



Research article

Exploring the diversity of andean berries from northern Peru based on molecular analyses

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ABSTRACT

More than 12,000 species have been listed under the category of berries, and most of them belong to the orders Ericales and Rosales. Recent phylogenetic studies using molecular data have revealed disagreements with morphological approaches mainly due to diverse floral arrangements, which has proven to be a problem when recognizing species. Therefore, the use of multilocus sequence data is essential to establish robust species boundaries. Although berries are common in Andean cloud forests, diversity of these taxa has not been extensively evaluated in the current context of DNA-based techniques. In this regard, this study characterized morphologically and constructed multilocus phylogenies using four molecular markers, two chloroplast markers (*matK* and *rbcl*) and two nuclear markers (ITS and *GBSSI-2*). Specimens did not show diagnostic features to delimit species of berries. A total of 125 DNA-barcodes of andean berries were newly generated for the four molecular markers. The multilocus phylogenies constructed from these markers allowed the identification of 24 species grouped into the order Ericales (*Cavendishia* = 1, *Clethra* = 2, *Disterigma* = 2, *Gaultheria* = 4, *Thibaudia* = 4, *Vaccinium* = 3) and Rosales (*Rubus* = 8), incorporating into the Peruvian flora four new records (*Disterigma ecuadorensis*, *Disterigma synanthum*, *Vaccinium meridionale* and *Rubus glabratus*) and revealing the genus *Rubus* as the most diverse group of berries in the Amazonas region. The results of this study showed congruence in all the multilocus phylogenies, with internal transcribed spacer (ITS) showing the best resolution to distinguish the species. These species were found in coniferous forests, dry and humid forests, rocky slopes, and grasslands at 2,506–3,019 masl from Amazonas region. The integration of morphological and DNA-based methods is recommended to understand the diversity of berries along the Peruvian Andean cloud forest.

Abstract in Quechua language

Qhawayraqan astawan chunka iskayniyuq waranqa especiekuna bayasmanta huch'uy mit'a maypichus hatun rak'i chayaqi ordenkunata Ericaleswan Rosaleswan. Chayraqpi Khuski filogeneticamanta rurachiy allincharqan chani-kuna molecularkuna willarqan ayñi rikunawanta morfologocokunamanta, qaylla llapan rantichay t'ika tiktutaywan ñawray, ima kay kaqta qhawacgirqan kay huk champay pachaman riqsiyqa especiekunamanta. Hina kaqtiñtaq, chanikuna qatikipaykunamanta multilocus hat'alliy tiksipmi takyachiypaq saywakuna sinchikuna especiekunamanta. Pana bayaskuna kanku allatinkuna sach'a-sach'api phuyusqa anti runap, ñawran manan karqan achka kamaykuy kunan pacha allwiyaraykupi takyasqakuna ADN. Chayrayku, Noqanchispa taqwi allincharqan huk filogenia multilocus, rarachikupünmi tawa molecular marcadorkuna, caspa iskay markadorkunawan cloroplastomanta (*matK*, *rbcl*) iskay markadorkunawan nuclearkunamanta (ITS, *GBSSI-2*). Kaykunawan filogeniamanta huniqamuran kikinichay iskay chunka tawayoq especies ima tantaqamuran q'anchis generospi (*Cavendishia*=1, *Clethra*=2, *Disterigma*=2, *Gaultheria*=4, *Thibaudia*=4, *Vaccinium*=3, *Rubus*=8), kaykunata huñuyqamuranta piruwanu lllacha kamay tawa musuq quillqakamachikuta (*Disterigma ecuadorensis*, *Disterigma synanthum*, *Vaccinium meridionale*, *Rubus glabratus*). Nocaykuq llusqisqan kuwirinti rikuchirurqan llapankuna filogeniaspi multilocusmanta, kaspaspa espaciador transcrito interno (ITS) pi rikuchina kutuwi mihur rantichay riqsiyqaq especiekunata.

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Abstract in Awajun language

Dekanauwai juú weantug 12000 sag nagkaikiut, júna nejég tente ainawai nuintushkam kuashtai Ericales nuigtu Rosales weantui. Molecularesjai takasmaug júki filogeneticos augtus yamá dekai antugnainasmauwa nuna Morfológicosjai disa umikmaug, júka wainawai kuashag yagkunum, juwai dekaata tamanum kuashat utugchata ama nunuka. Nunui asamtai multilocus takasmauwa nujai dekanui wajukut ainawa pipish tumaig aidaush. Tujashkam kuashtai tentee nejég ainaug ikam naig yujagkim amuamua nunuig, wajupá kuashtakit tusajig ashi dekapasjig ADNjain dischamui. Nuni tamaugmak, ii augtusag dúka takasé filogenia multilocus dekamua nujai, takasji ipák usumat marcadores molecularesjai, jimag marcadores cloroplastosjai (*matK* nuigtu *rbcl*) nuigtu jimag marcadores nuclearesjai (ITS nuigtu *GBSSI-2*). Juu filogenias dekaji 24 sag nagkaikiut tuwaka 7 generosnug tuwaka awa nunu (*Cavendishia*=1, *Clethra*=2, *Disterigma*=2, *Gaultheria*=4, *Thibaudia*=4, *Vaccinium*=3, *Rubus*=8), juui dekanai yamajam ipák usumat ajag perunum awanunu (*Disterigma ecuadorensis*, *Disterigma synanthum*, *Vaccinium meridionale* nuigtu *Rubus glabratus*).

1. Introduction

Botanically, berries refer to small, rounded, shiny, sweet, sour, multi-seeded fruits from different ovaries of a single flower (Mazzoni et al., 2017). In common usage, the meaning of 'berry' certainly differs from this scientific definition. For instance, strawberries, raspberries, and blackberries are considered berries, but these are excluded by botanical circumscription since they are aggregate fruits (Xiang et al., 2017). Berries are consumed worldwide mainly because of the high concentrations of various phytochemicals, such as phenolic compounds, anthocyanins, and flavonoids (Mazzoni et al., 2017; López et al., 2021; Hotchkiss et al., 2021).

Regarding diversity, approximately 12,000 species have been listed under the category of berries (Rose et al., 2018), and most of them belong to the orders Ericales and Rosales (Phipps, 2014; Chase et al., 2016). The larger genera includes species of berries in Ericales are *Impatiens* (~1000 spp.), *Rhododendron* (~1,000 spp.), *Diospyros* (~700 spp.), *Erica* (~700 spp.), *Vaccinium* (~500 spp.), and *Primula* (~400 spp.) (Bouchenak-Khelladi et al., 2015; Schwery et al., 2015). These genera include many well-known tropical and temperate groups that are biogeographically widespread as pantropical and cosmopolitan (Chartier et al., 2017), mainly due to long-distance dispersal or vicariance scenarios (Thomas et al., 2015). In Rosales, the highest diversity of berries includes genera within the family Rosaceae (3,000 species), such as *Rubus* (~750 spp.), *Potentilla* (~400 spp.), *Alchemilla* (~400 spp.), and *Prunus* (~200 spp.) (Focke, 1911; Kalkman, 1993; Phipps, 2014). The great diversity of this group is due to polyploidy, agamospermy and constant hybridization of closely related species (Song and Hancock, 2011; Pedraza-Peñalosa and Luteyn, 2011; Mimura and Suga, 2020). Berry diversity in Rosaceae has a wide distribution, particularly in the temperate forests of the Northern Hemisphere (Hummer and Janick, 2009).

The Andean orogeny is considered one of the most significant events for radiation of vascular plants and the biogeographic history of neotropical species (including andean berries) in South America (Barthlott et al., 2011; Luebert and Weigend, 2014). This is clearly observed in Andean cloud forest ecosystems where high levels of biodiversity and endemism have been reported among different group of vascular plants (Ledo et al., 2012). Additionally, in the Peruvian Andes, the highest number of endemic plants has been found on slopes between 2,500 and 3,000 masl (Van der Werff and Consiglio, 2004). Currently, 113 species of berries in Rosaceae (Rosales) and 385 in Ericales have been reported from Peru (Ulloa-Ulloa et al., 2004; León, 2006a), and most of these species have been reported on the basis of morphological analyses alone (Coico et al., 2016). Many of these species are considered endemic and distributed in meso-andean and montane forest regions and others in natural areas (León, 2006a). However, this diversity has not been confirmed molecularly since phenomena such as high phenotypic plasticity or crypticism might over or under represent diversity, respectively (Calderon et al., 2021).

Recent phylogenetic studies of berries within Ericales have revealed disagreement with morphological approaches, such as those reporting wide floral diversity among species (Schönenberger et al., 2010; Rose et al., 2018). Accordingly, the proper taxonomic positions of these

species and families were mainly resolved using molecular data (Chartier et al., 2017). The initial classification in Rosales (Rosaceae) was based on morphology and the number of chromosomes (Potter et al., 2002, 2007); however, intergeneric hybridization occurring within subfamilies and tribes has proven to be problematic when delimiting species (Hummer and Janick, 2009). To correct this incongruence, molecular analyses (e.g., plastidial markers, plastomes) are an effective tool for examining systematics (Soltis et al., 2011; Rose et al., 2018; Diaz-Garcia et al., 2021). The molecular markers for phylogenetic analyses that have been most commonly used in berries (Rosales and Ericales) are those corresponding to plastidial regions (*matK*, *ndhF*, and *rbcl*), plastidial intergenic spacers (*trnL-trnF*, *trnS-trnG*, *psbA-trnH*), and nuclear regions (*rITS*, *GBSSI-2*) (Kron et al., 2002; Powell and Kron, 2003; Potter et al., 2007; Soltis et al., 2011; Wang et al., 2016). These barcodes have provided information for testing hypotheses on morphology, genetics and evolutionary relationships in phenotypically diverse groups of Ericales and Rosales (Xiang et al., 2017; Okada et al., 2020).

Although berries are common in Andean cloud forests, the diversity of berries has not been extensively evaluated in the current context of DNA-based techniques. Only few reports on the basis of anatomical observations has been presented. Accordingly, the novelty of this study is to characterize molecularly and determine the phylogenetic positions of berries collected from northern Peru, analyzing the evolutionary relationships of these taxa based on two chloroplast markers (*matK* and *rbcl*), the internal transcribed spacer (ITS) region, and nuclear granule-bound starch synthase (*GBSSI-2*). This is the first integrated study using morphology and the generation of DNA-barcodes to explore the diversity of andean berries from Amazonas region.

2. Materials and methods

2.1. Specimen collection

A total of 48 specimens of Andean berries were sampled from eight localities throughout the province of Chachapoyas, Amazonas, in northern Peru (Molinopampa, Granada, Levanto, Chachapoyas, Maino, Leymebamba, La Jalca, and Huancas; Figure 1). A permit for scientific research on wild flora (RDG N° D000394-2020-MIDAGRI-SERFOR-DGGSPFFS, with authorization code N° AUT-IFL-2020-061) was provided by Servicio Nacional Forestal y de Fauna Silvestre (SERFOR). Tissue samples of approximately 50 mm² were taken from leaf tips for molecular analyses and placed in prelabelled 1.5 mL Safelock Eppendorf tubes. For each site, the date, time, and GPS coordinates were recorded. Photographs were taken to record sampling locations and site features. In addition, inflorescences, leaves, and fruits were collected for morphological examination. Samples were morphologically characterized according to Focke (1910, 1911); Middleton and Wilcock (1990); Sleumer (1967); Middleton (1991); Smith (1933); Kron et al. (2002) and Vander and Dickinson (2009) and were deposited in the herbarium of Universidad Nacional Toribio Rodríguez de Mendoza (KUELAP), Peru (Table 1) (Thiers, 2016). Furthermore, the records and morphologies of

berries were revised and contrasted from databases and collections such as the Global Biodiversity Information Facility (<https://www.gbif.org/>), Tropicos from Missouri Botanical Garden (<http://www.tropicos.org>), the New York Botanical Garden Steere herbarium (<http://sweetgum.nybg.org/science>), and JSTOR Global Plants (<https://plants.jstor.org>).

2.2. DNA sequencing and alignment preparation

Genomic DNA was extracted from leaf tissue using the NucleoSpin Plant II Kit (Macherey-Nagel, Düren, Germany) following the Tineo et al. (2020). Briefly, samples were homogenized in a freeze-crush apparatus (SK-100, Funakoshi, Japan). 550 μ l of lysis buffer was added and incubated at 65 °C overnight and then centrifuged at 11000 rpm for 60s. Then, 480 μ l of binding buffer was added and centrifuged at 11000 rpm for 60s. Then, two washing steps of 600 μ l of washing buffer was performed and centrifuged at 13000 rpm for 60s. Finally, 50 μ l of elution buffer was added and centrifuged at 11000 rpm for 60s. DNA concentration was quantified by a Quantus™ Fluorometer (Promega, Madison, USA) (Table 1), and quality was measured by 1% agarose gel electrophoresis and visualized on a photodocumenter (SmartView Pro UVCI-1000, Major Science, Saratoga, USA) (Figure 2). Two chloroplast markers (*matK* and *rbcl*) and two nuclear markers (*nrITS* and *GBSSI-2*) were sequenced. Each gene was amplified

using polymerase chain reaction (PCR) with MasterMix (Promega, Wisconsin, USA) in the following reaction mixture: 10 ng of DNA and 0.25–0.5 pmol of forward and reverse primers for a total volume of 10 μ l. The PCR protocols followed Bustamante et al. (2021) and Tineo et al. (2020), and primer combinations are summarized in Table 2. Amplicons were purified using the NucleoSpin™ Gel and PCR Clean-up Kit protocol (Macherey-Nagel™, Düren, Germany). The sequences of the forward and reverse strands were determined commercially by Macrogen Inc. (Macrogen, Seoul, Korea). The sequences were manually edited with Chromas V.2.6.6 software. The 125 newly generated sequences (DNA-barcodes) from the four markers (*matK*, *rbcl*, *nrITS* and *GBSSI-2*) were deposited in GenBank. These sequences and others obtained from GenBank (Table 3) were initially aligned with Muscle algorithms (Thompson et al., 1994) and were adjusted manually with MEGA10 software (Kumar et al., 2018) (Figure 3).

