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Ecuadorian bumble bees (Apidae: *Bombus*): Species diversity, distribution, and floral associations

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Abstract. Ecuador's bee diversity, particularly bumble bees, remains underexplored despite their significant ecological role. This study provides an updated species list, identification keys in both English and Spanish, potential distribution maps based on Ecological Niche Models (ENM), and a summary of known plant associations. Our dataset includes 1,756 records, comprising 408 museum specimens, 1,234 observations from iNaturalist, and 114 field observations recorded by the first author. We document 13 species distributed across two subgenera. *Bombus* (*Cullumanobombus*): *B. butteli*, *B. ecuadorius*, *B. funebris*, *B. handlirschi*, *B. hortulanus*, *B. melaleucus*, *B. robustus*, *B. rubicundus*, and *B. vogti*. *Bombus* (*Thoracobombus*): *B. excellens*, *B. pauloensis*, *B. pullatus*, and *B. transversalis*. Most species are associated with high Andean ecosystems above 2,300 m, though several extend into lower elevations, with records ranging from 180 to 4,719 m. The compiled data span five decades and include records from 17 of 24 provinces in Ecuador. Bumble bees were documented visiting 143 plant species across 39 families, highlighting their broad trophic interactions and potential importance for native vegetation. The ENM-based potential distribution maps offer updated insights into the geographic ranges of those species with sufficient occurrence data, providing a foundation for future ecological and conservation assessments. This study synthesizes the most comprehensive information currently available on Ecuadorian bumble bees, contributing to improved taxonomic knowledge, a deeper understanding of their trophic interactions, and clearer biogeographic insights for the group. Our findings also highlight the importance of continued monitoring and research, particularly to evaluate how these species respond to environmental change and to better understand their functional roles within both Andean and lowland ecosystems.

Resumen. La diversidad de abejas en Ecuador, en particular los abejorros, sigue estando poco explorada a pesar de su importante función ecológica. Este estudio proporciona una lista actualizada de especies, claves de identificación en Inglés y Español, mapas de distribución potencial basados en Modelos de Nicho Ecológico (MNE) y un resumen de las asociaciones conocidas con plantas. Nuestro conjunto de datos incluye 1.756 registros, compuestos por 408 especímenes de museo, 1.234 observaciones de iNaturalist y 114 observaciones de campo registradas por el primer autor. Documentamos 13 especies de abejorros distribuidas en dos subgéneros. *Bombus* (*Cullumanobombus*): *Bombus butteli*, *B. ecuadorius*, *B. funebris*, *B. handlirschi*, *B. hortulanus*, *B. melaleucus*, *B. robustus*, *B. rubicundus* y *B. vogti*. *Bombus* (*Thoracobombus*): *Bombus excellens*, *B. pauloensis*, *B. pullatus* y *B. transversalis*. La mayoría de las especies están asociadas con ecosistemas altoandinos por encima de los 2.300 m, aunque varias se extienden

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hacia elevaciones más bajas, con registros que van desde los 180 hasta los 4.719 m. Los datos recopilados abarcan cinco décadas e incluyen registros de 17 de las 24 provincias del Ecuador. Se documentó que los abejorros visitan 143 especies de plantas pertenecientes a 39 familias, lo que resalta sus amplias interacciones tróficas y su posible importancia para la vegetación nativa. Los mapas de distribución potencial basados en ENM ofrecen información actualizada sobre los rangos geográficos de las especies con suficientes datos de ocurrencia, proporcionando una base para futuras evaluaciones ecológicas y de conservación. En conjunto, este estudio sintetiza la información más completa disponible actualmente sobre los abejorros del Ecuador, contribuyendo a mejorar el conocimiento taxonómico, profundizar en la comprensión de sus interacciones tróficas y aclarar los patrones biogeográficos del grupo. Nuestros hallazgos también resaltan la importancia de continuar con el monitoreo y la investigación, especialmente para evaluar cómo responden estas especies al cambio ambiental y para comprender mejor sus roles funcionales tanto en ecosistemas andinos como de tierras bajas.

INTRODUCTION

Bees (Apoidea) of Ecuador, although diverse and ecologically important, remain relatively understudied and poorly known. This is true even for one of the most common and easily observed bee genera, such as *Bombus* Latreille, 1802 (bumble bees). These large, social bees have robust bodies covered in dense pilosity and possess a charismatic appearance. They inhabit in Ecuador both Andean and Amazonian ecosystems (Pinilla-Gallego *et al.,* 2017). As colony-forming, polylectic bees (*i.e.*, generalists in their pollen preferences), they are highly dependent on floral resources such as nectar and pollen for sustenance and colony maintenance (Martel *et al.,* 2024). This ecological role makes them active flower visitors in both natural and agricultural ecosystems (Padrón, 2025). Furthermore, the current global ecological crisis threatens biodiversity, including bees, and the essential ecosystem services they provide. Among these, pollination is widely recognized, with bumble bees playing a crucial role in the pollination of plants in both natural and agricultural ecosystems (Wahengbam *et al.,* 2019; Cameron & Sadd, 2020; Abrol *et al.,* 2021). Recent evidence indicates that bumble bees are being affected by global change (Soroye *et al.,* 2020), leading to population declines (Goulson *et al.,* 2008), range contractions (Kerr *et al.,* 2015), and disrupted synchrony with the plants they visit (Pyke *et al.,* 2016). These negative effects are expected to be more pronounced in high-altitude ecosystems such as the Andes (Gonzalez *et al.,* 2022; Nascimento *et al.,* 2022), where bumble bees are especially abundant, making their study a priority. Ecological Niche Model estimation has recently been applied to bumble bee species in Colombia (Rojas-Arias *et al.,* 2023), integrating occurrence data with climatic variables. This approach enables the identification of potential distribution areas, facilitates the identification of suitable habitats and informs us about overall habitat requirements.

In Ecuador, particularly in the high Andes, species like *B. funebris* have been recognized by Indigenous groups for generations, leading to the existence of a species-specific common name in the Kichwa language, "Puzu Bunga," which is otherwise rare for insects. "Puzu" can be used as an adjective describing a mottled gray, white, and black coloration (Ministerio de Educación de Ecuador, 2009), a pattern present on the scutum and last metasomal segments of the species. "Bunga", according to Encalada (2022), is considered an onomatopoeic reference to the buzzing sound produced by the insect in flight. These characteristics accurately describe the coloration pattern of *B. funebris*, one of the most common and observed species in Andean ecosystems, particularly in anthropized habitats.

Bombus includes approximately 300 species (Williams, 2023), most of which are distributed across the Palearctic, Oriental, and Nearctic regions, with fewer species occurring in the Neotropical region. In the Neotropics, 46 species have been recorded (Williams, 2025), the majority of which are found in mountainous ecosystems. This makes *Bombus* one of the most conspicuous bee genera in the Andes (Pinilla-Gallego *et al.,* 2017), aside from the introduced European honey bee, *Apis mellifera* Linnaeus, 1758. Bumble bees are notably present in both natural and agricultural ecosystems, where they pollinate many commercial and agriculturally important plants. Despite their ecological, economic, and cultural significance, the study of bumble bees in Ecuador has not been extensive, and even basic aspects such as their alpha diversity remain uncertain. The lack of fundamental information, combined with the limited availability of identification resources, has contributed to the scarcity of ecological studies on these bees.

The earliest records of bumble bees in Ecuador date back centuries and are limited to brief mentions (Cieza, 1962), species lists (Smith, 1854; Franklin, 1913), and locality records (Osculati *et al.,* 1846; Whymper, 1892). Below, we chronologically describe this historical documentation. The Spanish chroniclers who arrived in Ecuador (then part of the Viceroyalty of Peru) after the conquest were tasked with describing the American lands, including their natural history. One such chronicler was Cieza de León, who, in his work *Crónica del Perú* (1550), provided observations on various aspects of nature and Indigenous cultures, including bees. His account describes several animals, including birds, insects, and fish from what are now the southern regions of Ecuador. However, despite his detailed documentation of the fauna, Cieza de León briefly mentions some bees (Cieza, 1962) but does not reference the presence of bumble bees. This omission is also evident in the writings of Jesuit priest Juan de Velasco (1727–1792), who provided a more extensive description of Ecuadorian bees but likewise failed to mention bumble bees (De Velasco, 1841). It is noteworthy that, despite referencing various types of bees, the early chroniclers and naturalists did not document bumble bees, despite their large size and conspicuous presence in Andean ecosystems. This absence in historical records suggests that these insects either did not attract the attention of early naturalists, perhaps because they were non-honey-producing bees, or were simply grouped under general descriptions of "bees". Although these historical descriptions of bees are not as detailed or extensive as those of other natural elements, they remain valuable as early testimonies of the knowledge of these insects in the region.

The first confirmed records of bumble bees in Ecuador date back to the 19th century. Osculati *et al.* (1846) mentioned the presence of species of this genus in the country, reporting *B. excellens* Smith, 1879, and *B. rubicundus* (as *napensis*) Smith, 1854, collected along the Quijos and Napo rivers. Subsequently, in the Catalogue of Hymenoptera of the British Museum of Natural History, a queen of *B. funebris* collected in Quito was mentioned and described by Smith (1854). Later, Meunier (1890a) referred to this specimen again, and in a separate work, Meunier (1890b) described a new species, *B. ecuadorius*, based on a specimen collected by the missionary Boetzkes in Quito at 2,000 m of altitude.

In 1892, Whymper, in his list of species collected during his expedition through the Ecuadorian Andes, mentioned bumble bees and highlighted the abundance of a black-and-white species like a Chilean species: *"Among these, a black and white Bombus, closely resembling a Chilian species, is particularly common"* (Whymper, 1892). This was likely *B. funebris*, a species, as previously mentioned, common in the high Andes and exhibiting the described coloration. Cameron (1903) reported the presence of two species in Ecuador: *B. funebris* and *B. robustus*, collected by Whymper. The specimen of *B. robustus* was collected in Pichincha at 3,500 m, while the *B. funebris* specimens were from locations near Quito. Friese (1903) described two additional species for Ecuador: *B. bicolor*, a junior synonym of *B. rubicundus*, from a female collected in Cuenca (2,200 m), and *B. butteli*, from another female. A year later, Friese (1904) mentioned two more species: *B. robustus* var. *hortulanus* and *B. weisi*, which might have been an incorrect identification of *B. robustus*. Friese himself questioned this identification, writing at the end of the paragraph: *"Gehört vielleicht als schwarzafterige Form zu robutus?"* [*"Perhaps belongs, as a black-abdomened form, to robustus?"*].

The first species list of *Bombus* in Ecuador was proposed by Franklin (1913), who reported 16 species, including *B. butteli* Friese, 1903, *B. ecuadorius* Meunier, 1890b, *B. funebris* Smith, 1854, *B. robustus* Smith, 1854, *B. rubicundus* Smith, 1854, *B. vollucelloides* Gribodo, 1892, *B. handlirschi* Friese, 1903, *B. carolinus* Friese, 1903, *B. guatemalensis* (Cockerell, 1912), *B. kohli* (Swederus, 1787) (as *B. morio* (Swederus, 1787), *B. medius* Cresson, 1863 [as *B. transversalis* (Olivier, 1789)], *B. mexicanus* Cresson, 1878, *B. niger* Franklin, 1913 (*as B. pullatus* Franklin, 1913), *B. pullatus*, *B. steindachneri* Handlirsch, 1888, and *B. ephippiatus* Say, 1837. He also erroneously mentioned that the type specimen used for the description of *B. wilmattae* Cockerell, 1912 queen came from Ecuador, along with three workers. Additionally, Franklin cited *B. pullatus*, whose holotype originated from the country.

However, it is important to reassess these historical records considering modern taxonomy. For example, *B. ephippiatus* is not currently considered part of the Ecuadorian fauna. Although Franklin associated a female specimen from Ecuador with *B. ephippiatus* Say, subsequent taxonomic revisions have clarified that this was a misidentification and not a redescribed valid occurrence of *B. ephippiatus*. Several of the names listed by Franklin have since been revised or synonymized. We provide a cross-referenced table (Table S1) linking Franklin's original names to their current taxonomic status, based on Milliron (1973a,b) and Moure's online database (Moure *et al.*, 2025), which is based on Moure *et al.* (2007) with updated literature.

Frison (1925) expanded knowledge on this group by reporting seven species for Ecuador: *B. robustus*, *B. rubicundus*, *B. funebris*, *B. kohli*, *B. mexicanus*, *B. pauloensis* (as *B. atratus*) and *B. pullatus*. Additionally, he described four variations (currently not recognized as distinct species or subspecies) based on material from Ecuador: *B. robustus* var. *curiosus*, *B. robustus* var. *gaigei*, *B. robustus* var. *hortulans*, and *B. rubicundus* var. *bicolor*.

Milliron (1960) recorded three bumble bee species in Ecuador: *Bombus rubicundus* (as *B. bicolor*), *B. funebris*, and *B. robustus var. hortulans*. Later, Milliron (1971) expanded the list with *B. pauloensis* (as *B. atratus*), *B. excellens*, *B. opifex*, and *B. pullatus*. In a subsequent revision, Milliron (1973b) further documented *B. melaleucus*, *B. ecuadorius*, *B. hortulanus*, *B. robustus*, *B. vogti*, *B. funebris* (as *B. funebris funebris* and, speculating about the presence of *B. funebris rohweri*), *B. rubicundus*, *B. handlirschi*, and *B. coccineus*. Additionally, he suggested that *B. volucelloides* and *B. butteli* were likely present in Ecuador.

Abrahamovich & Díaz (2002) reported 14 species, including: *Bombus handlirschi*, *B. pauloensis* (as *B. atratus*), *B. excellens*, *B. mexicanus*, *B. morio*, *B. opifex*, *B. pullatus*, *B. funebris*, *B. ephippiatus*, *B. ecuadorius*, *B. hortulanus*, *B. melaleucus*, *B. robustus*, and *B. rubicundus*. This publication positioned Ecuador as the second most diverse country in terms of bumble bee species in Central and South America, after Mexico (19 species).

In 2004, Rasmussen presented a preliminary list of bee species from the provinces of El Oro, Loja, and Zamora, reporting the presence of *B. pauloensis* (as *B. atratus*) as a common element of Loja's local bee fauna and mentioning the presence of *B. ecuadorius*. Since these publications, there has been no update on the number of bumble bee species present in the country. As can be observed, there is significant variation in the number of species reported for Ecuador over time, highlighting the need for an updated species list to better understand the diversity of this insect group.

Other studies on *Bombus* in Ecuador have focused on aspects of their natural history, including the nesting behavior of *B. transversalis* (Olesen, 1989) and *B. pauloensis* (as *B. atratus*) (Gonzalez *et al.*, 2004). More recently, phoretic interactions between *B. funebris* and beetles of the genus *Antherophagus* (Coleoptera: Cryptophagidae) have also been documented (Vanegas & Padrón, 2022; Martel *et al.*, 2024). The limited number of ecological studies on *Bombus* in the country may, in part, be due to the lack of an updated species checklist and accessible tools for accurate species identification.

Reliable taxonomic identification is fundamental for obtaining meaningful ecological data, as it underpins assessments of biodiversity, species interactions, and changes in community composition. It also ensures the validity of ecological analyses, supports monitoring efforts, and informs decision-making in conservation and environmental management. Without robust taxonomy, the interpretation and applicability of ecological findings are significantly hindered. However, to achieve this in Ecuador, it is essential to determine which species are present, where they occur, how to identify them, and what floral resources they use.

In this study, we aim to address the limited knowledge of Ecuadorian bumble bees by synthesizing data from several years of fieldwork across diverse ecosystems, complemented by the examination of specimens deposited in national and international entomological collections. Our objectives are to provide an updated list of the *Bombus* species present in the country, develop a dichotomous key with photographs to facilitate accurate species identification, and generate potential distribution maps based on available occurrence records. Additionally, we compile a preliminary list of plant species visited by these bumble bees and summarize known aspects of their natural history. Through this work, we seek to establish a foundation that promotes and supports future ecological, taxonomic, and conservation research on bumble bees in Ecuador.

