A new species of *Escallonia* (Escalloniaceae) from the inter-Andean tropical dry forests of Bolivia (#31449)

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A new species of *Escallonia* (Escalloniaceae) from the inter-Andean tropical dry forests of Bolivia

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Over the last two decades, renewed fieldwork in poorly explored areas of the tropical Andes has dramatically increased the comparative material available to study patterns of inter- and intraspecific variation in tropical plants. In the course of a comprehensive study of the genus Escallonia, we found a group of specimens with decumbent branching, small narrowly elliptic leaves, inflorescences with up to three flowers, and flowers with red petals. This unique combination of traits was not present in any known species of the genus. To evaluate the hypothesis that these specimens belonged to a new species, we assessed whether morphological variation between the putative new species and all currently known Escallonia species was discontinuous. The lack of overlap in tolerance regions for vegetative and reproductive traits combined with differences in habit, habitat, and geographic distribution supported the hypothesis of the new species, which we named Escallonia harrisii. The new species grows in sandstone inter-Andean ridges and cliffs covered with dry forest, mostly on steep slopes between 1,300 - 2,200 m in southern Bolivia. It is readily distinct in overall leaf and flower morphology from other Escallonia species in the region, even though it does not grow in sympatry with other species. Because E. harrisii is locally common it may not be threated at present, but due to its restricted geographic distribution and the multiple threats of the tropical dry forests it could become potentially vulnerable.

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ABSTRACT

Over the last two decades, renewed fieldwork in poorly explored areas of the tropical Andes has dramatically increased the comparative material available to study patterns of inter- and intraspecific variation in tropical plants. In the course of a comprehensive study of the genus *Escallonia*, we found a group of specimens with decumbent branching, small narrowly elliptic leaves, inflorescences with up to three flowers, and flowers with red petals. This unique combination of traits was not present in any known species of the genus. To evaluate the hypothesis that these specimens belonged to a new species, we assessed whether morphological variation between the putative new species and all currently known *Escallonia* species was discontinuous. The lack of overlap in tolerance regions for vegetative and reproductive traits combined with differences in habit, habitat, and geographic distribution supported the hypothesis of the new species, which we named *Escallonia harrisii*. The new species grows in sandstone inter-Andean ridges and cliffs covered with dry forest, mostly on steep slopes between 1,300 - 2,200 m in southern Bolivia. It is readily distinct in overall leaf and flower morphology from other *Escallonia* species in the region, even though it does not grow in sympatry with other species. Because *E. harrisii* is locally common it may not be threated at present, but due to its restricted geographic distribution and the multiple threats of the tropical dry forests it could become potentially vulnerable.

INTRODUCTION

The tropical Andes harbor an exceptional concentration of endemic plant species and are considered one of the hottest global biodiversity hotspots (Myers et al., 2000). Patterns of species richness and endemicity in these mountains vary with elevation as a result of the evolutionary history of resident lineages. The low elevation tropical dry forest stands out as a remarkable biome that includes more species-poor but endemic-rich clades than other Andean biomes due to the persistence of old lineages that have diversified over the last 20 my. (Särkinen et al., 2011). Unfortunately, these evolutionarily unique forests are highly threatened (Banda-R et al., 2016). Therefore discovering, describing, and documenting their biodiversity is of significant interest to evolutionary and conservation biologists alike.

Escallonia Mutis ex L.f. (Escalloniaceae) is a morphologically and ecologically diverse genus of shrubs and small trees widely distributed in the neotropical mountains (Zapata, 2013; Sede and Denham, 2018). It is characterized by its sympodial growth with distinctive long- and short-shoot construction. The leaves are always simple, spiral, and with serrate margins. Flowers are borne singly or in inflorescences of few to many flowers. The flowers are always pentamerous, with free petals at maturity and inferior ovaries. There is an intrastaminal nectary disk, and always a characteristic large discoid stigma. All *Escallonia* species have bilocular septicidal capsules enclosing about 100 minute seeds. The species examined so far show the same chromosome morphology and base number (n=12) (Zielinski, 1955; Sanders et al., 1983; Hanson et al., 2003). Some species have a long history in horticulture and are widely used as ornamentals (Sleumer, 1968; Denaeghel et al., 2018).

Escallonia, with 39 species, is one the most species-rich genera in the Escalloniaceae (APG, 2016). Although relationships within Escalloniaceae and between Escalloniaceae and other Campanulids are not fully resolved (Tank and Donoghue, 2010; Beaulieu and O'Meara, 2018), the monophyly of *Escallonia* is strongly supported (Sede et al., 2013; Zapata, 2013). Most *Escallonia* species are distributed along the Andes, from northern Venezuela to southern Argentina, and the mountains of Costa Rica. Some species are restricted to the mountains of southeastern Brazil, and one species occurs in Juan Fernández Island. Most species have comparatively broad geographic ranges, and only few species are extremely narrow endemics (Sleumer, 1968). The phylogeny of *Escallonia* shows considerable phylogenetic geographic structure with major clades restricted to geographic regions (Zapata, 2013). This suggests that old divergences are associated with geographic isolation and that recent divergences are associated with bioclimatic differentiation along elevation gradients within geographic regions.

Historically, *Escallonia* has been relatively well-collected in some areas such as the southern Andes (Kausel, 1953; Sleumer, 1968; Sede and Denham, 2018). Renewed field exploration in poorly-known and highly threatened regions of the tropical Andes has made available new comparative material to study broad patterns of variation and reassess species boundaries in the genus. In this study, we present and describe a new species of *Escallonia* restricted to the dry forests of southern Bolivia. We include a detailed description and illustration, and a discussion of the eco-phenotypic differences between the new species and other species that occur in the region.

MATERIALS & METHODS

Species concept

In the present study, we follow the general lineage species concept (de Queiroz, 1998), which proposes that species are independently evolving segments of population-level lineages and that any evidence of lineage separation (i.e., distinct morphology, differences in ecological niche, monophyly of alleles) is sufficient to infer the existence of separate species (De Queiroz, 2007). Here, we assess discontinuities in continuous morphological traits using the approach proposed by Zapata and Jiménez (2012), in combination with differences in habit, habitat and geographic distribution.