2.3. Phylogenetic analysis of concatenated sequence data

The phylogenies were based on concatenated data of the four molecular markers (Table 2). An exploratory phylogeny consisting of Ericales and Rosales (340 sequences) was performed to identify the main lineages where Andean berries were embedded. Additionally, separate phylogenies for each lineage were evaluated. Selection of the best-fitting nucleotide

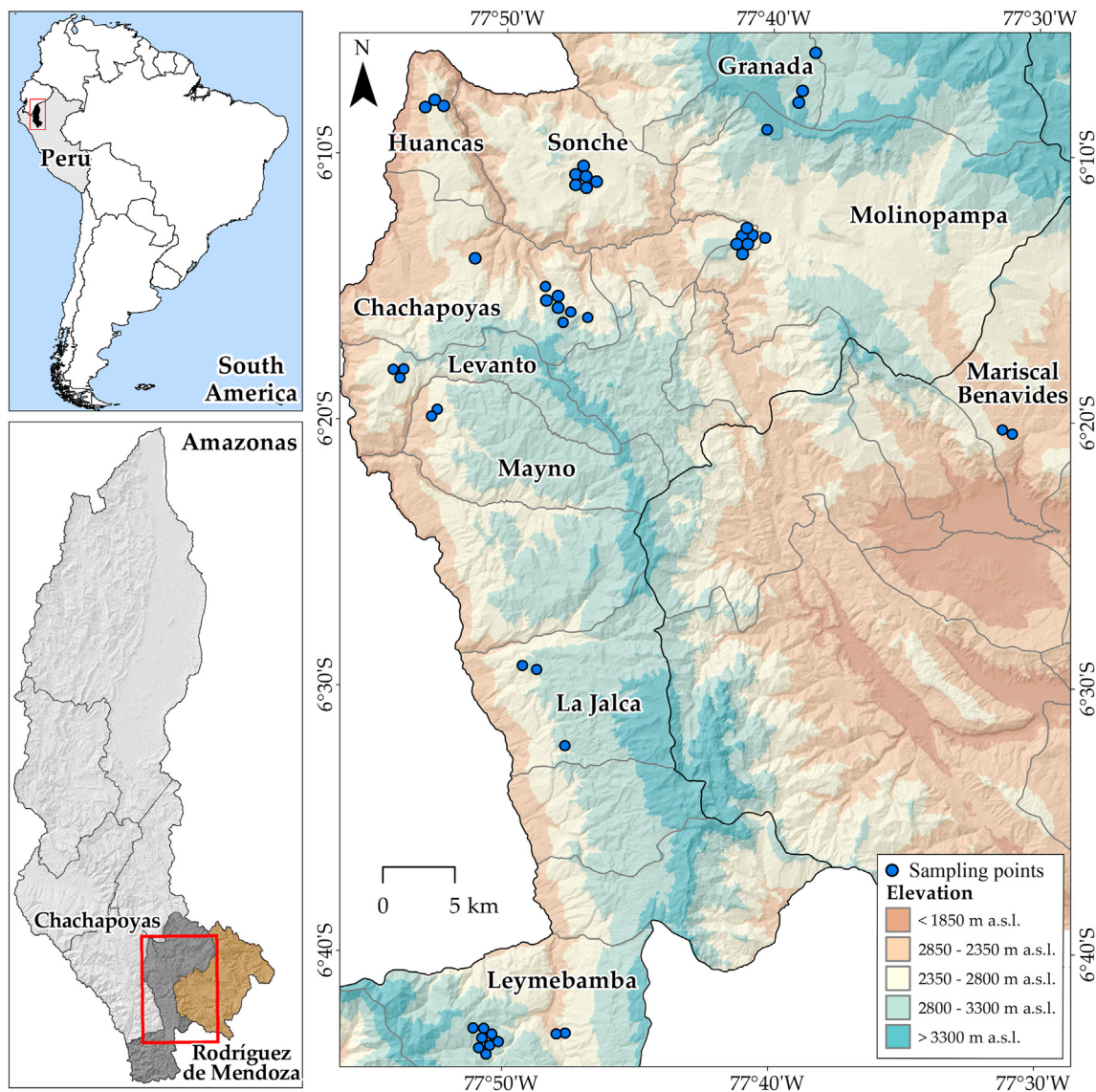


Figure 1. Map showing the sampling of Andean berry specimens from Region Amazonas, northern Peru.

substitution model was conducted using PartitionFinder (Lanfear et al., 2012) for exploratory analysis (using the four partitions *matK*, *rbcL*, *nrITS* and *GBSSI-2*) and for separate phylogenies (using three partitions each) (Table 4). The best partition strategy and model of sequence evolution were selected based on the Bayesian information criterion (BIC) for each phylogeny (Table 4). Maximum likelihood (ML) analyses were conducted with the RAxML HPC-AVX program (Stamatakis, 2014), implemented in the raxmlGUI 1.3.1 interface (Silvestro and Michalak, 2012) using Table 4 models with 1000 bootstrap replications. Bayesian inference (BI) was

performed with MrBayes v. 3.2.6 software (Ronquist et al., 2012) using Metropolis-coupled MCMC and the Table 4 models. Two runs each with four chains (three hot and one cold) were conducted for 10,000,000 generations, sampling trees every 1,000 generations.

3. Results

A total of 125 DNA-barcodes of andean berries were newly generated for the four molecular markers that allowed the construction of

Table 1. List of samples of Andean berries collected in northern Peru including genomic DNA QC using fluorometer.

Species	Code	Herbarium Voucher	Place	Date	Elevation (m.a.s.l)	Latitude (South)	Longitude (West)	DNA concn. (ng/μL)
<i>Cavendishia punctata</i>	IARAN006	KUELAP-267	La Palma	5/07/2017	2934	6° 43' 26.36"	77° 50' 42.30"	50.20
<i>Cavendishia punctata</i>	IARAN018	KUELAP-279	Olmal	13/07/2017	2506	6° 10' 54.69"	77° 47' 07.72"	56.10
<i>Cavendishia punctata</i>	IARAN032	KUELAP-293	Opelele	5/08/2017	2572	6° 15' 18.68"	77° 48' 05.35"	86.30
<i>Cavendishia punctata</i>	IARAN050	KUELAP-311	Santa Rosa	14/08/2017	2794	6° 18' 06.26"	77° 53' 51.48"	80.70
<i>Cavendishia punctata</i>	IARAN046	KUELAP-307	Maino	14/08/2017	2598	6° 19' 35.92"	77° 52' 36.40"	81.02
<i>Clethra ovalifolia</i>	IARAN021	KUELAP-282	Sonche	23/07/2017	2507	6° 10' 40.69"	77° 47' 09.79"	43.00
<i>Clethra retivenia</i>	IARAN034	KUELAP-295	Chachapoyas	5/08/2017	2627	6° 15' 35.49"	77° 47' 59.39"	25.00
<i>Disterigma ecuadorensis</i>	IARAN024	KUELAP-285	La Jalca	28/07/2017	2851	6° 32' 13.45"	77° 47' 42.39"	93.30
<i>Disterigma synanthum</i>	IARAN014	KUELAP-275	Espadilla	13/07/2017	2536	6° 13' 16.64"	77° 40' 51.62"	21.30
<i>Disterigma synanthum</i>	IARAN003	KUELAP-264	La Palma	5/07/2017	2887	6° 43' 28.98"	77° 50' 45.47"	12.00
<i>Gaultheria secunda</i>	IARAN017	KUELAP-278	Espadilla	13/07/2017	2542	6° 13' 16.92"	77° 40' 52.56"	21.00
<i>Gaultheria secunda</i>	IARAN005	KUELAP-266	La Palma	5/07/2017	2912	6° 43' 28.99"	77° 50' 43.98"	8.70
<i>Gaultheria secunda</i>	IARAN023	KUELAP-284	Olmal	23/07/2017	2496	6° 10' 56.73"	77° 47' 08.38"	46.56
<i>Gaultheria secunda</i>	IARAN027	KUELAP-288	La Jalca	28/07/2017	2837	6° 29' 23.55"	77° 48' 47.56"	42.05
<i>Gaultheria secunda</i>	IARAN040	KUELAP-301	Opelele	5/08/2017	2827	6° 15' 30.71"	77° 48' 24.23"	94.72
<i>Gaultheria</i> sp. 1	IARAN041	KUELAP-302	Levanto	14/08/2017	2720	6° 18' 09.99"	77° 53' 51.59"	56.08
<i>Gaultheria</i> sp. 2	IARAN047	KUELAP-308	Levanto	14/08/2017	2770	6° 18' 11.66"	77° 53' 51.18"	79.00
<i>Gaultheria</i> sp. 3	IARAN028	KUELAP-289	La Jalca	28/07/2017	2,700	6° 29' 12.74"	77° 49' 19.11"	17.00
<i>Thibaudia angustifolia</i>	IARAN022	KUELAP-283	Olmal	23/07/2017	2509	6° 10' 44.94"	77° 47' 11.12"	95.01
<i>Thibaudia moricandi</i>	IARAN037	KUELAP-298	Opelele	5/08/2017	2625	6° 16' 04.98"	77° 46' 53.43"	76.30
<i>Thibaudia obovata</i>	IARAN011	KUELAP-272	Espadilla	13/07/2017	2502	6° 13' 11.16"	77° 40' 48.18"	19.03
<i>Thibaudia ovalifolia</i>	IARAN038	KUELAP-299	Tañapampa	5/08/2017	2372	6° 13' 56.99"	77° 51' 13.92"	22.08
<i>Vaccinium floribundum</i>	IARAN001	KUELAP-262	La Palma	5/07/2017	2942	6° 43' 31.76"	77° 50' 42.14"	7.40
<i>Vaccinium floribundum</i>	IARAN004	KUELAP-265	La Palma	5/07/2017	2906	6° 43' 28.99"	77° 50' 43.94"	21.20
<i>Vaccinium floribundum</i>	IARAN007	KUELAP-268	La Palma	5/07/2017	3019	6° 43' 21.11"	77° 50' 33.62"	7.30
<i>Vaccinium floribundum</i>	IARAN012	KUELAP-273	Espadilla	13/07/2017	2515	6° 13' 13.72"	77° 40' 49.62"	23.00
<i>Vaccinium floribundum</i>	IARAN016	KUELAP-277	Espadilla	13/07/2017	2544	6° 13' 17.18"	77° 40' 52.96"	38.09
<i>Vaccinium floribundum</i>	IARAN020	KUELAP-281	Sonche	23/07/2017	2494	6° 10' 47.96"	77° 47' 07.36"	49.86
<i>Vaccinium floribundum</i>	IARAN026	KUELAP-287	Leymebamba	28/07/2017	2857	6° 43' 03.77"	77° 47' 44.91"	12.43
<i>Vaccinium floribundum</i>	IARAN029	KUELAP-290	Huancaurco	2/08/2017	2680	6° 07' 59.65"	77° 52' 34.45"	86.09
<i>Vaccinium floribundum</i>	IARAN031	KUELAP-292	Huancaurco	2/08/2017	2699	6° 08' 10.84"	77° 52' 27.79"	32.00
<i>Vaccinium floribundum</i>	IARAN036	KUELAP-297	Opelele	5/08/2017	2626	6° 15' 24.92"	77° 47' 58.95"	43.32
<i>Vaccinium floribundum</i>	IARAN051	KUELAP-312	Santa Rosa	14/08/2017	2597	6° 19' 38.43"	77° 52' 36.31"	14.00
<i>Vaccinium mathewsii</i>	IARAN002	KUELAP-263	La Palma	5/07/2017	2906	6° 43' 31.46"	77° 50' 43.66"	64.30
<i>Vaccinium mathewsii</i>	IARAN025	KUELAP-286	Leymebamba	28/07/2017	2855	6° 43' 03.79"	77° 47' 45.14"	23.10
<i>Vaccinium mathewsii</i>	IARAN039	KUELAP-300	Opelele	5/08/2017	2827	6° 15' 30.87"	77° 48' 24.53"	65.30
<i>Vaccinium mathewsii</i>	IARAN030	KUELAP-291	Huancaurco	2/08/2017	2727	6° 07' 58.84"	77° 52' 39.03"	32.20
<i>Vaccinium meridionale</i>	IARAN009	KUELAP-270	Espadilla	13/07/2017	2399	6° 13' 04.40"	77° 40' 19.82"	24.90
<i>Vaccinium meridionale</i>	IARAN013	KUELAP-274	Espadilla	13/07/2017	2519	6° 13' 14.60"	77° 40' 49.79"	78.00
<i>Vaccinium meridionale</i>	IARAN019	KUELAP-280	Sonche	23/07/2017	2514	6° 10' 48.38"	77° 47' 07.56"	56.00
<i>Rubus adenothallus</i>	IR003	KUELAP-256	Granada	4/04/2019	2822	6° 06' 07.01"	77° 38' 28.79"	129.20
<i>Rubus andicola</i>	IR001	KUELAP-254	Izcuchaca	4/04/2019	2188	6° 20' 15.31"	77° 31' 06.41"	111.00
<i>Rubus floribundus</i>	IR002	KUELAP-255	Izcuchaca	4/04/2019	2156	6° 20' 15.30"	77° 31' 06.40"	130.00
<i>Rubus glabratus</i>	IR008	KUELAP-261	Calla Calla	4/04/2019	2887	6° 43' 19.29"	77° 50' 45.41"	143.60
<i>Rubus lechleri</i>	IR005	KUELAP-258	Granada	4/04/2019	2923	6° 07' 34.69"	77° 38' 59.81"	110.20
<i>Rubus loxensis</i>	IR006	KUELAP-259	Granada	4/04/2019	2949	6° 07' 34.92"	77° 38' 59.97"	160.00
<i>Rubus sparsiflorus</i>	IR007	KUELAP-260	Granada	4/04/2019	3068	6° 07' 56.21"	77° 38' 59.97"	132.10
<i>Rubus weberbaueri</i>	IR004	KUELAP-257	Molinopampa	4/04/2019	3251	6° 08' 59.48"	77° 40' 16.09"	120.00

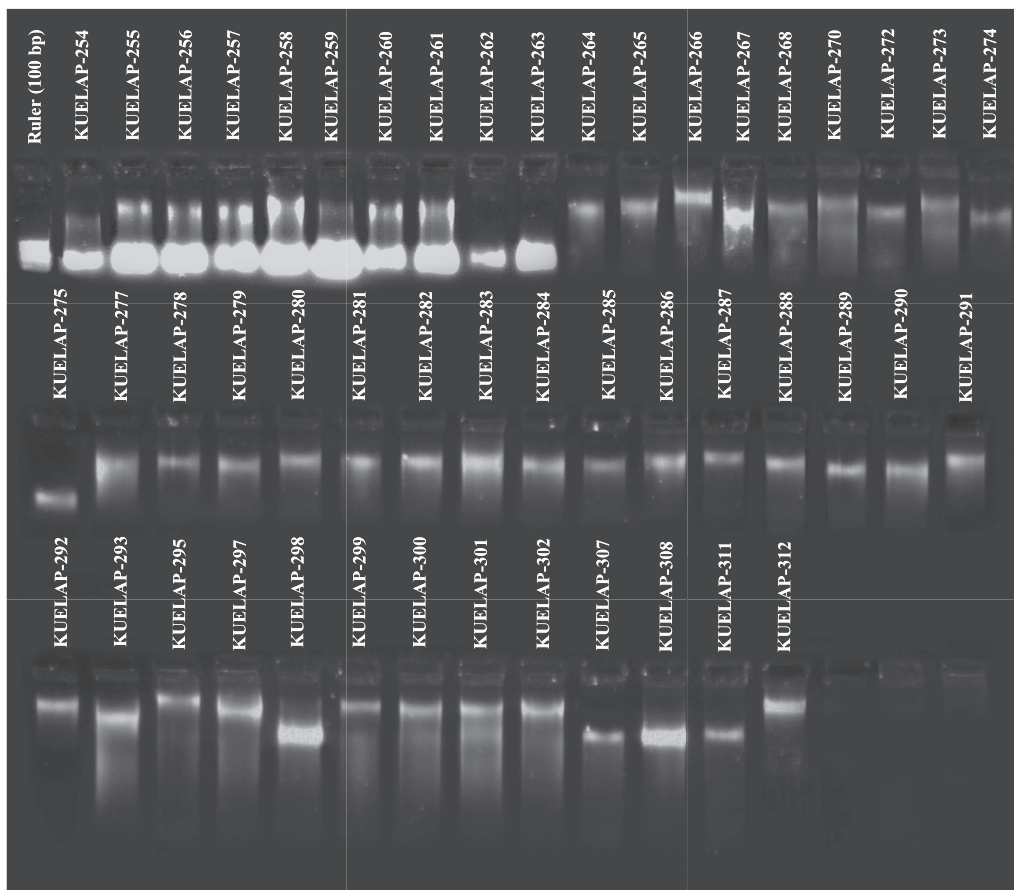


Figure 2. Genomic DNA QC using standard Gel Electrophoresis for Andean berries specimens from Region Amazonas, northern Peru.

multilocus phylogenies. In the exploratory phylogeny, the analyzed data matrix included a total of 3,324 base pairs (bp) (1,487 bp for *matK*, 666 bp for *rbcL*, 716 bp for ITS, and 455 bp for *GBSSI*) from 340 individuals (Table 3). This multilocus phylogeny obtained from the ML and BI analyses molecularly confirmed 24 species from 48 specimens embedded in the order Ericales and Rosales. This exploratory phylogenetic tree showed six monophyly lineages belonging to Ericales [*Cavendishia* Lindl., *Clethra* L., *Disterigma* (Klotzsch) Nied, *Gaultheria* L., *Thibaudia* Ruiz & Pav., and *Vaccinium* L.] and one belonging to Rosales (*Rubus* L.) (Figure S1).