MATERIALS AND METHODS

Field Work

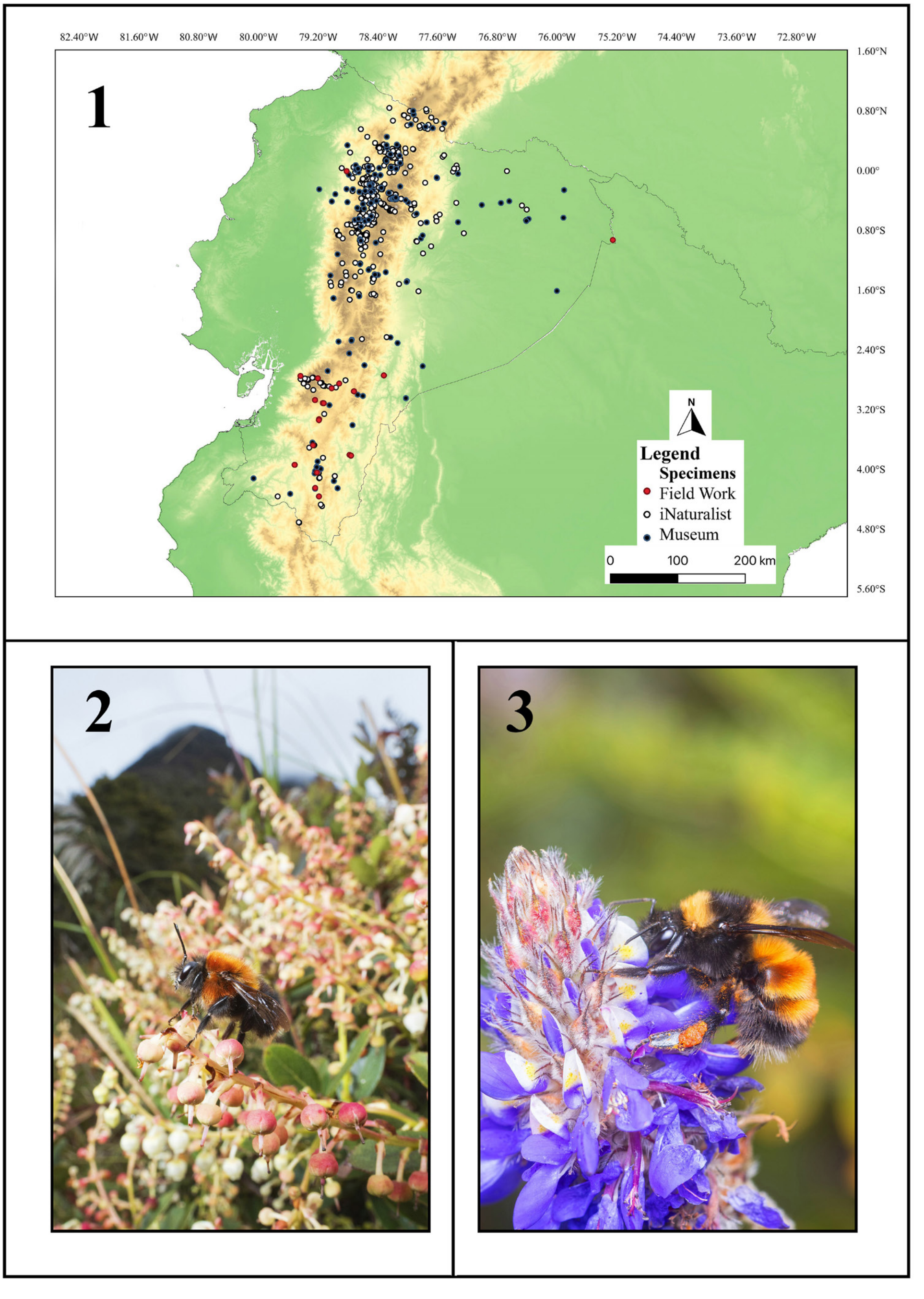
From February 2021 to March 2025, 33 field surveys were conducted across 19 localities representing a variety of ecosystems in the provinces of Azuay, Cañar, Chimborazo, Cotopaxi, Latacunga, Loja, Morona Santiago, Napo, Orellana, Pastaza, Pichincha, and Zamora Chinchipe (Fig. 1). During these surveys, habitats were systematically explored to locate bumble bees, with particular attention to documenting their flower visitation events. Although floral visits were recorded, we did not quantify whether individuals collected pollen, nectar, or both, nor whether they contacted the floral reproductive structures while foraging. Most surveyed sites were situated above 2,000 m and encompassed Andean grasslands, montane forests, and páramo ecosystems, while a smaller number of surveys were conducted in lowland Amazonian habitats (Figs. 2, 3). Together, these surveys provide a broad environmental representation of the regions where *Bombus* species occur in Ecuador.

Review of Museum Collections

Visits were conducted to examine specimens of *Bombus* from Ecuador, housed in the country's main collections, namely the Instituto Nacional de Biodiversidad, Quito (INABIO), and the Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ). In addition, we included specimens from Claus Rasmussen's Collection, Aarhus University, Denmark (CRC), and the National Museum of Natural History, Washington, USA (USNM). Images of specimens available in online databases were also reviewed.

Citizen Science Data

Citizen science is becoming an increasingly important source of information for biological records. Due to their large size compared to other bees and their presence in both natural and agricultural ecosystems, bumble bees are frequently recorded on platforms such as iNaturalist (iNaturalist, 2025). As of March 11 2025, there were 1,780 records of *Bombus* in iNaturalist Ecuador (https://ecuador.inaturalist.org/observations?place_id=7512&taxon_id=52775). These photos are often accompanied by valuable biological information that can be assessed, such as interactions with



Figures 1–3. Bumble bees of Ecuador. **1.** Map showing the localities of the specimens and their sources. **2.** *Bombus rubicundus* Smith male perching on an inflorescence in the Maylas area, Azuay province. **3.** *Bombus robustus* Smith worker feeding on flowers of *Dalea coerulea* (Fabaceae) in Azuay province.

flowers, making this source particularly useful for studying bumble bees. For this study, we conducted a search for *Bombus* records on iNaturalist-Ecuador (iNaturalist community). The retrieved records were downloaded and individually reviewed. Most of these identifications were checked and verified on the platform by the second author (CR) and many other experts (see acknowledgment for the most active). These determinations were based primarily on the dominant color patterns characteristic of each species rather than on the use of a photographic key. We did not classify records by sex or caste. Coordinates were extracted from each record, and information on plant-flower interactions was recorded whenever available or visible from the image of the bee. The data were then curated by individually assessing and verifying the identification of each *Bombus* species. Records in which species identification could not be reliably confirmed through photo review were excluded from the final dataset.

Occurrence Data

The data obtained from these sources, *i.e.*, museums, fieldwork, and citizen science portals, were divided into two categories: records of specimens examined in museum collections and observational records from the iNaturalist platform and field observations. These records are presented in Appendix S1 and Dataset S1. The records are organized alphabetically by province, with the province name written in uppercase and bold (*e.g.*, **AZUAY**)**.** Within each province, records are formatted as follows: if a record includes multiple specimens, the number of individuals is noted first, followed by the name of locality, altitude in meters, latitude and longitude in decimal degrees, date of record, collector name, and the source of the record. If the specimen is housed in a museum, the corresponding acronym (*e.g.*, QCAZ) is included. If the record is from an observation (*e.g.*, iNaturalist or Sebastián Padrón), it is indicated accordingly. Below is an example of the record format used: **BOLÍVAR:** 7, Cashca-Totoras, 2,982 m, -1.7115 -78.97805, L. Coloma, QCAZ. It should be noted that the list is not separated by caste which was not recorded.

Geographic coordinates and elevation data missing from some museum specimens were estimated (Google Earth) and are presented in the records accordingly. Other unavailable information was omitted. This information is presented in Dataset S1. It includes detailed occurrence data organized by province and type of record, following the format described above. These supplemental materials serve as a comprehensive reference for the distributional data used in this study. In addition, to visualize the elevational distribution of the species recorded in Ecuador, we generated a range-plot showing the minimum and maximum elevation at which each species has been documented. The plot displays horizontal segments representing the elevational range of each species. All graphs were produced using the ggplot2 package in R.

Species Identification

We followed the subgeneric classification proposed by Williams *et al.* (2008), which employs four criteria to simplify the subgeneric classification system of the genus *Bombus*, reducing it to 15 subgenera globally. All original species descriptions were consulted (*i.e.*, Swederus, 1787; Olivier, 1789; Smith, 1854, 1879; Handlirsch, 1888; Meunier, 1890b; Friese, 1903, 1904, 1913), but identifications were based primarily on subsequent taxonomic treatments and identification keys. These include Franklin (1913), the revisions by Milliron (1971, 1973a,b), Rasmussen (2003) and more recent resources such as the online key to female coloration patterns by Williams (2025). Together, these sources provided the comparative framework necessary for consistent identification of female specimens based on external morphological traits. The coloration patterns are depicted following the scheme proposed by Williams (2007), which divides the mesothorax and metasoma of bumble bees into 24 color segments (Fig. 2). In this scheme, the dominant colors for each segment are represented. The color selection process involved sampling pixel colors from museum photographs using the Eyedropper tool in Photoshop. Additional taxonomic characters are those used by, or adapted from, Michener (2007). This includes numbered metasomal terga and sterna which are labelled from basal first to apical last.

Ecological Niche Models

The Ecological Niche Models (ENM) for each bumble bee species (with more than seven independent records) present in Ecuador were estimated. The number of records used per species was 592 for *B. funebris*, 562 for *B. robustus*, 7 for *B. ecuadorius*, 253 for *B. hortulanus*, 21 for *B. melaleucus*, 128 for *B. rubicundus*, 91 for *B. transversalis*, 16 for *B. excellens*, 66 for *B. pauloensis*, and 14 for *B. vogti*. This data was first georeferenced and reviewed by projecting each record onto an elevation layer of the country using QGIS 3.4 (QGIS Development Team, 2024). This projection allowed the identification of erroneous georeferencing, such as the presence of strictly high-Andean species (*B. funebris*, *B. hortulanus*, *B. rubicundus*, and *B. robustus*) in Amazonian ecosystems; such records were removed. Subsequently, the localities were reprojected in QGIS and an elevation layer of the country, and using the Point Sampling Tool from the toolbox, the elevation of each record was extracted. A species-specific data filtering process was then applied to eliminate or correct elevations that were significantly outside the average range for each species. These refined data were used for ENM development.

To estimate the potential distribution of bumble bees in Ecuador, the entire continental territory was considered. Nineteen environmental variable layers (Table S2) with a spatial resolution of 30 arc seconds (0.93 km^2) were obtained from the WorldClim v.2.1 database (Fick & Hijmans, 2017). The environmental variable data represent an average from 1970 to 2000. Ecological Niche Models were estimated using Maxent 3.4 (Phillips *et al.*, 2006). The parameters selected for ENM estimation in Maxent followed those used by Rojas-Arias *et al.* (2023), including a maximum of 500 iterations, 10% test points (CrossValidate), no extrapolation, cumulative output, a convergence threshold of 0.00001, a prevalence of 0.5, and a maximum of 10,000 background points. To validate and assess the generated models, the Jackknife test was used to estimate the importance of each variable. The AUC (Area Under the Curve) test was employed to evaluate model accuracy and predictive performance, with values ranging from 0 to 1, where 1 represents perfect prediction.

The resulting ENMs in raster format for each species were then reclassified into binary presence/absence maps using the Raster Calculator in QGIS 3.4. The ENMs, represented as raster layers with probability values ranging from 0 to 1, were rescaled by applying a fixed threshold of 0.5. The procedure involved loading the corresponding raster layer into QGIS and accessing the Raster Calculator tool (Raster > Raster Calculator). A conditional expression of the form "ENM_raster@1" > 0.5 was applied, where values greater than 0.5 were reclassified as 1 (Presence), and values equal to or less than 0.5 were classified as 0 (Absence). The resulting binary raster was saved in .tif format for further analysis. These final maps included areas with a suitability percentage above 50%.

Finally, each map was edited to remove trans-cordilleran areas where the estimated potential distribution of a species, restricted to one side of the Western or Eastern Cordillera, was projected onto the opposite side. To achieve this, Ecuador's watershed boundaries were delineated using digital elevation models (DEM) downloaded from the DIVA-GIS platform (Hijmans *et al.*, 2012). These DEMs, with a spatial resolution of 30 m, were processed in QGIS 3.4, using hydrological analysis tools from the SAGA GIS and GRASS GIS modules. The Fill Sinks tool from the SAGA GIS module was employed to correct topographic inconsistencies in the DEM. This corrected DEM was then used as input for calculating flow direction and flow accumulation. To estimate flow direction, the Flow Direction (D8) algorithm from SAGA GIS was applied, assigning each cell a runoff direction based on the Deterministic Eight Neighbor Method (D8). Flow accumulation was calculated using the Flow Accumulation tool, generating a raster in which each cell represents the amount of flow received from upstream cells. To identify watersheds, outlet points were established at sites of interest, selected based on the country's hydrographic network. A vector layer of points was created (Layer > Create Layer > New Point Layer), manually placing outlet points along the main drainage network. Then, the Watershed Delineation tool in SAGA GIS was used with the flow direction layer and outlet points as inputs, generating vector polygons representing watershed boundaries. To extract the drainage network from the delineated watersheds, the Drainage Network tool in SAGA GIS was applied, setting an appropriate flow accumulation threshold to identify primary and secondary watercourses. The results were analyzed and visualized in QGIS 3.4, enabling differentiation between the eastern and western slopes of the Andes. These layers were overlaid to remove trans-cordilleran areas projected in the ENMs. Additionally, to improve ENM predictions, an elevation-based filter was applied to eliminate projected distribution areas that fell outside the minimum and maximum elevation ranges recorded for each species from the three data sources used. These procedures allowed for a more accurate definition of potential distribution areas for bumble bee species.

Identification of Plants Visited by Bumble Bees in Ecuador

To compile an original list of plants visited by each bumble bee species, photographs obtained in the field and those from the iNaturalist platform were used. Only photos showing bumble bees actively feeding on flowers were considered for data extraction, while images of bumble bees merely perched on plants were excluded. The taxonomic identification of the visited plants was conducted using bibliographic sources such as Jørgensen & León-Yánez (1999) and León-Yánez *et al.* (2011). The information on plants visited by each bumble bee species includes the scientific name of the plant and its respective family. Additionally, all plant species were classified according to their biogeographic origin, as introduced, native to South America, and endemic to Ecuador. This classification was based on information from Jørgensen & León-Yánez (1999, 2011), and digital resources such as the Missouri Botanical Garden's Tropicos database (Missouri Botanical Garden, 2025).

Specimen Photography

Museum specimens were photographed using a Canon R5 camera 45 megapixels, paired with a Canon 100mm F/2.8 1X Macro lens or a Canon MP-E 65mm F/2.8 1-5X Macro lens. Specimen lighting was achieved using a single Yongnuo Flash IV 560, softened with an AK Diffuser. The photos were taken in RAW format and were subsequently edited using Adobe Photoshop 2024. This software was also used to compose the final figures and create the figures of the species' coloration patterns.

Species Illustrations

Coloration patterns in bumble bees are often species-specific traits and can therefore be useful for initial species identification (Williams, 1998). For this reason, we present dorsal-view illustrations of the female coloration patterns of the bumble bee species recorded in Ecuador. These illustrations are based on species descriptions, examinations, and photographs of multiple museum specimens.

RESULTS

Bombus Species of Ecuador

A total of 1,757 specimens were examined, including 408 museum specimens from INABIO (50), QCAZ (328) and USNM (30) and 1,348 field observations (1,234 from iNaturalist and 114 recorded by the first author). See Appendix S1 for details of the records. These combined data sources allowed us to capture a broad representation of the geographic and ecological variation of *Bombus* across Ecuador. Most surveyed sites were situated above 2,000 m and encompassed Andean grasslands, montane forests, and páramo ecosystems, which represent the primary habitats where bumble bees were recorded. Additionally, a smaller number of surveys were conducted in mid- and lowland Amazonian habitats, providing complementary data from tropical ecosystems, and extending the environmental gradient represented in our dataset.

The species records presented here span 55 years, from September 1970 to January 2025, and cover 17 provinces: Azuay, Bolívar, Cañar, Carchi, Chimborazo, Cotopaxi, Imbabura, Loja, El Oro, Morona Santiago, Napo, Orellana, Pastaza, Pichincha, Sucumbíos, Tungurahua, and Zamora Chinchipe. Seven provinces (Esmeraldas, Galápagos, Guayas, Los Ríos, Manabí, Santa Elena, and Santo Domingo de los Tsáchilas) do not have any *Bombus* records. These species occur at elevations ranging from 180 m to 4,719 m. The most abundant species in our records were *B. funebris* (592) and *B. robustus* (562).

The number of records for each species was as follows: *Bombus butteli* (7), *B. ecuadorius* (4), *B. excellens* (16), *B. funebris* (592), *B. handlirschi* (2), *B. hortulanus* (253), *B. melaleucus* (21), *B. pauloensis* (66), *B. pullatus* (1), *B. robustus* (562), *B. rubicundus* (128), *B. transversalis* (91), and *B. vogti* (15). For the previously reported species *B. opifex*, *B. coccineus*, and *B. morio*, no confirmed records exist in Ecuador, as discussed below. However, should they occur in Ecuador, all three species have been included in the identification key, and an overview of each is provided to facilitate future documentation.

In this publication, we report the confirmed presence of 13 bumble bee species grouped into two subgenera. *Bombus* (*Cullumanobombus*) Vogt, 1911, which include species that are predominantly short-faced (*e.g.*, Cameron *et al.*, 2007; Hines, 2008) mountain or montane grassland species (Williams *et al.*, 2008; Williams, 2023), and pocket makers. They built pollen storage pockets adjacent to brood cells and often nest underground. The other subgenus is *Bombus* (*Thoracobombus*) Dalla Torre, 1880, which have moderately long faces and long tongues (Cameron *et al.*, 2007; Williams *et al.*, 2022) and include all those described by Sladen (1912) as 'carder bees'. Many of them build nests on the ground surface, covered only by herbaceous plant material such as grass stems (*e.g.*, Cameron & Whitfield, 1996), although other species prefer to nest underground (Sakagami & Zucchi, 1965; Sakagami *et al.*, 1967; Janzen, 1971; Garófalo, 1979; Garófalo *et al.*, 1986; Olesen, 1989; Silva-Matos & Garófalo, 2000; Cortopassi-Laurino *et al.*, 2003; Ramírez & Cameron, 2003; Gonzalez *et al.*, 2004; Hoffmann *et al.*, 2004; Hines *et al.*, 2007; Almanza Fandiño, 2007; Riaño *et al.*, 2014; Posada-Flórez & Téllez-Farfán, 2021).

