DARWINIANA NUEVA SERIE
www.ojs.darwin.edu.ar
ISSN 0011-6793 impresa - ISSN 1850-1699 en línea

DARWINIANA, nueva serie 12(2): 204-219. 2024
Versión de registro, efectivamente publicada el 11 de septimbre de 2024
DOI: 10.14522/darwiniana.2024.122.1221

# TAXONOMIC STATUS, DISTRIBUTION AND CONSERVATION OF THE CRITICALLY ENDANGERED PLANT *PSYCHOTRIA ANGUSTATA* (RUBIACEAE), ENDEMIC TO FLOREANA ISLAND, GALAPAGOS

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**Abstract.** Simbaña, W.; A. Tye, T. J. Motley & U. Eliasson. 2024. Taxonomic status, distribution and conservation of the Critically Endangered plant *Psychotria angustata* (Rubiaceae), endemic to Floreana Island, Galapagos. *Darwiniana*, nueva serie 12(2): 204-219.

Two species of *Psychotria* have been recognised in the Galapagos Islands, both understorey shrubs endemic to the archipelago: *P. rufipes* Hook.f. occurs on seven islands, including Floreana, while *P. angustata* Andersson is endemic to Floreana. Since their mid-19th century discovery, the taxonomic and ecological status of these species has been uncertain. To clarify this, we examined historical specimens and numerous recent collections of both species, and surveyed their distribution on Floreana. Examination of the original description of *P. angustata* enables restriction of its type to the single specimen *Andersson 195*, which we designate the lectotype. We found differences in leaf venation, indumentum, shape and size, which confirm the existence of two clearly different forms that were originally referred to two species. Where these occur together no intermediate individuals were found. Differences also exist in the indumentum of twigs, inflorescences and flowers, but flower colour appears to be similar (white to cream) in the two taxa. These differences are of a degree commonly treated as infra-specific in other species of *Psychotria*. We conclude that the two taxa hitherto recognised as species are better regarded as varieties within *P. rufipes* and provide the consequent new combination *Psychotria rufipes* var. *angustata* W. Simbaña & Tye **stat. nov.** Both taxa are threatened by humid forest destruction and introduced animals and plants. Surveys confirm the global Red-List status of *P. rufipes* var. *angustata* as Critically Endangered. Population age structure indicates regeneration of both taxa since the recent eradication of feral ungulates from Floreana, but invasive plants still threaten them.

Keywords. Charles Darwin; morphology; Nils Johan Andersson; population; speciation; threats; typification.

**Resumen.** Simbaña, W.; A. Tye, T. J. Motley & U. Eliasson. 2024. Estado taxonómico, distribución y conservación de la planta en peligro crítico *Psychotria angustata* (Rubiaceae), endémica de la isla Floreana, Galápagos. *Darwiniana*, nueva serie 12(2): 204-219.

Dos especies de *Psychotria* han sido reconocidas en las islas Galápagos, ambas arbustos del sotobosque, endémicas para el archipiélago: *P. rufipes* Hook.f. está presente en siete islas, incluyendo Floreana, mientras *P. angustata* Andersson es endémica de Floreana. Desde su descubrimiento a mediados del siglo 19, el estado taxonómico y ecológico de estas especies ha sido dudoso. Para aclarar esto, examinamos las muestras históricas y numerosas colecciones recientes de ambas especies, e investigamos su distribución en Floreana. Un examen de la descripción original de *P. angustata* permite restringir su material tipo a la muestra *Andersson 195*, la cual designamos lectotipo. Constatamos diferencias de la venación, indumento, forma y tamaño de las hojas, que confirman la existencia de

Original recibido el 14 de abril de 2024, aceptado el 3 de septiembre de 2024
Editor Asociado: Diego L. Salariato

dos formas claramente diferentes, que originalmente fueron referidas a dos especies. También existen diferencias en el indumento de las ramas pequeñas, de las inflorescencias y de las flores, pero el color de las flores parece ser similar (blanco a color crema) en los dos taxones. Estas diferencias son de un grado comúnmente considerado como de nivel infra-específico en otras especies de *Psychotria*. Por lo tanto, proporcionamos la nueva combinación necesaria *Psychotria rufipes* var. *angustata* W. Simbaña & Tye. **stat. nov.** Los dos taxones están amenazados por la destrucción del bosque húmedo y por los animales y plantas introducidos. La investigación de campo confirma el estado actual de *Psychotria rufipes* var. *angustata* en la Lista Roja mundial como En Peligro Crítico. La estructura de edades de las poblaciones sugiere la recuperación de los dos taxones desde la erradicación reciente de los ungulados ferales de Floreana, pero las plantas invasoras siguen amenazándolos.

Palabras clave. Charles Darwin; morfología; Nils Johan Andersson; población; especiación; amenazas; tipificación.

## INTRODUCTION

The genus *Psychotria* L. (Rubiaceae) comprises up to 2,000 species of shrubs and small trees, and is found throughout the tropics (Taylor, 2022). It is taxonomically complex (Hamilton, 1989; Taylor, 1996, 2016), particularly in oceanic archipelagos, where rapid evolution complicates its classification (Sohmer, 1978; Nepokroef et al., 1999). Two *Psychotria* species have been described from the Galapagos Islands, both endemic to the archipelago and occurring as understorey shrubs in closed vegetation of the humid middle to high altitude vegetation zones. *Psychotria rufipes* Hook.f. is widely distributed in the highlands (300-870 m a.s.l.) (CDS herbarium, 2018) of San Cristóbal, Fernandina, Santa Cruz, Santiago, Pinta, Isabela and Floreana islands (Andersson, 1854; Robinson, 1902; Stewart, 1911, 1915; Wiggins, 1971). Its leaves, twigs and inflorescences bear reddish hairs (Figs. 1A, B; 2A-D, I), particularly on the lateral veins of the abaxial surface of the elliptic-ovate to obovate (length 8-20 cm) leaves; its flowers have a white corolla (Hooker, 1847; Wiggins, 1971). It is classed as Vulnerable according to IUCN Red-List criteria (León-Yánez et al., 2011) owing to progressive destruction and degradation of its habitat on most of these islands. *Psychotria angustata* Andersson (Figs. 1C, 2E-G, J) is in contrast restricted to Floreana Island and is Critically Endangered (Tye, 2011). It was originally distinguished from *P. rufipes* by its glabrous leaves, twigs and inflorescences, a roseate corolla and broadly lanceolate leaves 8-10 cm long (Andersson, 1854; Wiggins, 1971).

The first specimens of *Psychotria* from Floreana were collected in 1835 by Charles Darwin. These, together with one of Darwin's specimens from James (Santiago) Island, were described by Hooker (1847) as *P. rufipes*, though he provisionally separated a distinctively glabrous specimen from Floreana as simply *Psychotria* sp. Nils Johan Andersson visited the Galapagos Islands on the Swedish frigate *Eugenie* on 11-22 May 1852 (not July, as stated by Wiggins & Porter, 1971), and collected on five islands including Floreana (Andersson, 1854). Andersson (1854) described *P. angustata* as a new species from his specimen *Andersson 195* (S05-1055) and determined two of his other specimens from Floreana as *P. rufipes* (*Andersson s. n.*: S08-14105 and S08-14106). Andersson's *Psychotria* specimens are at the Swedish Museum of Natural History (S).

Later, Robinson (1902) reported both species from Floreana based on the specimens of Andersson and on *Lee s. n.* (US25604). Stewart (1911) also listed both species for Floreana, although he apparently did not collect either species there and observed only plants that he referred to *P. rufipes*. Wiggins (1971) accepted both species as valid but did not report *P. rufipes* on Floreana and noted that *P. angustata* had not been found since the collections of Andersson and Darwin. Wiggins (1971) confirmed Andersson's (1854) description of *P. angustata* as essentially glabrous throughout, but found "a few linear-subulate, reddish setae or scales 0.2-0.6 mm long" at some of the junctions of the lateral veins with the midrib on the abaxial surface of leaves of Darwin's specimen sheet CGE00346=190. However, he noted that these were "insignificant" and easily overlooked, compared with the dense coating of pubescence in *P. rufipes*.

In 1981, Eliasson (1982) collected a specimen that he referred to *P. angustata* (*Eliasson 3689* two sheets GB-0132150 and GB-0132151, hereafter "*Eliasson 3689 A*" and "*3689 B*" respectively) but noted that this taxon was "perhaps hardly more than a glabrous form of *P. rufipes*".