Taxon sampling

A total of 809 herbarium specimens from all species of *Escallonia* and the new species were included in this study. *Escallonia salicifolia* Mattf. was not included here because only two specimens were available and the method used in this study requires a sample size larger than three (Zapata and Jiménez, 2012). Voucher information for all specimens is available in a git repository at `http://github.com/zapataf/ms_eharrisii`

Morphological measurements

The new species differs from other *Escallonia* species in overall leaf shape and flower number. Therefore, we measured leaf length and width, and counted the number of flowers per inflorescence in all specimens. On each specimen, we recorded leaf measurements from three different leaves and then averaged to generate mean leaf measurements. We counted flower number on one inflorescence per specimen.

Morphological discontinuities

We assessed morphological discontinuities in leaf shape and flower number between the new species and all *Escallonia* species using the method of Zapata and Jiménez (2012). For these analyses, we used a frequency cutoff of 0.15 and statistical confidence of 0.90. Therefore, we inferred morphological discontinuities when the proportions of the tolerance limits covering the morphological variation for each pair of species overlapped by less than 0.15. All analyses were carried out in R 3.4.3 (R Core Team, 2016); source code and the data used in these analyses are available in a git repository at `http://github.com/zapataf/ms_eharrisii`

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Code of Nomenclature for algae, fungi, and plants (ICN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. In addition, new names contained in this work which have been issued with identifiers by IPNI will eventually be made available to the Global Names Index. The IPNI LSIDs can be resolved and the associated information viewed through any standard web browser by appending the LSID contained in this publication to the prefix "http://ipni.org/". The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central, and CLOCKSS.

RESULTS & DISCUSSION

Discontinuities in leaf morphology

The new species has small narrowly elliptic leaves, which are uncommon in *Escallonia* (Figure 1). The weigh of the evidence supporting a morphological discontinuity in leaf morphology is strong between the new species and the following 20 species: *E. angustifolia* C. Presl, *E. bifida* Link & Otto, *E. chlorophylla* Cham. & Schltdl., *E. farinacea* A. St.-Hil., *E. herrerae* Mattf., *E. hispida* (Vell.) Sleumer, *E. illinita* C. Presl, *E. laevis* (Vell.) Sleumer, *E. micrantha* Mattf., *E. millegrana* Griseb., *E. myrtoidea* Bertero ex DC., *E. obtusissima* A. St.-Hil., *E. paniculata* (Ruiz & Pav.) Roem. & Schult., *E. pendula* (Ruiz & Pav.) Pers., *E. petrophila* Rambo & Sleumer, *E. piurensis* Mattf., *E. pulverulenta* (Ruiz & Pav.) Pers., *E. reticulata* Sleumer, *E. revoluta* (Ruiz & Pav.) Pers., and *E. schreiteri* Sleumer (Figure 2). These results support the hypothesis of a species boundary between the new species and 20 currently known *Escallonia* species.

Discontinuities in flower number

The new species has inflorescences with up to three flowers, which are uncommon in *Escallonia* (Figure 3). There is support for a morphological discontinuity in flower number between the new species and 30 species, 19 of which are also separated by a discontinuity in leaf morphology (see above, all species except *E. petrophila*). The remaining 11 species separated only by a morphological discontinuity in flower number are: *E. alpina* Poepp. ex DC., *E. cordobensis* (Kuntze) Hosseus, *E. discolor* Vent., *E. florida* Poepp. ex DC., *E. hypoglauca* Herzog, *E. leucantha* J. Rémy, *E. megapotamica* Spreng., *E. resinosa* (Ruiz & Pav.) Pers, *E. rubra* (Ruiz & Pav.) Pers., *E. tucumanensis* Hosseus, and *E. virgata* (Ruiz & Pav.) Pers. (Figure 4). These results support the hypothesis of a species boundary between the new species and 30 currently known *Escallonia* species.

Support for the new species boundary

Taken together, the results described above show there is evidence supporting a species boundary between the new species and 31 currently known *Escallonia* species. In most cases the new species boundary spans differences in both leaf and flower traits (19 species). In other cases, the species boundary is supported with evidence from one of the traits (12 species). This is consistent with the species concept we apply in this study (De Queiroz, 2007). For instance, *E. micrantha* and the new species differ in both leaf shape and flower number, whereas *E. florida* and the new species differ in flower number but are broadly similar in leaf shape (Figure 2, Figure 4). No material for DNA sequencing was available to place the new species in the *Escallonia* phylogeny, therefore it is not possible to discern whether morphological similarities between the new species and other species reflect convergent evolution or recent divergence with little differentiation.

Lack of support for morphological discontinuities, differences in habit and habitat, and alternative explanations

The weigh of the evidence supporting a morphological discontinuity between the new species and the following seven species was weak: *E. callcottiae* Hook. & Arn., *E. gayana* Acevedo & Kausel, *E. ledifolia* Sleumer, *E. myrtilloides* L. f., *E. polifolia* Hook., *E. rosea* Griseb., and *E. serrata* Sm.. There are three non-exclusive reasons to explain why this result does not undermine the hypothesis of a species boundary between the new species and any of these seven species: *i) Habit and habitat*. *E. myrtilloides*, *E. polifolia*, *E. rosea*, *E. serrata*, and the new species all differ in habit and habitat. *E. myrtilloides* are small trees with thick branches and it is restricted to the páramos and jalcas in the tropical Andes above 2,600 m. *E. polifolia* are small shrubs with revolute, tomentulose leaves, and it is endemic to the jalcas in the Cha-Chapoyas region (northern Perú) above 2,800 m. *E. rosea* are shrubs from the wet temperate forests of southern Chile (Valdivian forests). *E. serrata* are procumbet shrubs endemic to Patagonia in southern Chile and Argentina. In contrast, the new species are profusely branched sub-shrubs with decumbent branching and slender twigs, and it is endemic to the dry forest in southern Bolivia at around 1,700 m.

ii) Geographic sampling. One could propose that the new species is an allopatric population of any of the seven species. This would predict there could be unsampled populations from any of the seven species across the geographic range of *Escallonia*. This is highly unlikely because other *Escallonia* species have been sampled thoroughly at intervening localities (Figure 5) and we have examined around 3,900 *Escallonia* herbarium specimens that indicate that the geographic range of the seven species is well sampled, and *iii) Statistical power*. The sample size for *E. callcottiae*, *E. gayana*, and *E. ledifolia* is very low (Table 1), which lowers the statistical power of the method we used to diagnose morphological discontinuities (Zapata and Jiménez, 2012). Therefore the lack of evidence supporting a morphological discontinuity in these cases may just be a statistical artifact.