Identification Key to bumble bees of Ecuador (Workers and Queens)

The key is produced to facilitate identification based on field observations mostly without the need for magnification and includes species whose presence in Ecuador has not yet been confirmed but are potentially to be found. To keep the language less technical in the key, we used thorax and abdomen for the mesosoma with the fused propodeum and metasoma, respectively.

1. Body entirely or almost entirely black 2
—. Body with distinct coloration (can be white hair bands or patches) 5

[All dark bees]
2(1). Wings with a violet reflection .... *B. morio* (not confirmed in Ecuador)
—. Wings without a clear violet reflection 3

3(2). Dorsal thorax black with intermixed gray hairs; abdomen black with at the most few pale hairs .... *B. vogti* (Figs. 46–49).
—. Thorax and abdomen completely black ………………………………….......... 4
4(3). Posterodistal angle of the metabasitarsus smooth though sharp; wings apical dark with veins dark and sharply defined against membrane .... *B. pauloensis* (Figs. 55–57)
—. Posterodistal angle of the metabasitarsus sharply defined; wings pale brown and relatively uniform in tone, veins faint and only slightly darker than surrounding membrane.. *B. pullatus* (Figs. 58–62)
5(1). Thorax entirely or almost entirely black ……......………………………................. 6
—. Thorax not completely black 10

[Bees with dark thorax]
6(5). Terga I, II ochre; tergum III black; terga IV–VI white.. 7
—. Tergum I black; following terga black, white or red... 8
7(6). Dorsal thorax black with scattered gray hair .... *B. butteli* (Figs. 5–8)
—. Dorsal thorax entirely black .... *B. ecuadorius* (Figs. 10–13)
8(6). Terga I–III black; terga IV–VI white .... *B. melaleucus* (Figs. 30–33)
—. Tergum I black; terga II, III red 9
9(8). Terga II–VI red; thorax black but dorsally intermixed with gray hairs .... *B. excellens* (Figs. 51–53)
—. Terga II, III red; tergum IV reddish-white; terga V, VI white; thorax black .... *B. coccineus* (potentially present in Ecuador) (Figs. 69–70)

[Bees with colors on thorax]
10(5). Thorax mostly black with a large white dorsal patch; terga IV–VI white .... *B. funebris* (Figs. 15–18)
—. Thorax yellow, red, or orange (see also lateral view)....................................... 11
11(10). Thorax with yellow bands or yellow segments 12
—. Thorax red or orange (see also lateral view).. 15
12(11). Tergum I yellow.. 13
—. Tergum I entirely or partly black.. 14
13(12). Thorax segments 1, 5, and 6 yellow; terga I–III yellow; tergum IV black; terga V–VI white ……………......……………….................... *B. robustus* (Figs. 35–38)
—. Thorax segments 1, 2, 5, and 6 yellow; terga I–III yellow; terga IV–VI reddish .... *B. opifex* (potentially present in Ecuador) (Figs. 71–72)
14(12). Thorax segments 1, 5, and 6 yellow; tergum I partly black at least basally .... *B. hortulanus* (Figs. 25–28)
—. Thorax segments 1, 5, and 6 yellow; terga III yellow-ochre; terga I, II, IV–VI black .... *B. transversalis* (Figs. 65–68)
15(11). Thorax with orange hairs (at least laterally); tergum I with mixed orange hairs; terga II, III orange-brown; terga IV–VI orange; orange hairs on margin of hind tibiae.. *B. handlirschi* (Figs. 20–23)
—. Thorax red; abdomen entirely red or terga I and IV–VI red and terga II, III black; black hairs on margin of hind tibiae............... *B. rubicundus* (Figs. 40–44)

Clave de identificación para las especies de *Bombus* de Ecuador (Obreras y Reinas)

La clave se ha elaborado para facilitar la identificación basada en observaciones de campo, generalmente sin necesidad de aumento, e incluye especies cuya presencia en Ecuador aún no ha sido confirmada pero que potencialmente podrían encontrarse allí. Para mantener un lenguaje menos técnico, usamos tórax para el mesosoma con el propodeo fusionado y abdomen para el metasoma.

1. Cuerpo completamente o casi completamente negro 2
—. Cuerpo con coloración distinta (pueden ser bandas o parches de pelos blancos) 5

[Abejas completamente oscuras]
2(1). Alas con reflejo violeta .... *B. morio* (no confirmado en Ecuador)
—. Alas sin un reflejo violeta claro.. 3
3(2). Tórax dorsal negro con pelos grises entremezclados; abdomen negro con, algunos pocos pelos pálidos .... *B. vogti* (Figs. 46–49)
—. Tórax y abdomen completamente negros 4
4(3). Ángulo posterodistal del metabasitarso liso aunque agudo; alas oscuras en el ápice con venas oscuras y claramente definidas contra la membrana .... *B. pauloensis* (Figs. 55–57)
—. Ángulo posterodistal del metabasitarso bien marcado; alas marrón claro y relativamente uniformes en tono, venas tenues y solo ligeramente más oscuras que la membrana circundante .... *B. pullatus* (Figs. 58–62)
5(1). Tórax total o casi totalmente negro 6
—. Tórax no completamente negro 10

[Abejas con tórax oscuro]
6(5). Tergos I, II ocre; tergo III negro; tergos IV–VI blancos 7
—. Tergo I negro; siguientes tergos negros, blancos o rojos 8
7(6). Tórax dorsal negro con pelos grises dispersos .... *B. butteli* (Figs. 5–8)
—. Tórax dorsal completamente negro .... *B. ecuadorius* (Figs. 10–13)
8(6). Tergos I–III negros; tergos IV–VI blancos .... *B. melaleucus* (Figs. 30–33)
—. Tergo I negro; tergos II, III rojos 9
9(8). Tergos II–VI rojos; tórax negro pero dorsalmente con pelos grises entremezclados .... *B. excellens* (Figs. 51–53)
—. Tergos II, III rojos; tergo IV rojizo-blanco; tergos V, VI blancos; tórax negro ....*B. coccineus* (potencialmente presente en Ecuador) (Figs. 69–70)

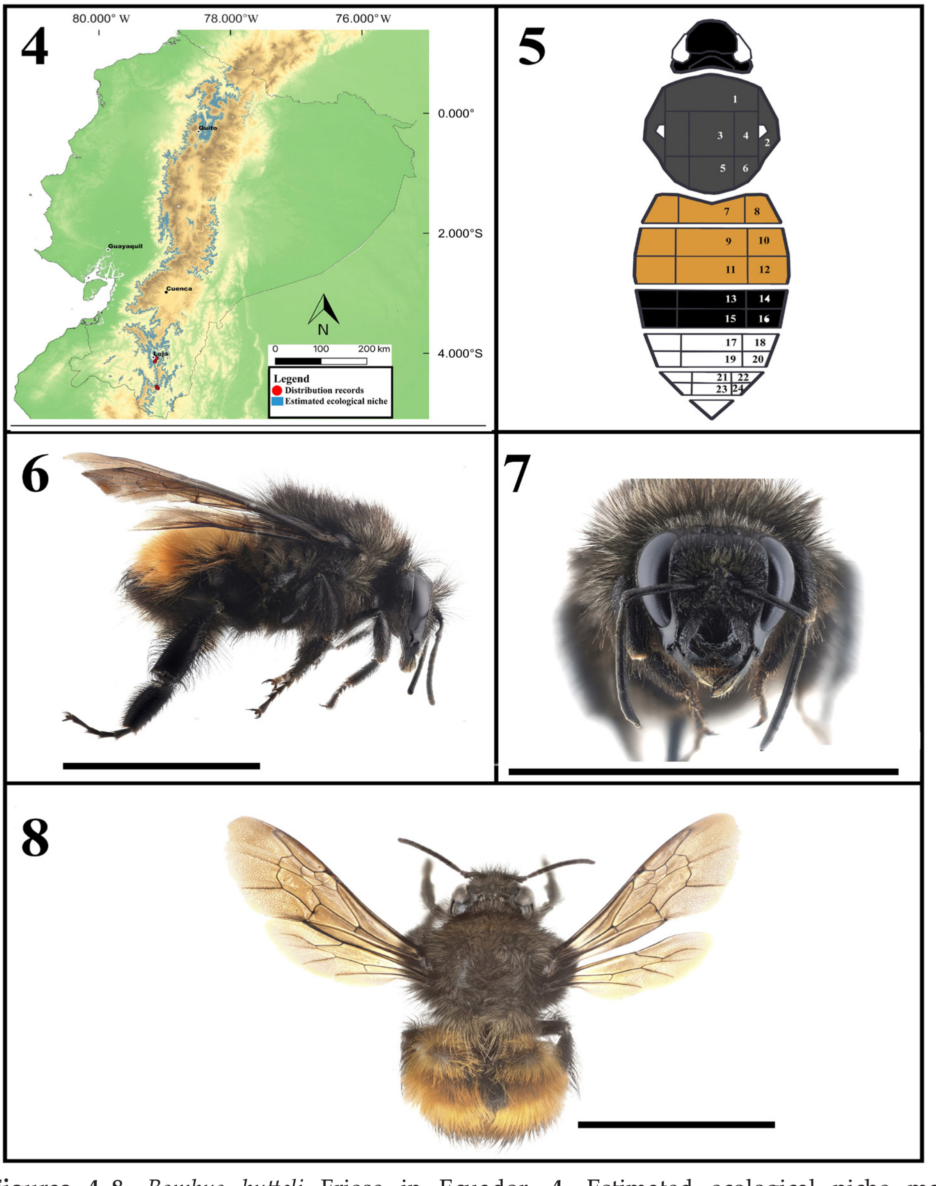
[Abejas con bandas de color en el tórax]
10(5). Tórax mayormente negro con un gran parche dorsal blanco; tergos IV–VI blancos .... *B. funebris* (Figs. 15–18)
—. Tórax amarillo, rojo u naranja (ver también vista lateral) 11
11(10). Tórax con bandas o segmentos amarillos 12
—. Tórax rojo u naranja (ver también vista lateral) 15
12(11). Tergo I amarillo 13
—. Tergo I total o parcialmente negro 14
13(12). Segmentos torácicos 1, 5 y 6 amarillos; tergos I–III amarillos; tergo IV negro; tergos V, VI blancos .... *B. robustus* (Figs. 35–38)
—. Segmentos torácicos 1, 2, 5 y 6 amarillos; tergos I–III amarillos; tergos IV–VI rojizos .... *B. opifex* (potencialmente presente en Ecuador) (Figs. 71–72)
14(12). Segmentos torácicos 1, 5 y 6 amarillos; tergo I parcialmente negro, al menos basalmente .... *B. hortulanus* (Figs. 25–28)
—. Segmentos torácicos 1, 5 y 6 amarillos; tergo III amarillo-ocre; tergos I, II y IV–VI negros .... *B. transversalis* (Figs. 65–68)
15(11). Tórax con pelos naranjas (al menos lateralmente); tergo I con pelos naranjas mezclados; tergos II, III naranja-marrón; tergos IV–VI naranjas; pelos naranjas en el margen de las tibias posteriores .... *B. handlirschi* (Figs. 20–23)

—. Tórax rojo; abdomen completamente rojo o tergo I y IV–VI rojos y tergos II, III negros; pelos negros en el margen de las tibias posteriores …………………..…… ………………………………………………….............. *B. rubicundus* (Figs. 40–44)

Overview of the *Bombus* species with confirmed presence in Ecuador

Subgenus *Bombus* (*Cullumanobombus*)

Bombus butteli Friese, 1903
(Figs. 4–8)



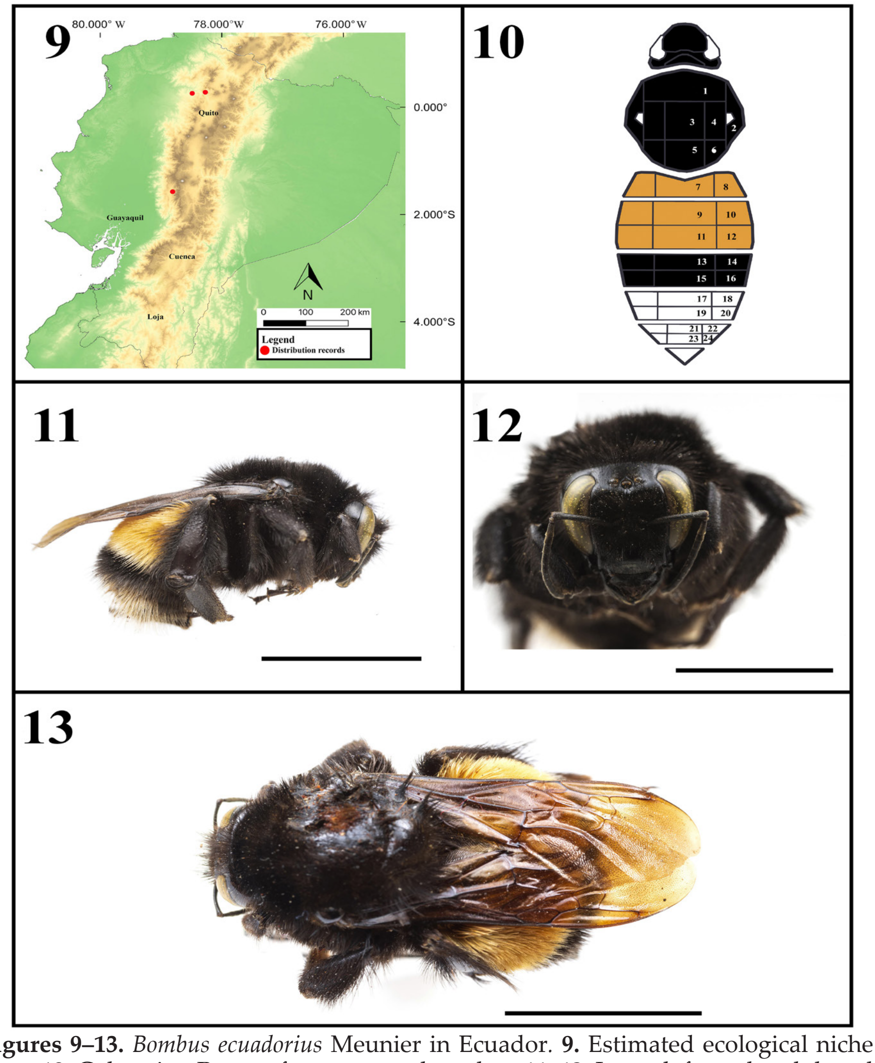
Figures 4–8. *Bombus butteli* Friese in Ecuador. **4.** Estimated ecological niche map. **5.** Coloration pattern for queen and worker. **6–8**. Lateral, frontal and dorsal views of the worker, respectively. Scale line = 1 cm.

Identification: The dorsal thorax is cinereous or gray, with the interalar area darker, sometimes almost yellowish hair band instead of the usual grayish cast. Metasoma coloration is variable: Terga I–II are yellow to ochre or reddish-brown, tergum III is black (sometimes with yellow or reddish-brown at the base), terga IV–V are pale yellowish white, and tergum VI is dark medially with pale sides. Wings are moderately infuscated, darker distally. *Bombus butteli* closely resembles *B. ecuadorius* but differs in having a black thorax with intermixed gray hairs, whereas *B. ecuadorius* has a completely black thoracic dorsum. In *B. ecuadorius* tergum VI is all white (Figs. 10–13).

Distribution: A species restricted to Ecuador, Peru, and Bolivia (Milliron, 1973b). In Ecuador, it has been observed in the southern regions of the country, in the provinces of Loja and Zamora-Chinchipe. Here it has been recorded at a mid and high elevation from 2,419 to 2,700 m (Fig. 4).

Host plants: Two species belonging to two families (Table S3).

Bombus ecuadorius Meunier, 1890b
(Figs. 9–13)

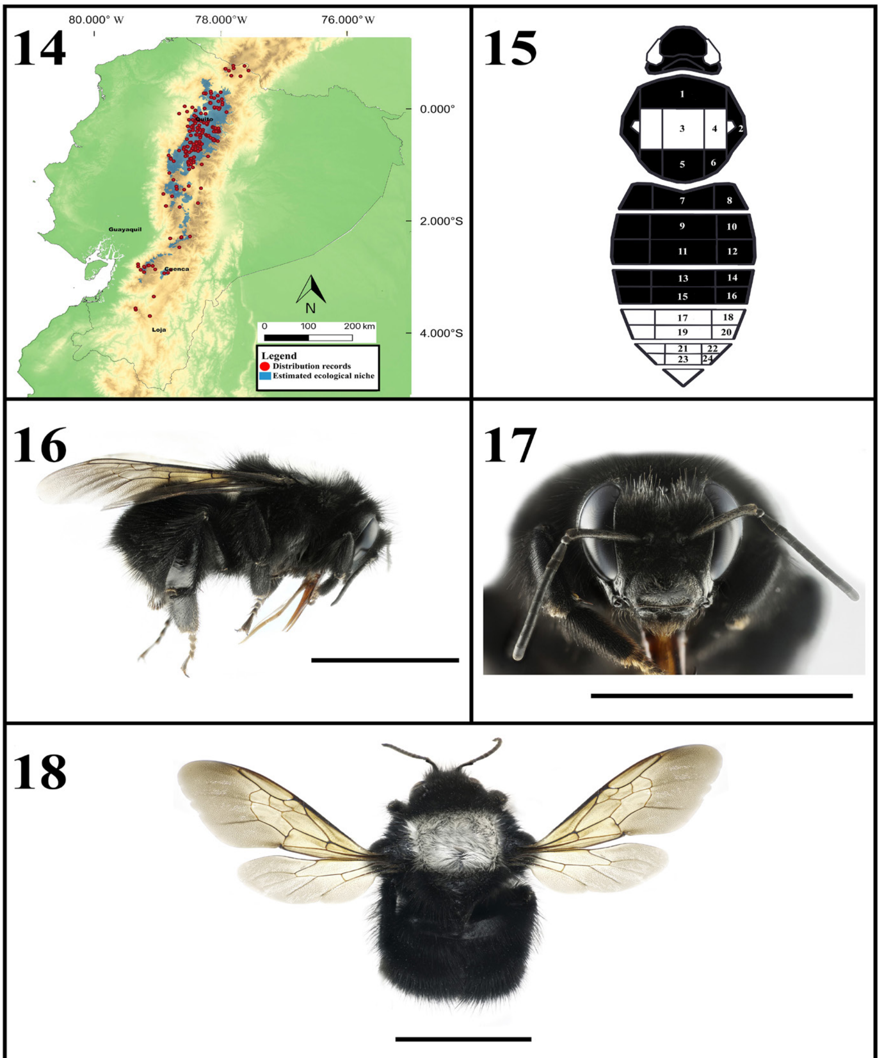


Figures 9–13. *Bombus ecuadorius* Meunier in Ecuador. **9.** Estimated ecological niche map. **10.** Coloration Pattern for queen and worker. **11–13.** Lateral, frontal and dorsal views of the queen, respectively. Scale line = 1 cm.