Up to 2007, six specimens of *Psychotria* from Floreana were available at the Charles Darwin Research Station herbarium (CDS), all having originally been identified as *P. angustata*, perhaps in part because Wiggins (1971) did not report *P. rufipes* from the island. However, in 2001 A. Tye re-determined three of them (*Huttel 351 A*, CDS5032;

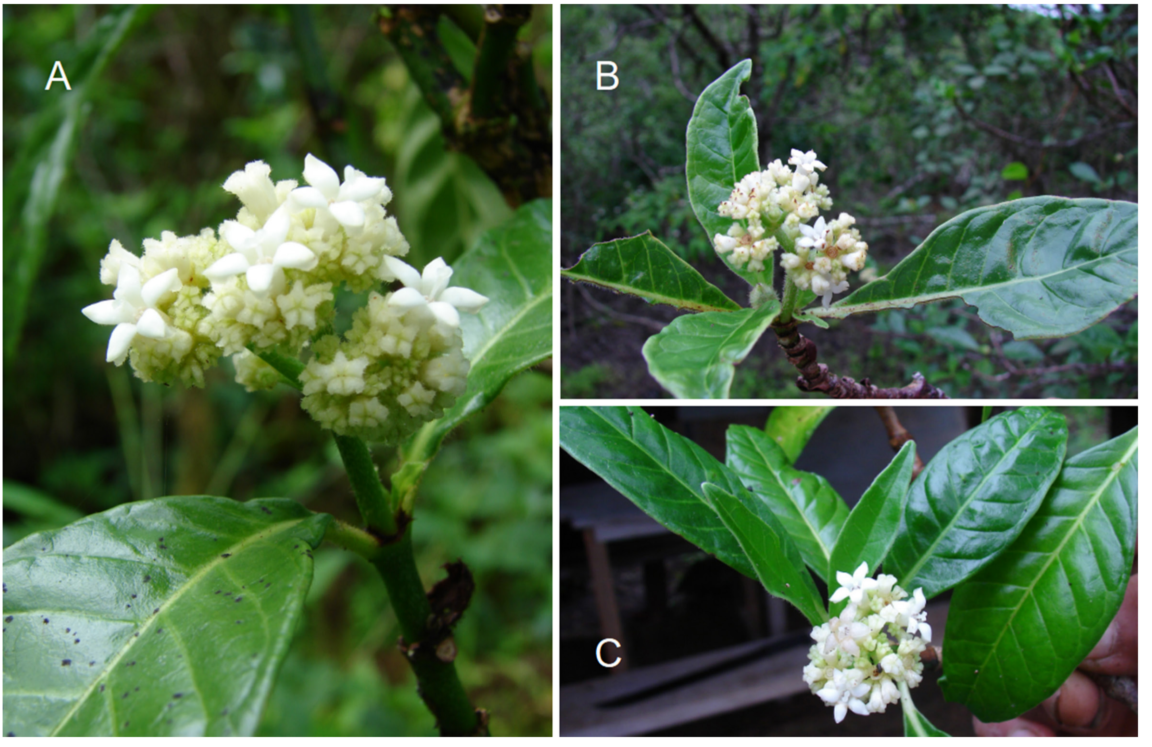


**Fig. 1.** Flowering branches. **A,** *Psychotria rufipes* on Santa Cruz Island. **B,** *P. rufipes* in Cerro Pajas, Floreana. **C,** *P. angustata* from Cerro Pajas. Both species have white corollas. A, by Rachel Atkinson; B and C, by W. Simbaña.

*Aldaz 108*, CDS7942 and *109*, CDS7943) as *P. rufipes*, based on the white corolla and the reddish hairs on the abaxial surface of the leaves, particularly between the secondary veins. Duplicates of *Huttel 351*, i.e. *351 B* (QCNE74305) and *351 C* (QCA98491), also show these hairs, including on the inflorescences and fruits of QCA98491.

Darwin (1839) and Andersson (1854) collected their *Psychotria* specimens on the highland plateau (now the island's Agricultural Zone) and Cerro Pajas (called "Sadelberget" or "Saddle Hill" by Andersson, 1854) (Fig. 3). Andersson (1854) reported both species from Sadelberget, which is the most prominent volcanic cone on the island, rising to 550 m (not 2000 feet or 640 m as stated by McBirney & Williams, 1969 and Hamann, 1981). It is circular, of diameter c. 1 km and internal depth c. 250 m from the highest walls on the north side. The vegetation of the outer slopes above its base at c. 320 m is primarily shrubland with patches of trees, many epiphytes and a rich ground layer of grasses, ferns, lichens, mosses and liverworts, whereas the prevailing moist winds strike the open southeast side of the crater and result in the vegetation of the interior reflecting more humid conditions than usual for this altitude in Galapagos, with evergreen forest dominated by *Scalesia pedunculata* Hook.f. and a canopy reaching about 6-12 m in height.

Stewart (1911, 1915) wrote that *P. rufipes* occurred as one of a number of species of occasional or common bushes in the woodland of the "plateau region, around an elevation of 1000 ft" (300 m). *Psychotria angustata* has seldom been collected and has mainly been reported within the crater of Cerro Pajas. Eliasson (1982) and Lawesson (1990) also found it in Cerro Alieri, a small crater just northeast of Cerro Pajas (Fig. 3). Mauchamp et al. (1998), reported a healthy population in 1992-1994 of 200 individuals of *P. angustata* in Cerro Pajas, and two other "much smaller" populations, at Cerro Verde and Cerro de los Burros, two hills east of the agricultural area (Fig. 3; I. Aldaz pers. comm.). At least four of the six prior specimens of *Psychotria* from Floreana at CDS were from inside or around Cerro Pajas, with the others northwest of Cerro Verde (*Aldaz 109*, CDS7943) and probably (judging from its site description) at Cerro Alieri (*Lawesson 2817 A* and *B*, CDS4827).

The taxonomic status and geographical distribution of the *P. angustata-rufipes* group has been uncertain since its discovery, with questions over the validity of *P. angustata*. Specimens of both taxa from Floreana were few, corolla

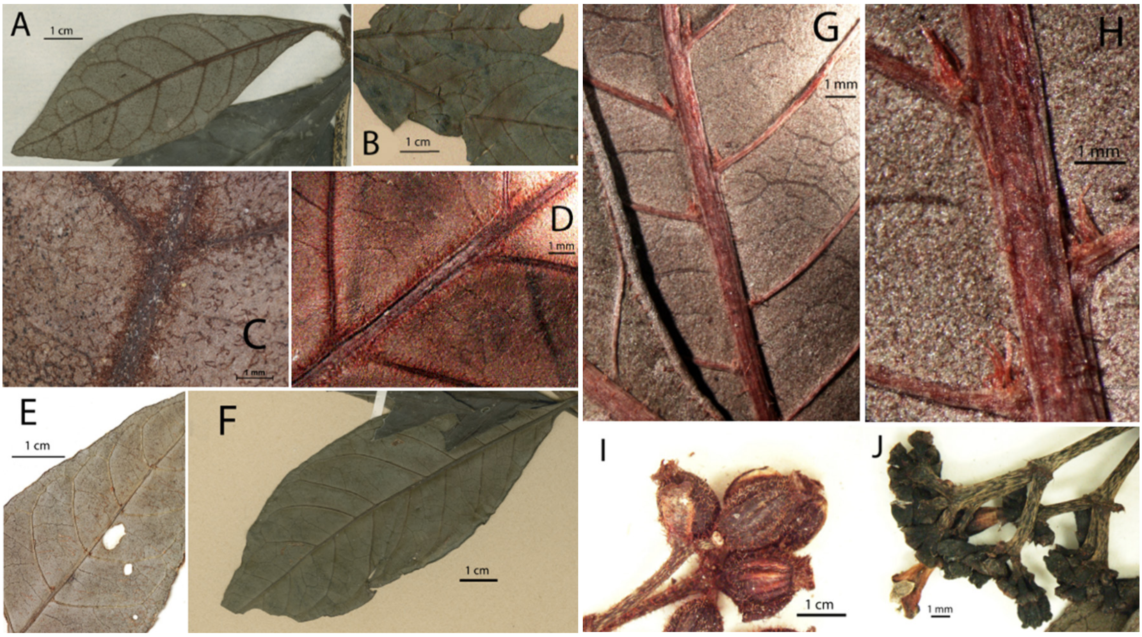


**Fig. 2.** Images of the reddish hairs along the veins of the abaxial surface of herbarium specimens of *P. rufipes* (**A,** *Darwin s. n.,* K000432936. **B,** *Andersson s. n.,* S08-14105. **C,** *Lee s. n.,* US25604. **D,** *Eliasson 363*, GB-0132154) contrast with the few tufts of red hairs between the mid-vein and primary lateral veins of *P. angustata* (**E,** *Darwin s. n.,* CGE00346. **F,** *Andersson 195*, S05-1055. **G-H,** *Eliasson 3689 B*, GB-0132151). Reddish hairs on the peduncle and mature fruits of *P. rufipes* (**I,** *Eriksson s. n.,* GB-0146898) contrast with *P. angustata* inflorescences where hairs are absent (**J,** *Eliasson 3689 A*, GB-0132150). A, by Marie Briggs © The Board of Trustees of the Royal Botanic Gardens, Kew, reproduced with the consent of the Royal Botanic Gardens, Kew. B and F, by Mia Ehn, S. C, by Ingrid Lin, courtesy of the United States National Herbarium, US. D, G-I), by W. Simbaña. E, by Christine Bartram, CGE.

colour has been lost on many specimens and was sometimes not recorded, and information on the distribution of the two species on the island was limited to collection notes and observations from *ad hoc* plant surveys. Further investigation of such poorly known plant groups is essential to clarify species distributions, taxonomic relationships and conservation priorities in the Galapagos Islands (McMullen et al., 2008; Tye & Francisco-Ortega, 2011). We therefore made extensive new collections of *Psychotria* from Floreana and compared them with the types and other previous specimens, in order to clarify the descriptions, taxonomic status, nomenclature and typification of the two Galapagos taxa, provide recent data on their distribution and population structure, and re-assess their conservation status.