3.1. *Cavendishia*

The phylogeny of *Cavendishia* included concatenated data (1,265 bp for *matK*, 551 bp for *rbcL*, and 631 bp for ITS) from 25 individuals. The specimens KUELAP-211, KUELAP-267, KUELAP-279, KUELAP-293, and KUELAP-307 were recognized as *Ca. punctata* (Ruiz & Pav. ex J.St.-Hil.) Sleumer. This species is characterized by pink peduncles, dark-red

pedicels, pinkish-red calyx, and pale green flowers (Figure 9A, Table 5). This species was placed in sistership with *Ca. bracteata* (Ruiz & Pav. ex A.St.-Hil.) Hoerold. The genetic divergences between these species were over 0.9% for *matK* and 0.4% for ITS (Figures 4, S2, S3). The intraspecific divergences of *Ca. punctata* were 0.7% for *matK*, 0.3% for *rbcL*, and 0.2% for ITS.

3.2. *Clethra*

The multilocus phylogeny of *Clethra* (1,323 bp for *matK*, 532 bp for *rbcL*, and 716 bp for ITS) included 21 individuals. Two species were identified among the specimens, *Cl. ovalifolia* Turcz (KUELAP-282) and *Cl. retivenia* Sleumer (KUELAP-295) (Figure 5). *Cl. ovalifolia* was characterized by oval leaves with stipules in the edges (Figure 9B), while *Cl. retivenia* was diagnosed with pubescent leaves and ferruginous back side leaves (Figure 9C, Table 6). *Cl. retivenia* resolved sistership to the clade composed of *Cl. fimbriata* Kunth, *Cl. ovalifolia* and *Cl. revoluta* (Ruiz & Pav.) Spreng., and genetic divergences were over 0.5% for ITS (Figure S4).

Table 2. Sets of primer combinations for *matK*, *rbcL*, nrITS and *GBSSI-2* markers used for specimens from Ericales and Rosales (listed 5' → 3').

Gene or spacer region	Amplified length (bp)	Primers sequence (5'–3')	References
<i>GBSSI-2</i>	550	F: 5'–TGGTCTTGGTGATGTTCTTGG–3'	Rousseau–Gueutin et al., 2009
		R: 5'–GTGTAGTTGGTTGTCCTTGTAAATCC–3'	Rousseau–Gueutin et al., 2009
ITS	650	F: 5'–GGAAGTAAAAGTCGTAACAAGG–3'	White et al., 1990
		R: 5'–TCCTCCGCTATATGATATGC–3'	White et al., 1990
<i>rbcL</i>	1600	F: 5'–ATGTCACCACAAACAGAACTAAAGC–3'	Chase et al. (2016)
		R: 5'–CTTTTAGTAAAAGATTGGCCGAG–3'	Chase et al. (2016)
<i>matK</i>	1500	F: 5'–CTATATCCACTTATCTTTCAGGAGT–3'	Ooi et al. (1995)
		R: 5'–AAAGTTCTAGCAAGAAAGTCGA–3'	Ooi et al. (1995)

Table 3. List of taxa used in molecular analyses along with voucher numbers followed by GenBank accession numbers. Sequences generated in the present study are in bold.

Species	Voucher/N° Taxon	ITS	matK	rbcl
<i>Cavendishia angustifolia</i>	Pedraza 1749	KJ788223	KJ788254	–
<i>Cavendishia arizonensis</i>	Luteyn 15286	–	KP729914	–
<i>Cavendishia bomareoides</i>	Pedraza 1752	KJ788224	KJ788255	–
<i>Cavendishia bracteata</i>	Luteyn 14223	AY331867	AY331894	–
<i>Cavendishia callista</i>	Clarke 5241	–	KP729912	MF786429
<i>Cavendishia capitulata</i>	Powell 10	AY331868	AY331895	–
<i>Cavendishia complectens</i>	Pedraza 1749	KM209386	–	–
<i>Cavendishia grandifolia</i>	NY/L. 8023	AY331869	AY331896	–
<i>Cavendishia isernii</i>	Salinas 707	KP729959	–	–
<i>Cavendishia leucantha</i>	Pedraza 1768	KJ788226	–	–
<i>Cavendishia lindauiana</i>	Pedraza 1766	KJ788227	KJ788258	–
<i>Cavendishia mariae</i>	Luteyn 15198	KP729960	KP729913	–
<i>Cavendishia martii</i>	Luteyn 15443	AF382658	AF382747	–
<i>Cavendishia micayensis</i>	Pedraza 1888	KJ788228	AF382748	–
<i>Cavendishia nobilis</i>	Lewis 3414	KP729961	KP729916	–
<i>Cavendishia pilosa</i>	Pedraza 1743	KJ788229	KJ788260	–
<i>Cavendishia pubescens</i>	Pedraza 1038	KJ788230	KJ788261	–
<i>Cavendishia punctata</i>	KUELAP–267	OL361763	OL706727	OL707640
<i>Cavendishia punctata</i>	KUELAP–311	OL361767	OL706731	OL707644
<i>Cavendishia punctata</i>	KUELAP–307	OL361766	OL706730	OL707643
<i>Cavendishia punctata</i>	KUELAP–293	OL361765	OL706729	OL707642
<i>Cavendishia punctata</i>	KUELAP–279	OL361764	OL706728	OL707641
<i>Cavendishia quereme</i>	Pedraza 1707	KJ788231	KJ788262	–
<i>Cavendishia tarapotana</i>	Pedraza 1958	KJ788232	KP729915	–
<i>Cavendishia zamorensis</i>	Salina 721	KP729966	KP729917	–
<i>Cavendishia litensis</i>	–	AY331890	–	–
<i>Thibaudia floribunda</i>	–	AF382709	–	–
<i>Thibaudia parvifolia</i>	–	AF382713	–	–
<i>Clethra acuminata</i>	Leonard et al., 1849	AY190572	–	JQ594906
<i>Clethra alnifolia</i>	CCDB–20334–D03	AY190571	MF350258	MG224565
<i>Clethra alnifolia</i>	CCDB–20334–C04	MG220127	AJ429281	MG222185
<i>Clethra arborea</i>	Hedenas & Bisang s.	AY190569	–	–
<i>Clethra arjakana</i>	Sleumer & Vink 4380	AY190568	–	–
<i>Clethra barbinervis</i>	Anderberg & Lundin 11	AY190573	AB697681	AF421089
<i>Clethra canescens</i>	224281	AY190564	–	–
<i>Clethra castaneifolia</i>	S.V&D. 9109	AY190567	–	–
<i>Clethra cubensis</i>	Rova et al., 2248	AY190560	–	–
<i>Clethra delavayi</i>	Aldén et al., 1717	AY190570	–	–
<i>Clethra fimbriata</i>	Harling 27133	AY190563	–	–
<i>Clethra hartwegii</i>	H.S.Gaultheria 2135	AY190574	–	–
<i>Clethra mexicana</i>	C&V 1831	AY190558	–	JQ591083
<i>Clethra ovalifolia</i>	H&A.21905	AY190561	–	–
<i>Clethra ovalifolia</i>	KUELAP–282	OL361761	OL706732	OL707645
<i>Clethra pachyphylla</i>	Emanuelsson 261	AY190565	–	–
<i>Clethra peruviana</i>	S.V et al., 10006	AY190566	–	–
<i>Clethra retivenia</i>	KUELAP–295	OL361762	OL706733	OL707646
<i>Clethra revoluta</i>	Persson 515	AY190562	–	–
<i>Clethra scabra</i>	Oliveira 297	AY190559	–	MG833484
<i>Clethra vicentina</i>	W&M 23234	AY190557	–	–
<i>Ternstroemia</i> sp.	–	–	HQ437950	–
<i>Franklinia alatamaha</i>	–	–	AF380082	MF349693
<i>Diospyros aculeata</i>	–	–	MG201641	–
<i>Disterigma acuminatum</i>	PP1098	FJ001669	–	–
<i>Disterigma agathosmoides</i>	L15190	–	KC175470	–
<i>Disterigma alaternoides</i>	L15074	FJ001672	AY331901	–
<i>Disterigma appendiculatum</i>	PP1113	FJ001673	–	–
<i>Disterigma balslevii</i>	PP998	FJ001674	–	–
<i>Disterigma bracteatum</i>	PP1016	FJ001675	–	–

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Table 3 (continued)

Species	Voucher/N° Taxon	ITS	matK	rbcl
<i>Disterigma chocoanum</i>	PP1121	FJ001696	–	–
<i>Disterigma codonanthum</i>	L15117	FJ001677	–	–
<i>Disterigma cryptocalyx</i>	L14993	FJ001678	–	–
<i>Disterigma dumontii</i>	L15177	FJ001679	–	–
<i>Disterigma ecuadorensis</i>	KUELAP–285	OL361760	OL706736	OL707648
<i>Disterigma empetrifolium</i>	CP7	FJ001680	–	–
<i>Disterigma hiatum</i>	PP1112	FJ001681	–	–
<i>Disterigma humboldtii</i>	P1075	FJ001684	–	–
<i>Disterigma luteynii</i>	LPP14797	FJ001687	–	–
<i>Disterigma micranthum</i>	PP1229	FJ001688	–	–
<i>Disterigma noyesiae</i>	PP1155	FJ001690	–	–
<i>Disterigma ollaceum</i>	PP1528	FJ001697	–	–
<i>Disterigma ovatum</i>	LPP15457	FJ001692	AY331902	–
<i>Disterigma pallidum</i>	PP1506	AF382674	–	–
<i>Disterigma parallelinerve</i>	JB12532	KC175459	–	–
<i>Disterigma pentandrum</i>	L15085	FJ001693	KC175465	–
<i>Disterigma pernettyoides</i>	L15441	–	AF382762	–
<i>Disterigma pseudokillipiella</i>	PP1143	FJ001694	KC175471	–
<i>Disterigma rimbachii</i>	PP1018	FJ001695	AY331903	–
<i>Disterigma staphelioides</i>	PP1062	FJ001698	–	–
<i>Disterigma stereophyllum</i>	L15206	FJ001699	–	–
<i>Disterigma synanthum</i>	KUELAP–264	–	OL706734	OL707647
<i>Disterigma synanthum</i>	KUELAP–275	OL361759	OL706735	–
<i>Disterigma trimerum</i>	L15568	FJ001700	–	–
<i>Disterigma ulei</i>	PP1515	FJ001701	–	–
<i>Disterigma verruculatum</i>	PP1138	FJ001703	–	–
<i>Notopora schomburgkii</i>	–	AF382683	AF382768	–
<i>Orthaea venamensis</i>	–	AF382687	AF382772	–
<i>Orthaea apophysata</i>	–	AF382685	–	–
<i>Gaultheria acuminata</i>	1091527	JF801586	JF801333	–
<i>Gaultheria adenothrix</i>	586107	FJ010595	–	–
<i>Gaultheria antipoda</i>	672075	JF801617	JF801372	KT626709
<i>Gaultheria borneensis</i>	VacciniumK.2101092, ACAD	JF801598	AF366629	JF941568
<i>Gaultheria bracteata</i>	1091528	JF801593	JF801341	–
<i>Gaultheria buxifolia</i>	1091526	–	JF801359	–
<i>Gaultheria cardiosepala</i>	LuLu–06–0022–1	JF976341	HM597394	JF941573
<i>Gaultheria corvensis</i>	1091531	JF801614	–	–
<i>Gaultheria cumingiana</i>	VacciniumK.3101092, ACAD	AF358882	–	–
<i>Gaultheria cuneata</i>	S.D. Z&L. Lu 031543	HM597250	–	–
<i>Gaultheria discolor</i>	GLGS32542	–	HM597366	JN098404
<i>Gaultheria dolichopoda</i>	L. Lu et al., 060005	HM597318	HM597405	–
<i>Gaultheria domingensis</i>	679020	JF801594	JF801342	–
<i>Gaultheria dumicola</i>	LuLu–GLGS20245	–	HM597346	JF941588
<i>Gaultheria eciliata</i>	LuLu–LL–07149–1	–	HM597421	–
<i>Gaultheria erecta</i>	L.13813, NY	JF801585	AF366631	–
<i>Gaultheria eriophylla</i>	763043, RBGE	–	U61317	L12618
<i>Gaultheria foliolosa</i>	L.15075, NY	JF801610	–	–
<i>Gaultheria glomerata</i>	L.15327, NY	JF801592	AF366633	–
<i>Gaultheria gracilis</i>	1091532	JF801587	JF801335	–
<i>Gaultheria hapalotricha</i>	1091533	JF801596	–	–
<i>Gaultheria heteromera</i>	L. Lu et al., 07316A	–	HM597358	–
<i>Gaultheria hispidula</i>	VacciniumK.s.n., ACAD	JF801562	AF366634	MG223840
<i>Gaultheria hookeri</i>	S.D. Z&W.B. Yu 009	–	HM597364	–
<i>Gaultheria humifusa</i>	FF132	FJ665708	JF801346	KX678317
<i>Gaultheria hypochlora</i>	LuLu–GLGS16817–1	JF976381	HM597410	JF941640
<i>Gaultheria insana</i>	672082	JF801604	JF801354	–
<i>Gaultheria lanigera</i>	L.15062, NY	JF801590	–	–
<i>Gaultheria leucocarpa</i>	VacciniumK. 318896, ACAD	JF976385	JF801306	–
<i>Gaultheria macrostigma</i>	176244	FJ665711	JF801369	–

(continued on next page)

Table 3 (continued)