TAXONOMIC TREATMENT

Escallonia harrisii Zapata & Villarroel, sp. nov. (Figure 6)

Type: BOLIVIA. Santa Cruz. Vallegrande. San Blas (abajo) y La Estancilla, 58 Km de la ciudad de Vallegrande. 18° 29′ S, 63° 59′ W, 2200 m, 19 November 1994 (fl), *Vargas, I.G.* 3673 (holotype: MO, isotypes: NY; USZ).

Paratype: BOLIVIA. Chuquisaca. 4 km de la comunidad de San Bartolo, sobre el camino a Nuevo Mundo, 19° 39′ S, 64° 02′ W, 1350 m, 14 December 2013 (fl, fr), *Villarroel et al.* 2322 (UB; USZ).

Diagnosis: Decumbent branching, small narrowly elliptic leaves, inflorescences with up to three flowers, flowers with red petals

Description: Perennial sub-shrub, to 2 m tall, profusely branched, branches decumbent, 1.9-1.0 mm diameter, angular to terete, outer bark scaly, grey, new growth branches angular, outer bark smooth, reddish, densely puberulent, hairs simple, white, 0.1-0.2 mm long. Leaves spiral; petiole 0.6-0.8 mm long; lamina oblanceolate, 14.5-19.7 mm long, 1.6-3.7 mm wide, basally attenuate, apically acute, abaxially dull with scattered glands, minutely puberulent (simple hairs), adaxially lustrous green, glabrous; margin slightly serrate, glandular; secondary veins three to four pairs, brochidodromous. Inflorescences terminal, 1 to 3-flowered. Flowers hermaphrodite, pentamerous. Pedicels 2-4.7 mm long, 0.4-0.6 mm diameter, terete, densely puberulent (simple hairs). Ovary inferior, turbinate, 1.5-3 x 2.4-3.8 mm, puberulent. Calyx tube 0.5-0.7 mm long; lobes narrowly triangular-subulate, 5.8-10 x 0.8-1.3 mm, abaxially and adaxially puberulent, margin glandular, sparsely ciliate, sometimes recurved. Corolla actinomorphic, glabrous; petals red, spatulate, 6.7-7.9 x 0.9-1.17 mm at base, 1.5-1.75 mm at the widest point, margin minutely crenulate. Stamens 5; filaments glabrous, terete, 4.2-4.9 mm long; anthers versatile, sub-basifixed, narrowly oblong 1.30 x 0.44 mm. Style terete, 4.4-6.3 mm long. Stigma discoid. Disk flat. Fruit brown, turbinate, 3.10-4.12 x 3.41-4.70 mm, dehiscence septicidal. Seeds linear, 0.04 mm long, striate.

Additional Specimens Examined: BOLIVIA. Chuquisaca. Calvo. Serranía Incahuasi. 10-15 km from Muyupampa on road to Lagunillas, 19° 21′ 51″ S, 63° 50′ 09″ W, 1500 m, 8 March 1998 (fl, fr), *Wood et al.* 13266 (K); Chuquisaca. Calvo. Serranía del Incahuasi, 10-15 km de Muyupampa sobre el camino a Lagunillas, 19° 49′ 39″ S, 63° 43′ 31″ W, 1580 m, 25 March 2013 (fl, fr), *Wood et al.* 27640 (K; USZ); Chuquisaca. Calvo. Serranía Incahuasi, entre Muyupampa y Lagunillas, 19° 49′ 38″ S, 63° 43′ 30″ W, 1580 m, 13 December 2013 (fl, fr), *Villarroel et al.* 2321 (UB; USZ); Tarija. O'Connor. On w side of easternmost pass on road from Entre Rios to Palos Blancos, 21° 25′ 28″ S, 63° 54′ 47″ W, 1400 m, 17 January 2001 (fr), *Wood and Goyder* 16822 (K).

Etymology: The specific epithet is in honor of Whitney R. Harris, who supported the center that now bears his name, the Whitney R. Harris World Ecology Center at the University of Missouri-St. Louis. Through the support provided by this center, several generations of biologists from throughout the world have been able to contribute to the study, understanding, and conservation of temperate and tropical ecosystems worldwide.

Phenology: Flowering and fruiting specimens have been collected between November and March. There are no observations yet on pollination or dispersal biology.

Distribution: Restricted to the south of Bolivia (Figure 7). Locally common.

Habitat: Plants of this species grow on rocky outcrops and ridges of red sandstone, mostly on steep slopes and summits between 1,300-2,200 m elevation. The dominant vegetation in the region where *E. harrisii* grows is dry forest on the slopes (i.e., Chaco Serrano forest) and semi-deciduous forests on the mountaintops (i.e., Tucumano Boliviano forest)

Conservation status: Although *E. harrisii* has been collected in few localities, it is locally common and it may not be threatened at present. Because it is restricted to the tropical dry forest, one of the most threatened tropical habits (Banda-R et al., 2016), it could become potentially vulnerable. However, more data and population-level studies are needed to assess the conservation status of this species. An IUCN category of Data Deficient (DD) is assigned, according to IUCN criteria (IUCN, 2012).

Affinities: Because we did not have access to good quality DNA, *E. harrisii* has not been included in a molecular phylogenetic study of *Escallonia* and its closest relatives are not known. Morphologically, *E. harrisii* displays similarities in leaf shape and flower number with *E. callcottiae*, *E. gayana*, *E. ledifolia*, *E. myrtilloides*, *E. polifolia*, *E. rosea* and *E. serrata* (Table 1). However, none of these species has decumbent branching, slender twigs and narrow oblanceolate leaves.

Ecologically, no other species of *Escallonia* has been found in sympatry with *E. harrisii*. Only *E. millegrana*, *E. micrantha*, *E. pendula* and *E. herrerae* grow at equivalent elevations and in similar habitats (i.e. dry forests in inter-Andean valleys). These four species are strikingly different in all morphological traits compared to *E. harrisii* (Table 1). Although *E. millegrana* also occurs in Bolivia, plants of this species are tall deciduous shrubs (up to 4 m) with long leaves (up to 15 cm), spines in young shoots, and inflorescences with around 850 flowers (Table 1).

[tbp]

Table 1. Descriptive statistics. N = sample size, m = minimum, Me = mean, M = maximum, LL = leaf length, LW = leaf width, FN = flower number, E = elevation. New species in bold. *Species occurring in Bolivia.