## MATERIALS AND METHODS

### Prior herbarium specimens and new collections

Throughout this paper herbarium abbreviations follow Thiers (2023). W. Simbaña examined and took digital photos of *Psychotria* specimens from GB on loan at ODU, and specimens at CDS, QCNE and QCA. Andersson's specimens at S were examined by U. Eliasson, Mia Ehn, Jens Klackenberg and Niklas Wikström. Specimens at MO were examined by Charlotte Taylor, and at US by Mark Strong. The two Darwin *Psychotria* specimens at CGE were studied there by A. Tye. The numbering system used for Darwin's specimens at CGE has recently been changed from a 3-digit number to a different 5-digit number (e.g. CGE190 becomes CGE00346). The 3-digit system was based on Hooker's numbers, which were not written on the sheets themselves but on folders, whereas the 5-digit system refers to barcodes printed on the sheets. To facilitate comparison with earlier publications on these specimens, we cite both numbers herein, in the form: CGE00346=190. Digital scans of all of the specimens mentioned above, as well as of specimens at CAS and two Darwin duplicates at K, were provided by the herbaria concerned.

In total, 83 prior specimens comprising a total of 121 herbarium sheets (including duplicates, triplicates or quadruplicates) were examined, including 14 specimens (20 sheets) from Floreana

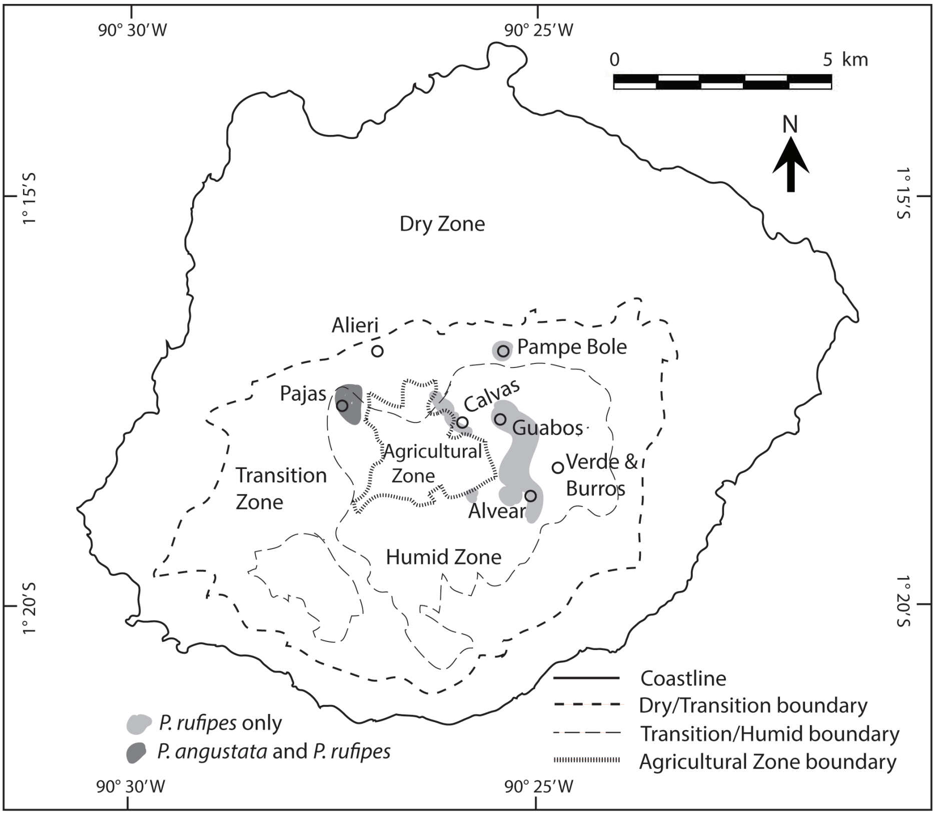


**Fig. 3.** Floreana Island, showing vegetation zones, the Agricultural Zone, sites (hills) mentioned in the text (open circles), and the approximate distribution of the two *Psychotria* taxa in 2008.

of which five specimens (eight sheets) had been labelled as *P. angustata* and nine specimens (12 sheets) as *P. rufipes*, and 69 specimens (101 sheets) of *P. rufipes* from other islands.

Between September 2007 and January 2008, W. Simbaña, accompanied by field assistants from Floreana, collected new specimens of *Psychotria* at various sites in the highlands of the island, including the crater of Cerro Pajas. The 16 new specimens comprised 22 sheets (including duplicates and triplicates), of which six specimens (nine sheets) were determined as *P. angustata*, and ten specimens (13 sheets) as *P. rufipes*. These were deposited and studied at CDS. The field work and collections were permitted as part of the Annual Plan for 2007-2008 of the Charles Darwin Research Station, as approved by the Galapagos National Park Directorate.

Including the prior herbarium specimens and the new collections, a total of 99 specimens comprising 143 herbarium sheets (including duplicates, triplicates or quadruplicates) were examined, all of which are listed in Appendix 1, where they are named according to our own determinations.

## Morphometrics

Lending of some herbarium material was restricted, several specimens were infertile, and the state of preservation of flowers (where present) was often so poor that for most specimens measurements could be made only on leaves. However, we compare the floral and fruiting characters of the two taxa as far as possible using both qualitative characters and the limited measurements we were able to obtain. Means are presented with standard deviation.

For principal coordinate analysis (PCoA) and cluster analysis (CA) of leaf traits, 2-5 leaves were examined on each herbarium sheet where possible, and the mean for each individual specimen was calculated from these measurements, in effect assuming that an individual specimen (including duplicates) represents one plant. Six leaf traits, including one qualitative and five quantitative (Table 1), were measured or scored for each leaf. These traits were chosen based on the differences between taxa mentioned by Andersson (1854), Wiggins (1971) and Hamilton (1989), as well as on our own observations. Leaves were examined

**Table 1.** Leaf traits used in the principal coordinates and cluster analyses of *Psychotria* herbarium specimens.

| N° | Character | Type | Unit or coding | Abbreviation |
|---|---|---|---|---|
| 1 | Leaf length | Continuous | cm | LENL |
| 2 | Leaf width | Continuous | cm | WIDL |
| 3 | Petiole length | Continuous | mm | PELE |
| 4 | Petiole width | Continuous | mm | PEWI |
| 5 | Number of secondary nerves on each side of midrib | Discrete | n | NSN |
| 6 | Indumentum of abaxial leaf surface | Categorical | 0 = Subglabrous/glabrous<br>1 = Pubescent | TEXL |

with a light stereo-microscope and measured with a ruler or graticule. Similar measurements using ImageJ 1.37v software (Rasband, 2006) were made on digital images of the specimens *Darwin s. n.* (K00174121), *Andersson 195* and *Andersson s. n.* (S08-14105 and S08-14106).

All six leaf traits were measured on 84 specimens (116 sheets), comprising 13 specimens (18 sheets) of *P. angustata* and 17 specimens (23 sheets) of *P. rufipes* from Floreana, as well as 54 specimens (75 sheets) of *P. rufipes* from various other islands. The PCoA and CA both used Gower's dissimilarity coefficient, the measure of choice when the data matrix contains both continuous and binary data (Gower, 1971; Gower & Legendre, 1986). The CA used the unweighted pair-group method (UPGMA) to visualize groups of specimens. PCoA is often recommended to evaluate the phenetic relationship among specimens in an ordination space (Marhold, 2011; Kaplan & Marhold, 2012). Prior to these analyses the full data matrix was standardised (mean = 0, SD = 1). All statistical calculations were made using the software Past v. 4.02 for Windows (Hammer et al., 2001).

### Population status and distribution

At sites where *Psychotria* was located during the 2007-2008 surveys, each plant was mapped by GPS-GIS, the habitat and vegetation were described, and the state of the *Psychotria* plants (signs of damage etc.) was recorded. Individuals with main stem basal diameter ≤ 1 cm were considered seedlings, those of 1.01-2 cm juveniles, and > 2 cm adults.

Preliminary conservation re-assessments were made following IUCN Red List criteria (IUCN, 2012), based on past and present distribution revealed by the herbarium specimens examined, published literature, unpublished records at the Charles Darwin Research Station, and the new field work.

## RESULTS

### Type material of Psychotria angustata

Andersson (1854) described *P. angustata* as a new species from his specimen *Andersson 195* (S05-1055). Other dates have been attributed to Andersson's publication owing to the production of several reprints, but the version that appears to have been published first (cited herein as Andersson, 1854) is dated 1854 and was apparently issued that year, while a version dated 1853 was not issued until 1855 (Stafleu & Cowan, 1976; C. Wijkström, Royal Swedish Academy of Sciences, pers. comm.). The date of description of Andersson's new taxa, including *P. angustata*, should therefore be 1854.