Identification: The dorsal thorax is completely black. Metasoma pubescence is dense: terga I–II are ochre to light golden-yellow, tergum III is black (sometimes with a few yellow hairs), terga IV–V are whitish, and tergum VI is dark medially with whitish sides. The wings are deeply infuscated, appearing almost black. The taxonomic status of this species remains unresolved; it is here treated as distinct taxon from *B. butteli* (Franklin, 1913; Milliron, 1973b), a species with which it shares many similarities (Figs. 5–8) (See discussion under *B. butteli*).

Distribution: This species is restricted to Ecuador, Peru, and Bolivia (Milliron, 1973b). In Ecuador, it has been recorded sporadically from 1,800 m to 2,981 m (Fig. 9), three at the QCAZ museum, and recently was also reported on iNaturalist from the Reserva Geobotánica Pululahua near Quito.

Bombus funebris Smith, 1854
(Figs. 14–18)



Figures 14–18. *Bombus funebris* Smith in Ecuador. **14**. Estimated ecological niche map. **15.** Coloration pattern for queen and worker. **16–18.** Lateral, frontal and dorsal views of the queen, respectively. Scale line = 1 cm.

IDENTIFICATION: This species is easily recognized by its distinctive coloration, unique among Ecuadorian bumble bees. The body is predominantly black, with the anterior mesoscutum and mesoscutellum black, and a broad patch of light greyish-white hairs between the wing bases (segments 3 and 4) (Fig. 15). The metasomal terga I–III are black and terga IV–VI are white (Fig. 15), sometimes with a pale rufescent tinge. Unlike other high-elevation species, such as *B. hortulanus*, *B. robustus*, *B. rubicundus*, and *B. handlirschi*, it lacks any yellow or red coloration. The species also has a relatively large head, robust mandibles, and long antennae. The queen and worker are similar in appearance, with size being the most evident difference as in most other Ecuadorian bumble bees (*B. rubicundus* and *B. handlirschi* being exceptions). However, males tend to show slightly more diffuse white coloration, which can extend across multiple metasomal terga, distinguishing them from queens and workers.

DISTRIBUTION: This species is primarily distributed at high altitudes in the Andes, covering regions of Colombia, Ecuador, Peru, and Bolivia (Abrahamovich *et al.,* 2004). It inhabits mountainous areas, cloud forests, and páramos. In Ecuador, it is commonly found in the Andes at an elevation range from 938 m to 4,719 m, making it the highest-flying bumble bee species in the country (Fig. 14).

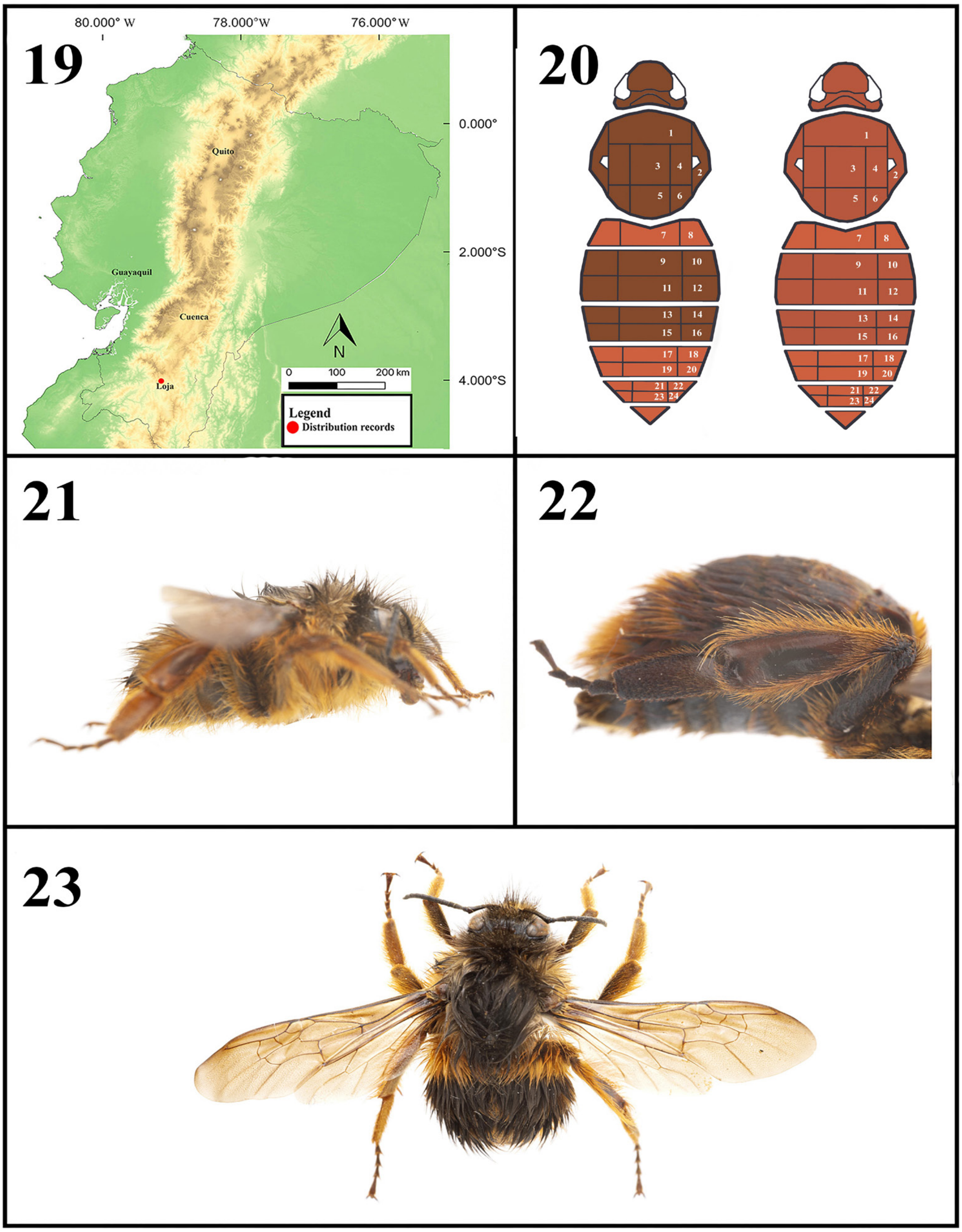
HOST PLANTS: 63 species belonging to 16 families (Table S3).

NATURAL HISTORY: *Bombus funebris* is the Andean species recorded at the highest altitude, with an individual collected at 4,750 m in Colombia (Pinilla-Gallego *et al.,* 2017), and in Ecuador, here we report a specimen at 4,719 m in Cotopaxi National Park. Paradoxically, despite its wide distribution and frequent presence in both natural and productive ecosystems, very little is known about its natural history. However, in recent years, Vanegas & Padrón (2022) and Martel *et al.* (2024) described the phoretic interaction of beetles from the genus *Antherophagus* with this bumble bee species in the Ecuadorian Andes. Individuals have been observed attached to bumble bees in the páramos of Azuay and Pichincha. Additionally, it was recorded that these beetles use the inflorescences of *Chuquiraga jussieui* as transfer stations to other bumble bees (Martel *et al.,* 2024).

Bombus handlirschi Friese, 1903
(Figs. 19–23)

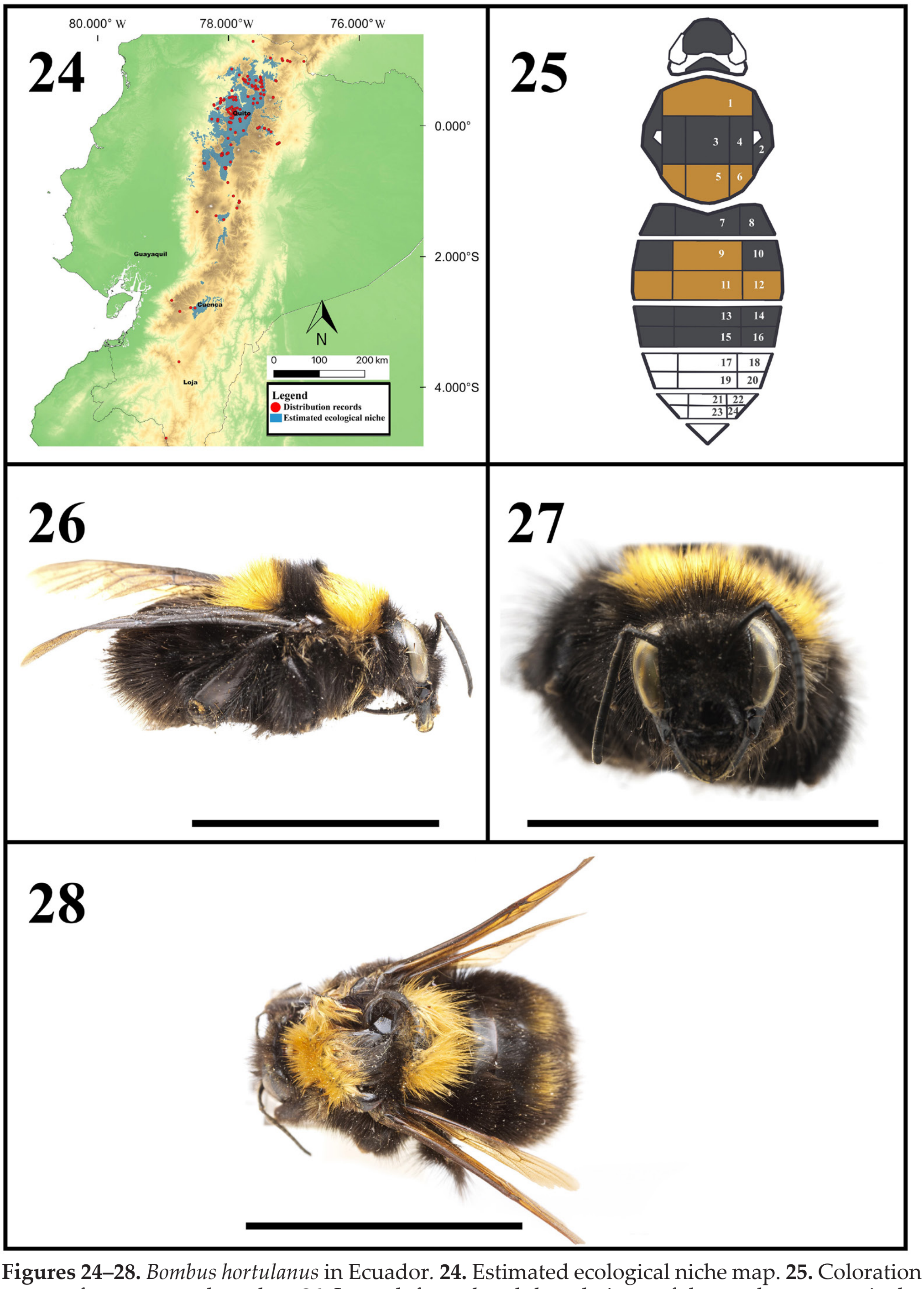
IDENTIFICATION: The pubescence is fine, dense, and even, except for longer hairs on the vertex, posterior mesoscutellum, and metasomal terga IV and V, with sparse hairs along the middle of terga I–V (Fig. 20). The head is brownish-black with fine, short orange-yellow intermixed on the face and pale reddish-orange on the occiput. The thorax is reddish-orange with black hairs intermixed, black predominating on the disc, especially between the wings, while the legs are mostly pale reddish-orange. The metasoma is reddish-orange, with faint brownish patches on terga II and III, terga IV–VI, and the sterna are somewhat paler. The wings are uniformly brown with a violaceous reflection under certain lights. Terga I–VI show varying shades of orange and orange-brown, with terga II and III being orange-brown and terga IV–VI orange (Fig. 20). Milliron (1973b) described the queen as larger than the workers, measuring approximately 27 mm in length. The head is trapezoidal, with noticeably larger, more rounded eyes, while the face bears short yellow and dark hair like those of the workers. The thorax is predominantly reddish orange with black areas, especially between the wings, but the pubescence is longer on the head and posterior metasoma than in workers. The legs are mainly reddish orange, with short, dense hair on the hind tibiae and tarsi (Fig. 22). The metasoma has diffused brown patches and a paler ventral surface. The wings are larger and uniformly dark, with a faint violaceous reflection. Although the queens of *B. handlirschi* and *B. rubicundus* share certain similarities, they can be distinguished by the coloration of the hairs along their hind tibiae: red in *B. handlirschi* (Fig. 22) and black in *B. rubicundus* (Fig. 44).

Distribution: It is distributed from Venezuela to Bolivia (Abrahamovich & Díaz 2002; Rasmussen 2003; Abrahamovich *et al.*, 2004). *Bombus handlirschi* has been reported for Ecuador by Abrahamovich & Díaz (2002), although this record is based on Milliron (1973b), who documented a worker from Ecuador without specifying the locality (only the year 1900). In this study, we report two specimens from the southern part of Ecuador, where it is uncommon and found in the high-altitude regions of the Andes 3,300 m (Fig. 19).



Figures 19–23. *Bombus handlirschi* Friese in Ecuador. **19.** Estimated ecological niche map. **20.** Coloration pattern, worker (left) and queen (right). **21.** Lateral view of the worker. **22.** Detail of the hind tibia of the queen. **23.** Dorsal view of the worker. Photos not to scale.

Bombus hortulanus Friese, 1904
(Figs. 24–28)



Figures 24–28. *Bombus hortulanus* in Ecuador. **24.** Estimated ecological niche map. **25.** Coloration pattern for queen and worker. **26.** Lateral, frontal and dorsal views of the worker, respectively. Scale line = 1 cm.

Identification: The dorsal thorax is light fulvous to golden-yellow (segments 1, 5, and 6), with a narrow, well-defined interalar black band (segments 2–4). Metasoma tergum I is basolaterally black, with the remainder yellow to entirely black; terga II and III range from yellow to black, often with pale distal hairs; terga IV and V are white; and tergum VI is black medially and white at the sides. Additionally, terga VII and VIII are black, tergum II includes yellow segments 9, 11, and 12, and black segment 10; tergum III is black, and terga IV–VI are white (Fig. 25). The wings are rather deeply infuscated with brown (Fig. 28). Although this species is similar in appearance to *B. robustus* (Figs. 35–38), it can be distinguished from this by the color of the first metasomal tergum. In *B. robustus*, this tergum is entirely yellow, whereas in *B. hortulanus* it always shows at least some black, providing a reliable feature for distinguishing the two species in the field (Fig. 26).

Distribution: It can be found in Venezuela, Colombia, and Ecuador (Milliron, 1973b). In Ecuador, it is in the middle and high parts of the Andes (Fig. 24), within an altitudinal range from 1,283 m to 4,253 m.

Host plants: 50 species belonging to 11 families (Table S3).

Natural history: It has been identified as an efficient pollen transporter of granadilla (*Passiflora*) (Cortés-Gómez *et al.,* 2023) in agricultural systems. In Colombia, Riveros *et al.* (2006) described the differences in foraging behavior of this species with others and found that *B. hortulanus* collected nectar by robbing through holes at the base of flowers, likely due to its shorter glossa and smaller body size. Its nest is unknown, but it has been observed in Colombia to potentially nest in areas with a low to moderate level of disturbance (Nates-Parra *et al.,* 2006).