	N	mLL	MeLL	MLL	mLW	MeLW	MLW	mFN	MeFN	MFN	mE	ME
E. alpina	40	9.2	16.6	26.5	4	7.0	9.8	1	8.1	14	20	2300
E. angustifolia	13	39.5	54.6	74	5	11	17	16	70.3	155	1600	3280
E. bifida	36	41.7	55.9	79	13.3	17.4	23.3	25	83.1	150	70	2300
E. callcottiae	6	21.7	29.2	42.3	9.7	13	21.7	12	23.7	55	40	800
E. chlorophylla	13	37.3	47.6	56.7	12.6	17.6	23.4	27	42.1	60	0	1312
E. cordobensis	11	29.7	40.6	53.5	6	7.9	10.9	7	12.7	22	1000	2400
E. discolor	5	48.7	59.0	76.7	17.7	20.9	23.3	65	103	150	2500	3300
E. farinacea	18	35	48.6	62.3	10	14.6	18.3	6	13.9	22	812	1810
E. florida	10	16	18.8	23	3	3.7	6	10	31.3	61	624	2000
E. gayana	7	13.3	16.9	21.7	4.3	5.6	7.1	28	48	100	100	800
E. harrisii	**6**	**14.5**	**16.8**	**19.7**	**1.6**	**2.8**	**3.7**	**1**	**1.8**	**3**	**1350**	**2200**
E. herrerae	8	103.7	152.1	174.3	24.3	35	46	115	157	250	1800	3450
E. hispida	8	35	47.2	55.8	16.2	20	22.2	16	20.3	34	600	1500
**E. hypoglauca*	24	18	30.3	48.3	7.3	13.3	22.3	7	10.9	24	2200	3500
E. illinita	25	37.7	45.8	58.7	8.3	16.4	21.7	22	49.5	150	40	2650
E. laevis	27	20.3	37	57.4	9.6	13.8	21	7	14	30	0	2750
E. ledifolia	10	27.7	35.9	43	5	7.4	9.7	2	5.6	8	950	1150
E. leucantha	14	15.7	22.7	31	5.3	8.3	11	33	61.2	80	50	707
E. megapotamica	29	21	31.2	48	5.5	8.9	16	19	49.11	95	30	1000
E. micrantha	11	88.3	118.8	142.3	23	32.4	43.3	800	881.8	950	1850	2500
**E. millegrana*	21	73.3	104.8	146.3	22.5	32.5	46	700	835.7	950	1228	2950
**E. myrtilloides*	56	6.7	14.4	30.3	3.8	7.1	18	1	1	1	2351	4100
E. myrtoidea	15	31.7	45	72	15.3	20.9	26	35	73.8	115	120	2000
E. obtusissima	6	52	61.2	69.3	19	22.7	27.7	27	32.8	45	800	1200
**E. paniculata*	66	40.7	75.7	112	16.3	24	37	40	148.9	800	1200	3492
E. pendula	30	116.7	175.4	217.7	22.3	38.3	55.7	80	169.3	280	1300	3100
E. petrophila	8	55.8	84.6	98.7	20.9	25.9	29	5	7	11	800	1131
E. piurensis	12	24	36.5	44.7	9.7	11.4	13.7	20	44.9	75	2500	3300
E. polifolia	9	13.8	17.6	19.5	2.3	2.8	3.8	1	1	1	2900	3500
E. pulverulenta	25	41.9	54.6	72.9	17.3	26.5	37	140	171.5	200	0	1200
E. resinosa	46	20.7	34.1	52.7	5.7	8.6	13	10	56.4	130	2200	3776
**E. reticulata*	21	55.7	68.7	80	15	23.7	28.3	25	55.8	100	1300	2400
E. revoluta	21	31.7	39.1	49.3	12.8	18.7	25.7	27	75.3	180	1	1642
E. rosea	30	15	33.5	51	5	12.8	24.3	5	16.7	55	185	1662
E. rubra	46	21.7	36.6	58.3	6.3	16.7	32	5	15.5	45	0	1605
**E. schreiteri*	18	42.3	56.6	74	8.3	11.1	14.7	20	42.6	60	1600	2954
E. serrata	20	8.2	14.4	21.2	4.3	6.6	9.5	1	1	1	5	400
E. tucumanensis	18	31.7	50.5	76	11	18.3	30.7	6	14.2	30	800	2800
E. virgata	20	9.5	11.7	14.7	3.5	4.5	5.7	6	13.1	28	61	3000

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REFERENCES

APG (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean ...*, pages 1–20.

Banda-R, K., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., Pullan, M., Quintana, C., Riina, R., Rodriguez M, G. M., Weintritt, J., Acevedo-Rodriguez, P., Adarve, J., Alvarez, E., Aranguren B, A., Arteaga, J. C., Aymard, G., Castano, A., Ceballos-Mago, N., Cogollo, A., Cuadros, H., Delgado, F., Devia, W., Duenas, H., Fajardo, L., Fernandez, A., Fernandez, M. A., Franklin, J., Freid, E. H., Galetti, L. A., Gonto, R., Gonzalez-M, R., Graveson, R., Helmer, E. H., Idarraga, A., Lopez, R., Marcano-Vega, H., Martinez, O. G., Maturo, H. M., McDonald, M., McLaren, K., Melo, O., Mijares, F., Mogni, V., Molina, D., Moreno, N. d. P., Nassar, J. M., Neves, D. M., Oakley, L. J., Oatham, M., Olvera-Luna, A. R., Pezzini, F. F., Dominguez, O. J. R., Rios, M. E., Rivera, O., Rodriguez, N., Rojas, A., Sarkinen, T., Sanchez, R., Smith, M., Vargas, C., Villanueva, B., and Pennington, R. T. (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. *Science (New York, N.Y.)*, 353(6306):1383–1387.

Beaulieu, J. M. and O'Meara, B. C. (2018). Can we build it? Yes we can, but should we use it? Assessing the quality and value of a very large phylogeny of campanulid angiosperms. *American Journal of Botany*, 88:163–16.

de Queiroz, K. (1998). The General Lineage Concept of Species, Species Criteria, and the Process. In Harrison, R. G. and Berlocher, S. H., editors, *Endless forms: Species and speciation*, pages 57–75. New York.

De Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology*, 56(6):879–886.