*Andersson 195* and Darwin's glabrous specimen *Darwin s. n.* are sometimes termed syntypes of *P. angustata* (e.g. www.tropicos.org), but it seems clear from the wording of Andersson's (1854) description that he had not actually seen Darwin's specimen. Beneath his formal description of *P. angustata*, Andersson (1854: 193) wrote "Psychotriae species (the leaves and whole plant quite glabrous) Hook. fil. l. c. p. 220?", where the question mark implies that Andersson merely suspects but cannot confirm that Darwin's glabrous specimen mentioned by Hooker (1847) is of the same species as the one he himself collected, i.e. he cannot have seen Darwin's specimen. Andersson (1854) then refers to the habitat of the species as "Hab. locis maxime sylvestribus regionis editioris insulae Charles (Ipse et *Darwin?*).", again with a question mark after "Darwin", indicating that this habitat description was based on his own specimen, and perhaps (the question mark indicating Andersson's uncertainty) could also be referred to that of Darwin. Andersson's (1854) protologue thus does not clearly identify a holotype, and his tentative references to Darwin's specimen cannot be taken as designating it as a syntype. Therefore, we here select *Andersson 195* (S05-1055) as the lectotype of *Psychotria angustata* Andersson.

## Multivariate Analyses

PCoA and CA produced similar results. The PCoA plot separated the specimens into two distinct groups along the first two axes (Fig. 4). One group, in the lower right part of the plot, represents *P. angustata* and is clearly distinct from *P. rufipes*. Specimen *Andersson s. n.,* S08-14106, originally determined by Andersson as *P. rufipes*, is associated with the *P. angustata* group (Fig. 4). This specimen is almost completely glabrous, but has various tufts of red hairs on the abaxial surface of the leaf as described below for all the specimens of *P. angustata* (including the *Andersson 195* lectotype and *Darwin s. n.*) and observed in Figs. 2E-H. The upper group included all the specimens of *P. rufipes* from Floreana and other islands. The first three coordinate measures were responsible for 61.1% of the total variation (36.8%, 18.6%, and 5.7%, respectively; Table 2).

The CA also produced two groups, similar to those of the PCoA (Fig. 5). One group (G1) includes specimens previously classified as *P. angustata*, and the second (G2) contains the majority of the *P. rufipes* specimens, in three subgroups that mix the specimens from Floreana among those from other islands. The cophenetic correlation coefficient of the analysis was 0.77, indicating a good fit of the dendrogram to the similarity matrix.

## Descriptive comparisons and re-determination of some prior herbarium specimens

The *P. rufipes* sheets CGE00347=191 and K000432936 of *Darwin s. n.* show dense red pubescence in patches under the leaves, as described by Wiggins (1971): “pilosulous beneath, the hairs more densely crowded in angles of lateral veins than on intervein surface of blade”. In addition, Wiggins (1971) drew attention to the “closely rufo-pilosulous” stipules, the “usually rufo-pilosulous” inflorescence branches, “densely pilosulous” flower bracts, “rufo-pilosulous” calyx and “hirsutulous” outer surface and margins of the corolla in *P. rufipes*. In contrast to these and other specimens referable to *P. rufipes* from Floreana, which have dense reddish hairs concentrated along the midrib and lateral veins, those from other islands (e.g. from Santa Cruz, see Appendix 1) have even denser pubescence over the whole abaxial surface of the leaf (including midrib, primary and secondary veins, lamina and petiole). The leaves are broadly elliptic-ovate to broadly oblanceolate, 4-19 (9.9 ± 2.7) cm long, 1.8-7.6 (4.2 ± 1.2) cm wide; petioles 3-17 (8.5 ± 2.6) mm long, 0.5-2.2 (3.7 ± 0.4) mm wide, scarcely short-pilosulous; secondary veins 6-13 (7.9 ± 1.0) pairs, eucamptodromous. Inflorescences are terminal, cymose, 1.8-9 (4.9 ± 1.7) cm long, 1-2 (1.6 ± 0.3) mm wide; branches of inflorescences usually rufo-pilosulous; corolla white, 4-10 (5.5 ± 0.8) mm long, the apices of the corolla lobes thickened into the form of a hook or horn, hirsute.

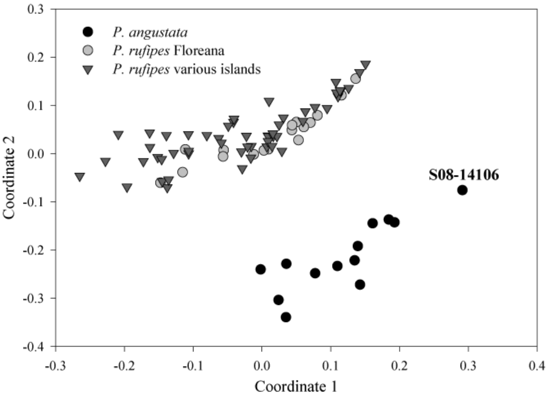


**Fig. 4.** PCoA plot of the first two principal coordinates showing the distribution of 84 specimens based on six morphological characters. S08-14106 is the *Andersson s. n.* specimen, here referred to *P. angustata*.

The lectotype of *P. angustata* (*Andersson 195*, S05-1055) is glabrous on the abaxial leaf surface, except for some tufts of red hairs at the junctions of the veins, and the calyx is ciliate (J. Klackenberg pers. comm.). This matches Wiggins’ (1971) description of the *Darwin s. n.* “syntype” of *P. angustata*. Sheets Eliasson *3689 A* and *B* almost perfectly match Andersson’s type specimen, with mature leaves essentially glabrous on both sides, including the elevated mid-vein on the abaxial surface and the lateral veins. Young leaves have some scattered, tapering, brownish trichomes 0.2-0.8 mm long on the mid-vein below, as well as along the often involute margins (Fig. 2G, H). However, these are so inconspicuous that the leaves would normally be described as glabrous,

**Table 2.** Eigenvalues and percentages of variance for the first three PCoA coordinates, from six characters using all 84 *Psychotria* specimens.

| Principal coordinates: | 1 | 2 | 3 |
|---|---|---|---|
| Eigenvalue | 2.01 | 1.02 | 0.31 |
| Percentage of variance | 36.80 | 18.62 | 5.70 |
| Cumulative percentage | 36.80 | 55. 42 | 61.12 |

and the trichomes seem to be shed during the further development of the leaf. Sparse, scattered, minute trichomes of the same type as on the leaves also occur on the stipules, on the apex of the campanulate calyx, and on the central axis and branches of the inflorescences. However, the glabrous abaxial side of the mature leaves and the glabrous or subglabrous inflorescence branches and corolla lobes of *P. angustata* contrast with the corresponding parts of *P. rufipes*, where the pubescence is mostly rich and conspicuous.

Of the other two Andersson specimens (*s. n.*, S08-14105 and S08-14106) from Floreana, both determined by him as *P. rufipes*. S08-14105 is indeed quite hairy on the abaxial leaf surface, particularly along the whole length of the midrib and primary veins but also on the lamina (J. Klackenberg, pers. comm.), with longer hairs (0.15-0.35 mm long) than the Type of *P. angustata*. Also, its peduncles and the apex of the campanulate calyx are hairy. Although its leaves are not as densely pubescent as in most specimens of *P. rufipes* (i.e. the syntypes, and specimens from other islands), in our view it corresponds with *P. rufipes.* In contrast, S08-14106, which was also named by Andersson as *P. rufipes*, seems to have been misclassified, as it has the same pattern of leaf pubescence as S05-1055 (the lectotype of *P. angustata*) and other specimens that clearly belong to *P. angustata*, such as Eliasson *3689 A* and *B* (J. Klackenberg, pers. comm.), and Darwin's specimen of *P. angustata* (CGE00346=190, K000174121). The fruits, which are more mature than the very young ones of S05-1055, are glabrous, with some hairs only at the persisting calyx lobes. The corolla colour cannot be determined on any of these specimens. Of the later Floreana specimens identified as *P. rufipes* (with which we concur), *Lee s. n.* (US25604) has reddish hairs on the abaxial surface of the leaves, denser on the mid-vein and primary lateral veins (Fig. 2C), as does *Eliasson 363* (GB-0132154; Fig. 2D). The flower peduncles have only a few reddish hairs; the four calyx lobes also have reddish hairs and the stipules have reddish hairs abaxially only (M. Strong, pers. comm.).

Of our new Floreana specimens, ten match the descriptions of *P. rufipes* by Hooker (1847) and Wiggins (1971), with conspicuous reddish hairs on the inflorescences (peduncles and pedicels) and along the lateral and central veins of the abaxial surface of the leaves, a white corolla with hirsute lobes (Fig. 1B), and red fruits that also bear reddish hairs.

Six of our new specimens match the description of *P. angustata*, at least in most respects: they have a few inconspicuous reddish hairs (0.1-1.2 mm long) on the abaxial surface of mature leaves and at the unions of the main lateral veins with the mid-vein. However, the corolla of these specimens and of all plants seen in flower was white (Fig. 1C right), and the corolla lobes glabrous, in contrast to the description by Andersson (1854), but as noted on the labels of four of the six previous specimens of *Psychotria* from Floreana at CDS (*Lawesson 2817 A* and *B*, *Aldaz 108*, *109* and *149*); the corolla colour of the other two specimens at CDS was not noted by the collector. Similarly, two *P. angustata* plants at Cerro Alieri, photographed by U. Eliasson in 1981, had white flowers.