Species	Voucher/N° Taxon	ITS	matK	rbcl
<i>Gaultheria megalodonta</i>	157515	AF358890	AF366639	
<i>Gaultheria miqueliana</i>	1636–77, AA	AF358891	–	AF124590
<i>Gaultheria mucronata</i>	586115	FJ010604	FJ010622	–
<i>Gaultheria myrsinoides</i>	L.14814, NY	AF358892	AF366640	–
<i>Gaultheria notabilis</i>	L. Lu et al., 07005	–	HM597370	–
<i>Gaultheria nubigena</i>	672084	JF801600	JF801350	–
<i>Gaultheria ovatifolia</i>	CCDB–23363–F06	JF801597	–	MG222845
<i>Gaultheria parvula</i>	672087	FJ665715	JF801371	–
<i>Gaultheria praticola</i>	861407	–	JF801383	–
<i>Gaultheria procumbens</i>	Powell s.n., WFU	–	AF366643	MG222887
<i>Gaultheria prostrata</i>	S.D.Z&W.B.Yu ZY011	JF801603	JF801348	JN098405
<i>Gaultheria pseudonotabilis</i>	GLGS 16565	–	HM597382	–
<i>Gaultheria pyroloides</i>	95633	HM597252	JF801349	–
<i>Gaultheria reticulata</i>	L.15077, NY	AF358897	AF366645	–
<i>Gaultheria schultesii</i>	586118	FJ010601	–	–
<i>Gaultheria sclerophylla</i>	L.5331, NY	AF358898	AF366646	–
<i>Gaultheria secunda</i>	KUELAP–278	–	OL706744	OL707650
<i>Gaultheria secunda</i>	KUELAP–284	OL361752	OL706738	OL707651
<i>Gaultheria secunda</i>	KUELAP–301	OL361754	OL706741	OL707654
<i>Gaultheria secunda</i>	KUELAP–288	OL361753	OL706739	OL707652
<i>Gaultheria secunda</i>	KUELAP–266	OL361751	OL706737	OL707649
<i>Gaultheria semi–infera</i>	L. Lu et al., 07312	–	HM597388	–
<i>Gaultheria serrata</i>	1091539	JF801595	JF801343	–
<i>Gaultheria shallon</i>	DNA 185, WFU	JF801581	JF801329	MG221678
<i>Gaultheria sleumeriana</i>	1091540	JF801613	–	–
<i>Gaultheria straminea</i>	L. Lu et al., 07306	–	HM597390	–
<i>Gaultheria strigosa</i>	L.15358, NY	JF801608	AF366647	–
<i>Gaultheria suborbicularis</i>	1045346	JF801563	–	–
<i>Gaultheria tasmanica</i>	1977–5050, RBGK	AF358901	JF801370	–
<i>Gaultheria thymifolia</i>	586120	–	HM597396	–
<i>Gaultheria tomentosa</i>	L.15076, NY	AF358902	AF366648	–
<i>Gaultheria trichophylla</i>	LuLu–ZY–013–1	–	HM597416	JF941727
<i>Gaultheria vaccinioides</i>	1091543	–	JF801331	–
<i>Gaultheria viridicarpa</i>	1842756	–	–	KU564802
<i>Gaultheria</i> sp. 01	KUELAP–302	OL361755	OL706742	OL707655
<i>Gaultheria</i> sp. 02	KUELAP–308	–	OL706743	OL707656
<i>Gaultheria</i> sp. 03	KUELAP–289	–	OL706740	OL707653
<i>Leucothoe griffithiana</i>		FJ010598	FJ010616	–
<i>Leucothoe tonkinensis</i>		MH558159	–	–
<i>Leucothoe davisiae</i>		JF801553	FJ010617	–
<i>Thibaudia ovalifolia</i>	KUELAP–299	OL361758	Yes	OL707660
<i>Thibaudia moricandi</i>	KUELAP–298	–	Yes	OL707659
<i>Thibaudia obovata</i>	KUELAP–272	OL361756	–	OL707657
<i>Thibaudia costaricensis</i>	WFU/EAP016	AY331887	AY331914	–
<i>Thibaudia densiflora</i>	MM001	–	AF382790	–
<i>Thibaudia diphylla</i>	NY/L15459	AY331888	AY331915	–
<i>Thibaudia floribunda</i>	NY/L15090	AF382709	–	–
<i>Thibaudia inflata</i>	NY/L15029	–	AY331916	–
<i>Thibaudia jahnii</i>	180744	–	AF382792	–
<i>Thibaudia litensis</i>	NY/L15020	AY331890	–	–
<i>Thibaudia macrocalyx</i>	NY/L15444	AF382711	AF382793	–
<i>Thibaudia martiniana</i>	NY/L15028	AY331891	AY331918	–
<i>Thibaudia angustifolia</i>	KUELAP–283	OL361757	OL706745	OL707658
<i>Thibaudia pachyantha</i>	NY/L15189	AF382712	–	–
<i>Thibaudia parvifolia</i>	NY/L5212	AF382713	–	–
<i>Thibaudia tomentosa</i>	NY/L15502	AY331892	AY331919	–
<i>Vaccinium posanum</i>	–	AF382736	–	JQ594910
<i>Disterigma trimerum</i>	–	FJ001700	–	–
<i>Vaccinium alvarezii</i>	KIG, HGG, P–659–L	KM209414	–	–

(continued on next page)

Table 3 (continued)

Species	Voucher/N° Taxon	ITS	matK	rbcL
<i>Vaccinium amarianum</i>	TI:Ohi-Toma s.n	–	LC168877	–
<i>Vaccinium ambivalens</i>	C.Koster BW 13699-L	KM209415	–	–
<i>Vaccinium andersonii</i>	RG-9104-L	KM209418	–	–
<i>Vaccinium arboreum</i>	FLAS:M-4609	KM209419	–	KY626810
<i>Vaccinium arctostaphylos</i>	ACAD/VK-23991	AF419774	AF419702	–
<i>Vaccinium berberidifolium</i>	FRF-51757-L	KM209424	–	–
<i>Vaccinium boninense</i>	1004256	–	AB623168	–
<i>Vaccinium bulleyanum</i>	1633929	–	LC168878	–
<i>Vaccinium caespitosum</i>	ACAD/VK-313887	AF419775	AF419703	KX678256
<i>Vaccinium calycinum</i>	ACAD/VacciniumK-630886	AF419776	AF419704	–
<i>Vaccinium caudatifolium</i>	RBGE 1993-4020	AF382715	AF382797	–
<i>Vaccinium cercidifolium</i>	RBGE 1982-0845	AF382716	–	–
<i>Vaccinium cereum</i>	ACAD/VacciniumK-316992	KM209431	AF419705	–
<i>Vaccinium ciliatum</i>	445570	AB623188	–	–
<i>Vaccinium corymbosum</i>	ACAD/VacciniumK-ABS7	AF419778	AF419706	MG223027
<i>Vaccinium crassifolium</i>	WFU/K&P-DNA208	AF382718	–	–
<i>Vaccinium crenatum</i>	NY/L14171	AF382719	–	–
<i>Vaccinium cruentum</i>	1633933	KM209436	–	–
<i>Vaccinium cylindraceum</i>	180753	AF382720	AF382800_	–
<i>Vaccinium deliciosum</i>	ACAD/VK-529879	AF419790	AF419707	KX678227
<i>Vaccinium dentatum</i>	RBGE 1011085	AF382721	AF382801	–
<i>Vaccinium emarginatum</i>	174252	–	AB623166	–
<i>Vaccinium erythrocarpum</i>	ACAD/VK-81981	AF419779	AF419710	–
<i>Vaccinium exul</i>	1633938	–	–	KU568131
<i>Vaccinium filiforme</i>	RBGE 1980-1411	AF382722	–	–
<i>Vaccinium floribundum</i>	180757	–	AF382804	–
<i>Vaccinium floribundum</i>	KUELAP-312			OL707676
<i>Vaccinium floribundum</i>	KUELAP-268		OL706747	OL707663
<i>Vaccinium floribundum</i>	KUELAP-273	–	–	OL707665
<i>Vaccinium floribundum</i>	KUELAP-281	OL360763	OL706752	OL707668
<i>Vaccinium floribundum</i>	KUELAP-265	OL360759	OL706746	OL405713
<i>Vaccinium floribundum</i>	KUELAP-277	OL360761	OL706750	OL707667
<i>Vaccinium floribundum</i>	KUELAP-287	–	OL707625	OL707670
<i>Vaccinium floribundum</i>	KUELAP-262	–	–	OL707661
<i>Vaccinium floribundum</i>	KUELAP-290	OL360765	OL706753	OL707671
<i>Vaccinium floribundum</i>	KUELAP-297	OL360768	OL707628	OL707674
<i>Vaccinium floribundum</i>	KUELAP-292	OL360767	OL707627	OL707673
<i>Vaccinium fragile</i>	ACAD/VacciniumK-128796	AF382725	AF382805	–
<i>Vaccinium gaultheriifolium</i>	RBGE 1992-0332	AF382726	LC168880	–
<i>Vaccinium hirsutum</i>	ACAD/VacciniumK-83981	AF419780	AF419709	–
<i>Vaccinium hirtum</i>	RBGE 1921-9886	AB623185	AB623169	–
<i>Vaccinium horizontale</i>	180761	–	AF382808	–
<i>Vaccinium latissimum</i>	1633959	KM209449	–	–
<i>Vaccinium leucobotrys</i>	1633944	KM209451	–	–
<i>Vaccinium macrocarpon</i>	13750	AF382730	U61316	MG221913
<i>Vaccinium madagascariense</i>	LB-11063-L	KM209442	–	–
<i>Vaccinium mathewsii</i>	KUELAP-286	OL360764	OL707624	OL707669
<i>Vaccinium mathewsii</i>	KUELAP-300	OL360769	OL707629	OL707675
<i>Vaccinium mathewsii</i>	KUELAP-263	–	–	OL707662
<i>Vaccinium mathewsii</i>	KUELAP-291	OL360766	OL707626	OL707672
<i>Vaccinium membranaceum</i>	ACAD/VK-133979	AF419782	AF419711	MH926046
<i>Vaccinium meridionale</i>	ACAD/VacciniumK-s.n.	AF382731	–	AF124576
<i>Vaccinium meridionale</i>	KUELAP-274	OL360760	OL706749	OL707666
<i>Vaccinium meridionale</i>	KUELAP-270		OL706748	OL707664
<i>Vaccinium meridionale</i>	KUELAP-280	OL360762	OL706751	
<i>Vaccinium moupinense</i>	S.M, A.F. 079	KM209457	–	–
<i>Vaccinium myrtilloides</i>	S/Anderberg s.n.	AF382732	AF382810	MG221208
<i>Vaccinium nummularia</i>	180764	–	LC168882	–
<i>Vaccinium oldhamii</i>	ACAD/VacciniumK-426886	AF419783	AB623174	–

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Table 3 (continued)

Species	Voucher/N° Taxon	ITS	matK	rbcl
<i>Vaccinium ovalifolium</i>	ACAD/VK-1419886	AF419784	–	KX679055
<i>Vaccinium ovatum</i>	ERM1383	FJ001692	–	KX678497
<i>Vaccinium oxycoccos</i>	HERB0230	–	LC168883	KX677905
<i>Vaccinium padifolium</i>	ACAD/VK-5141090	AF382734	AF382812	–
<i>Vaccinium phillyreoides</i>	989263-L	KM209465	–	–
<i>Vaccinium praestans</i>	ACAD/VK-Vacc813	AF419785	AF419714	–
<i>Vaccinium pratense</i>	SCBGP385_2	KP092616	–	–
<i>Vaccinium reticulatum</i>	ACAD/VacciniumK-324992	AF382737	AF382814	–
<i>Vaccinium scoparium</i>	ACAD/VacciniumK-731883	AF419787	AF419716	MG222739
<i>Vaccinium sieboldii</i>	TNS:175ws-20100513	AB623191	AB623175	–
<i>Vaccinium smallii</i>	ACAD/VK-725886	AF382739	AB623170	–
<i>Vaccinium summfaucais</i>	RBGE 1963-0610	AF382740	AF382817	–
<i>Vaccinium tenellum</i>	WFU/K& P-DNA209	AF382741	AF382818	–
<i>Vaccinium uliginosum</i>	ACAD/VK-217995	AF419788	AF419717	KX677950
<i>Vaccinium varingifolium</i>	229200	AY274564	–	–
<i>Vaccinium vitis idaea</i>	RBGE 1977-3274A	AH011361	MN150141	MG222697
<i>Vaccinium wrightii</i>	1004259	AB623192	–	–
<i>Vaccinium yakushimense</i>	1004255	AB623183	–	–
<i>Vaccinium yatabei</i>	ACAD/VK-419886	AF419789	AF419718	–
<i>Z. pulverulenta</i> (Outgroup)	AF358906	AF124571	–	–
<i>A. polifolia</i> (Outgroup)		AF358872	LC168873	–
Species	Voucher/N° Taxon	ITS	GBSSI	rbcl
<i>Rubus acuminatus</i>	R2007	–	–	KU881197
<i>Rubus adenothallus</i>	KUELAP-256	OL348471	OL707633	OL707678
<i>Rubus amabilis</i>	R01-14-SICUA	FJ472909	KU926726	KU881200
<i>Rubus andicola</i>	KUELAP-254	OL348470	OL707636	OL707677
<i>Rubus assamensis</i>	R0118	AH006024	KU926729	KU881203
<i>Rubus australis</i>	Gardner 1539, MO	H006022	–	–
<i>Rubus biflorus</i>	R2504	KU881063	KU926733	KU881207
<i>Rubus bifrons</i>	Alice 98-9, M	AF055775	–	–
<i>Rubus bollei</i>	Bol_col14	KM037227	–	–
<i>Rubus caesius</i>	Karlen 243, S/75065	AF055776	–	FN689382
<i>Rubus calycinus</i>	R2519	KU881065	KU926735	KU881209
<i>Rubus canadensis</i>	A&C 98-10, M/MOBOT.S.27940	AF055777	–	KY427303
<i>Rubus caudifolius</i>	R2021	KU881067	KU926737	KU881211
<i>Rubus chamaemorus</i>	Alice, R17, M	AF055740	–	–
<i>Rubus chingii</i>	R2128	KU881068	–	KU881212
<i>Rubus corchorifolius</i>	PDBK 2008-0160	–	–	MH593651
<i>Rubus coreanus</i>	321593	MT078683	KU926741	MN732644
<i>Rubus cuneifolius</i>	Alice 5, M/A.22485	AF055778	–	KJ773846
<i>Rubus deliciosus</i>	Alice, 98-1, M	AF055733	–	–
<i>Rubus ellipticus</i>	R2512/R0112	KU881060	KU926746	KU881223
<i>Rubus eucalyptus</i>	R2354	–	KU926749	KU881226
<i>Rubus eustephanus</i>	R2518	KU881083	KU926750	KU881227
<i>Rubus loxensis</i>	KUELAP-259	OL348474	OL707635	OL707679
<i>Rubus flagellaris</i>	Alice 61:WKU/BM 2008/273	AY083372	–	HM850313
<i>Rubus foliosus</i>	Fol_col08	KM037335	–	–
<i>Rubus floribundus</i>	KUELAP-255	OL351854	OL707632	–
<i>Rubus geoides</i>	Dudley et al., 1538a, MO	AF055799	–	–
<i>Rubus glabratus</i>	Rubus5132 QCA	HM453950	–	–
<i>Rubus glabratus</i>	KUELAP-261	OL348476	OL707639	OL707681
<i>Rubus glaucus</i>	PI 548906	AY083361	–	–
<i>Rubus gracilis</i>	Grac_col05	KM037377	–	–
<i>Rubus gunnianus</i>	Wells 96-1, M	AF055749	–	–
<i>Rubus hirsutus</i>	ODdo/R2225	AY818208	KU926758	KU881236
<i>Rubus hypomalacus</i>	Hma_col07	KM037395	–	–
<i>Rubus hypopitys</i>	R2533	KU881094	–	KU881238
<i>Rubus idaeus</i>	Alice, R8, MAINE	AF055755	–	JX848533
<i>Rubus lasiococcus</i>	Merello et al., 827, MO	AF055750	–	–

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Table 3 (continued)