Denaeghel, H. E. R., Van Laere, K., Leus, L., Lootens, P., Van Huylenbroeck, J., and Van Labeke, M.-C. (2018). The Variable Effect of Polyploidization on the Phenotype in Escallonia. *Frontiers in Plant Science*, 9:36–17.

Hanson, L., Brown, R. L., Boyd, A., Johnson, M. A. T., and Bennett, M. D. (2003). First Nuclear DNA C-values for 28 Angiosperm Genera. *Annals of Botany*, 91:31–38.

IUCN (2012). *IUCN Red List Categories and Criteria, Version 3.1.* IUCN, Gland, Switzerland, Cambridge, United Kingdom, 2 edition.

Kausel, E. (1953). Revisión del género "Escallonia" en Chile. *Darwiniana*, 10:169–255.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403:853–858.

R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Sanders, R. W., Stuessy, T. F., and Rodriguez, R. (1983). Chromosome numbers of the flora of the Juan Fernandez Islands. *American Journal of Botany*, 70(6):799.

Särkinen, T., Pennington, R. T., Lavin, M., Simon, M. F., and Hughes, C. E. (2011). Evolutionary islands in the Andes: persistence and isolation explain high endemism in Andean dry tropical forests. *Journal of Biogeography*, 39(5):884–900.

Sede, S. M. and Denham, S. S. (2018). Taxonomic Revision of Escallonia(Escalloniaceae) in Argentina. *Systematic Botany*, 43(1):364–396.

Sede, S. M., Duernhoefe[illegible] I., Morello, S., and Zapata, F. (2013). Phylogenetics of Escallonia (Escalloniaceae) based on plastid DNA sequence data. 173(3):442–451.

Sleumer, H. O. (1968). Die Gattung Escallonia. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde*, pages 1–149.

Tank, D. C. and Donoghue, M. J. (2010). Phylogeny and phylogenetic nomenclature of the Campanulidae based on an expanded sample of genes and taxa. *Systematic Botany*, 35(2):425–441.

Zapata, F. (2013). A multilocus phylogenetic analysis of Escallonia (Escalloniaceae): diversification in montane South America. *American Journal of Botany*, 100(3):526–545.

Zapata, F. and Jiménez, I. (2012). Species delimitation: inferring gaps in morphology across geography. *Systematic Biology*, 61(2):179–194.

Zielinski, Q. B. (1955). Escallonia: the genus and its chromosomes. *Botanical Gazette*, pages 166–172.

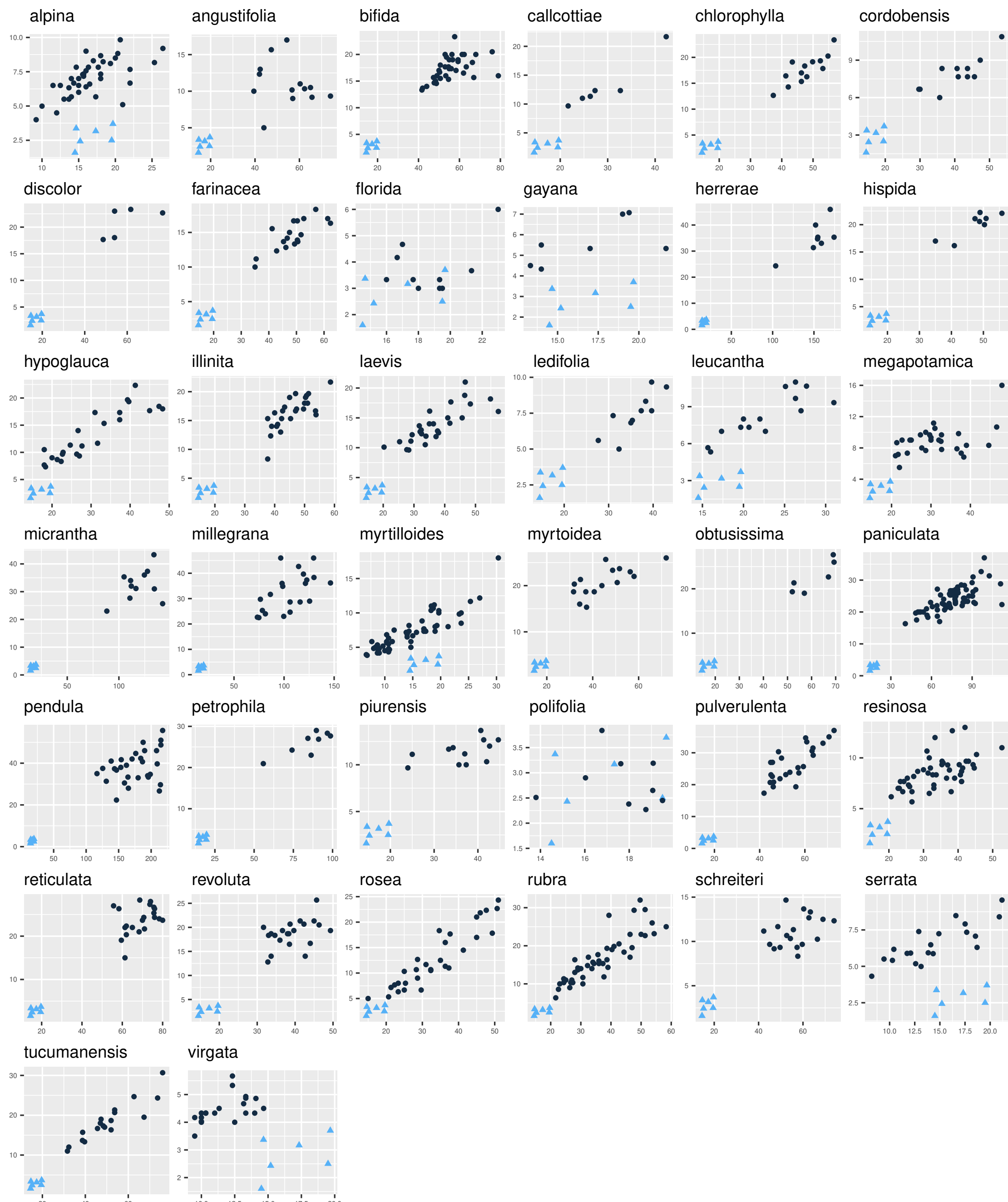

Figure 1. Bivariate plots for variation in lamina length (mm) on the X-axis and lamina width (mm) on the Y-axis. In each panel, new species in light triangles, currently known species in dark circles, species name of the currently known species on top.