## Revised descriptions of the two taxa

According to our measurements of the specimens examined, combined with our field observations and measurements of living plants, *P. rufipes* on Floreana is a shrub up to 4.6 m tall (1.8 ± 0.8, n = 112 mature plants), with basal diameter 2-6 cm (3.0 ± 1.0, n = 112); leaves opposite, simple; blade broadly elliptic-ovate to obovate or oblanceolate, 5-15 cm long (9.3 ± 2.0, n = 124), 2.0-5.6 cm wide (3.7 ± 0.9, n = 124), adaxial surface glabrous, abaxial surface covered with reddish hairs on the lamina and more densely along the midrib and primary and secondary veins; eucamptodromous, secondary veins 7-11 pairs (8.1 ± 0.9, n = 124); petioles 4-15 mm long (7.7 ± 2.5, n = 124) , 0.4-2 mm wide (1.1 ± 0.4, n = 124), rufo-pilosulous; stipules ovate, 6-8 mm long (7 ± 1.4, n = 2), 5-6 mm wide (5.0 ± 0.7, n = 2), scarcely short-pilosulous. Inflorescences terminal, cymose, 2.0-7.7 cm long (4.2 ± 1.3, n = 19), peduncles 1-2 mm wide (1.5 ± 0.4, n = 19), tomentulose to hirtellous to glabrous; branches of inflorescences usually rufo-pilosulous; corolla white to cream, 4-6 mm long (5.1 ± 0.5, n = 13), tube cylindrical, white pubescent in throat, abaxial surface of lobule apex thickened to form a "horn", hirsute. Fruit ellipsoid-globose with red hairs, the flesh at maturity yellow then red, juicy; when dry 4-6 mm long (5.0 ± 0.6, n = 30), 2-4 mm diameter (3.3 ± 0.7, n = 30).

*P. angustata* is a shrub that grows up to 3.5 m in height (1.8 ± 0.5, n = 157 mature plants), with main stem 2-7 cm (3.0 ± 0.9, n =157) in basal diameter. Leaf blades are broadly lanceolate, 5.5-15.8 cm long (8.8 ± 1.9, n = 116), 1.8-5.7 cm wide (3.3 ± 0.7, n = 116); adaxial surface glabrous, abaxial surface subglabrous with few brownish trichomes 0.2-1.9 mm long (0.8 ± 0.5, n = 14) at the angles where the primary veins join the midrib; secondary veins 7-13 pairs (8.8 ± 1.3, n = 116), eucamptodromous; petioles 4-13 mm long (7.3 ± 2.3, n = 116), 0.8-2.0 mm wide (1.1 ± 0.2, n = 116); stipules 6-11 mm long (9.3 ± 1.5, n = 8), 4.3-10 mm wide (6.3 ± 2.2, n = 8). Inflorescences axillary and terminal, 1-8 cm long (3.2 ± 1.6, n = 25); peduncles 1.0-2.0 mm wide (1.4 ± 0.4, n = 25); corolla white to cream (the pink colour reported

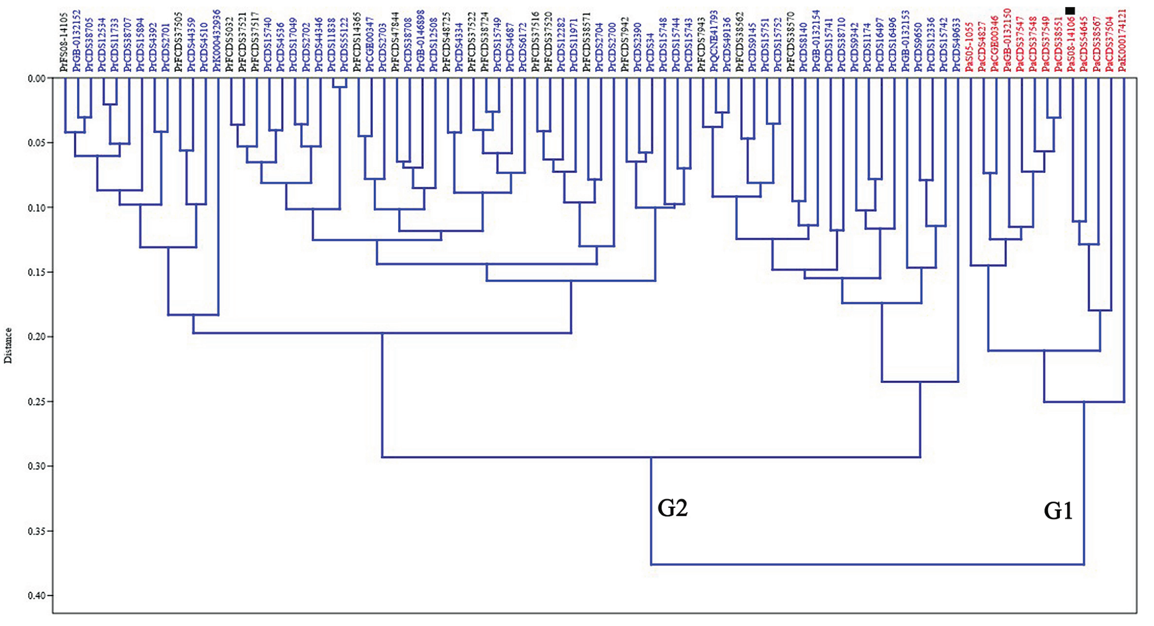


**Fig. 5.** Cluster analysis dendrogram using UPGMA and Gower's similarity coefficient. Group G1 corresponds to *P. angustata* (red), and G2 to *P. rufipes* from various islands (blue) and Floreana (black). The black square indicates *Andersson s. n.* S08-14106, here confirmed as *P. angustata*. The specimens are indicated by initials of genus and species, (Pa or Pr) followed by an F for *P. rufipes* on Floreana only, followed by the herbarium number (e.g. *P. angustata* PaCDS37504; *P. rufipes* Floreana PrFCDS37521; *P. rufipes* other islands PrK000432936).

by Andersson has not been confirmed by others), 3-6 mm long (4.4 ± 0.9, n = 17), abaxial surface of lobule apex thickened to form a "horn", glabrous. Fruit subglobose, glabrous, the flesh at maturity turning yellow then red, juicy; when dry 4-6 mm long (5.5 ± 0.6, n = 35), 2.0-3.6 mm diameter (3.1 ± 0.5, n = 35).

Although the corolla was white in all live plants found and all the recent specimens otherwise referable to *P. angustata*, and although specimens referable to *P. angustata* generally present sparse hairs in specific places under the leaves, all prior specimens and new collections seemed to fall clearly into one or other morphological type ("*rufipes*" or "*angustata*") based on the extent and density of pubescence, with no evidence of obvious intermediates or intergradation between them. These groups correspond with those based on leaf characters that were identified in the PCoA and CA.

## Distribution, threats and population structure

We found plants matching *P. rufipes* in five localities on Floreana, on the upper edges and steep slopes of several hills including Cerro Pajas (Fig. 3), at altitudes of 300-550 m (Table 3). We found plants referable to *P. angustata* in only one population, in Cerro Pajas (Table 3), but did not visit the Cerro Verde and Cerro de los Burros sites mentioned by Mauchamp et al. (1998). *Psychotria angustata* was also reportedly found at Cerro Alvear on 4 October 2007 (J. Moreno and S. Mora, pers. comm.), but no specimen has yet been collected there. Our searches, including the north side of Cerro Pajas and in the neighbouring Cerro Alieri where Eliasson (1982) and Lawesson (1990) reported *P. angustata*, did not reveal any *Psychotria* there or anywhere else below 350 m a.s.l. (Table 3), so we presume it is now extinct there.

*Psychotria angustata* may thus be extant at four localities (Cerros Alvear, de los Burros, Pajas and Verde). We were not able to visit Cerros Burros and Verde, or to obtain population data from Cerro Alvear, so for assessing conservation status we assume that the population at Cerro Alvear had density and structure similar to that at Cerro Pajas and that the status of the populations at the two small unvisited sites had not changed since the observations of Mauchamp et al. (1998).

In all five sites where we found *Psychotria*, both species occurred in closed vegetation, usually below the canopy of the Galapagos endemic trees *Scalesia pedunculata* (only in Cerro Pajas) and *Lippia salicifolia* Andersson, and often close to

**Table 3.** *Psychotria angustata* and *P. rufipes* population sizes (comprising seedlings, juveniles and adults) on Floreana in 2008.

| Site* | Species | Latitude (°S) | Longitude (°W) | Elevation (m a.s.l.) | Number of plants counted |
|---|---|---|---|---|---|
| Pajas | ***P. angustata*** | 1.295 | 90.457 | 350-550 | **857** |
| Pajas | *P. rufipes* | 1.295 | 90.457 | 450-550 | 100 |
| Alvear | *P. rufipes* | 1.314 | 90.430 | 400 | 329 |
| Guabos | *P. rufipes* | 1.3029 | 90.4343 | 400 | 174 |
| Pampe Bole | *P. rufipes* | 1.2911 | 90.4331 | 390 | 9 |
| Calvas | *P. rufipes* | 1.3039 | 90.4391 | 390 | 11 |
| all five | *P. rufipes* total | | | | 623 |

*All sites are hills, known as "Cerro" in Spanish (e.g. Cerro Pajas, Cerro Alvear, etc.).

small *Zanthoxylum fagara* Sarg. trees (native) and the endemic shrubs *Croton scouleri* Hook.f. and *Macraea laricifolia* Hook.f. Other understorey shrubs present included *Tournefortia rufo-sericea* Hook.f. (endemic), *Chiococca alba* Hitchc. (native) and *Volkameria mollis* (Kunth) Mabb. & Y.W. Yuan (native).