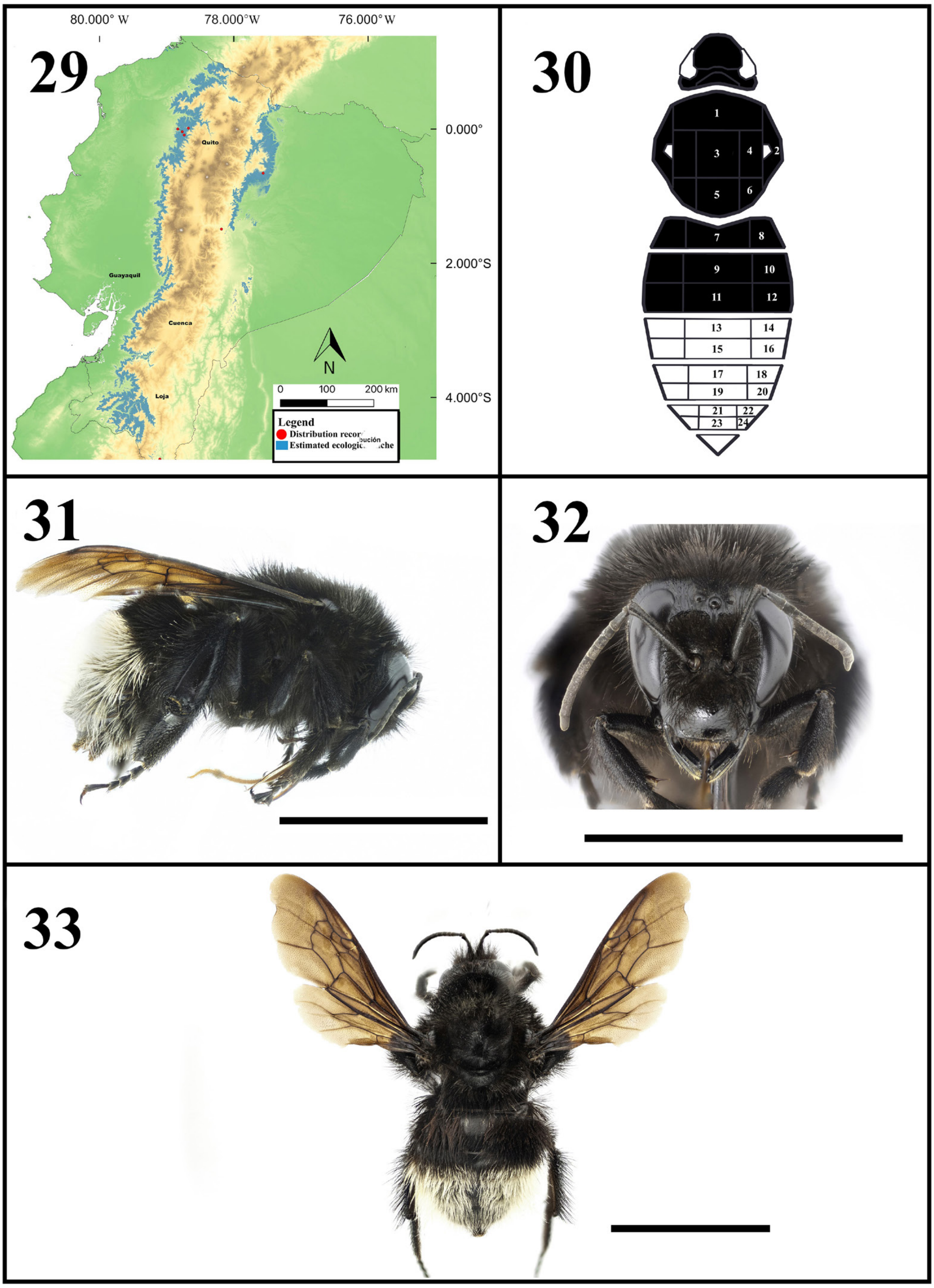
Bombus melaleucus Handlirsch, 1888
(Figs. 29–33)

Identification: Thorax is black, not intermixed with grey hairs, the metasoma, terga I and II are black, and terga I, III, V and VI are white (Fig. 30).

Distribution: It is distributed in Central America (Costa Rica and Panama) and South America in Venezuela, Colombia, Ecuador, and Peru (Abrahamovich & Díaz, 2002; Abrahamovich *et al.,* 2004). In Ecuador, it has been recorded in both the eastern and western foothills of the Andes at altitudes ranging from 1,132 m to 1,826 m (Fig. 29). The first author found a population of this species flying near Mindo (see below).

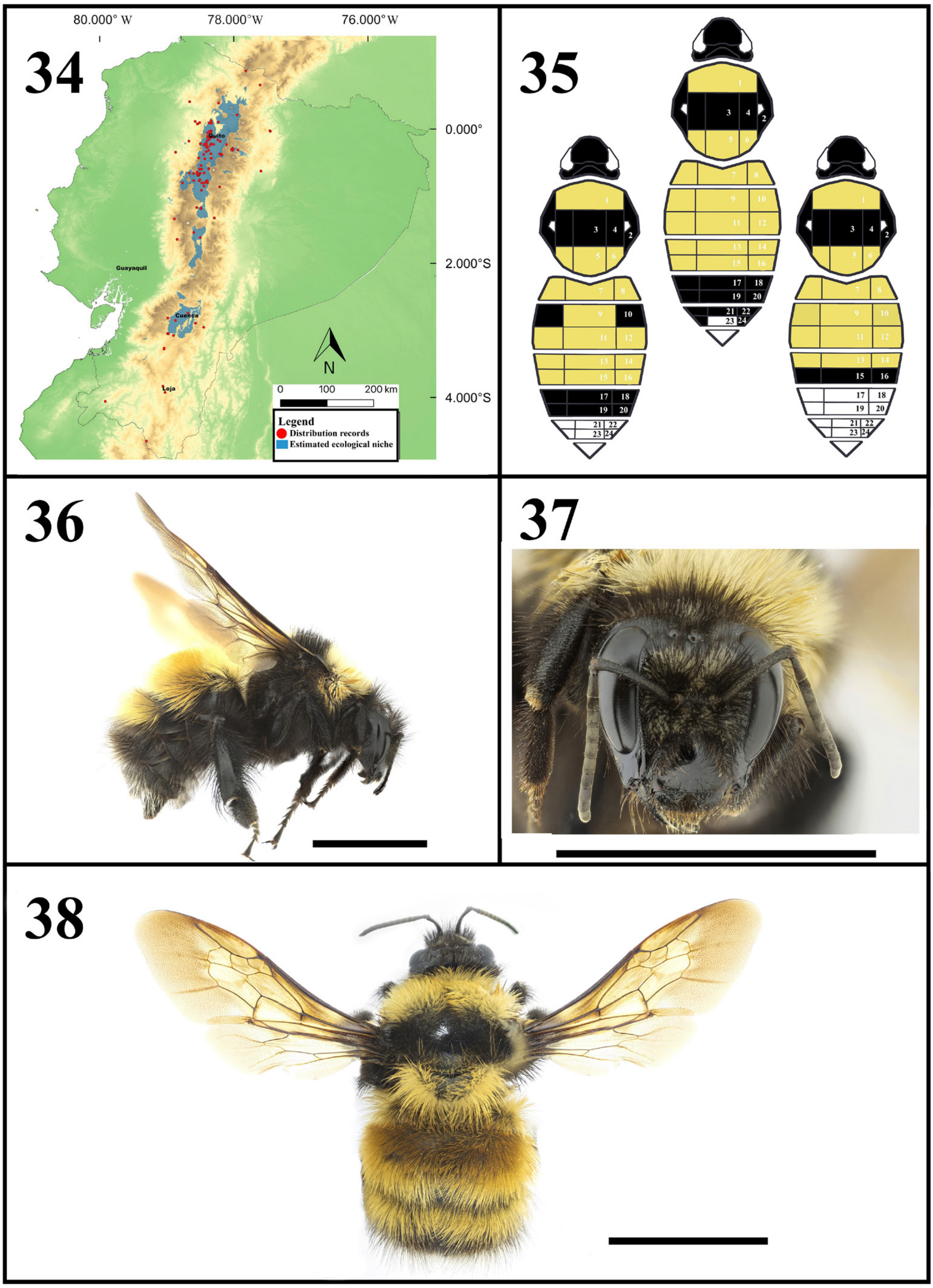
Host plants: One species belonging to one family (Table S3).

Natural history: *Bombus melaleucus* is generally an uncommon species in Ecuador, but in certain areas, it can be locally abundant. In the Mindo area of Pichincha, several individuals were observed along with other bees visiting the flowers of *T. diversifolia* (Asteraceae), which are known to produce toxic chemicals for bees, such as isochlorogenic acid (Liu *et al.,* 2015). This, coupled with concerns that this species may be endangered in Colombia as mentioned by Hoffmann *et al.* (2004) and Pinilla-Gallego *et al.* (2017), raises further issues. Little is known about its biology, though Hoffmann *et al.* (2004) described the nest, nesting biology, and colony development of *B. melaleucus* in Colombia.



Figures 29–33. *Bombus melaleucus* Friese in Ecuador. **29.** Estimated ecological niche map. **30.** Coloration pattern for queen and worker. **31.** Lateral view of the queen. **32, 33.** Frontal and dorsal views of the worker. Scale line = 1 cm.

Bombus robustus Smith, 1854
(Figs. 34–38)



Figures 34–38. *Bombus robustus* Smith in Ecuador. **34.** Estimated ecological niche map. **35.** Variable coloration pattern for queen and worker. **36–38.** Lateral, frontal and dorsal views of the queen, respectively. Scale line = 1 cm.

Identification: The dorsal thorax is yellow (segments 1, 5, and 6) with a moderately wide interalar black band, lateral black, and segments 2, 3, and 4 are black (Fig. 35). Metasoma can exhibit three variations in its color pattern. In the first variation, terga I–III are yellow, tergum IV is black, tergum V has segments 21, 22, and 24 as white, and segment 23 as black, and tergum VI is white (Fig. 35). In the second variation, terga I–III are yellow, tergum II has segments 9, 11, and 12 as yellow, and segment 10 as black; tergum IV is black, and terga V and VI are white (Fig. 35). In the third variation, terga I and II are yellow, tergum III has segments 13 and 14 as yellow, and segments 15 and 16 as black, while terga IV–VI are white (Fig. 35). Despite this variability, it can be separated from the similar-looking *B. hortulanus* (Figs. 25–28), its only known sympatric congener in Ecuador, by the coloration of tergum I: In *B. robustus* it is yellow while there is some black in *B. hortulanus*.

Distribution: *Bombus robustus* is restricted to the tropical Andes, specifically in the Andean regions, in countries such as Venezuela, Colombia, Ecuador, and Peru (Rasmussen, 2003; Abrahamovich *et al.*, 2004). In Ecuador, it is primarily distributed in the Andean region, occupying habitats between 1,400 and 4,000 m (Fig. 34).

Host plants: 51 species belonging to 11 families (Table S3).

Natural history: This species is primarily associated with páramo ecosystems, cloud forests, and other high-altitude areas, where it plays a key role in the pollination of numerous plant species. However, aspects related to its natural history remain unknown. During a fieldwork in the Azuay province, near Girón, at an altitude of 3,050 m, the first author recorded the presence of a *B. robustus* nest beneath a fallen *Eucalyptus* log in 2019. The presence of the nest was detected by observing several individuals foraging on a group of flowers from a shrub located approximately 10 m from the nest entrance. The nest was in a grassland surrounded by native vegetation. Upon approaching the site, several bumble bees were observed at the entrance, seemingly as guards. When the observation was made from about 3 m away, the individuals reacted defensively, emerging from the nest and exhibiting aggressive behavior. One of the specimens stung the observer's hand, prompting the retreat from the area.

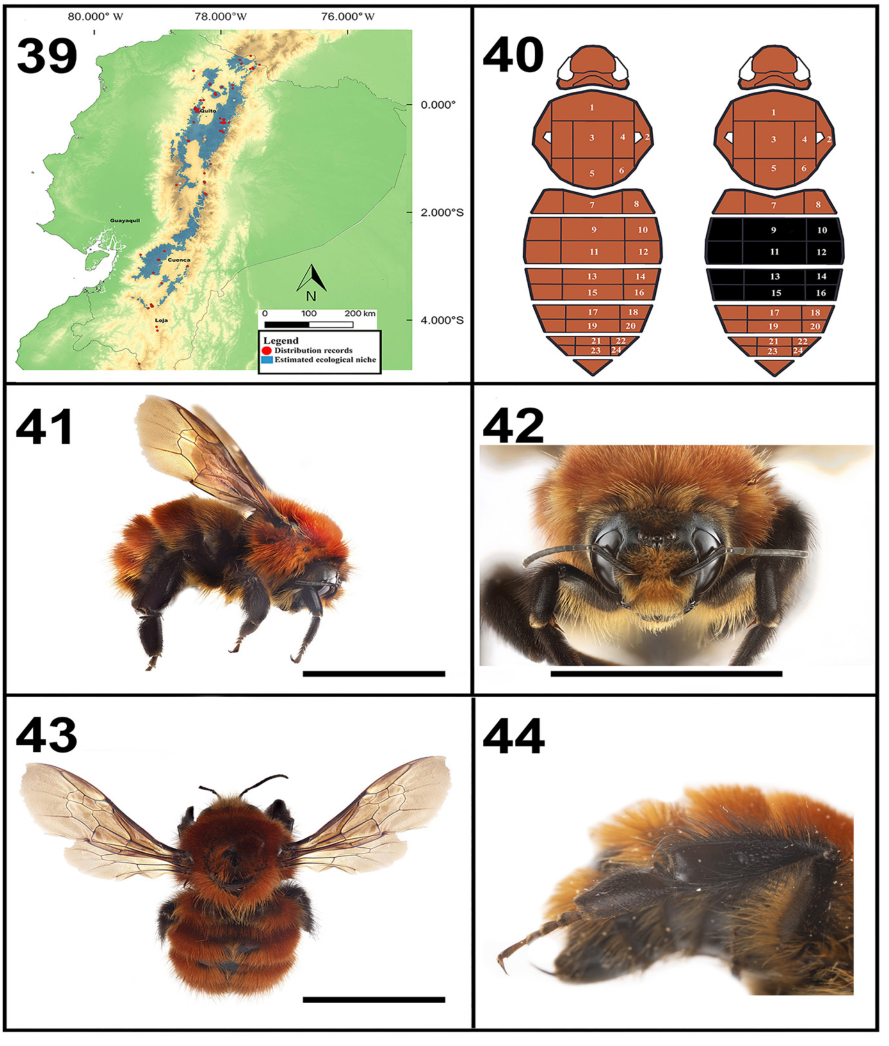
Bombus rubicundus Smith, 1854
(Figs. 39–44)

Identification: The pubescence is fine, dense, and uneven, with longer, looser hairs on the scutellum and metasoma terga IV and V. The female castes exhibit two color patterns: the queen is entirely reddish, while the workers have a red thorax, red tergum I, black terga II and III, and red terga IV and VI (Fig. 40). The head is pale reddish with little black (Fig. 42), the thorax and metasomal terga are coppery red, and the legs are black with a trace of reddish pile on the coxae and femora (Figs. 41, 42). The wings are uniformly stained with brownish-black (Fig. 43). Milliron (1973b), described the queen as larger than the workers, with a trapezoidal head and broadly rounded temples. The compound eyes are noticeably larger and more rounded than those of workers, and the face bears short yellow and dark hair like those seen in workers. The thorax is predominantly reddish-orange with black areas, particularly between the wings, and the pubescence on the head and posterior metasoma is longer than in workers. The legs are mainly reddish-orange, with short, dense hair on the hind-tibiae and hind-tarsi. The metasoma displays diffuse brown patches and a paler ventral surface, while the wings are large, uniformly dark, and show a faint violaceous reflection. It is important to note that queens of *B. rubicundus* and *B. handlirschi* look somewhat similar, but the hind tibiae are bordered with black hair in *B. rubicundus* (Fig. 44) and with red hair in *B. handlirschi* (Fig. 22).

Distribution: This species is distributed from Venezuela to Bolivia (Abrahamovich & Díaz, 2002; Rasmussen, 2003; Abrahamovich *et al.*, 2004). In Ecuador, along with *B. funebris*, *B. robustus*, *B. handlirschi*, and *B. hortulanus*, it is found among the bumble bee species present in the higher regions of the Andes (1,413–4,409 m), including páramo ecosystems (Fig. 39).