Species	Voucher/N° Taxon	ITS	matK	rbcl
<i>Rubus lechleri</i>	KUELAP-258	OL348473	OL707637	OL707682
<i>Rubus macilentus</i>	R2501	KU881118	KU926783	KU881262
<i>Rubus macraei</i>	59494	AF055763	–	–
<i>Rubus matsumuranus</i>	PDBK 2012-0085	–	–	MH593654
<i>R. moorrei</i>	Streimann 8207, GH	AF055765	–	–
<i>Rubus mesogaeus</i>	ALTA:120202	KU881122	KU926787	KU881266
<i>Rubus moschus</i>	Mos01_col04	KM037437	–	–
<i>Rubus niveus</i>	R0101	KU881126	KU926791	KU881270
<i>Rubus nubigenus</i>	1257, NCGR	AF055769	–	–
<i>Rubus odoratus</i>	Alice, R14, M	AF055734	–	–
<i>Rubus parviflorus</i>	Richards, 666, M	AF055735	–	–
<i>Rubus parvifolius</i>	R2035	KU881132	KU926797	GU363802
<i>Rubus parvus</i>	Alice 97-3, M/CHR:688824	AF055766	–	KT626843
<i>Rubus pectinellus</i>	680-MO	AF055797	–	–
<i>Rubus pedemontanus</i>	Martensen s.n.	AF055783	–	–
<i>Rubus pentagonus</i>	R0223	–	KU926801	KU881280
<i>Rubus phoenicolasius</i>	Alice, 96-2, M	AF055759	KU926803	–
<i>Rubus pinfaensis</i>	R0102	–	KU926811	KU881291
<i>Rubus platyphyllus</i>	Sva_col04	KM037581	–	–
<i>Rubus praecox</i>	Pra01_col01	KM037481	–	–
<i>Rubus pungens</i>	R2337	KU881153	KU926818	KU881297
<i>Rubus radula</i>	Rad_col06	KM037522	–	–
<i>Rubus reflexus</i>	S.10331/S.0492L	JN407524	–	JN407362
<i>Rubus robustus</i>	Steinbach 247, GH	AF055771	–	–
<i>Rubus roseus</i>	L&14402, M	AF055770	–	–
<i>Rubus sanctus</i>	Thibaudia Eriksson 714, S	AF055785	–	–
<i>Rubus saxatilis</i>	Thibaudia Eriksson 719, S	AF055746	–	–
<i>Rubus schizostylus</i>	TKM201536	KT634247	–	–
<i>Rubus schleicheri</i>	Schl_col05	KM037537	–	–
<i>Rubus scissoides</i>	1546356	KM037543	–	–
<i>Rubus setosus</i>	Alice 113, MAINE	AF055787	–	–
<i>Rubus silvaticus</i>	Sil_col08	KM037557	–	–
<i>Rubus simplex</i>	R2321	–	KU926832	KU881312
<i>Rubus sparsiflorus</i>	KUELAP-260	OL348475	OL707638	OL707680
<i>Rubus sulcatus</i>	Martensen 1325.12	AF055789	–	–
<i>Rubus sumatranus</i>	R2111	KU881182	KU926845	KU881326
<i>Rubus tephrodes</i>	Yao, 9231, MO	AF055767	–	–
<i>Rubus thibetanus</i>	Q186	MH711174	–	–
<i>Rubus trifidus</i>	C, 3.001/A, 98-2, M	AF055737	–	–
<i>Rubus trilobus</i>	Ruiz, 889, MO	AF055738	–	–
<i>Rubus trivialis</i>	Alice 55, M/Abbott 26055	AF055790	–	KJ773847
<i>Rubus ursinus</i>	197, NCGR/Alice 98-8, M	AF055794	–	–
<i>Rubus vigorosus</i>	Martensen 2518.32	AF055793	–	–
<i>Rubus weberbaueri</i>	KUELAP-257	OL348472	OL707634	OL707683
<i>Fullgaria paradoxa</i>		U90805	AM116869	U06802
<i>Waldsteinia fragarioides</i>			–	U90822
<i>Geum urbanum</i>			AM116871	U90802

3.3. *Disterigma*

The phylogeny of *Disterigma* included concatenated data (1274 bp for *matK* and 686 bp for ITS) from 32 individuals. Based on the multilocus tree obtained from the ML and BI analyses (Figure 6), the specimens were identified as *D. synanthum* Pedraza (KUELAP-264, KUELAP-275) and *D. ecuadorensis* Luteyn (KUELAP-285). The former species was characterized by pale green floral bracts and a white corolla (Figure 9D). This species was sister to *D. alaternoides* (Kunth) Nied (BS/BI = 85/1.0), differing by 0.2% for the ITS. Additionally, *D. ecuadorensis* was characterized by a green calyx, pink corolla, and white berry (Figure 9E, Table 7). This species was sister to *D. ulei* Sleumer, differing by 2.3% for ITS (Figures S5, S6).

3.4. *Gaultheria*

The multilocus phylogeny of *Gaultheria* (1487 bp for *matK*, 550 bp for *rbcl* and 659 bp for ITS) included 67 individuals (Figure 7). The materials comprise four species within *Gaultheria*. One of this species was identified as *G. secunda* J. Rémy (KUELAP-266, KUELAP-278, KUELAP-284, KUELAP-288, KUELAP-301) based on the red calyx and pale-white corolla (Figure 9F, Table 8). This species was resolved in sistership to the clade composed of *G. foliolosa* Benth and *G. mucronata* (L. fil.) J. Rémy. The intraspecific divergences of *G. secunda* were 0.2% for *matK*, 0.2% for *rbcl*, and 2.4% for ITS (Figures S7, S8, S9). The other three species remained unidentified. *Gaultheria* sp. 1 (KUELAP-289) (Figure 9G) resolved sister to *G. myrsinoides* Kunth. Additionally,

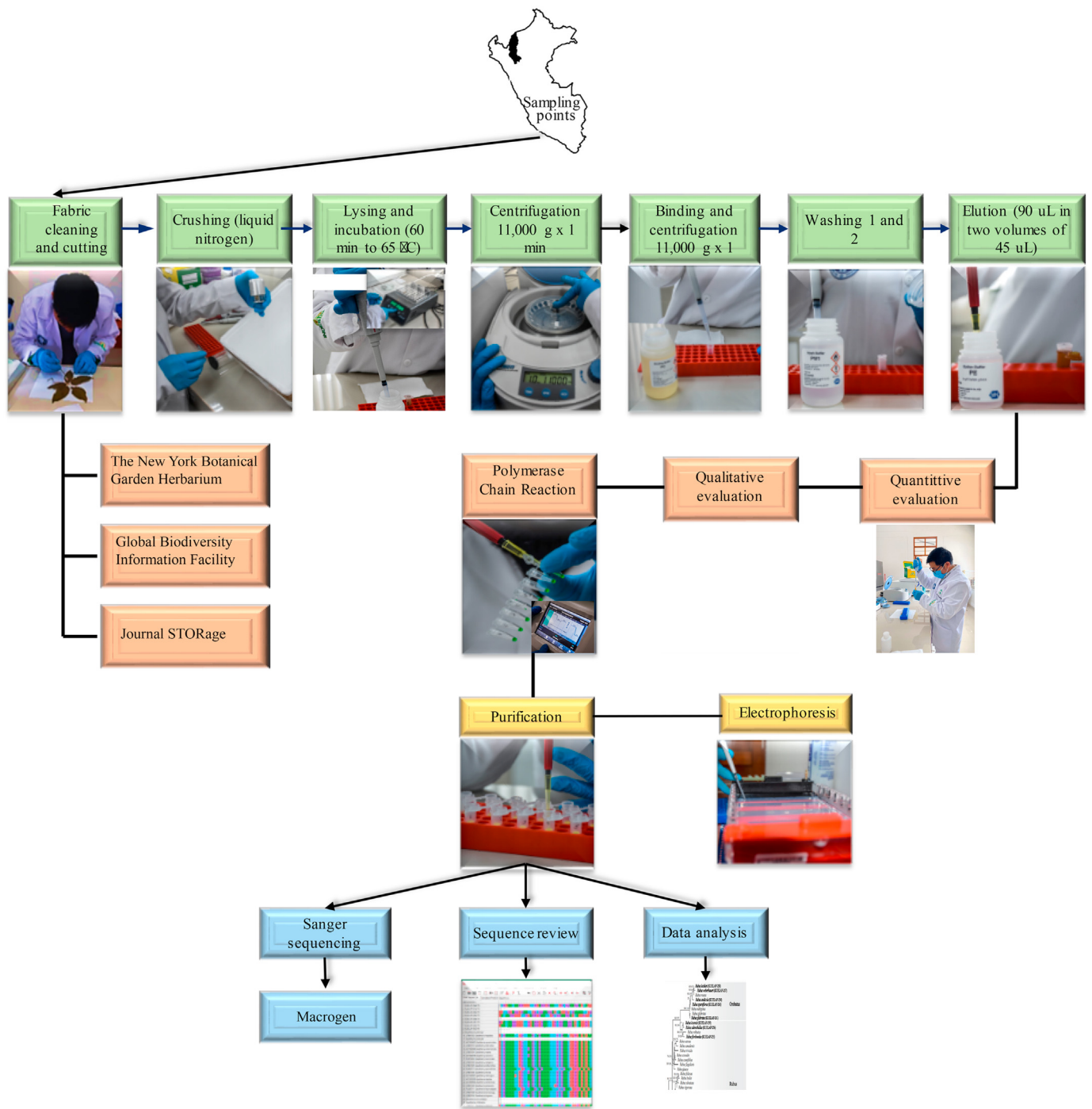


Figure 3. Experimental procedures for sampling, identification, DNA extraction, amplification, purification and data analysis for Andean berries specimens from Region Amazonas, northern Peru.

Gaultheria sp. 2 (KUELAP-308) (Figure 9H) and *Gaultheria* sp. 3 (KUELAP-302) (Figure 9I) were sister species, and both were sister to *G. glomerata* (Cav.) Sleumer.

3.5. *Thibaudia*

The phylogeny of *Thibaudia* included concatenated data (1,262 bp for *matK*, 551 bp for *rbcl* and 650 bp for ITS) from 18 individuals. The materials comprised four species in *Thibaudia* (Figure 8). *T. ovalifolia* A.C.Sm. (KUELAP-299) and *T. moricandi* Dunal (KUELAP-298) were recognized as sister species, and both differed by 0.1% for *matK* and

0.1% for *rbcl*. *T. ovalifolia* was characterized by glabrous flowers and rugose calyxes (Figure 9L), whereas *T. moricandi* was characterized by a pubescent corolla (Figure 9K, Table 9). These two species were sister to *T. obovata* A.C.Sm. (KUELAP-272), and both differed from the latter by over 0.1% for *rbcl* and 0.1% for ITS (Figures S10, S11). *T. obovata* was characterized by obovate-oblong leaves, pilose calyx and pedicels, and tomentose corolla (Figure 9M). Moreover, the clade composed of these three species and *T. nutans* Klotzsch ex Mansf. was closely related to *T. angustifolia* Hook (KUELAP-283). *T. angustifolia* was diagnosed by the presence of a bright red corolla and purple berries (Figure 9J).

Table 4. Evolutionary models for phylogenetic analyses of specimens from Ericales and Rosales.

	Group	Bayesian inferences	Maximum likelihood
Exploratory phylogeny	Figure S1	GTR + I+G	GTRGAMMAI
Separate phylogenies	Figure 2	GTR	K81
	Figure 3	TRNEF+G	TRNEF+G
	Figure 4	GTR	K81UF+I+G
	Figure 5	GTR+I+G	GTR+I+G
	Figure 6	GTR+I+G	GTR+I+G
	Figure 7	GTR	K81UF+G
	Figure 8	GTR+I+G	GTR+I+G

3.6. Vaccinium

The multilocus phylogeny of *Vaccinium* (1,253 bp for *matK*, 551 bp for *rbcL* and 673 bp for ITS) included 79 individuals. In this collection, three species were recognized in this genus, namely, *V. meridionale* Sw, *V. mathewsii* Sleumer, and *V. floribundum* Kunth. The former species (KUELAP-270, KUELAP-274, KUELAP-280) was characterized by dark berries and a bitter taste (Figure 9N). *V. meridionale* was sister to *V. arboreum* Marshall and genetically differed by 0.3% in *rbcL* and by 3.5% in the ITS. *V. mathewsii* (KUELAP-263, KUELAP-286, KUELAP-291, KUELAP-300) was morphologically characterized by a pinkish-white corolla and blue-black fruit (Figure 9O, Table 10). *V. mathewsii* was closely related to *V. crenatum* (G. Don) Sleumer, and genetic divergence of these taxa was 5.7% for ITS. *V. floribundum* (KUELAP-262, KUELAP-265, KUELAP-267, KUELAP-268, KUELAP-273, KUELAP-277, KUELAP-281, KUELAP-287, KUELAP-290, KUELAP-292, KUELAP-312) was diagnosed by having leathery leaves with pinkish-white flowers and dark berries (Figure 9P) and showed high intraspecific divergences (1.2% for *matK*, 0.3% for *rbcL*, and 3.7% for ITS), while the general appearance remained identical among all specimens of this study, suggesting cryptic diversity. *V. floribundum* was sister to *V. ovatum* Pursh, differing by 0.7% for *rbcL* (Figures S12, S13, S14).

3.7. Rubus

The phylogeny of *Rubus* (666 bp for *rbcL*, 455 bp for *GBSSI*, and 639 bp for ITS) included 81 individuals. In this collection, eight species were recognized in *Rubus* and grouped into two subgenera (Orobatus and *Rubus*, Figure 10). The subgenus Orobatus consisted of *R. andicola* Focke, *R. glabratus* Kunth, *R. lecheri* Focke, *R. sparsiflorus* J.F. Macbr, and *R. weberbaueri* Focke, whereas the subgenus *Rubus* consisted of *R. adenthallus* Focke, *R. floribundus* J.F. Macbr. and *R. loxensis* Benth. These two subgenera were distinguished by glands without flexible bristles (Orobatus) and inflorescences in panicle or subracemose forms (*Rubus*). In the subgenera Orobatus (Figure 11); *R. andicola* (KUELAP-254) was characterized by elongated branches, spines with short, curved and compressed trichomes, with leaves pubescent on the underside (Figure 11C); *R. glabratus* (KUELAP-261) by having pink-rose petals and reddish-orange immature fruits (Figure 11A); *R. lecheri* (KUELAP-258) by its bristly pubescence on the back sides of leaves and purple petals (Figure 11E); *R. sparsiflorus* (KUELAP-260) by the presence of flowers in dense clusters, crepe-like petals and a pink corolla (Figure 11B); and *R. weberbaueri* (KUELAP-257) by having veins and spines on the back sides of the leaves, magenta flowers, and black fruits (Figure 11D, Table 11). Genetically, *R. weberbaueri* and *R. lecheri* were sister species, differing by 1.0% for *rbcL* and 0.2% for ITS. These two species were closely related to *R. roseus*, and the three species differed by over 0.2% for ITS. *R. andicola* was sister to the clade composed of these tree species, differing over 0.9% for *rbcL* and 0.2% for ITS. *R. sparsiflorus* was closely related to the clade composed of these four species and diverged over 0.9% for *rbcL* and 0.3% for ITS. *R. glabratus* was closely related to the clade composed of six species of the subgenus Orobatus and differed over 0.9% for *rbcL* and 0.8% for ITS. Conversely, in the subgenus *Rubus*, *R. floribundus* (KUELAP-255) was recognized as a sister species to *R. robustus*, and both differed by 0.9% for the ITS. *R. floribundus* had dense inflorescences with pyramidal-shaped paniculata extraaxillaris that tapered toward the lower branches (Figure 11F). These species were sister to the clade composed of *R. adenthallus* (KUELAP-256) and *R. loxensis* (KUELAP-259). *R. loxensis* had creeping-climbing stems and slightly ovate petals and sepals (Figure 11G), whereas *R. adenthallus* was

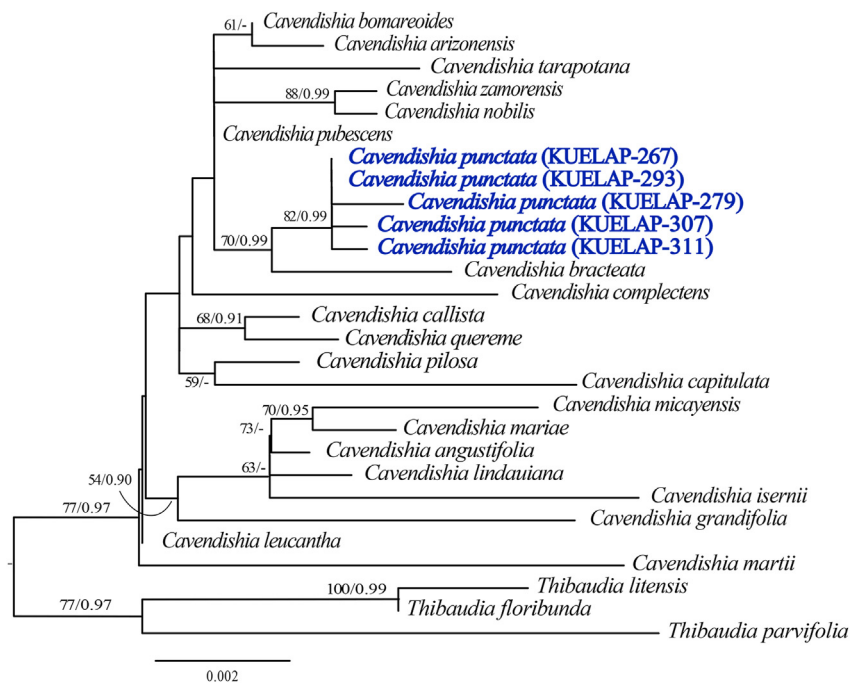


Figure 4. Phylogenetic tree of the *Cavendishia* lineage based on maximum likelihood inference of combined *matK*, *rbcL*, and ITS data. Maximum likelihood bootstrap values (BS; $\geq 50\%$)/Bayesian posterior probabilities (BPP; ≥ 0.9) are indicated above branches. Values lower than 50% (BS) or 0.90 (BPP) are indicated by hyphens (-). The scale bar indicates the number of nucleotide substitutions per site.