The introduced trees *Psidium guajava* L., *Cedrela odorata* L. and *Citrus* spp., and shrub *Lantana camara* L., all of which are among the most damaging invasive plants in Galapagos (Tye, 2001), were also present, often growing around *Psychotria* plants. At Cerro Alvear and Cerro Pampe Bole, adult *P. rufipes* plants had their branches broken and procumbent, apparently caused by feral pigs and domestic cattle. On the other hand, we found that *P. rufipes* often branches in all directions, forming a hemispherical shrub over humid soil, where it takes root at nodes and is thereby able to spread asexually.

In Cerro Pajas, the groups of plants of each *Psychotria* species occurred separately, although the distances between groups were not great (50-150 m). Of the 857 individuals of *P. angustata* that we marked and measured, distributed over a 1000 m² area of the crater, 369 (43%) were juveniles, 334 (39%) seedlings, and 154 (18%) adults. The total number of plants in the five populations of *P. rufipes* was 623, of which 318 (51%) were seedlings, 193 (31%) juveniles and 112 (18%) adults, dispersed over a total area of about 548 m² (Table 3). The populations of both species in 2008 were thus composed of a majority of seedlings and juveniles, indicating vigorous regeneration (Fig. 6).

*Psychotria angustata* is globally rare and at risk of extinction because of its restricted distribution (Area of Occupancy AOO < 0.1 km²) at four sites (Subpopulations) on one island (capitalised terms are as defined in IUCN, 2012), which produce an Extent of Occurrence (EOO) of < 2.25 km². Within the AOO we counted 154 adult plants (down from the 200 estimated by Mauchamp et al., 1998) and, taking into account the observations of Mauchamp et al. (1998) we estimate that Cerro Verde, Cerro

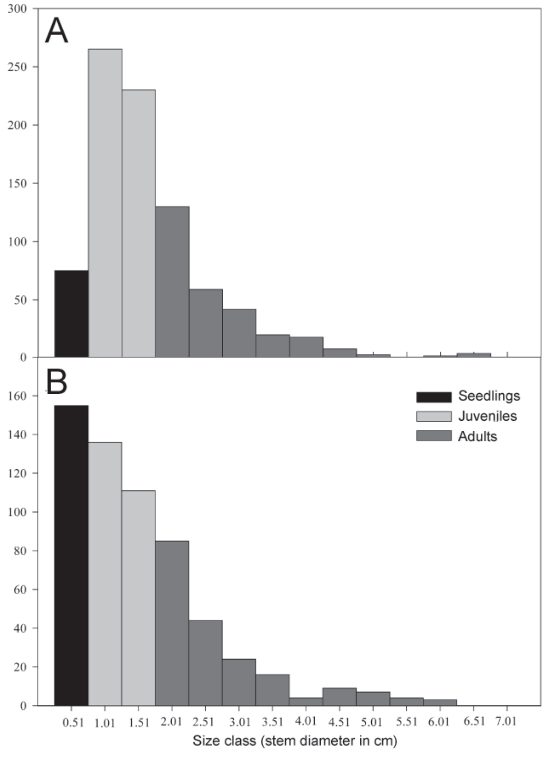


**Fig. 6.** Size class and age class distributions on Floreana in 2008. **A,** *Psychotria angustata* at Cerro Pajas (n = 857). **B,** *P. rufipes* (n = 598) at Cerros Alvear, Calvas, Guabos, Pampe Bole and Pajas.

de los Burros and Cerro Alvear combined could perhaps contain up to another 100, for a total global population of some 300 adults at all four sites. On this basis, and the fact that the threat from introduced ungulates has been reduced but pressure from introduced plants continues, *P. angustata* qualifies as Critically Endangered (CR) according to IUCN criteria B1ab(i-v), B2ab(i-v) (IUCN, 2012); this assessment is preliminary, pending acceptance by IUCN. Similarly, although *P. rufipes* is considered globally Vulnerable (Tye, 2011), it must be considered locally endangered on Floreana island under the same criteria as *P. angustata*.

## DISCUSSION

### Morphology and taxonomy

Our recent specimens and field observations confirm the presence of two distinct forms of *Psychotria* on Floreana. We found that flower colour, originally used to distinguish them, appears to be similar (white to cream) in both. Instead, we have shown that the two taxa are most clearly differentiated by the indumentum of the abaxial leaf surface, twigs, inflorescences and corolla lobes. These differences are of a degree commonly treated as infra-specific in other species of *Psychotria*. Although no intermediates have been found where the two forms grow close to each other, the major difference between them (pubescence) could result from a simple genetic control mechanism, as in rice *Oryza sativa* L. (Zeng et al., 2013) and cottons *Gossypium* L. (Yuan et al., 2021), with no implication of linked reproductive isolation between the two forms or of the production of intermediates. We conclude that the two taxa hitherto described as species are better treated as varieties within a single species, with the name *rufipes* having priority as the name of the species, and the taxon *angustata* becoming

*Psychotria rufipes* var. *angustata* W. Simbaña & Tye, **stat. nov.** Basionym: *P. angustata* Andersson, Om Galapagos-oärnes vegetation. Stockholm: P.A. Nordstedt & Söner; 1854: 193. Lectotype: *N. J. Andersson 195* (S05-1055).

We therefore propose a revised key to the Galapagos *Psychotria* taxa, based on Wiggins (1971) with modifications, as follows:

1. Leaves, twigs and inflorescences subglabrous; corolla white to cream (occasionally pink) with apex of lobules glabrous; leaves broadly lanceolate, abaxial surface with a few brownish trichomes at the angles where the primary veins join the mid-rib.......................................*P. rufipes* var. *angustata*

1. Leaves, twigs, and inflorescences hirsute with reddish hairs; corolla white to cream, with apex of lobules hirsute; leaves elliptic-ovate to obovate or oblanceolate, abaxial surface with reddish hairs coating the lamina and more densely along the midrib and primary veins.......................*P. rufipes* var. *rufipes*

The pink corolla sometimes reported for *P. rufipes* var. *angustata* (Andersson, 1854; Wiggins, 1971; McMullen, 1999) is evidently not a consistent character of taxonomic value: we do not know whether it is genetically fixed or influenced by the environment or state of maturation. Investigation using molecular markers is required to determine the genetic background to this and the other differences from *Psychotria rufipes* var. *rufipes*, as well as the origin of the Galapagos *Psychotria.* Molecular data so far suggest that *P. rufipes* is sister to *P. nervosa* Sw., a species restricted to the Caribbean Basin (Trusty et al. 2012), and visual inspection of specimens of *P. rufipes* and *P. nervosa* at MO, considering the general pattern of venation, shape and size of leaves, stipules and corolla, shape of inflorescence, development of bracts, length and shape of calyx limb, size and details of the shape of fruits, and pubescence, supports this relationship (C. M. Taylor, pers. comm.).

There are other examples in the Galapagos flora where local populations of a species deviate in certain characteristics from the range of morphological variation of the species found in the rest of its geographical area, for example in the *Alternanthera filifolia* (Hook.f.) J.T. Howell complex (Eliasson, 2004; Sánchez del Pino et al., 2012). Such populations may be incipient species illustrating evolution in progress.

### Threats and population status

Floreana is among the Galapagos islands most impacted by introduced species. Its native vascular flora has been devastated by feral ungulates and replaced in large areas by invasive plants. However, feral goats and donkeys were eradicated from the island between 2006 and 2009 (Carrión et al., 2011), and in 2007-2008 we noted evidence of physical damage by ungulates of *Psychotria* plants at only two of the five sites where we found one or other of the two taxa. In fact, our results and further monitoring show rapid recuperation of vegetation on the island (Atkinson et al., 2008; W. Simbaña pers. obs.), with the populations of both *Psychotria* taxa in 2008 composed of a majority of seedlings and juveniles (Fig. 6). Further, the adults present must have germinated and survived while introduced ungulates were common in their habitat, which may have been helped by a long-lived soil seed-bank and the hitherto unreported ability to reproduce vegetatively.

In the 1990s, the populations at Cerro Verde and Cerro de los Burros were much smaller than that at Cerro Pajas, comprising together some 50 mature plants, and while one of these populations was in a good state out of the reach of ungulates, the other was severely damaged by pigs (Mauchamp et al., 1998; I. Aldaz, pers. comm.) and continued to suffer such damage until at least mid-2006 (A. Altamirano, pers. comm.). The pigs and domestic cattle have since been brought under tighter management, but there is now an urgent need to expand the management of invasive plants. The Galapagos National Park Directorate began to control invasive plants in Cerro Pajas in 1995 and this became more intensive from 2006, probably contributing to the *Psychotria* regeneration noted in 2007-2008.

However, the invasive *Lantana camara* and *Psidium guajava* may still represent the greatest threat to *Psychotria* in all of the sites where we found it, with plants of both taxa often overgrown by these species. Measures should therefore be taken to ensure that all Floreana populations of *Psychotria* are preserved.