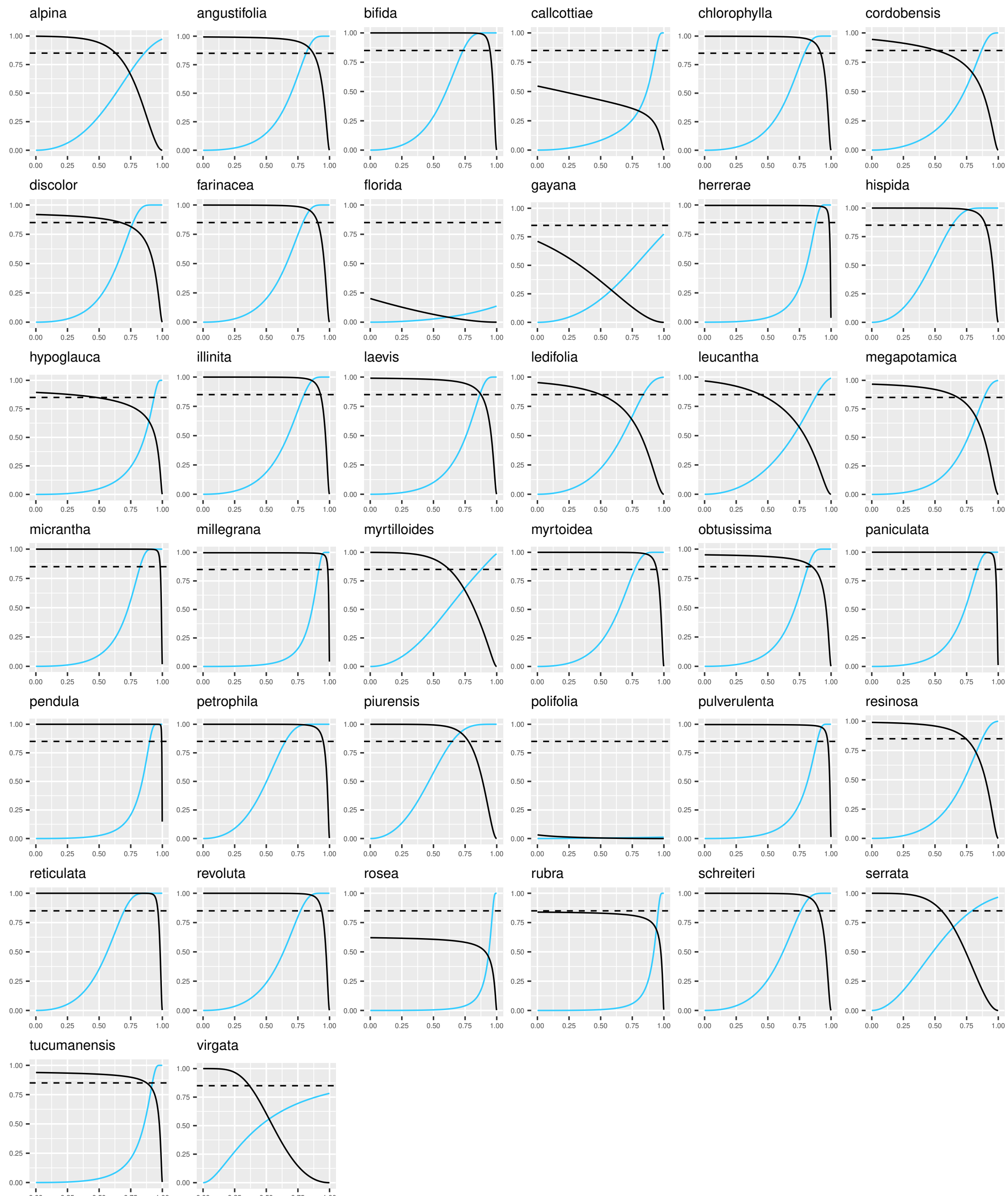

Figure 2. Proportion plots, the estimated proportion (Y-axis) covered by tolerance regions sharing a single point along the ridgeline manifold (X-axis). In each panel, new species in light color, currently known species in dark color, species name of the currently known species on top, dashed line corresponds to the cutoff threshold to infer a morphological discontinuity.

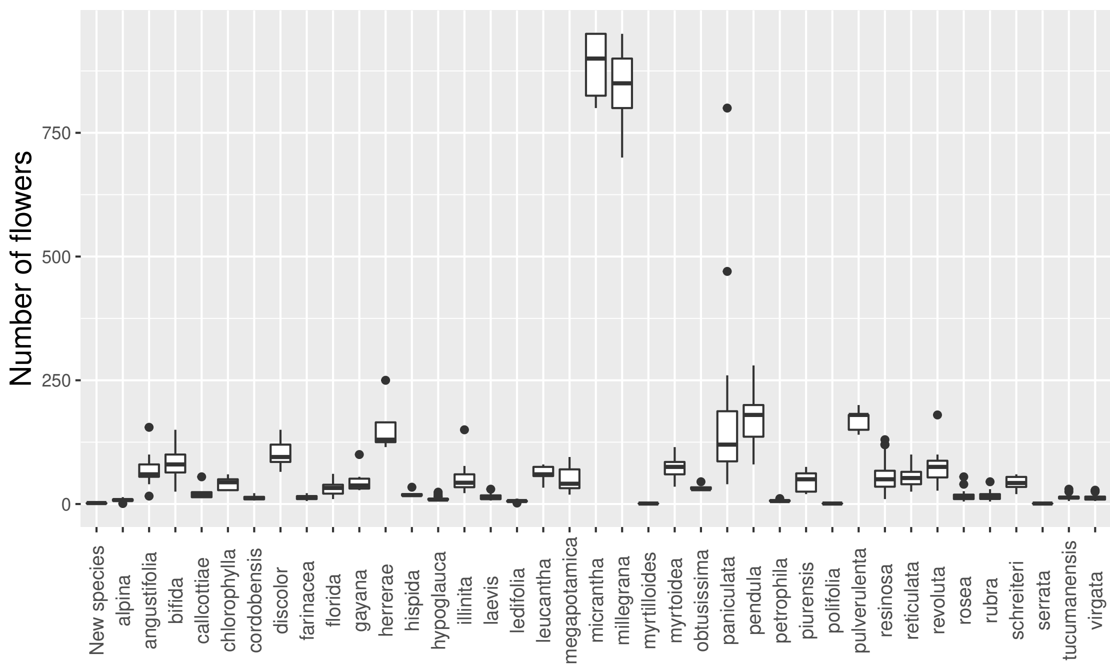

Figure 3. Variation in flower number in *Escallonia*.