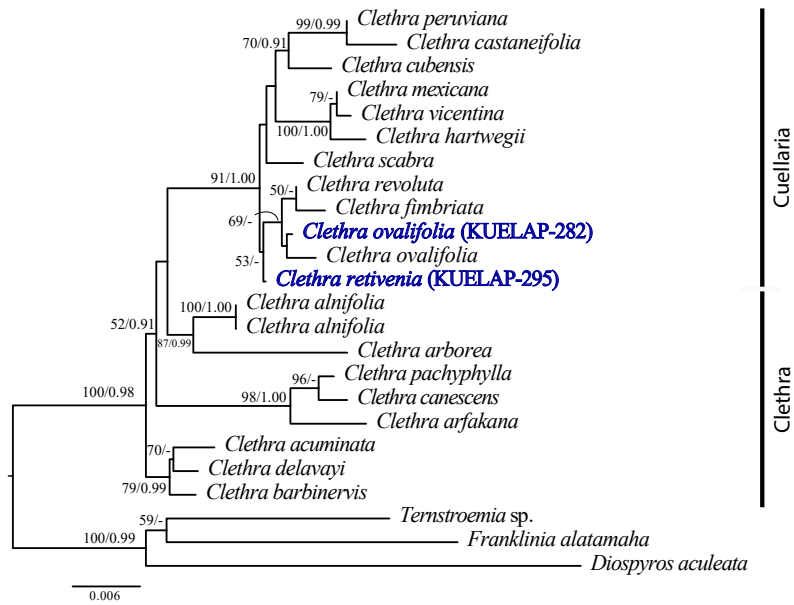


Figure 5. Phylogenetic tree of the *Clethra* lineage based on maximum likelihood inference of combined *matK*, *rbcl*, and ITS data. Maximum likelihood bootstrap values (BS; $\geq 50\%$)/Bayesian posterior probabilities (BPP; ≥ 0.9) are indicated above branches. Values lower than 50% (BS) or 0.90 (BPP) are indicated by hyphens (-). The scale bar indicates the number of nucleotide substitutions per site.

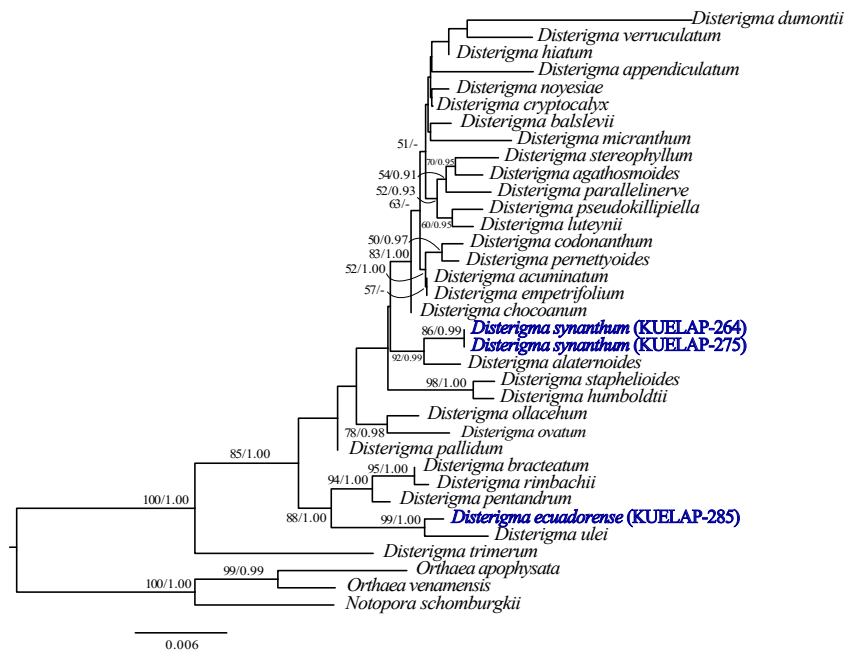


Figure 6. Phylogenetic tree of the *Disterigma* lineage based on maximum likelihood inference of combined *matK* and ITS data. Maximum likelihood bootstrap values (BS; $\geq 50\%$)/Bayesian posterior probabilities (BPP; ≥ 0.9) are indicated above branches. Values lower than 50% (BS) or 0.90 (BPP) are indicated by hyphens (-). The scale bar indicates the number of nucleotide substitutions per site.

characterized by small greenish-white flowers and elongated red-black baya (Figure 11H). *R. adenothallus* and *R. loxensis* differed by 0.3% for *rbcl* (Figures S15, S16, S17).

4. Discussion

Most berries from mountainous habitats tend to be more diverse than those from lowland habitats (Powell and Kron, 2003) due to the interactions of UV radiation with environmental (climate) and geographic

(relief) factors, which evoke species-specific responses leading to adaptation and diversification (Sedej et al., 2020). Using molecular markers, this study identified 24 species of andean berries (*Cavendishia* = 1, *Clethra* = 2, *Disterigma* = 2, *Gaultheria* = 4, *Thibaudia* = 4, *Vaccinium* = 3, *Rubus* = 8) from the Amazonas region. The majority of these species were found in coniferous forests, dry and humid forests, rocky slopes, and grasslands at 2,506–3,019 masl (Figure 12).

The genus *Cavendishia* has approximately 130 species distributed throughout the Andes of South America, and most of these species are

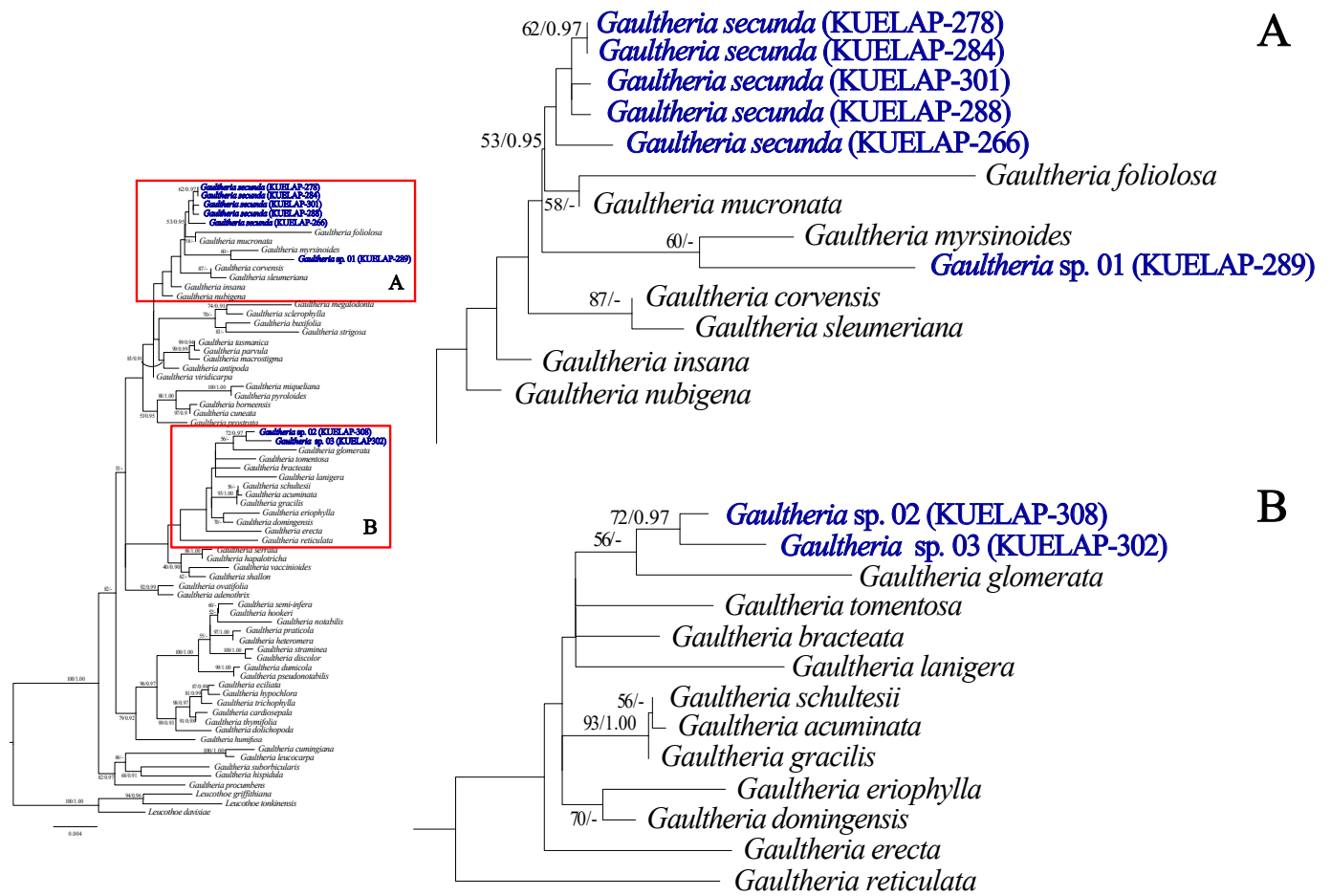


Figure 7. Phylogenetic tree of the *Gaultheria* lineage based on maximum likelihood inference of combined *matK*, *rbcL*, and ITS data. Maximum likelihood bootstrap values (BS; $\geq 50\%$)/Bayesian posterior probabilities (BPP; ≥ 0.9) are indicated above branches. Values lower than 50% (BS) or 0.90 (BPP) are indicated by hyphens (-). The scale bar indicates the number of nucleotide substitutions per site.

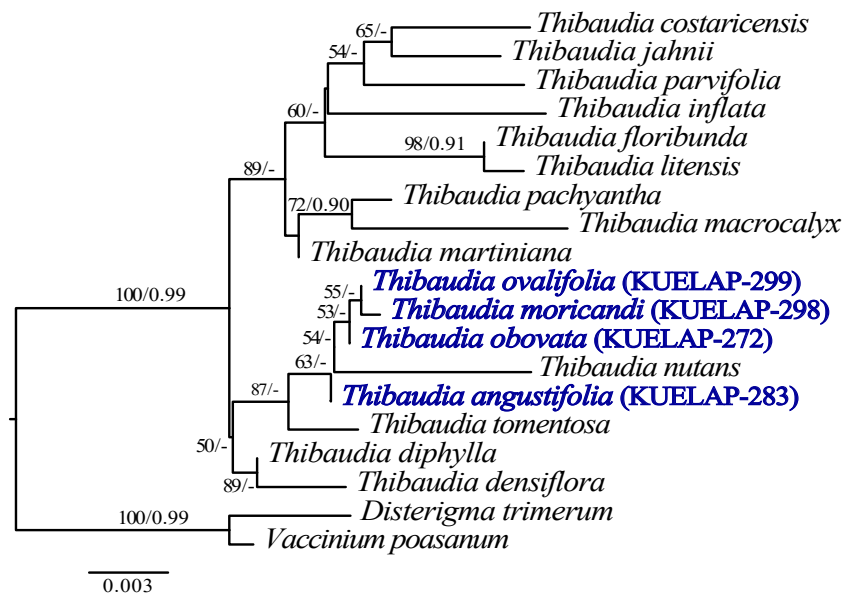


Figure 8. Phylogenetic tree of the *Thibaudia* lineage based on the maximum likelihood inference of combined *matK*, *rbcL*, and ITS data. Maximum likelihood bootstrap values (BS; $\geq 50\%$)/Bayesian posterior probabilities (BPP; ≥ 0.9) are indicated above branches. Values lower than 50% (BS) or 0.90 (BPP) are indicated by hyphens (-). The scale bar indicates the number of nucleotide substitutions per site.

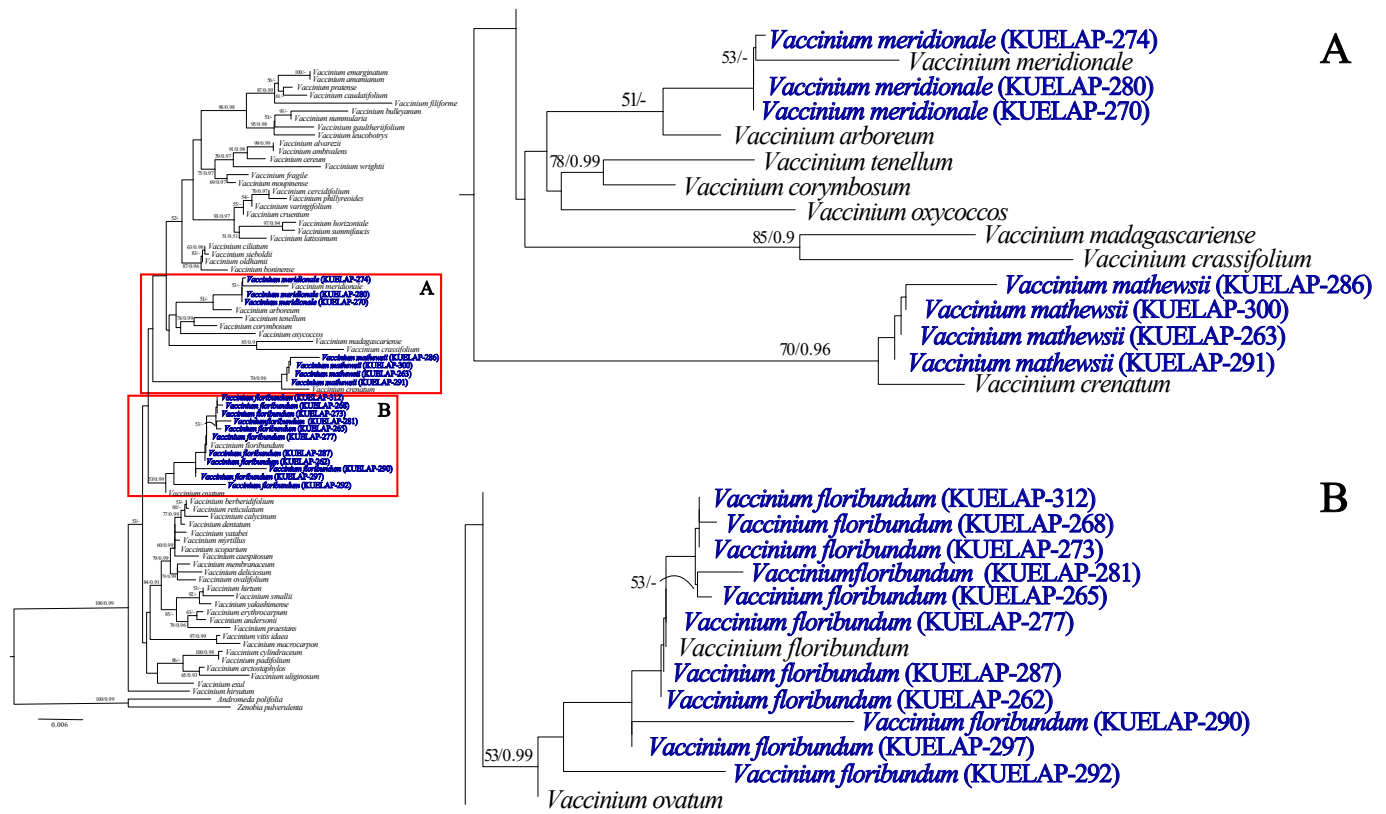


Figure 9. Phylogenetic tree of the *Vaccinium* lineage based on maximum likelihood inference of combined *matK*, *rbcL*, and ITS data. Maximum likelihood bootstrap values (BS; $\geq 50\%$)/Bayesian posterior probabilities (BPP; ≥ 0.9) are indicated above branches. Values lower than 50% (BS) or 0.90 (BPP) are indicated by hyphens (-). The scale bar indicates the number of nucleotide substitutions per site.