Floreana has been poorly studied and many parts of it have never been visited by botanists. The island is characterised by > 30 parasitic cones in the central highlands, many of which still await detailed survey. Several of these hills host other threatened Floreana endemic plants, e.g. *Linum cratericola* Eliasson (known only from Cerro Alieri: Simbaña & Tye, 2009), but our knowledge of the endemic flora of these areas, especially since the eradication of the ungulates, is still fragmentary. On every field trip to Floreana for the present study we found new populations of threatened plants, including *Psychotria* and three other single-island endemics (*Lecocarpus pinnatifidus* Decne, *Lippia salicifolia* and *Alternanthera nesiotes* I.M. Johnst. (unpubl. data). Searches of other potential sites should therefore be completed.

## CONCLUSIONS

Our analysis leads us to recognise two distinct *Psychotria* forms on Floreana, which correspond to the two named species but indicate a degree of distinction better considered to be at the infraspecific level. We confirm that the two taxa grow together in Cerro Pajas, with no intermediates having been found. Our investigation allows us to restrict the type of *P. angustata* to the specimen *Andersson 195* (S05-1055), to clarify the description of this taxon, and to re-evaluate the conservation status of both taxa on Floreana, but further investigation is required of the *Psychotria* complex across the Galapagos archipelago, including its genetics, reproductive biology, taxonomy and ecology, to complete its piece of the jig-saw puzzle of evolution in the Galapagos.

## ACKNOWLEDGEMENTS

WS and AT dedicate this paper to our late colleague and friend Dr Timothy J. Motley, who contributed insights from his important studies of plant evolution to early versions of this manuscript. WS's most recent field expeditions were part of a long-term CDRS study "Project Floreana" under permits granted by the GNPD; thanks to Dr Rachel Atkinson for her leadership of that project and to the CDRS for support. A special thanks to all the volunteers and students of the CDRS and the field assistants on Floreana, who helped with their enthusiasm to ease the long days of exploration, and the GNPD staff on Floreana, who provided valued logistical support. We thank Anne Guézou and Jorge Luis Rentería of CDRS, Charlotte Taylor of MO and Jesús Muñoz from RJBM, all of whom helped with bibliographic information. We express our gratitude to Mia Ehn and Jens Klackenberg (Swedish Museum of Natural History) and Niklas Wikström (Bergius Foundation, Department of Botany, Stockholm University) for examining specimens at S, Mark Strong for checking the Lee specimens at US, and Charlotte Taylor for reviewing specimens at MO. We thank the curators and directors of CDS, CGE, QCNE and QCA for providing access to their specimens, GB for the loan of theirs, CAS, CGE, K, MO, S and US for digital images, and Dr Rebecca Bray (ODU herbarium) for assisting with loan requests. WS also thanks Dr Tatyana Lobova and the ODU botany group for their support during his visit to the United States. This is contribution number 2628 of the Charles Darwin Foundation for the Galapagos Islands.

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## Appendix 1. Specimens examined.

Specimens are assigned to the two varieties according to our own determinations (for example, *Andersson s. n.* S08-14106 was formerly regarded as *P. rufipes* but is clearly a specimen of *P. rufipes* var. *angustata*).
* Specimens measured with a ruler or graticule; ** specimens measured using ImageJ.

### Psychotria rufipes var. angustata

Examined Material. ECUADOR. **Galapagos. Floreana Island (also known as Charles Island or Santa Maria).** Central part of island. 380 m s.m. 9-I-1981, *Eliasson 3689 A* (GB 0132150)* and *B* (GB 0132151)*. Cerro Pajas. 7-VIII-1994, *Aldaz 149* (CDS 54645, formerly CDS 6525)*. Dentro del crater, 1° 17' 47.4'' S, 90° 27' 23'' W, 380 m s.m., 2-X-2007, *Simbaña 702* (CDS 37504)*; 1° 17' 31'' S, 90° 27' 32.2'' W, 410 m s.m., 23-XI-2007, *Simbaña & Veintimilla 743* (CDS 37547)*; 1° 16' 58.8'' S, 90° 29' 29.7'' W, 410 m s.m., 23-XI-2007, *Simbaña et al. 744 A* and *B* (CDS 37548)*; 1° 16' 58.8'' S, 90° 29' 29.7'' W, 410 m s.m., 23-XI-2007, *Simbaña et al. 745* (CDS37549)*; 1° 16' 58.8'' S, 90° 29' 29.7'' W, 400 m s.m., 23-XI-2007, *Simbaña et al. 746* (CDS 38567)*; 1° 17' 42.4'' S, 90° 27' 21.9'' W, 400 m s.m., 23-XI-2007, *Simbaña et al. 747 A, B* and *C* (CDS 38551)*. In collapse about 50 m deep and its surrounding area. 11-II-1986, *Lawesson 2817 A* and *B* (CDS 4827)*. Location not specified. End of IX-1835, *Darwin s. n.* (CGE 00346=190, K 00174121 [photo seen])*. V-1852, *Andersson 195* (S 05-1055 lectotype, basionym [photo seen])**; *Andersson s. n.* (S 08-14106 [photo seen])**.

### Psychotria rufipes var. rufipes

**Fernandina (or Narborough) Island.** Camp crater. 2 Km S of camp crater, 450 m s.m., 22-VI-1974, *Adsersen 523* (CDS 2700)*; 450 m s.m., 6-VI-1977, *Adsersen 1985 A* (CDS 2703)* and *B* (QCA 98487)*. Southwest slope. 300 m s.m., 3-5-II-1964, *Fosberg 45009 A* (K 000174129 [photo seen]) and *B* (MO 1755206 [photo seen]).

**Floreana (Charles or Santa Maria) Island.** Cerro Albiar [*sic*]. 1° 18’ 48.6” S, 90° 25’ 41.7” W, 390 m s.m., 21-XI-2007, *Simbaña et al. 720 A, B* and *C* (CDS 37522)*. Cerro Pajas. 17-VIII-1984, *Huttel 351 A* (CDS 5032)*, *B* (QCNE 74305)* and *C* (QCA 98491)*. 28-III-1993, *Aldaz 108* (CDS 7942)*. Dentro del cráter, 1° 17’ 48.9” S, 90° 27’ 22.7” W, 380 m s.m., 2-X-2007, *Simbaña 703* (CDS 37505)*. Alrededor del cráter del Cerro Pajas, 1° 17’ 38.7” S, 90° 27’ 20.7” W, 370 m s.m., 13-II-2003, *Jaramillo 2110* (CDS 14365)*; Parcela 1, 1° 17’ 49.2” S, 90° 27’ 23” W, 320 m s.m., 12-I-2011, *Jaramillo et al. 3808 A* (CDS 47844)*; Parcela 1, 1° 17’ 49.2” S, 90° 27’ 23” W, 370 m s.m., 12-I-2011, *Jaramillo et al. 3808 B* (CDS 48096)*; Parcela 19, 1° 18’ 48.03” S, 90° 26’ 6.82” W, 330 m s.m., 13-I-2011, *Jaramillo et al. 3929* (CDS 48725)*. Cerro Pampe Bole. 1° 17’ 27.9” S, 90° 26’ 0.2” W, 386 m s.m., 19-II-2008, *Simbaña 834 A* and *B* (CDS 38724)*. Location not specified. *Andersson s. n.* (S 08-14105)**; 8-IV-1888, *Lee s. n.* (US 25604). Los Guabos. 1° 18’ 10.3” S, 90° 25’ 54.8” W, 400 m s.m., 19-Nov-2007, *Simbaña et al. 714* (CDS 37516)*; 1° 18’ 15.9” S, 90° 25’ 52.2” W, 420 m s.m., *Simbaña & Moreno 715* (CDS 37517)*; 1° 18’ 10.3” S, 90° 25’ 54.8” W, 390 m s.m., *Simbaña & Moreno 718* (CDS 37520)*; 1° 12’ 18.1” S, 90° 25’ 58” W, 400 m s.m., *Simbaña & Veintimilia 719* (CDS 37521)*; 1° 12’ 18.1” S, 90° 25’ 58” W, 380 m s.m., *Simbaña & Veintimilia 760* (CDS 38562)*; 1° 18’ 15.9” S, 90° 25’ 52.2” W, 350 m s.m., *Simbaña et al. 768* (CDS 38570)*; 1° 18’ 10.3” S, 90° 25’ 54.8” W, 350 m s.m., *Simbaña et al. 769* (CDS 38571)*. N.O. del Cerro Verde. 23-III-1993, *Aldaz 109* (CDS 7943)*.

**Isabela (or Albemarle) Island.** E. rim of Volcán Alcedo. 22-V-1974, *van der Werff 1177 A* (QCA 98493)* and *B* (K 000174124 [photo seen]). Volcán Sierra Negra. Finca de Pedro Cartagena (FI011), 0° 52’ 26.5” S, 91° 0’ 42.1” W, 12-IV- 2005, *Chamorro & Guerrero 2392* (CDS 17049)*. Santo Tomas, 350 m s.m., 31-VII-1977, *Adsersen 2419* (CDS 2704)*. 0° 50’ 53.2” S, 91° 1’ 22.4” W, 19-II-2003, *Trusty 590* (CDS 15751)* and *591* (CDS 15752)*. Callejón de la Sierra, 0° 53’ 40.3” S, 91° 11’ 6.4” W, 310 m s.m., 14-II-2004, *Jaramillo 2344* (CDS 16496)*; Callejón de la Sierra, 0° 53’ 41.2” S, 91° 11’ 7.3” W, 310 m s.m., 14-II-2004, *Jaramillo 2345* (CDS 16497)*. Cerro Verde. 300-500 m s.m., 15-XI-1985, *Lawesson 2409* (CDS 4510)*. Cerro Azul. Caleta Iguana, 0° 58’ 51.7” S, 91° 26’ 52.3” W, 15-I-2009, *Guézou 544* (CDS 49136)*. La Capilla, 0° 59’ 3” S, 91° 25’ 0.6” W, 480 m s.m., 16-I-2009, *Jaramillo 3466* (CDS 44359)*; Pega-Pega, 0° 58’ 59” S, 91° 26’ 22.2” W, 200 m s.m., 14-I-2009, *Jaramillo 3452 A, B* and *C* (CDS 44346)*.

