki 2000). Despite the fact that *Piofontia*'s inferred age 95% confidence interval of 1.71–11.37 can accommodate such incongruence, other primarily páramo genera like *Arcytophyllum, Brunfelsia, Jamesonia+Eriosorus, Lysipomia, Valeriana,* and *Vasconcellea* also show ages older than 4 Ma (Luebert and Weigend 2014). An explanation for this early origin could be that ancestors of these lineages inhabited the summits of middle elevation mountains (<2000 m) extant at that time. Mid-elevation tropical mountains often have open and semi-dry areas at upper elevations, which are somewhat physiologically similar to the páramo. These physiologically dry patches are caused by well-drained soils and strong winds similar to the contemporary *campos de altitude* and *campus rupestres* in Brazil (Safford 1999; Alves et al. 2014). It is possible that middle elevation mountaintops provided an early habitat for *Piofontia* ancestors before higher elevations were available at 4 Ma. A second alternative is that páramos were available before 2–4 Ma as suggested by Ehlers and Poulsen (2009). A third scenario is that *Piofontia* originated in the Sierra Nevada de Santa Marta (SNSM), a mountain range located in northern Colombia which is now separated from the main Andes Cordilleras; SNSM's paleoelevation remains largely unstudied (Villagómez et al. 2011). Our biogeographic analysis provides some evidence for the last hypothesis because the *Piofontia* species endemic to the SNSM (*P. coriacea, P. inesiana,* and *P. romeroi*) comprise a clade that that is sister to the rest of *Piofontia*, making the SNSM the second most likely area of origin for the genus after the Eastern Cordillera (Fig. 5).

The biogeographic analysis of *Piofontia* suggests that the Eastern Cordillera of Colombia played a major role in the diversification of the genus given the many extant and ancestral species whose distributional range include this area. The Eastern Cordillera contains the most

páramo land area and discrete patches (Londoño et al. 2014) making it ideal for autochthonous allopatric speciation. Our reconstruction also indicates that the Eastern Cordillera was the source for the colonization of three other mountain ranges: the Colombian Central and Western Cordilleras, as well as the Talamanca Cordillera in Central America.

Achenes of *Piofontia* are small and a have a pappus that allows for long-distance dispersal of their seeds by wind (Cuatrecasas 1969). Collectively, *Piofontia* is found on almost every páramo island, with the exception of the southernmost páramos, south of the Girón-Paute valley in Ecuador, which is a biogeographic barrier for numerous Andean genera (Jørgensen et al. 1995). Specific examples of long-distance dispersal in *Piofontia* are shown by the two species reported at the westernmost páramos, in Costa Rica, relatively isolated from other páramos. The first species, *P. costaricense* is endemic to Costa Rica but is probably a direct descendant of *P. alveolata*, which is found the Colombian Eastern Cordillera. The second Costa Rican species, *P. floribunda*, is also reported for Colombia and Ecuador (Vargas 2011; 2018).

CONCLUSIONS

Our comparative framework that incorporates phylogenetics, geographical distributions, and morpho-ecological characters unveiled a high signal of allopatric speciation, supporting it as the process driving most of the recent speciation events in *Piofontia*. The island-like distribution of the páramo is likely a primary factor of autochthonous allopatric speciation via geographic isolation, explaining the particularly high accumulation of plant species in páramo (Simpson and Todzia 1990) and their high speciation rates (Madriñán et al. 2013). Despite the comparatively small role parapatric ecological speciation identified in recent *Piofontia* sister taxa divergences, we propose that ecological divergence has a role that is infrequent but potentially powerful in

island-like systems. When ecological divergence does occur, it allows a lineage to colonize a new niche and then rapidly speciate by means of allopatric speciation between islands. Ecological divergence events that boost diversification are thus expected to be detectable at deeper geological time scales (> 1 Ma). We conclude that allopatric and parapatric ecological divergence are positively synergistic processes in the history of the diversification of páramo plants.

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CONFLICT OF INTEREST

We declare no competing interest.

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