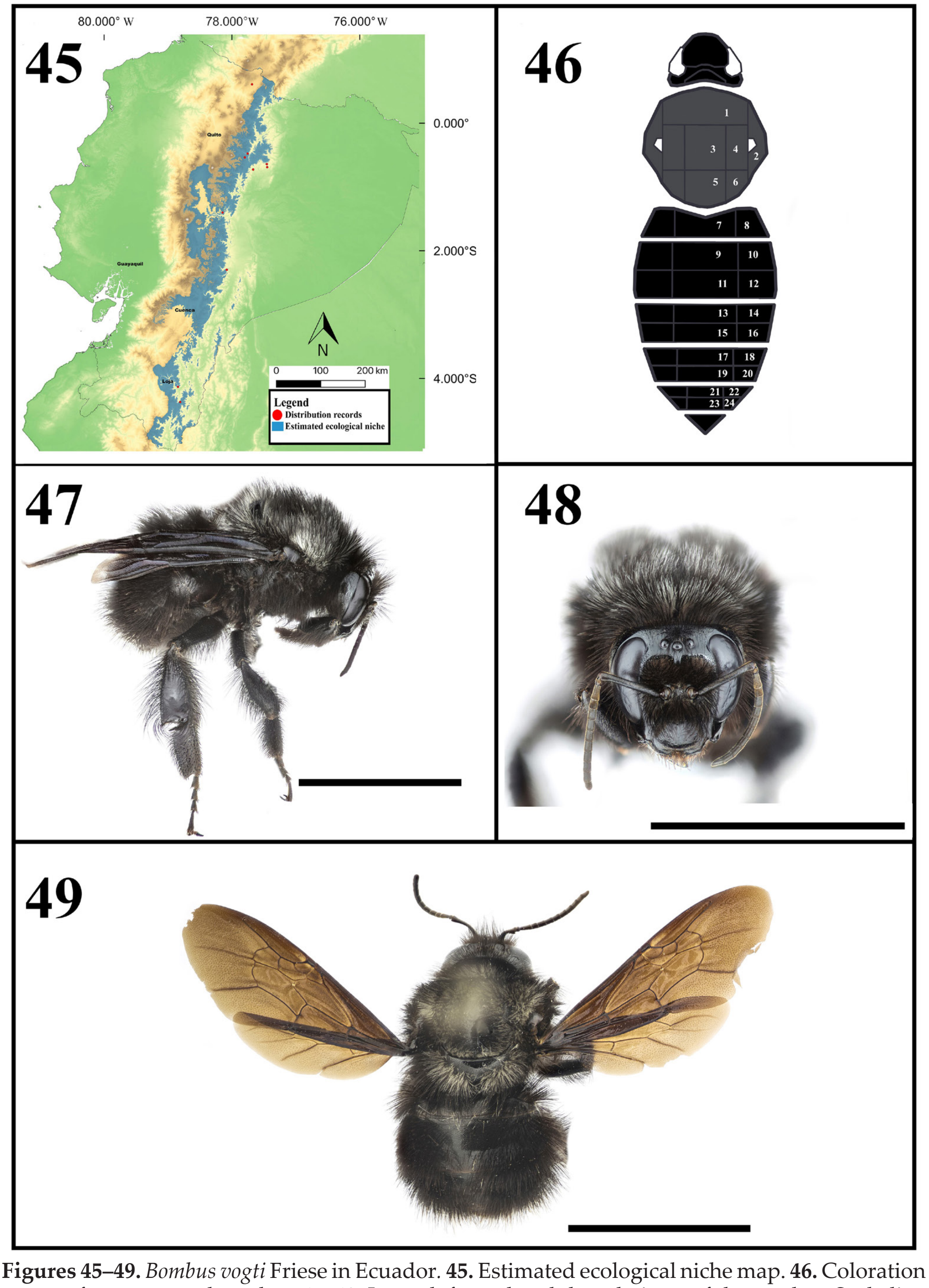
Host plants: 21 species belonging to 7 families (Table S3).

Natural history: Its nest has been described by Aguilar (2004) in Colombia. Riveros *et al.* (2006) described the differences in foraging behavior, they found that *B. rubicundus* engaged in nectar robbing, accessing nectaries through holes instead of pollinating the flowers. In recent years, a potential case of Batesian mimicry between this bumble bee and the fly *Mallota rubicunda* (Syrphidae) has been identified and quantified, finding a high level of external similarity between the two insects (PSP, in review). Also, in 2024, the first author observed several individuals entering a hole, possibly the entrance to a nest, which was located at the base of a tree. The soil around the entrance was covered in moss. This observation was made in a forest located in the Cajas National Park in Azuay at an elevation of 3,160 m.



Figures 39–44. *Bombus rubicundus* Smith in Ecuador. **39.** Estimated ecological niche map. **40.** Coloration pattern, queen (left) and worker (right). **41–44.** Lateral, frontal and dorsal views, and detail of the hind tibia of the queen. Scale line = 1 cm.

Bombus vogti Friese, 1903
(Figs. 45–49)



Figures 45–49. *Bombus vogti* Friese in Ecuador. **45.** Estimated ecological niche map. **46.** Coloration pattern for queen and worker. **47–49.** Lateral, frontal and dorsal views of the worker. Scale line = 1 cm

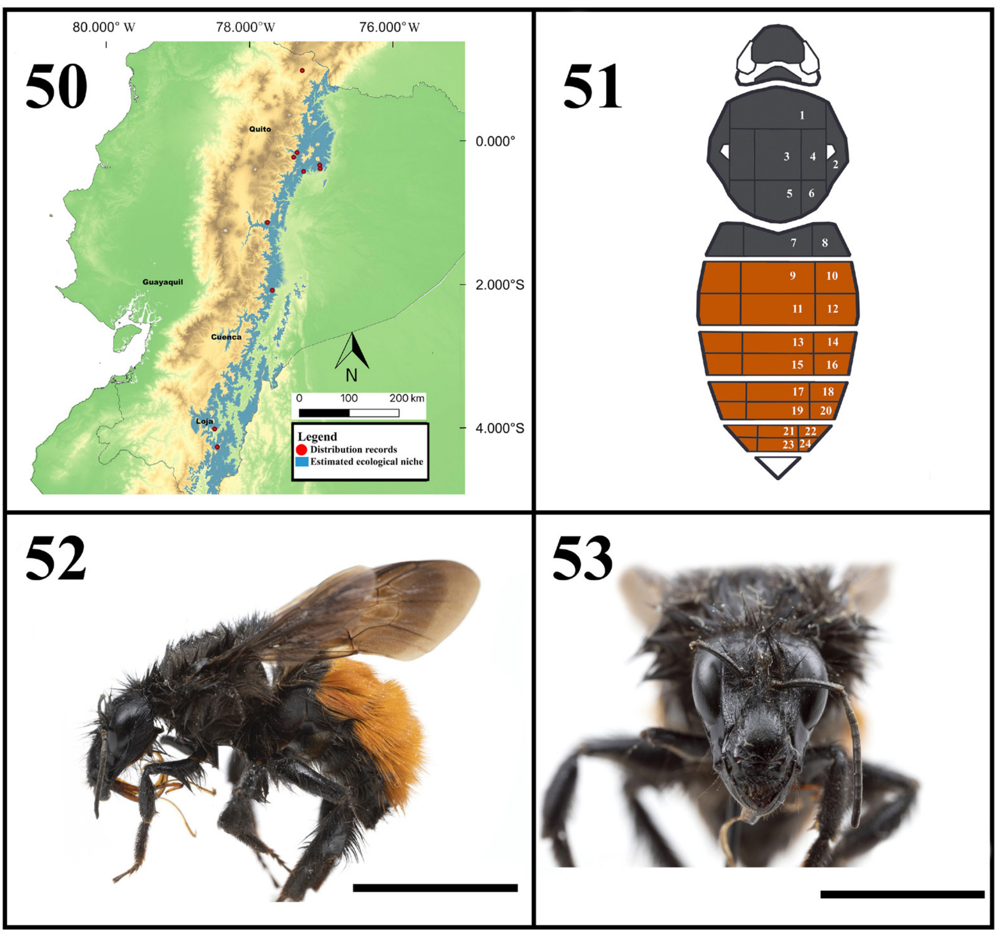
Identification: In our interpretation following Milliron (1973b), the thoracic pubescence is mostly short, even, and dense. The thorax is black with gray hair, and the metasoma is black, often with intermixed gray hair and occasionally even yellow hair (Figs. 46).

Distribution: It has been recorded in Ecuador, Peru, and Bolivia (Cockerell, 1912; Milliron, 1973b). Since its taxonomic status remains unclear, it has been treated in the past as *B. melaleucus* by Williams (1998) and followed by *e.g.*, Rasmussen (2003) and Abrahamovich *et al.* (2004). We here keep them separate to emphasize the knowledge gap in the taxonomy of certain species from the Andean region. In Ecuador, it has been recorded at elevations ranging from 1,724 to 3,414 m, primarily in the eastern foothills of the Andes (Fig. 45).

Host plants: One species belonging to one family (Table S3).

Subgenus *Bombus* (*Thoracobombus*)

Bombus excellens Smith, 1879
(Figs. 50–53)



Figures 50–53. *Bombus excellens* Smith in Ecuador. **50**. Estimated ecological niche map. **51.** Coloration pattern for queen and worker. **52, 53.** Lateral and frontal views of the queen. Scale line = 1 cm.

Identification: This species is characterized by a very elongated face with a long tongue and a notably long malar space (Fig. 53), much longer than the distance between the mandibular articulations. The thorax is completely black, sometimes appearing cinereous above, and bears elongated pubescence (Fig. 52). The metasoma is strikingly bicolored, with tergum I black, terga II–V (or VI) ferruginous (orange-red), and tergum VI black (Fig. 51). The wings are deeply infuscated with dark brown (Fig. 52). Queens, workers, and males are similar colored. Males differ from queens and workers mainly in head and antenna morphology, leg proportions, and pubescence. The male head is relatively narrower, with more strongly arched upper angles, closer-set ocelli, and a flatter vertical region. Overall pubescence is less dense and slightly shorter on the head, thorax, and metabasitarsal fringe compared to females.

Distribution: *Bombus excellens* is a species specialized in the primary tropical rainforests of the Andes, with a distribution range extending from Venezuela to Bolivia (Abrahamovich & Díaz, 2002; Rasmussen, 2003; Abrahamovich *et al.*, 2004). It is typically found at mid-altitudes of the Andes (Lievano *et al.*, 1991; Abrahamovich & Díaz, 2002). In Ecuador, it has been primarily recorded in the eastern foothills of the Andes between 1,267 to 3,300 m (Fig. 50). However, a specimen deposited at QCAZ indicates its collection in the city of Santo Domingo, at an altitude of 500 m, which we consider to be out of range and incorrect.

Host plants: Three species belonging to three families (Table S3).

Natural history: This species is rare within its distribution range and has been poorly documented in the field. According to Pinilla-Gallego *et al.* (2017), *B. excellens* may be endangered due to ongoing deforestation of its habitats. Recently, Hoffmann *et al.* (2024) described the first known nest of *B. excellens* in Norte de Santander, Colombia, at an altitude of 2,556 m. The nest was in a natural cavity formed among the roots of a tree, suggesting a preference for preexisting shelters for nesting. The worker bees foraged on a variety of plants, indicating a generalist diet within their ecosystem. The discovery and description of this nest provided valuable insight into its biology and highlights the need for further studies to assess its conservation status.

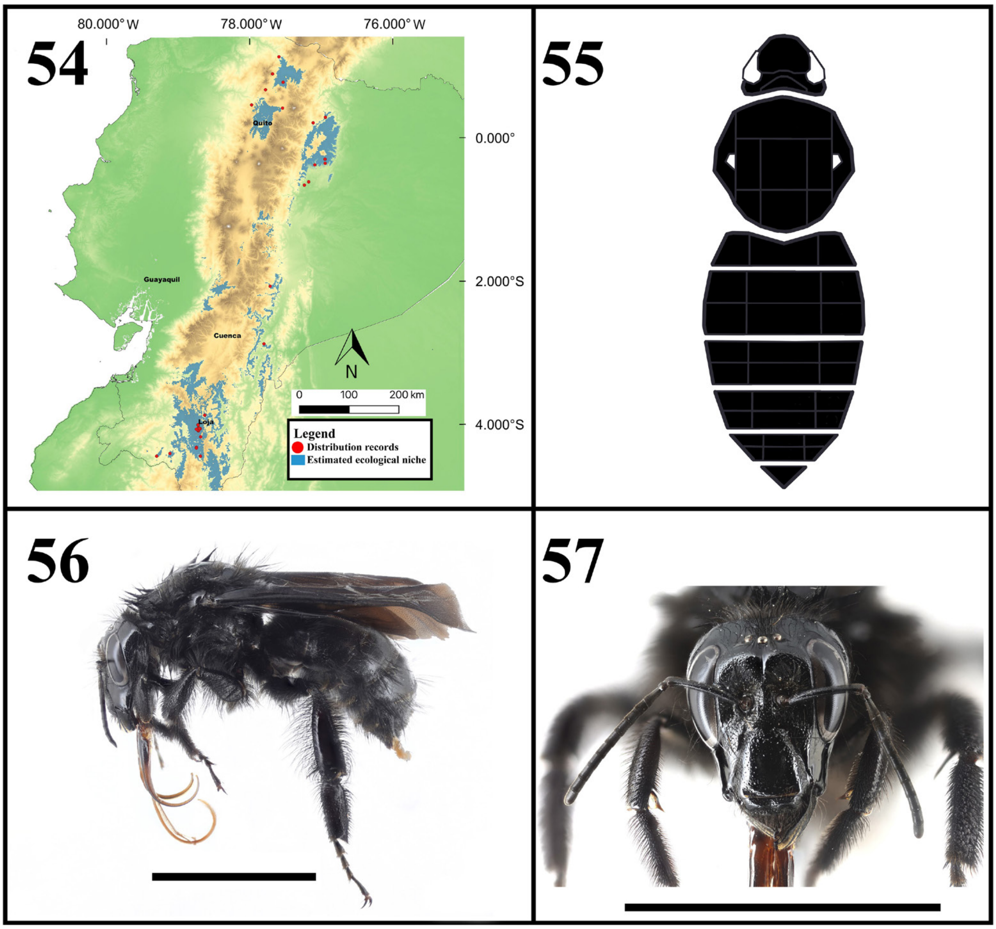
Bombus pauloensis Friese, 1913
(Figs. 54–57)

Identification: The species is in Ecuador entirely black with dark wings (Fig. 55). It can be distinguished from *B. morio* by most notably, a shorter malar space, and somewhat less violaceous wing reflections in females (Fig. 56). Elsewhere, in Colombia and eastern South America, this species frequently includes yellow bands, resembling *B. transversalis*. We have not yet confirmed this variation in Ecuador.

Distribution: It is distributed in Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, Uruguay, Paraguay, and Brazil (Abrahamovich *et al.*, 2004). In Ecuador, it is found in both eastern and western Andean slopes, where it has been recorded between 500 to 2,877 m (Fig. 54). *Bombus pauloensis* is also reported from the Guayaquil area (at least as the shipping port of the specimens), through the type localities of *Bombus cayennensis albidoanalis* Friese, 1931 and *Bombus cayennensis buchwaldi* Friese, 1931. If *B. pauloensis* truly occurs here, it would be in sympatry with *B. pullatus*. However, we note that the two species described by Friese (1931) do not represent typical forms of *B. pauloensis* from Ecuador: the first has yellow-white hairs on the thorax, and the latter has terga V and VI white. Milliron (1973a) referred to synonymies based on the main species, in Friese's interpretation, *B. pauloensis*, but we are not aware that these synonymies have ever been corroborated. Given this uncertainty, we do not record *B. pauloensis* as confirmed from Guyas (Guayaquil).

Host plants: Thirteen species belonging to four families (Table S3).

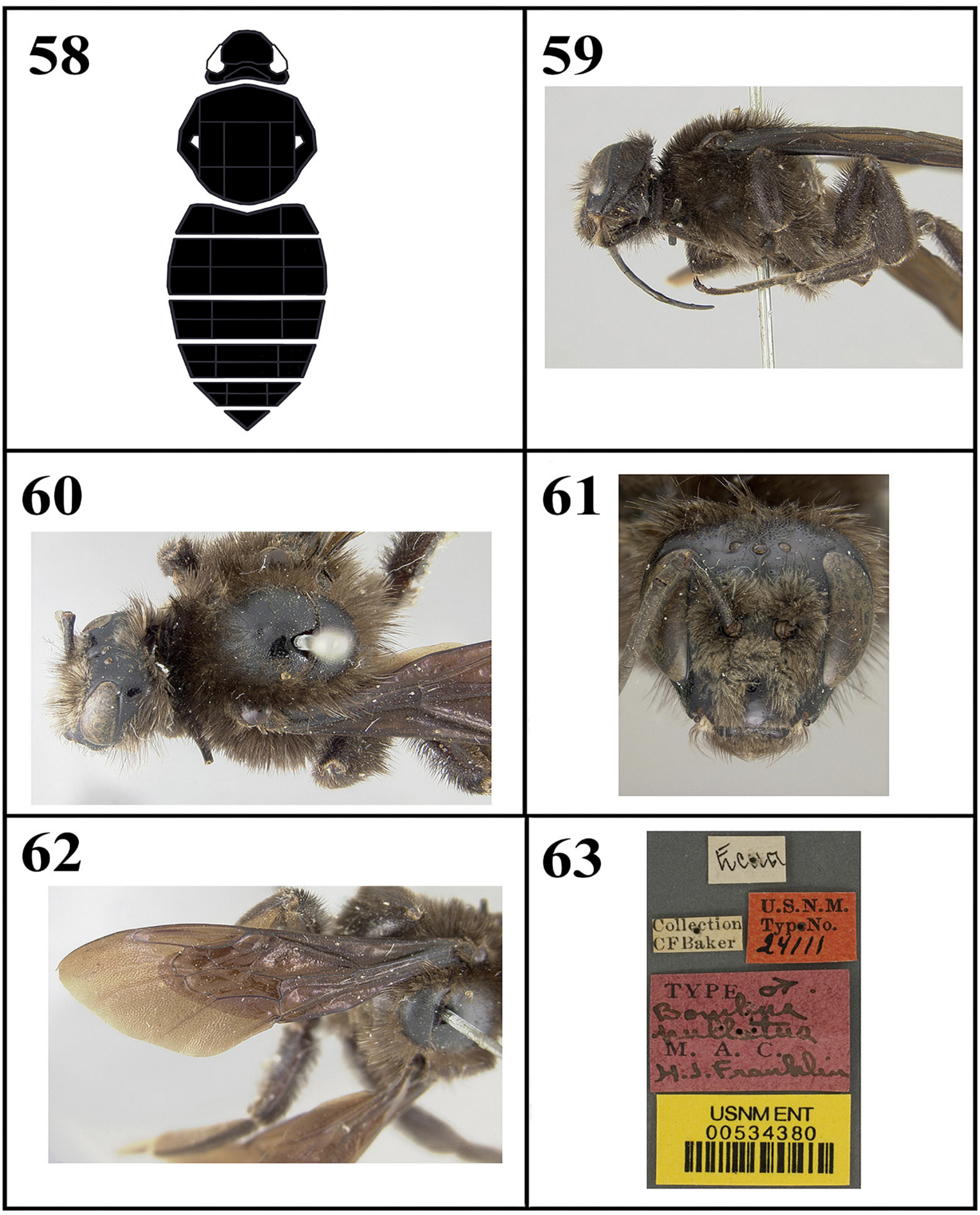
Natural history: *Bombus pauloensis* is perhaps the most studied bumble bee species reported here, and because of this, aspects of its natural history have been described.