**Pinta (or Abingdon) Island.** Central de la isla. Sendero que conduce a las parcelas permanentes de Hennig Adsersen, 0° 34’ 52.4” N, 90° 45’ 9.3” W, 600 m s.m., 2-II-2008, *Simbaña 818* (CDS 38707)*; Sendero que conduce a las parcelas permanentes de Hennig Adsersen, 0° 35’ 0.6” N, 90° 45’ 11.6” W, 611 m s.m., 2-II-2008, Simbaña *819* (CDS 38708)*; 0° 34’ 52.4” N, 90° 45’ 9.3” W, 600 m s.m., 2-II-2008, *Simbaña & Guézou 821* (CDS 38710)*. Ladera sur. 24-X-1984, *Huttel 408* (CDS 4334)*. Location not specified. 19-IX-1906, *Stewart 3517* (CAS 483743). Sector noroeste de la isla. Parte central del acantilado, 0° 34’ 43.3” N, 90° 46’ 30.8” W, 420 m s.m., 1-I-2008, *Simbaña 816* (CDS 38705)*. South slope. 400-610 m s.m., 8-XII-1985, *Lawesson 2672 A* and *B* (CDS 4687)*. San Cristóbal (or Chatham) Island. Academy Bay. 1-IV-1930, *Svenson 78* (K 000174126 [photo seen]). Canyon 2 Km NE of El Junco. 400 m s.m., 22-X-1974, *Adsersen 757 A* (CDS 2701)* and *B* (QCA 98488)*. Cuenca de la Honda, Guajavo forest. 450 m s.m., 18-X-1986, *Lawesson 3159* (CDS 4536)*. La Soledad. 0° 53’ 13.5” S, 89° 32’ 13.1” W, 6- II-2003, *Trusty 573 A, B* and *C* (CDS 15894)*; 0° 53’ 13.5” S, 89° 32’ 13.1” W, 6- II-2003, *Trusty 574* (CDS 15749)*. Mixed Guayabillo forest. 500 m s.m., 3 Km N of El junco, 20-IV-1977, *Adsersen 1702 A* (CDS 2702)* and *B* (QCA 98486)*. Southwest end, middle region. VI-1891, *Baur 148* (K000174125 [photo seen]). Wreck Bay. 27-I-1906, *Stewart 3518 A* (MO 1755208) [photo seen] and *B* (CAS 483740).

**Santa Cruz (or Indefatigable) Island.** 200 m s.m., 24-II-1963, *Snow s. n.* (CDS 34)*. 800-850 m s.m., 17-I-1981, *Eliasson 3777* (GB 0132152)*. Academy Bay. 9-XI-1905, *Stewart 3519* (CAS 0483746), *3520* (CAS 483744) and *3521* (CAS 483745). 5 miles north of Academy Bay, 800 m s.m., 13-III-1954, *Bowman 105* (MO 1755209 [photo seen]). Along the trail from Bella Vista to La Copa. 440 m s.m., 19-X-1966, *Eliasson 363* (GB 0132154)*. Along Puerto Ayora-Itabaca highway, just southwest of

Los Gemelos. Border of agricultural zone and Scalesia forest, 0° 38' 2.1'' S, 90° 23' 32.7'' W, 567 m s.m., *Jaramillo 4294* from field collection by A Schneider, R. Martínez and J. Vera (CDS 49633)*. Area immediately around casetta in Tortoise Reserve. 150 m s.m., 18-XI-1982, *Bentley 72 A* (QCNE 41793)*, *B* (QCA 98490)*, *C* (K 000174123 [photo seen]) and *D* (MO 1755212 [photo seen]). Between Horneman's Ranch and Fern-Sedge Zone, along trail to Mt. Crocker. 300 m s.m., 6-II-1964, *Wiggins 18530 A* (CDS 1174)* and *B* (K 000174127 [photo seen]). Carretera Gemelos-Itabaca. 0° 37' 5'' S, 90° 23' 1'' W, 540 m s.m., 14-V-1996, *Jaramillo 596* (CDS 9145)*. Cerro Crocker. Alrededor de las antenas, cuadrante AD4, 0° 38' 32.7'' S, 90° 19' 30.6'' W, 800 m s.m., 7-XII-2001, *Tobar & Herrera G12* (CDS 12534)*; Cuadrante AC3, 0° 38' 32.7'' S, 90° 19' 32.4'' W, 800 m s.m., 7-XII-2001, *Tobar & Herrera G25* (CDS 12508)*. N. slope of Mount Crocker, 690 m s.m., 4-III-1972, *Hamann 650* (CDS 8140)*. El Puntudo. Cuadrante # 19, 0° 39' 3.9'' S, 90° 19' 46.3'' W, 650 m s.m., 21-X-1998, *Jäger s. n.* (CDS 9342)*. Límite del Parque y Zona Agrícola (cerca a Los Gemelos). 0° 43' 7.4'' S, 90° 19' 50.7'' W, 180 m s.m., 5-X-1999, *Jaramillo 1466 A* and *B* (CDS 9650)*. Límite entre Parque Nacional y Zona Agrícola. Cuadrante 5, 0° 37' 57'' S, 90° 23' 49.4'' W, 500 m s.m., 5-X-1999, *Jaramillo 1507* (CDS 12336)*. Los Gemelos. 0° 37' 54.1'' S, 90° 23' 12.2'' W, 600 m s.m., 16-IV-2001, *Jaramillo & Ramírez 1771 A* and *B* (CDS 11733)*, *C* (QCNE 167699)* and *D* (QCNE 167700)*. 0° 37' 31.4'' S, 90° 23' 14.7'' W, 01-II-2003, *Trusty 568 A, B* and *C* (CDS 15748)*; 0° 37' 34.6'' S, 90° 23' 15.8'' W, 16-II-2003, *Trusty 585* (CDS 15744)* and *586* (CDS 15743)*; 16-II-2003, *Trusty 587 A* and *B* (CDS 15742)*; 0° 37' 33.2'' S, 90° 23' 5'' W, 16-II-2003, *Trusty 588* (CDS 15741)*; 0° 37' 31.4'' S, 90° 23' 14.7'' W, 16-II-2003, *Trusty 589 A* and *B* (CDS 15740)*. Media Luna. Miconia Zone, 11-III-1994, *Hagemann 68* (CDS 6172)*. Mina Granillo Rojo. Parcela B6K, 0° 37' 13.3'' S, 90° 21' 48'' W, 327 m s.m., 27-VII-2001, *Pozo & Herrera 3 A* and *B* (CDS 11971)*. Northwest side. 23-VII-1906, *Stewart 3522* (CAS 483741). Trail to Caseta 2 km down from St. Rosa. 12-IV-1980, *Adsersen 2* (K 000174130 [photo seen]). Scalesia forest. 700 m s.m., 17-IV-1974, *Adsersen 77 A* (CDS 2390)* and *B* (QCA 98489)*. Salasaca. 0° 7' 13'' S, 90° 30' 6.1'' W, 300 m s.m., 10-VII-1997, *Soria 030* (CDS 12282)*. Trail between Bellavista and abandoned village of Ponce Enrique. 200 m s.m., 26-I-1964, *Fosberg 44769 A* (MO 1287874 [photo seen]) and *B* (MO 1730641 [photo seen). Trail between Ponce Enrique (abandoned village) and "Table Mountain" (Los Negritos). 200-260 m s.m., 26-I-1964, *Fosberg 44797 A* (MO 1287873 [photo seen]) and *B* (MO-1730642 [photo seen]), *Fosberg 44798 A* (K 000174128 [photo seen]) and *B* (MO 1730640 [photo seen]). Vicinity of Bellavista. 7-XI-1966, *Eliasson 523 A* (GB 0132153)* and *B* (K 000174122 [Photo seen]).

**Santiago (San Salvador or James) Island.** James Bay. 3-I-1906, *Stewart 3523* (CAS 0483742). Borde E, interior del cuadrante lechoso. 0° 12' 45.2'' S, 90° 46' 49.5'' W, 750 m s.m., 29-XI-2000, *Simbaña 322 A* (CDS 11838)* and *B* (QCNE 168686)*. Cuadrante Jaboncillo. C1, 14-III-1991, *Valdebenito 149* (CDS 55122, formerly CDS 8778)*. In the forest region. 9-VI-1947, *Eriksson s. n.* (GB 0146898)*. Ladera sur. 1-XI-1984, *Huttel 464 A* (CDS 4392)* and *B* (QCA 98492)*. Location not specified. X-1835, *Darwin s. n.* CGE 00347=191 lectotype)*; *Darwin s. n.* (K 000432936 isolectotype [photo seen])*.