Figure 4. Box plots for variation in flower number. In each panel, new species in light color, currently known species in dark color, species name of the currently known species on top, dashed line is the upper tolerance limit for the new species, dotted line is the lower tolerance limit for the currently known species.

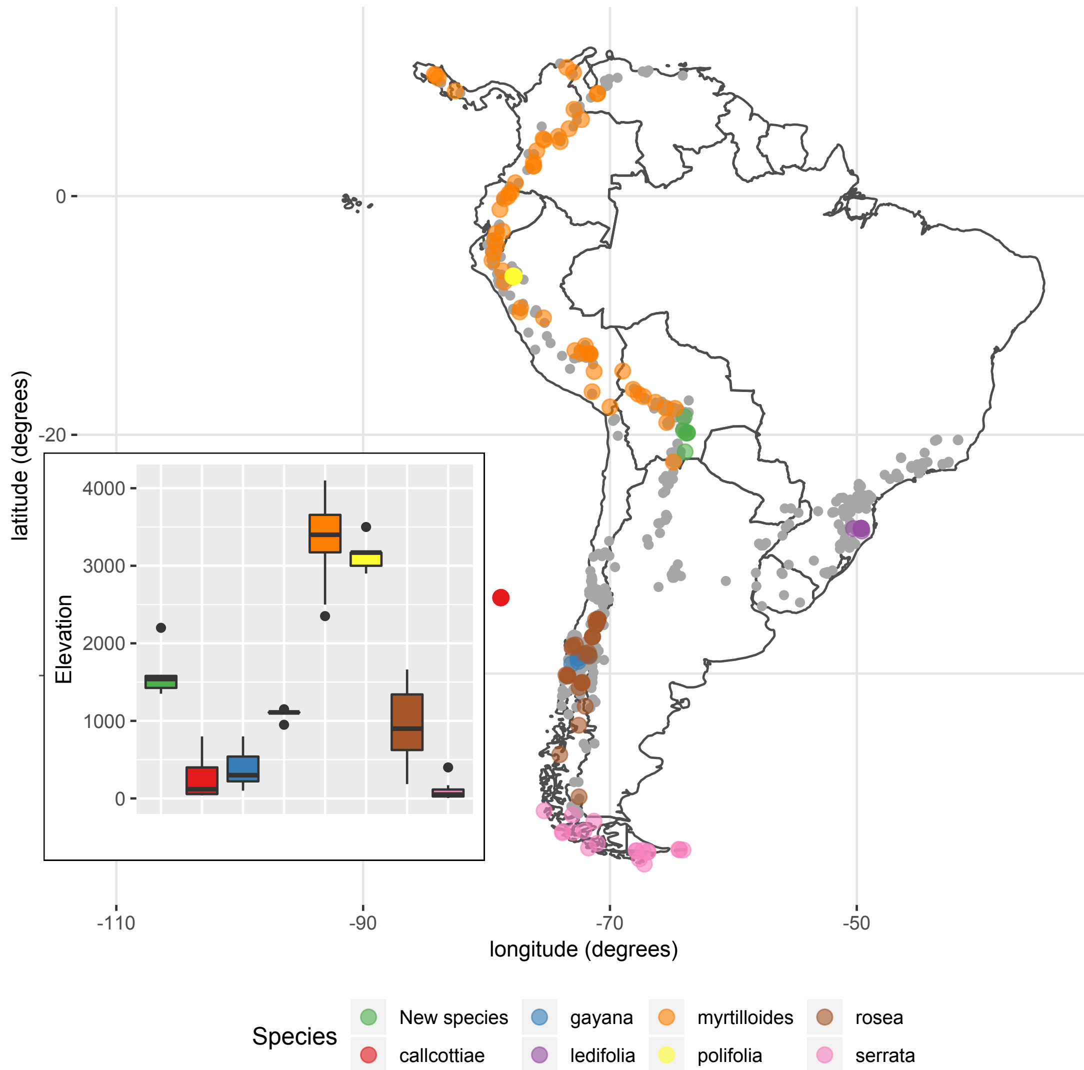

Figure 5. Geographic distribution of species lacking support for morphological discontinuities. Inset box plot for distribution along elevation.