Figures 54–57. *Bombus pauloensis* Friese in Ecuador. **54.** Estimated ecological niche map. **55.** Coloration pattern for queen and worker. **56, 57.** Lateral and frontal views of the queen. Scale line = 1 cm.

Many of the reports are published with the former name of *B. atratus*. Garófalo *et al.* (1986) studied the reproductive biology of this species, and later Garófalo (1995) made observations on the development of queen-less colonies under laboratory conditions, where the largest worker assumed the role of a false queen, mated, and produced female offspring. Subsequently, Gonzalez *et al.* (2004) described the nest of colonies in Colombia and Ecuador (Loja), providing data on nest architecture, offspring development, worker and guard behavior, seasonal cycles, and associated organisms, such as *Antherophagus* as a potential scavenger in the nests. Much research has been conducted on this species regarding its potential as a pollinator of commercially important cultivated plants (Aldana *et al.*, 2007; Riaño *et al.*, 2015; Báez *et al.*, 2020; Cavigliasso *et al.*, 2020; Salvarrey *et al.*, 2020; Alarcón *et al.*, 2022). This species has been bred in captivity (Salvarrey *et al.*, 2013). Riveros *et al.* (2006) described the differences in foraging behavior of three species of *Bombus* in Colombia and found that *B. pauloensis* was observed as a potential pollinator of *Digitalis purpurea*, using its long glossa and large body size to access the nectaries. Revainera *et al.* (2019) studied the association of phoretic mites on bumble bees, finding that the bumble bee caste was the most influential factor in the presence of mites and in the composition of the phoretic mite community. Also, Posada-Flórez & Téllez-Farfán (2021) reported the presence of several commensal, scavenger, and parasitic organisms, including *Antherophagus* beetles, in a nest of this species in Colombia. Finally, Fernandez de Landa *et al.* (2024) emphasized the importance of considering microbial dynamics in pollinator conservation strategies, highlighting the potential interactions between gut bacteria and pathogens in shaping bumble bee health.

Bombus pullatus Franklin, 1913
(Figs. 58–63)



Figures 58–63. Male holotype of *Bombus pullatus* Franklin (Photos from USNM https://collections.nmnh.si.edu/search/ento/). **58.** Coloration pattern. **59.** Lateral habitus. **60.** Dorsal habitus. **61.** Frontal view of the face. **62.** Wing detail. **63.** Detail of the holotype labels. Photos not to scale.

Identification: Workers looks similar to *B. pauloensis* (Figs. 58–62) in being an all-black and long-faced bumble bee (Figs. 67, 68). The presence of multiple black or melanic morphs of different species of *B.* (*Thoracobombus*) across Central and South America makes identification particularly challenging. While males can be reliably distinguished based on genitalia characters when dissected (Williams, 2025), queens and workers are not easily identified. Diagnostic features used to differentiate them from the all-black *B. pauloensis* includes a relatively sharp, rather than a smoother, acute, posterodistal angle of the metabasitarsus (Milliron, 1973a). This rather subtle character is best used in combination with other characters, such as the male genitalia, and sometimes it is helpful to note that in *B. pullatus*, the mesobasitarsus is app. 4x longer than wide (against 3x longer than wide in *B. pauloensis*), the clypeus is weakly convex, sloping laterally, and well punctate (against evenly convex, irregularly punctate, smoother mid-ventrally in *B. pauloensis*). The male type of *B. pullatus*, described from an unspecified locality in Ecuador, had its genitalia illustrated by Franklin (1913).

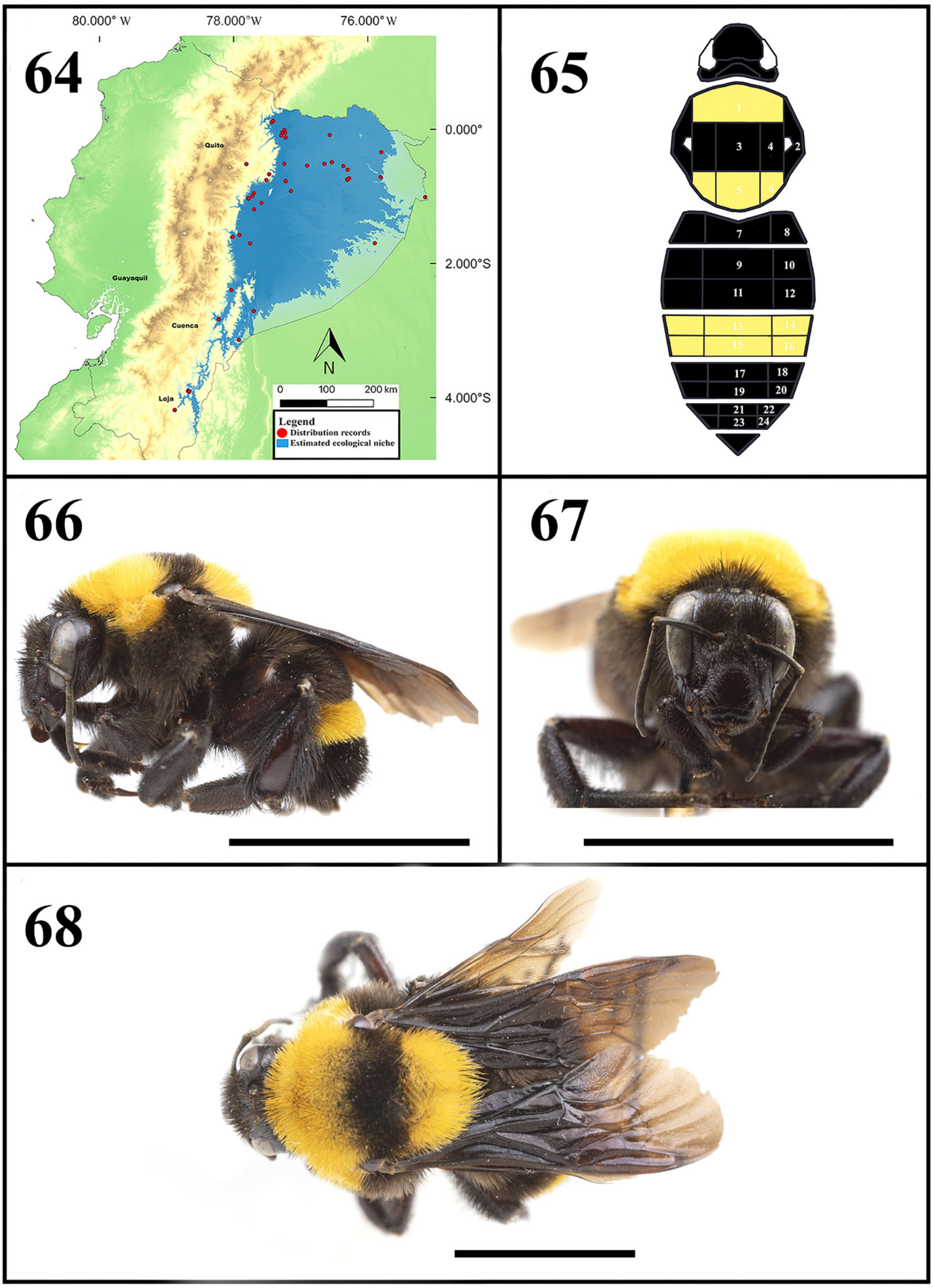
Distribution: The species is distributed from Central America to northeastern South American including Ecuador, Colombia, and Venezuela (Moure *et al.*, 2007). However, the southern limits are not well defined and might be due to the taxonomic confusion amongst the all-black bumble bees in the region (Williams, 2025). Franklin (1913) described *B. pullatus* from Ecuador based on an individual labelled "Ecuador" and "Coll. CFBaker" (Fig. 63). There is no further information about this individual which came from the Charles Fuller Baker [1872–1927] collection and must have been purchased or exchanged sometime before 1913. Baker collected from South America in both Colombia (H.H. Smith expedition) and Brazil (Pará), but we are unaware if he visited Ecuador, and if he did, to which region. We therefore assume this was received by Baker from another collector, before ending at UNSM. We have been unable to confirm any other records from Ecuador of the species and are uncertain whether the holotype specimen was mislabeled as being from Ecuador, or it simply represents an under-recorded species for the country. Milliron (1973a), also reported a specimen from the Guayaquil area, which would be congruent with a biogeographical region Central America to Chocó, such as what is known for some of the stingless bee species extending from Central America down to southwestern Ecuador (*e.g.*, *Partamona peckolti*, Camargo & Pedro, 2003). Further studies of all black bumble bees in Ecuador should confirm if the species is present in the country and if limited to the lower western parts only. Records on iNaturalist (211228059 and 191153350) suggest there are all black bumble bees in southwestern provinces Guayas and Manabi, but it is not possible to confirm if they are *B. pullatus* from the pictures.

Natural history: Studies on *B. pullatus* highlight its ecological and behavioral adaptations in tropical forests. Janzen (1971) documented arboreal nesting in Costa Rica. Later, Chavarría (1996) reported coexistence with leaf cutter ants *Acromyrmex octospinosus*, and Hines *et al.* (2007) described nest architecture, large perennial colonies, and foraging behavior. These findings show the species' social complexity and adaptation to humid tropical environments.

Bombus transversalis (Olivier, 1789)
(Figs. 64–68)

Identification: The thorax is golden-yellow (segments 1, 5, and 6), except for a narrow, well-defined interalar black band (segments 2–4) (Fig. 65). The metasoma has black terga I and II, IV, V, and VI, with tergum III in yellow ochre (Fig. 65, 66). The wings are black, with dull violaceous reflections under certain light (Fig. 68). The different castes (queen, worker, and male) all exhibit the same color pattern; they only vary in size and sex specific characters (male vs. worker/queen).

Distribution: The species is distributed across several South American countries, including Venezuela, Colombia, Ecuador, Peru, Bolivia, French Guiana, and Brazil (Abrahamovich *et al.*, 2004). In Ecuador, it is found exclusively on the eastern slopes



Figures 64–68. *Bombus transversalis* (Olivier) in Ecuador. **64.** Estimated ecological niche map. **65.** Coloration pattern for queen and worker. **66–68.** Lateral, frontal and dorsal views of the queen. Scale line = 1 cm.

of the Andes, within an altitudinal range between 180 and 1,242 m. This bumble bee species is characterized by being the lowest-elevation inhabitant within the genus *Bombus*, constituting a common component of the bee fauna in the lowland tropical areas of the Ecuadorian Amazon region (Fig. 64).

Host plants: Six species belonging to three families (Table S3).

Natural history: Several descriptions of the nests of *B. transversalis* exist (Dias, 1958; Olesen, 1989; Cameron *et al.*, 1999). One of them, conducted by Olesen (1989), details the behavior and structure of the nest in the Amazon of Ecuador. Cameron *et al.* (1999) described an interesting aspect of the natural history of this species in Peru: the use of a path constructed and maintained by the workers to access the nest. Later, Taylor & Cameron (2003) characterized nesting sites and nest architecture in Colombia, Brazil, Ecuador, and Peru. They also documented how the workers build the nests, modify the forest soil, and clean patches without leaf litter nearby. In 2001, Whitfield *et al*. described new species of parasitic wasps from the Braconidae family, which parasitize carrion moths from the Tineidae family (Lepidoptera) found in the nests of several colonies of *B. transversalis* in Colombia, Ecuador, and Peru. Finally, Dornhaus & Cameron (2003) documented a food alert mechanism used by this species as part of its recruitment behavior.

Overview of *Bombus* Species Potentially Occurring in Ecuador

Subgenus *Bombus* (*Cullumanobombus*)

Bombus coccineus Friese, 1903
(Figs. 69–70)

Identification: The pubescence is fine, dense, and shorter on the thoracic dorsum, with longer hairs elsewhere, except very short on Tergum VI. The thorax and metasomal tergum I are typically black, while terga II–IV are bright coppery red (sometimes tergum I is also red along the distal margin). Tergum V ranges from pale rufescent to whitish, and tergum VI is brown to black with pale rufescent to whitish at the sides. The wings are subhyaline or lightly infuscated with reddish-brown, with dark brown venation. The thorax is black, tergum I is black, terga II and III are red, tergum IV is reddish-white, and terga V and VI are white (Fig. 69).

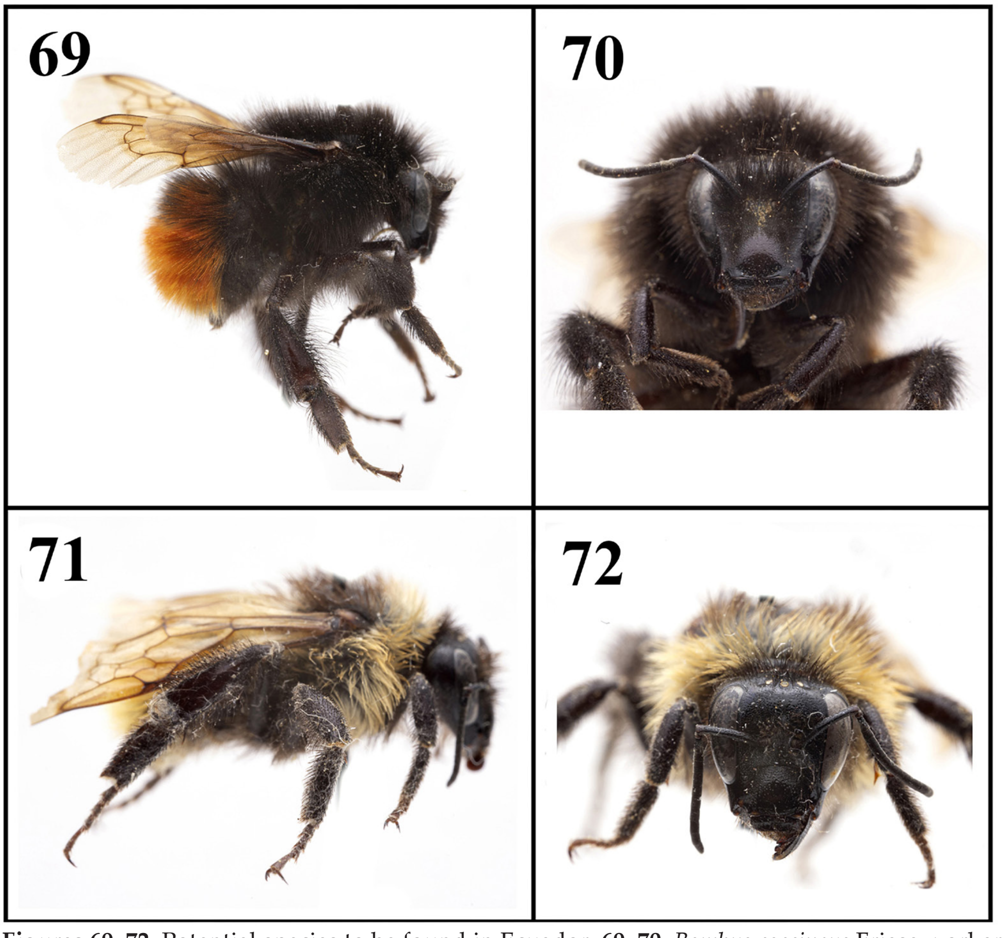
Distribution: Known only from Peru (Frison, 1925; Milliron, 1973a; Rasmussen, 2003). Abrahamovich & Díaz (2002) stated that the specimens reported from Ecuador by Milliron (1973a) are wrong, this is true for seven of the eight specimens he reported, as they originate from Peruvian localities in the departments of Cuzco, Junín, Pasco, and an unspecified department, rather than Ecuador. However, one specimen, with an unknown locality and no specific date, is labeled with the numbers 18177 and 96463 and is deposited at Secretaria de Agricultura, Departamento de Zoologia, Instituto Biológico, São Paulo, Brazil is reported from Ecuador. This could be a case of mislabeling and we will not confirm the presence in Ecuador based on this specimen which we did not examine.

Subgenus *Bombus* (*Thoracobombus*)

Bombus morio (Swederus, 1787)

Identification: The entire body is black, with the wings appearing black, exhibiting a violet reflection under certain lighting. Best distinguished by the other all-black bumble bees by the longer malar space compared to *B. pauloensis* and *B. pullatus.*

Distribution: Found in Venezuela, Colombia, Ecuador, Peru, Bolivia, Uruguay, Paraguay, and Argentina (Cockerell, 1912; Abrahamovich & Díaz, 2002; Rasmussen, 2003; Abrahamovich *et al.,* 2004). It has since been removed from the Peruvian checklist (CR, unpublished). In Ecuador, it was reported from the provinces of Pichincha and Tungurahua by Abrahamovich *et al.* (2004), possibly based on an assumption that *Bremus robustus curiosus* Frison, 1925, described from Baños, was a junior synonym of *B. morio*. However, the original description, Milliron (1973a), and Moure *et al*. (2025) suggest that it is rather a junior synonym of *B. vogti*. Therefore, we do not consider the real *B. morio* to be distributed in Ecuador or Peru.