Table 5. Morphological comparisons among species of the genus *Cavendishia*.

Species	Habitat	Altitude (masl)	Height (m)	Immature fruit	Mature fruit	Flowers	Corolla	References
<i>Cavendishia bracteata</i>	Shrub	1400–3500	1–3	Green	Black	Lilac	Pink	Luteyn (1983) WCVP (2021)
<i>Cavendishia isernii</i>	Shrub terrestrial	660–1200	1.8–3	Reddish–green	Greenish–white	Lilac	–	Luteyn (1983)
<i>Cavendishia punctata</i>	Shrub	2000–3000	2–3.5	Reddish–green	Purple	Pedicel and garnet calyx	Greenish	Luteyn (1983), this study
<i>Cavendishia sirensis</i>	Shrub hemi–epiphyte	600–1700	1.5–3	Green	Purple	White, red calyx	Tubular	Luteyn (1983)
<i>Cavendishia tarapotana</i>	Shrub	1200–1500	2.5–5	–	Lilac	Fuchsia red	Rose–yellow, white–yellow	Luteyn (1983)

endemic to Colombia (Pedraza-Peñalosa et al., 2015; WCVP, 2021). Only nine species of *Cavendishia* have been reported from Peru (León, 2006a; Pedraza-Peñalosa et al., 2015; WCVP, 2021), and two of these were from the Amazonas region. In addition to *Ca. isernii* Sleumer and *Ca. sirensis*

Luteyn (León, 2006a; Salinas, 2015), this study confirms the presence of *Ca. punctata* (KUELAP-267, KUELAP-279, KUELAP-293, KUELAP-307, KUELAP-311) in cold and humid habitats in the Amazonas region. *Ca. punctata* was already recorded from central (Junín and Pasco) and

Table 6. Morphological comparisons among species of the genus *Clethra*.

Species	Habitat	Altitude (masl)	Height (m)	Leaf shape	Immature fruit	Mature fruit	Flowers	Corolla	References
<i>Clethra fimbriata</i>	subshrub	2800–3600	2–3	Coriaceous	Brown	Brown	White	White	León (2006a,b), Sleumer (1967)
<i>Clethra ovalifolia</i>	Shrub	2000–3100	1–3	–	–	Brown	Cream	White	Sleumer (1967)
<i>Clethra retivenia</i>	Shrub	1500–3200	3	Coriaceous	–	–	White	White	León (2006a,b), this study
<i>Clethra revoluta</i>	Tree	2350	10–16	Coriaceous	–	–	White	White	Sleumer (1967)
<i>Clethra scabra</i>	Tree	1700–2000	4–8	–	Green	Brown–Reddish	Pink	Pink	Sleumer (1967)

Table 7. Morphological comparisons among species of the genus *Disterigma*.

Species	Habitat	Altitude (masl)	Height (m)	Calyx	Immature fruit	Mature fruit	Flowers	Corolla	References
<i>Disterigma synanthum</i>	Shrub-epiphyte	2500–3000	0.5–1	Green pale	Green pale	Brown	White–pink	white, style white	Pedraza–Peñalosa (2008), this study
<i>Disterigma alaternoides</i>	Shrub terrestrial	1500–2960	1.5–2	Green	Whitish–green	Brown	White–pink	White tubular	León (2006a,b), Pedraza–Peñalosa (2008)
<i>Disterigma ecuadorensis</i>	Shrub terrestrial	2500–3000	1	Green	–	White	White	Whitish–pink	Smith (1933), León (2006a,b), this study
<i>Disterigma ulei</i>	Epiphytic grass, Shrub terrestrial	2000–2800	0.5–1	Light green	Light green	Ocbonicos lilac	Greenish		Pedraza–Peñalosa (2008), Smith (1933)

Table 8. Morphological comparisons among species of the genus *Gaultheria*.

Species	Habitat	Altitude (masl)	Height (m)	Calyx	Immature fruit	Mature fruit	Flowers	Corolla	References
<i>Gaultheria foliolosa</i>	Shrub terrestrial	2000–3000	0.5–3	Cream	-	Blue–black	White	Cream	Middleton (1990, 1991)
<i>Gaultheria glomerata</i>	Shrub terrestrial	1000–3000	0.5–3	Red–rose	Greenish	Black	Lilac, red	–	Middleton (1990, 1991)
<i>Gaultheria myrsinoides</i>	Shrub terrestrial	2000–2800	1–2	Green	Green	Purple	White	White	Middleton (1990, 1991)
<i>Gaultheria mucronata</i>	Shrub terrestrial	2000–3120	1–2	Green	Green	Lilac	Pink	Cream at base rose distally	Middleton (1990, 1991)
<i>Gaultheria secunda</i>	Shrub, half–terrestrial	2500–3500	1–2	Rose–red	Green	Red–rose	Rose–pink	Pale pinkish–white	Middleton (1990, 1991), WCVP (2021), this study
<i>Gaultheria</i> sp 1	Shrub	2000–2720	1–2	Rose–red	Green	Red–rose	Rose–pink	Pale pinkish–white	This study
<i>Gaultheria</i> sp 2	Shrub	2000–2700	1–2	Rose–red	Green	Red–rose	Rose–pink	Pale pinkish–white	This study
<i>Gaultheria</i> sp 3	Shrub	2000–2700	1–2	Rose–red	Green	Red–rose	Rose–pink	Pale pinkish–white	This study

Table 9. Morphological comparisons among species of the genus *Thibaudia*.

Species	Habitat	Altitude (masl)	Height (m)	Calyx	Flowers	Corolla	References
<i>Thibaudia angustifolia</i>	Shrub	2000–2800	0.5–2	Red–rose	Bright red	Bright red	León (2006a,b), WCVP (2021), this study
<i>Thibaudia diphylla</i>	Shrub	1000–2400	2–4	Pale–pink	White pink	Rich pink	León (2006a,b), WCVP (2021)
<i>Thibaudia moricandii</i>	Shrub	1500–2600	0.5–2	Red	Red	Pubescent, throat, lobes white	León (2006a,b), this study
<i>Thibaudia nutans</i>	Herbaceous–bush	1000–1900	0.5–3	Green	Cauliflorous	Dark–red	León (2006a,b)
<i>Thibaudia ovalifolia</i>	Shrub	2100–2700	0.5–2	Rugose	glabrous flowers	–	León (2006a,b), WCVP (2021), this study
<i>Thibaudia obovata</i>	Shrub	1600–2200	1–3	Pilose pedicels		Tomentose	León (2006a,b), WCVP (2021), this study
<i>Thibaudia tomentosa</i>	Shrub terrestrial	–	0.5–1.5	Globose bell–shaped	Bright red, curved	Orange	León (2006a, b)

Table 10. Morphological comparisons among species of the genus *Vaccinium*.

Species	Habitat	Altitude (masl)	Height (m)	Immature fruit	Mature fruit	Flowers	Corolla	References
<i>Vaccinium arboreum</i>	Shrub	-	2–5	Green	Black	White	White	Bracko and Zurucchi (1993), León et al. (2017)
<i>Vaccinium crenatum</i>	Shrub terrestrial	1000–2800	–	Green	Reddish, blue–black	White–pink	Rose–red	Vander Kloet and Dickinson (2009), León et al. (2017)
<i>Vaccinium floribundum</i>	Shrub	2000–3000	0.5–1	Green	blue–black	White, red tips	white	Bracko and Zurucchi (1993), León et al. (2017), this study
<i>Vaccinium mathewsii</i>	Shrub	2000–3000	1–2	Green	blue–black	pinkish–white	Pinkish–white	Bracko and Zurucchi (1993), León et al. (2017), this study
<i>Vaccinium meridionale</i>	Shrub	1800–2800	0.5–2	Green–reddish	dark	White–pink	White	Vander Kloet and Dickinson (2009), this study
<i>Vaccinium ovatum</i>	Shrub	-	-	Green	red	White–pink	Pink	Bracko and Zurucchi (1993), León et al. (2017)

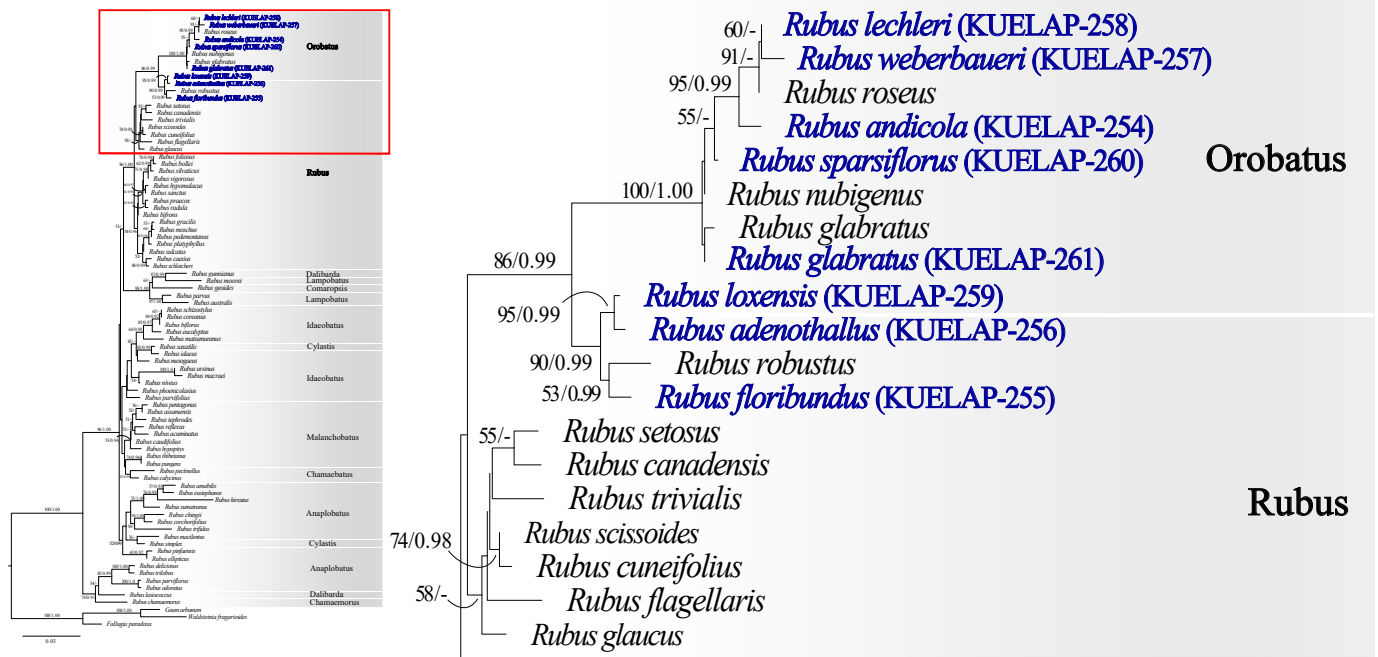


Figure 10. Phylogenetic tree of the *Rubus* lineage based on maximum likelihood inference of combined *rbcl*, *GBSSI*, and *ITS* data. Maximum likelihood bootstrap values (BS; $\geq 50\%$)/Bayesian posterior probabilities (BPP; ≥ 0.9) are indicated above branches. Values lower than 50% (BS) or 0.90 (BPP) are indicated by hyphens (-). The scale bar indicates the number of nucleotide substitutions per site.

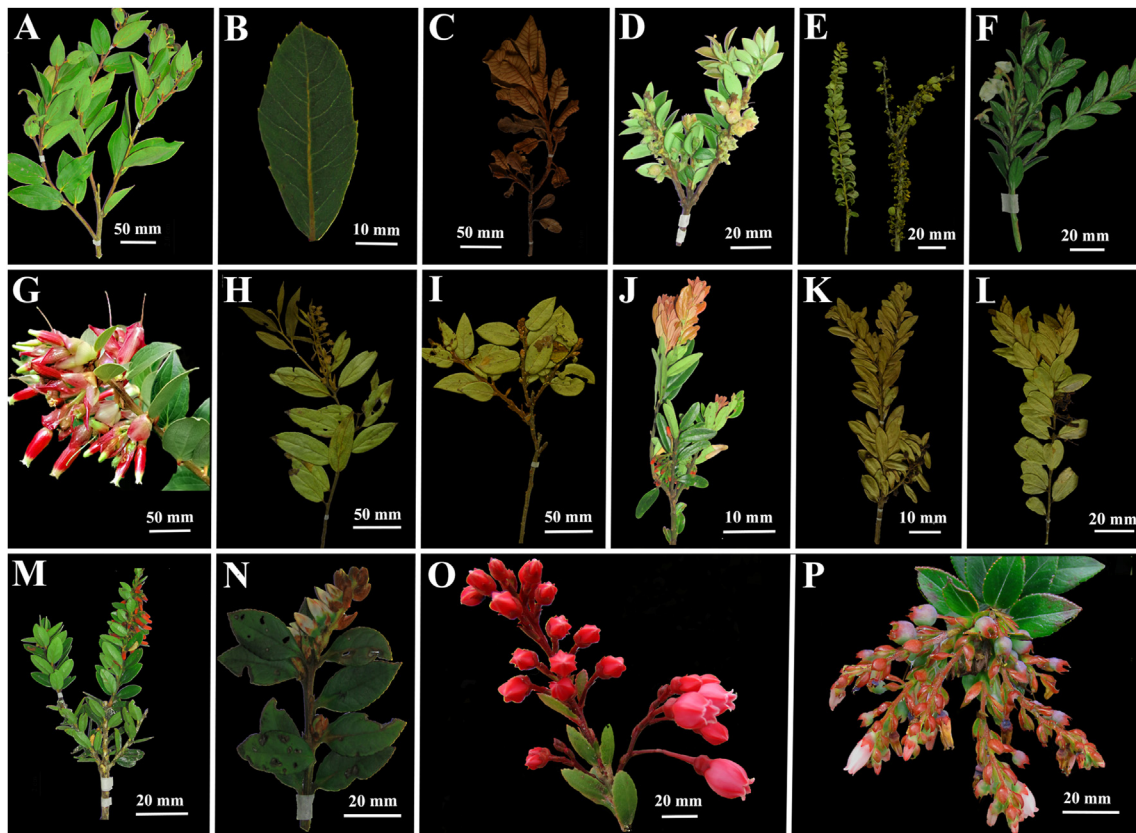


Figure 11. Diversity of Andean berries belonging to Ericales. A. *Cavendishia punctata*. B. *Clethra ovalifolia*. C. *Clethra retivenia*. D. *Disterigma synanthum*. E. *Disterigma ecuadorensis*. F. *Gaultheria secunda*. G. *Gaultheria* sp. 01. H. *Gaultheria* sp. 02. I. *Gaultheria* sp. 03. J. *Thibaudia angustifolia*. K. *Thibaudia moricandi*. L. *Thibaudia ovalifolia*. M. *Thibaudia obovata*. N. *Vaccinium meridionale*. O. *Vaccinium mathewsii*. P. *Vaccinium floribundum*.