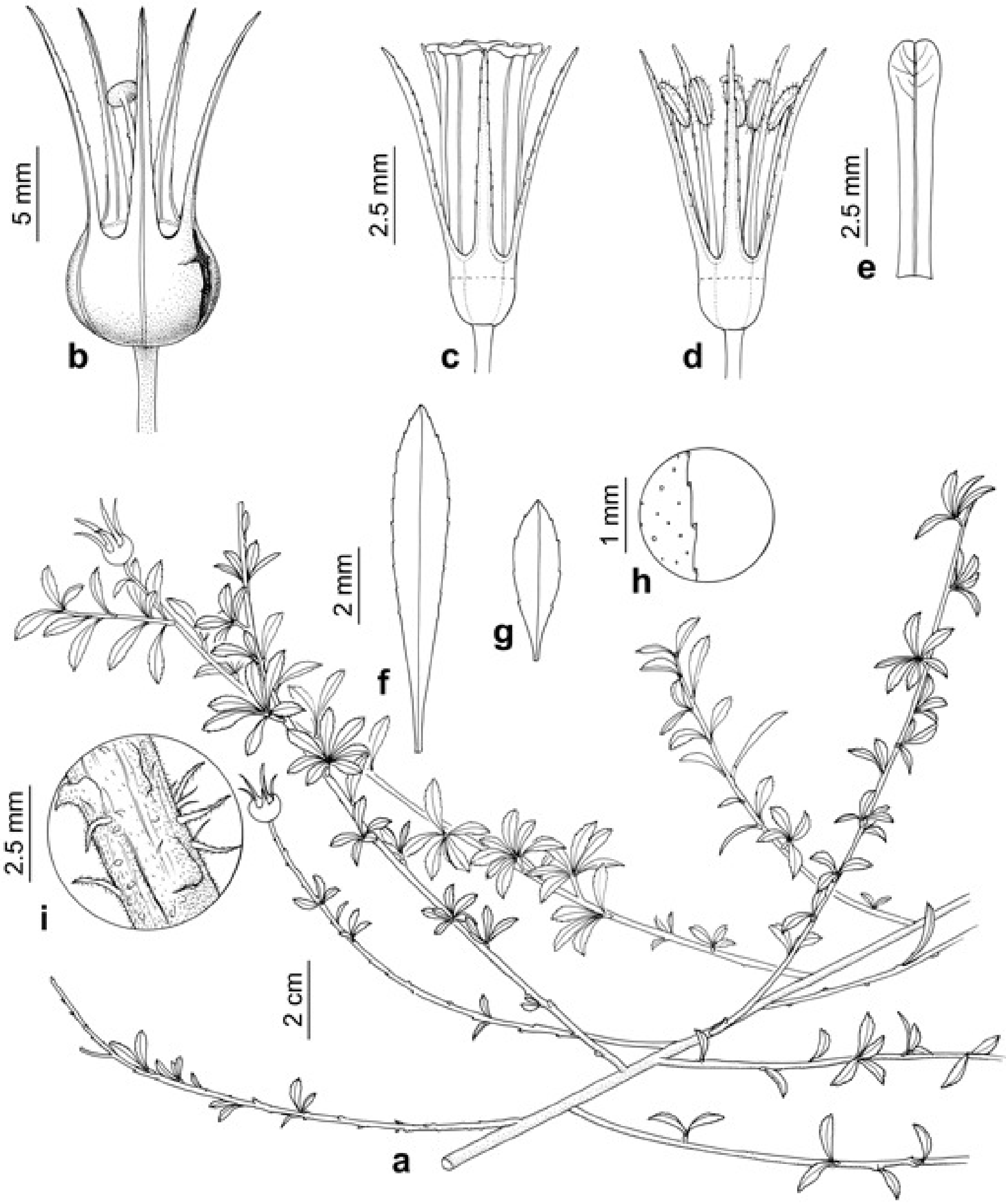

Figure 6. *Escallonia harrisii*. Zapata & Villarroel. a. Habit, b. Fruit, c. Flower, d. Flower with petals removed, e. Petal, f. Mature leaf, g. Young leaf, h. Detail of leaf margin, i. Detail of outer bark in mature shoot. Illustration by B. Alongi.

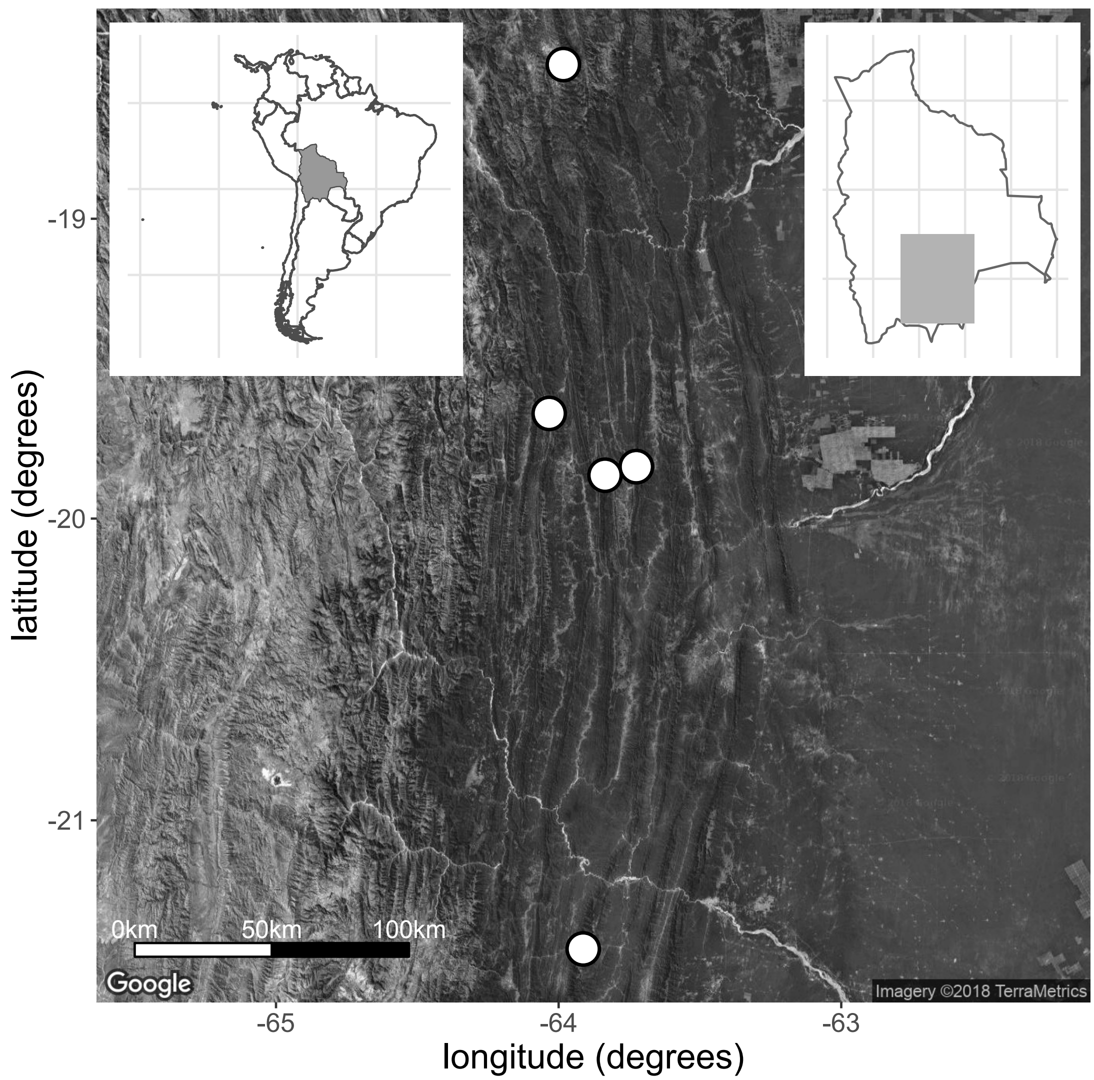

Figure 7. Collection sites of *Escallonia harrisii*. Topleft inset map of South America, Bolivia shaded. Topright inset map of Bolivia, area of the main figure shaded