Figures 69–72. Potential species to be found in Ecuador. **69, 70.** *Bombus coccineus* Friese worker from Peru in lateral and frontal views. **71, 72.** *Bombus opifex* Smith worker from Peru in lateral and frontal views. Photos not to scale.

Bombus opifex Smith, 1879
(Figs. 71–72)

Identification: The thorax is yellow, except for a rather wide interalar black band, which is typically more or less circular with a less definitive outline. The first three thoracic segments (1, 2, and 5) are yellow, while segments 3 and 4 are black. The metasomal terga I–III are yellow, while terga IV–VI are reddish. The wings are rather deeply infuscated with brown (Fig. 71).

Distribution: Species distributed in Peru, Bolivia, Argentina, and Paraguay (Abrahamovich & Diaz, 2002; Rasmussen, 2003). In Ecuador four specimens are reported by Milliron (1973a), one worker from "Esmeraldas, Ambato (XI-56, J.F., 2600 m [HEM]", three males one from "Esmeraldas: 1 Ambato, XI-XII-56, J.F., 2600 m" and two males from "Esmeraldas: Ambato, XII-56, J.F., 2600 m [all H. E. Milliron personal collection]. We have been unable to trace the specimens at the Canadian National Collection of Insects, Arachnids and Nematodes (S. Cardinal, pers. comm). We also note that the province name "Esmeraldas" is wrong and must be Tungurahua where the city of Ambato is found at an elevation of "2600 m". Esmeraldas is a lower elevation coastal area. Abrahamovich *et al.* (2004) already corrected the province to Tungurahua.

However, since these are the only known records of this species in Ecuador and the fact that the collector, "J.F." is identical with Juan Foerster (Kager, 1989), a German naturalist residing in Paraguay and later Argentina, with collecting trips to at least Bolivia, Ecuador, Colombia, and Uruguay, we suspect based on the biogeography that they are mislabeled individuals from his visits further south. Foerster collected multiple series of *B. opifex* from at least Bolivia (Milliron, 1973a). We therefore remove this species from the species list of Ecuador. This high-altitude species is not found in northern Peru, but rather in the southern Peruvian highlands, and it is therefore uncertain if it is even to be expected in Ecuador.

Natural history: Associations between *B. opifex* and flowers have been described in Argentina (Abrahamovich *et al.*, 2001). Revainera *et al.* (2019) described the association of phoretic mites with this species, finding that several species of mites can be found on the bodies of the bees, and that the mites have a strong preference for specific areas of the bumble bee's body.

Plants Visited by Bumble Bees in Ecuador

We purposefully recorded only original plant interactions observed in Ecuador. Additional floral records from within the range of the different species of *Bombus* can be found in Abrahamovich *et al.* (2001) and Rasmussen (2003). A total of 856 bumble bee visits to flowers were documented in Ecuador. From these observations, it was possible to identify that 10 bumble bee species visited a total of 143 plant species (from 1 to 63 different plant species) across 39 families (Table S3).

Bombus funebris visited 63 plant species from 24 families, with Asteraceae and Fabaceae being the most frequently visited. *Bombus robustus* was recorded visiting 51 plant species across 16 families, with Fabaceae, Asteraceae, Lamiaceae, and Solanaceae being the most visited. *Bombus hortulanus* visited 50 plant species in 19 families, primarily from Asteraceae, Fabaceae, and Lamiaceae. *Bombus rubicundus* visited 21 plant species in 10 families, with Asteraceae being the most frequently visited. *Bombus pauloensis* visited 13 plant species in 8 families, mainly from Fabaceae and Asteraceae. *Bombus transversalis* visited 6 plant species from 6 different families, with Verbenaceae being the most visited. *Bombus excellens* visited 3 plant species from 3 families, while *B. butteli* visited 2 plant species from 2 families. *Bombus melaleucus* and *B. vogti* each visited a single plant species from two different families. Among those plants visited were both native plants and introduced plants (Table S3). These results indicate a general preference for plant species in the Asteraceae and Fabaceae families. However, a considerable diversity of plant species from other families was also observed, highlighting the ability of *Bombus* species to visit a wide range of plant species in their environment.

DISCUSSION

This study provides an updated overview of the bumble bee diversity of Ecuador, including a revised species list, identification keys, potential distribution projections, and a catalog of visited plants. Our findings confirm the presence of 13 *Bombus* species in the country, positioning Ecuador as the third most diverse nation for bumble bees in the Neotropics, following Mexico (19 species) (Abrahamovich & Díaz, 2002), and Peru (14 species) (Rasmussen, 2003). Within South America, Ecuador ranks as the second most species-rich country, followed by Colombia with 9 species (Pinilla-Gallego *et al.*, 2017). While current records suggest that Ecuador's bumble bee diversity is well-documented, the possibility of new species records remains, particularly in the southern region and under-sampled areas such as the western foothills of the south, the Cóndor Mountain Range, and the Cutucú region. The original species records compiled in this study span 55 years and provide a valuable foundation for future research, offering essential tools for ecological studies, conservation planning, and policy development aimed at protecting these vital pollinators in Ecuador and beyond.

Unresolved Taxonomic Status

Although the species list presented here is the most accurate to date, it is evident that inconsistencies still exist in the taxonomy of certain species. The taxonomic status of several species reported remains unresolved. Potential synonymies among *B. ecuadorius* and *B. butteli*, *B. volucelloides* and *B. melaleucus*, and *B. robustus* and *B. vogti*, which have historically been treated as either distinct species or synonyms, warrant further investigation (Franklin, 1913; Williams, 1998). With the current information, few available specimens, and the use only of morphological characters, it is not possible to resolve these issues. What is needed is the incorporation of molecular markers, morphology, distribution, and biology across the range to enable a thorough revision of these species in the future. Additionally, it is important to recognize that some taxonomic inconsistencies within Ecuadorian bumble bees may stem from identification errors that cannot be resolved through morphology alone. Incorporating multigene datasets, together with detailed morphological, biogeographic, and biological information, will be essential for clarifying these taxonomic uncertainties and enabling a comprehensive revision in the future.

Citizen Science Data

Citizen science platforms, particularly iNaturalist, have become an increasingly important source of biodiversity information in Ecuador, with usage expanding rapidly in recent years (Páez-Vacas *et al.*, 2023). These records have already supported multiple entomological studies in the country (Vega *et al.*, 2021; Padrón *et al.*, 2023; Padrón, 2025), highlighting their value for documenting species distributions and ecological interactions, especially in studies focused on flower visitation by bees, including bumble bees, as recently demonstrated in Padrón (2025). However, as noted in other works (Hochmair *et al.*, 2020; Shirey *et al.*, 2021), the use of citizen-generated data requires careful validation, including the removal of dubious records and expert curation, procedures we applied in this study. Citizen-science datasets carry inherent biases: observations tend to cluster in densely populated or touristic areas, and species with more colorful or conspicuous phenotypes are overrepresented, a pattern also evident in our dataset. Despite these caveats, iNaturalist offers significant benefits for entomology (*cf.*, Callaghan *et al.*, 2022). It enables rapid accumulation of large datasets at minimal cost, facilitates the extraction of novel ecological interaction data (Gazdic & Groom, 2019), and can even quantify specific behaviors such as bee petal-cutting (Mead, 2023). Additionally, it supports ecosystem restoration planning by providing accessible plant-pollinator information (Bruninga-Socolar *et al.*, 2023). Given these strengths, continued promotion of insect observations, ideally capturing both pollinators and the flowers they visit, represents a valuable pathway for improving biodiversity knowledge in Ecuador.

Species Distribution

The elevational distribution of the *Bombus* species recorded in Ecuador (Fig. 73) corresponds well with knowledge from elsewhere. *Bombus transversalis* is a lowland rainforest species, whereas *B. pauloensis* occurs mostly in montane forests, extending into the higher lowland rainforest. Other montane species include *B. butteli*, *B. ecuadorius*, *B. excellens*, and *B. melaleucus*, while the remaining species extend from montane forest into, to varying degrees, the high Andean grasslands. *Bombus handlirschi* is only known from a few higher-elevation records in Ecuador, but in Peru it is primarily a montane cloud forest species (C.R. pers. obs.).

The distribution of bumble bee species in Ecuador is strongly influenced by the country's diverse topography of the Andes Mountain range which runs through the length of the country where all but one of the species are found. Notably, at least five

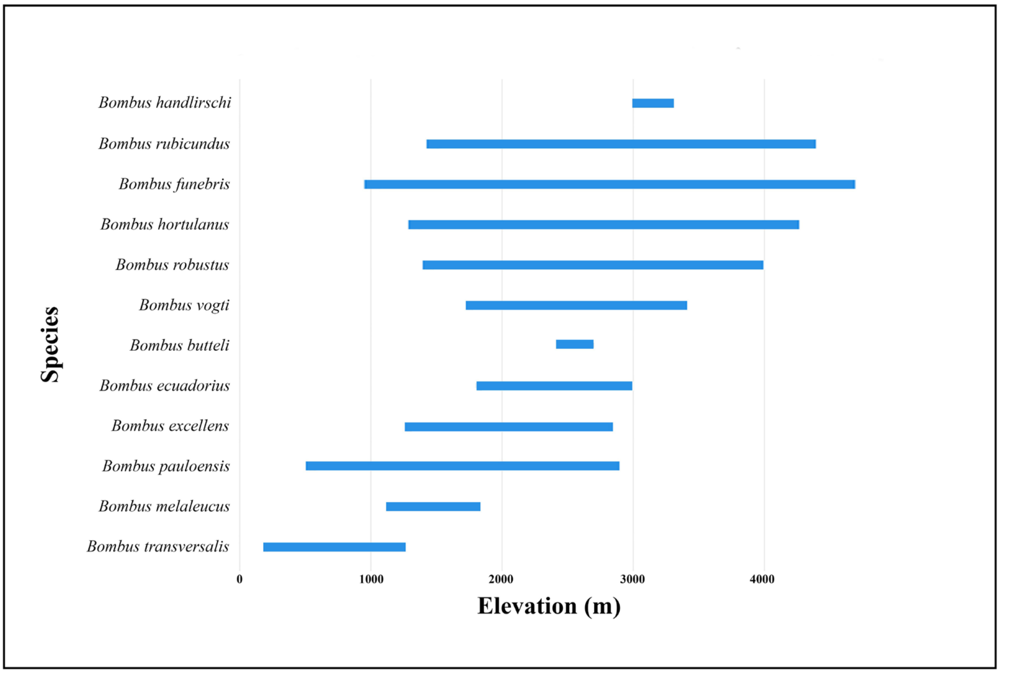


Figure 73. Elevational ranges of *Bombus* species in Ecuador. Species are distributed across lowland rainforest (~200–800 m), premontane or lower montane forest (~800–1,500 m), montane cloud forest (~1,500–2,800 m), high montane and elfin forest (~2,800–3,200 m), and, finally, the páramo and high Andean grasslands (~3,200–4,500 m).

species inhabit the páramo ecotone, highlighting the mutual importance of this high-altitude ecosystem and bumble bee diversity. In addition, some species extend their distribution into the eastern foothills, while fewer species are found in the western foothills, demonstrating a more limited presence in these areas. Interestingly, *B. transversalis* is the only species with a distribution in the lowlands of the Amazon, indicating that bumble bees in Ecuador also occupy tropical lowland ecosystems.

Our confirmed specimen data gathered from 1970 to 2025 spans over five decades and covers 16 out of the 24 provinces in Ecuador. These species have been recorded at a wide range of elevations, from as low as 180 meters to as high as 4,719 meters, reflecting the adaptability of bumble bees to varied environmental conditions across the country. However, there remain gaps in sampling, particularly in the southern and less-explored regions of the country, such as the western foothills of the southern Andes and the Cordillera Cóndor and Cutucú, which could hold unreported species. Ecological Niche Models (ENM) have demonstrated to be effective in estimating potential distribution areas for bumble bees in South America, as shown by Rojas-Arias *et al.* (2023) and performs well even with limited occurrence records (Elith *et al.*, 2006), which is particularly relevant for species in Ecuador represented by only a few observations (*i.e.*, seven records). Nevertheless, the interpretation of ENMs in Ecuador must be approached with caution. Species distribution modelling is inherently challenging, particularly in complex mountainous regions such as the Andes, where climatic layers are often interpolated from limited weather stations (Fernández *et al.*, 2013) and may not capture fine-scale environmental variability (Graham *et al.*, 2011). These uncertainties can influence model predictions, especially for species with few occurrence records or those restricted to narrow elevational bands (Jeliazkov *et al.*, 2022). Thus, the ENM-derived maps presented here should be viewed as informed approximations rather than definitive range limits, and future work incorporating higher-resolution climatic data and additional field surveys will be essential to refine these models and enable a more robust discussion of their implications.

Host Plants

The results of this study highlight the diversity of interactions between bumble bees and the plant species they visit in Ecuador. A marked preference for plants from the Asteraceae and Fabaceae families was identified, suggesting that these families may play a key role in the ecology of bumble bees as sources of nectar and pollen. However, the wide range of plant species visited indicates that bumble bees are generalist pollinators, capable of exploiting various floral resources in their environment. This generalist behavior may enhance their ecological resilience, allowing them to adapt to changes in floral resource availability due to seasonal fluctuations or habitat modifications.

Although a visit to a flower does not necessarily guarantee effective pollination, the high frequency of visits observed suggests that bumble bees play a likely important role in the reproduction of many of these plants. Previous studies have shown that frequent floral visits contribute to successful pollen transfer and seed set in various ecosystems (*e.g.*, Bueno *et al.*, 2023). Therefore, further research is needed to quantify pollination effectiveness across different *Bombus* species and plant taxa in Ecuador. This would provide valuable insights into the trophic interactions of different bumble bee species and their contributions to ecosystem stability.

It is also important to mention that, although the significance of native bees as key pollinators is well recognized, to our knowledge, this is the first preliminary list presenting interaction data for native bees in the country. This opens opportunities for future studies in which this list can be expanded and patterns in the use of floral resources can be analyzed. By incorporating additional observations from different regions and elevations, researchers could better understand how environmental variables influence pollinator-plant interactions.

One plant interaction pattern we were able to observe and compare across the *Bombus* species from Ecuador was their preference for native flora. Excluding species with no (*B. handlirschi, B. pullatus, B. ecuadorius*) or few host plant data (<10 plant species; *B. vogti*, *B. transversalis*, *B. excellens*, *B. melaleucus*), we identified three groups: those with less than 25% of total visits to introduced plants (*B. butteli*, *B. rubicundus*), those with 25–50% of visits (*B. funebris*, *B. pauloensis*), and finally those that visited introduced plants in more than 50% of their observed flower visits (*B. hortulanus*, *B. robustus*). Pollinators favoring non-native flora may provide these plants with a competitive advantage over native species and apparently both *B. butteli* and *B. rubicundus* are strongly favoring natural vegetation or areas with less anthropogenic impact.

Future studies should also explore the effects of anthropogenic pressures on bumble bee foraging behavior and pollination networks. Habitat loss, agricultural expansion, introduction, and expansion of non-native bee species competing for resources and pesticide use have been identified as major threats to tropical pollinators (Freitas *et al.,* 2009; Barbosa *et al.,* 2015; Toledo-Hernández *et al.,* 2022). Investigating how these factors impact *Bombus* populations in Ecuador could inform conservation strategies aimed at maintaining pollination services. Additionally, genetic studies on local bumble bee populations could provide insights into their adaptability and resilience to environmental changes. Overall, this study contributes to the growing body of knowledge on bumble bee-plant interactions in Ecuador, emphasizing the need for continued research and conservation efforts to preserve these important pollinators and their ecological functions.

What to study in the future about bumble bees in Ecuador?

Future research on bumble bees in Ecuador should focus on key aspects of their natural history and ecology, including nesting behavior, life cycles, and floral resource use across different ecosystems. Understanding their interactions with other pollinators and the potential competition for resources will provide valuable insights into their trophic interactions.

The study of pollination effectiveness among different *Bombus* species and their contribution to fruit and seed production in both native and cultivated plants is crucial for assessing their ecosystem function. Likewise, evaluating the effects of habitat loss on pollination networks will help predict potential cascading impacts on biodiversity. Anthropogenic disturbances, such as landscape homogenization, pesticide exposure, and habitat fragmentation, significantly influence bumble bee distribution, colony health, and long-term population viability. Investigating how these factors interact will be essential for developing conservation strategies. Moreover, the adaptation of bumble bees to urban environments and shifts in floral diet under changing conditions warrants further exploration.

Climate change poses additional challenges, as temperature and precipitation shifts may drive altitudinal or latitudinal range shifts. Understanding the resilience mechanisms of *Bombus* species to extreme climatic events will be fundamental for predicting their future distributions. From an evolutionary perspective, the role of mimicry in predator avoidance and the selective pressures shaping bumble bee coloration across different environments remain underexplored. Further research in this area could provide new insights into the evolutionary dynamics of these pollinators.

Finally, effective conservation and management strategies must be grounded in scientific evidence. Identifying key factors that promote bumble bee population stability, restoring critical habitats, and assessing the feasibility of even restoring populations in degraded areas will be essential steps toward their preservation.

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SUPPLEMENTAL MATERIAL

Appendix S1. Label data for specimens examined in museum collections.
Dataset S1. Geographic coordinates of records from INaturalist and observations by Sebastián Padrón.
Table S1. Bumble bees of Ecuador and their current taxonomic status.
Table S2. Environmental variables used in the study.
Table S3. Plant species visited by bumble bees in Ecuador.

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