Table 11. Morphological comparisons among species of the genus *Rubus*.

Species	Habit	Altitude (masl)	Height (m)	Calyx	Immature fruit	Mature fruit	Flowers	Corolla	References
<i>Rubus andicola</i>	Shrub	800–2500	2–3	Green	Green whit trichomes	Red	White–pink	Pink	Focke (1910, 1911), Mendoza and León (2006), this study
<i>Rubus adenothallus</i>	Shrub terrestrial	2000–3500	2–5	Green	Light green	Red–black, red	greenish–white	Greenish–white	Focke (1910, 1911), Mendoza and León (2006), this study
<i>Rubus floribundus</i>	Shrub	1500–2000	1–3	Green	Green	Becoming black	White	Pink	Focke (1910, 1911), Mendoza and León (2006), this study
<i>Rubus glabratus</i>	Trailing–shrublet	2000–3400	0.5–1	Green	Reddish–orange	-	Pink, red	Pink–rose	Focke (1910, 1911), Mendoza and León (2006), this study
<i>Rubus lechleri</i>	Shrub	2000–3600	2–4	Green	Green	Red	White–purple	Purple	Focke (1910, 1911), Mendoza and León (2006), this study
<i>Rubus loxensis</i>	Shrub	2000–3000	2–3.5	Green–reddish	Green, red	Red	Greenish, lilac	Slightly ovate	Focke (1910, 1911), Mendoza and León (2006), this study
<i>Rubus nubigenus</i>	Supporting–shrub	2000–3500	2–3	Green	Green–reddish	Dark fruits	White–greenish, pink	White	Focke (1910, 1911), Mendoza and León (2006)
<i>Rubus robustus</i>	Shrub	1000–3000	1–2	-	-	Black	White–pink	White–pink	Focke (1910, 1911), Mendoza and León (2006)
<i>Rubus roseus</i>	climbing shrub	1600–3000	1–3	Green, purplish tint	-	Red	White–pink	Reddish–violet	Focke (1910, 1911), Mendoza and León (2006)
<i>Rubus sparsiflorus</i>	Shrub	2000–3500	1–4	Green, red–brown	-	Red–purple, black	Black	Crepe–linke pink, style red	Focke (1910, 1911), Mendoza and León (2006), this study
<i>Rubus weberbaueri</i>	Shrub terrestrial	2400–3600	1.5–2.5	Lead–green	-	Black	Pink–reddish	Magenta	Focke (1910, 1911), Mendoza and León (2006), this study

southern Peru (Cusco) at 1,800–2,360 masl, forming sympatric populations with *C. bracteata* (Pedraza–Peñalosa and Luteyn, 2011). This study also confirms the wider distribution of *Ca. punctata* along the Peruvian Andes (Table 5).

The genus *Clethra* consists of 85 species distributed in Africa, America, and Asia (Sleumer, 1967; Fior et al., 2003; WCVP, 2021). Six of the 12 species reported from Peru were registered in the Amazonas region (*Cl. castaneifolia* Meisn., *Cl. ovalifolia*, *Cl. pedicellaris* Turcz., *Cl. peruviana* Szyszyl, *Cl. retivenia* and *Cl. revoluta* Ruiz & Pav) (WCVP, 2021; León, 2006b). This study confirmed the presence of *Cl. ovalifolia* (KUELAP-282) and *Cl. retivenia* (KUELAP-295) in Amazonas using molecular data (*matK*, *rbcl* and ITS). These species were previously recorded from Cajamarca (northern Peru) and Ucayali (southern Peru) (León, 2006b), and this study found that they occurred in similar habitats (i.e., temperate to humid tropical environments, 2,507–2,800 masl) coexisting with *V. floribundum* and *V. meridionale* (Table 6).

Disterigma includes 37 species distributed along cold mountain ecosystems of Central and South America (Pedraza–Peñalosa, 2008, 2009). Of these, 11 species were reported from Peru (Pedraza–Peñalosa, 2008, 2009; WCVP, 2021), and only three species were reported in the Amazonas region (i.e., *D. baguense* Pedraza; *D. ulei* Sleumer and *D. weberbaueri* Hoerold) (Pedraza–Peñalosa, 2009; WCVP, 2021). This study found two new reports of *Disterigma* for the Peruvian flora, namely, *D. ecuadorensis* (KUELAP-285) and *D. synanthum* (KUELAP-264, KUELAP-275)

(Figure 6). Although *D. ecuadorensis* was considered endemic to Ecuador and *D. synanthum* to Colombia (Pedraza–Peñalosa, 2008), the analyses of this study confirmed the wider distribution of these species. *D. ecuadorensis* and *D. synanthum* were found in cold to humid tropical environments at 2,500–3,000 masl and coexisting with *V. floribundum* (Table 7).

The genus *Gaultheria* is composed of 130 species from America and Asia (Middleton, 1991; Powell and Kron, 2001; WCVP, 2021). Sixteen species of *Gaultheria* have been reported from the tropical Andes of Peru (Middleton, 1991; Powell and Kron, 2001). In the Amazonas region, only three species of *Gaultheria* have been recorded (i.e., *G. erecta* Vent., *G. rigida* Kunth, *G. secunda* J. Rémy) (León, 2006a). Using molecular markers, the presence of *G. secunda* (KUELAP-278, KUELAP-284, KUELAP-301, KUELAP-288, KUELAP-266) was confirmed from Amazonas. Compared with the average intraspecific divergence observed in other species of the genus (as 0.3% for ITS in *G. leucarpa* and 0.3% for *matK* in *G. appressa*) (Fritsch et al., 2011; Lu et al., 2010), this taxon showed high intraspecific genetic divergence (2.4% for ITS), suggesting the presence of a species complex. Phenotypic plasticity of leaf anatomy (i.e., ovate to elliptic, leaf margins with sharp to rounded apex) among specimens of *G. secunda* was also observed. These phenomena have been previously reported in *Gaultheria* under scenarios of a high rate of reticulate evolution and hybrid speciation (Lu et al., 2010; Fritsch et al., 2011; Ocaña–Pallarés et al., 2019). *G. secunda* was found in wet grasslands and

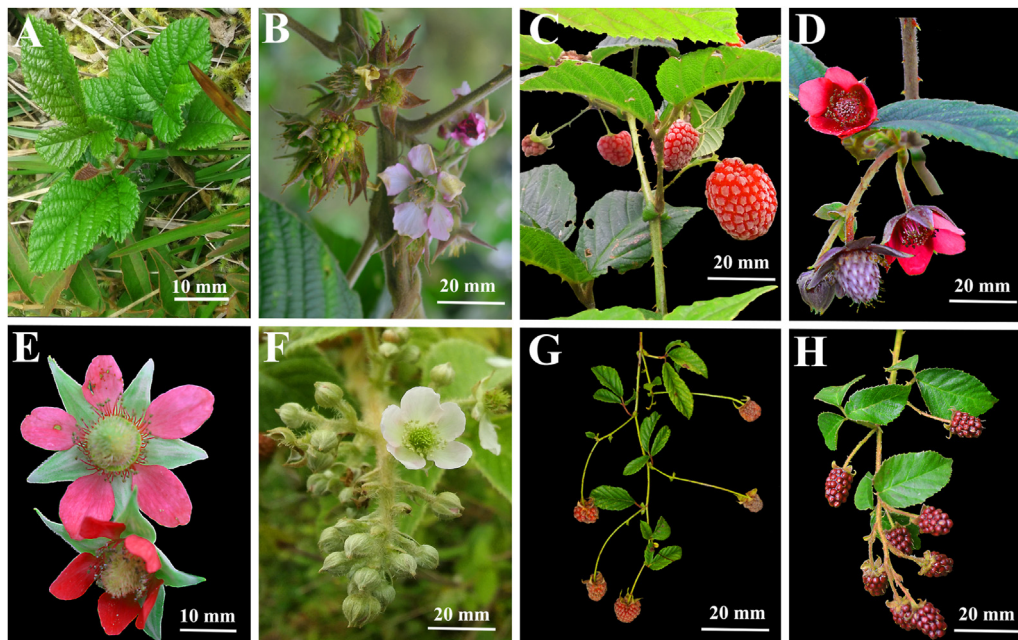


Figure 12. Diversity of andean berries belonging to Rosales. A. *Rubus glabratus*. B. *Rubus sparsiflorus*. C. *Rubus andicola*. D. *Rubus weberbaueri*. E. *Rubus lechleri*. F. *Rubus floribundus*. G. *Rubus loxensis*. H. *Rubus adenothallus*.

coniferous forest at 2,500–3,500 masl, coexisting with *D. synanthum*, *T. obovata*, *V. floribundum*, and *V. mathewsii*. This species has also been reported in Cusco, Pasco, Puno, Junin, and Ayacucho (central Peru). Additionally, another three species of *Gaultheria* (KUELAP-289, KUELAP-302, KUELAP-308) were found and this was not able to assign a species name because only one specimen was found and the diagnostic features of each species were not in good condition (Table 8). These unidentified species need further analyses with additional sampling and molecular markers to confirm their taxonomic status.

The genus *Thibaudia* consists of 73 species distributed in cloud forests from North to South America (Kron et al., 2002; Powell and Kron, 2003; WCVP, 2021). Approximately 29 species are distributed along areas of grass and shrubs (locally referred to as “pajonales”) and montane forests of the Peruvian Andes (2,500–4,000 masl) (León, 2006a,b; WCVP, 2021). Although six of these species have been previously reported from the Amazonas region (Powell and Kron, 2003; León, 2006a,b; WCVP, 2021), this study confirmed *T. angustifolia* (KUELAP-283), *T. moricandi* (KUELAP-298), *T. obovata* (KUELAP-272), and *T. ovalifolia* (KUELAP-299). The latter species was considered endemic to Junin (Central Peru) (León, 2006a). Ecologically, these species inhabit montane forests (2,000–2,800 masl), coexisting with *C. punctata*, *G. secunda*, *V. floribundum*, *V. meridionale*, and *V. mathewsii* (Table 9).

The genus *Vaccinium* consists of ~400 species distributed worldwide, except Australia (Asturizaga et al., 2006; Vander and Dickinson, 2009). Fifteen species have been reported from the tropical Andes and humid forests of Peru (Pedraza-Peñalosa and Luteyn, 2011; Coico et al., 2016; León et al., 2017; Mostacero et al., 2017; WCVP, 2021). Nine of these species have been recorded in the Amazonas region along steep rocky slopes and montane forests (León, 2006a; Coico et al., 2016). This study confirms the presence of *V. floribundum* and *V. mathewsii* and adds one new record of *Vaccinium* (i.e., *V. meridionale*) to the Peruvian flora. Although *V. meridionale* was originally reported as an endemic species from Colombia (Pedraza-Peñalosa and Luteyn, 2011), this study found it in montane forests from northern Peru (2,000–2,800 masl), suggesting that this species has a wider distribution along the Andes. Ecologically, *V. meridionale* shares the same habitat and coexists with *C. punctata*, *D. synanthum*, *G. secunda*, *V. florifundum*, and *V. mathewsii*. Previous intraspecific divergence reported on *Vaccinium* ranged from 0–0.1% for ITS in *V. reticulatum* (Kron et al., 2002), while molecular analyses of this

study revealed higher distance values within *V. floribundum* (3.7% for ITS). This could suggest high cryptic genetic diversity, although no morphological differences were found among specimens (Table 10). Sequencing additional markers or plastid genomes might reveal hidden taxa or overlooked interspecific introgression, which has been commonly reported in *Vaccinium* (Tsutsumi, 2011).

The genus *Rubus* encompasses ~700 species distributed worldwide (Focke, 1914; Thompson, 1995; Lu and Boufford, 2003; WCVP, 2021), and only 20 species have been reported from the montane and humid rainforests of Peru (Mendoza and León, 2006; WCVP, 2021). Previously, six species have been recorded from the Amazonas region (Mendoza and León, 2006). This study confirmed *R. adenothallus* and *R. weberbaueri* and reported the addition of six species of *Rubus* from the Amazonas region. Although *R. andicola*, *R. floribundus*, *R. glabratus*, *R. lechleri*, *R. loxensis*, and *R. sparsiflorus* were reported from distant regions such as Ayacucho (Central Peruvian Andes), Cusco (South Peruvian Andes) and San Martin (East Peruvian Andes), they inhabited Amazonas. Additionally, *R. glabratus* was originally described from Ecuador (Mendoza and León, 2006), and this study confirmed this species as having a wider distribution along the Andes. *R. adenothallus*, *R. lechleri*, *R. loxensis*, and *R. sparsiflorus* share the same habitat in humid forests above 3,300 masl. *R. andicola*, *R. floribundus*, and *R. weberbaueri* occur in the mountain undergrowth (sotobosque) at 1,800–2,500 masl. *R. glabratus*, *R. glaucus*, and *R. robustus* are found from montane rainforests to moorlands. The findings of this study reveal the genus *Rubus* as the most diverse group of berries in the Amazonas region (Table 11).

In the last decade, several of these species have been threatened by the high rate of deforestation, a serious concern that will eventually result in loss of biodiversity and uncontrolled genetic erosion of species with economic and ecological importance (Montesinos-Tubée, 2020; Walker et al., 2021). This study highlights not only the importance of sequencing several molecular markers in applying and validating the names of Andean berries, but also the need to integrate morphological and DNA-based methods to understand the diversity along the Peruvian Andean cloud forest (Bustamante et al. 2021, 2021, 2021; Tineo et al., 2020). The characterization of berries biodiversity is an important element in any future strategy to develop ambitious commitments and tackle research, monitoring and protection programs across the Amazonas region (Sánchez et al., 2021).

5. Conclusions

This study reported 24 species of andean berries distributed in coniferous forests, dry and humid forests, rocky slopes, and grasslands at 2,506–3,019 masl from the Amazonas region. These species are grouped into seven genera and included four new reports on the Peruvian flora. A total of 125 DNA-barcodes of andean berries were generated for four molecular markers (i.e., *GBSSI-2*, ITS, *matK*, *rbcl*). The results of this study suggest that the genetic marker ITS showed better resolution to distinguish species of the genera *Clethra*, *Disterigma*, *Thibaudia*, and *Rubus*, whereas the combination of the plastidial marker *matK* and the ITS properly resolved the relationships among species of the genera *Cavendishia*, *Gaultheria*, and *Vaccinium*. Accordingly, an initial screening regarding the diversity of andean berries should include amplification of these markers. This study also confirmed that morphological observations and mainly multilocus phylogeny are needed to reveal diversity of andean berries.

Declarations

Author contribution statement

Daniel Tineo, Danilo E. Bustamante & Martha S. Calderon: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Eyner Huaman: Contributed reagents, materials, analysis tools or data.

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Data availability statement

Data associated with this study has been deposited at <https://www.ncbi.nlm.nih.gov/genbank/>.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

Supplementary content related to this article has been published online at <https://doi.org/10.1016/j.heliyon.2022.e08839>.

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