

The Plant Family Ericaceae (“blueberries”) in Ecuador: Ecology, Diversity, Economic Importance, and Conservation

La familia de plantas Ericaceae (“mortiños”) en Ecuador: Ecología, Diversidad, Importancia económica y Conservación

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Abstract.- Species of the plant family Ericaceae found in Ecuador are generally discussed and characterized as to their diversity, economic importance, conservation, and ecology.

Key words: Andes, conservation, endemism, Neotropics, pollination

Resumen.- En el presente trabajo se discuten y caracterizan la diversidad, importancia económica, conservación y ecología de las especies de la familia de plantas Ericáceas de Ecuador.

Palabras clave: Andes, conservación, endemismo Neotrópico, polinización

Introduction

The plant family Ericaceae, locally known in Ecuador as “familia del mortiño”, is one of the key families of vascular plants in the threatened montane forest ecosystem of the Neotropics, where its diversification has been both recent and rapid (Churchill et al. 1995; Luteyn 2002, 2004; Kron & Luteyn 2005; Schwery et al. 2015). Many species are mycorrhizal and have large, showy flowers with colors in the red and orange range and are pollinated by hummingbirds; however, some species, and even entire genera, have rather inconspicuous flowers of muted colors more suitable for insect pollination (Naskrecki & Colwell 1998; Luteyn 2002). The fruits are mostly blue-black, juicy berries distributed by birds (Fig. 1); some berries are edible and have potential for commercial cultivation.

Taxonomy

In Ecuador, the Ericaceae are well represented with approximately 230 species, second only in the Neotropics to Colombia (with approx. 300 spp.)—131 Ecuadorean species (i.e., 57%) are endemic or nearly so (Luteyn 1996 and herein updated). Seventeen genera of Ericaceae in Ecuador have inferior ovaries (tribe Vaccinieae; approx. 82% of the overall species in Ecuador) characterized by berry fruits, the largest genera being *Ceratostema* (32 species), *Psammisia* (27 spp.), *Macleania* (22 spp.), *Cavendishia* (21 spp.), and *Disterigma* (23 spp.); Vaccinieae may be terrestrial or epiphytic in their habit. Four genera (approx. 18% of the species) have superior ovaries and capsular fruits, the largest being *Gaultheria* (16 spp.) and *Bejaria* (5 spp.); *Pernettya* has a berry fruit (see Luteyn 1985, 1995, 1996); all superior-ovary genera are terrestrial in habit. A full taxonomic description for the family and all Ecuadorean species has been provided by Luteyn (1996). For a color-photo field guide to the Ericaceae of Ecuador, see Luteyn 2006. It is felt that many new species are yet to be discovered, principally in the “Oriente”.

Ecology, Distribution, and Biogeography

General Ecology.—In Ecuador, species of Ericaceae are a conspicuous feature in montane cloud forests (between 1700–2500 m elevation), where the soils are well-drained, acidic, and high in organic matter, and where there is sufficient precipitation in the form of fog, mist, or rain; they are not found on the dry side of mountains. In their montane habitats, Ecuadorean Ericaceae are woody subshrubs 0.1–0.2 m tall, shrubs 1–3 m tall, or rarely trees to 10 m tall, and terrestrial or epiphytic in habit; some species are lianoid scramblers and at least one case of facultative hemiepiphytism has been documented in Ecuador (Zotz et al. 2021).



Figure 1. *Macleania* flowers and fruits. A) *M. pentaptera* flowers (Ecuador, Luteyn & Sylva S. 14719, NY); B) *M. pentaptera* fruits (Ecuador, Luteyn et al. 8026, NY); C) *M. rupestris* flowers (Ecuador, Luteyn et al. 14118, NY); D) *M. rupestris* fruits (Costa Rica, Luteyn s.n.). Photos: James L. Luteyn.

While most species are montane, some Ericaceae have adapted to the cooler, but not freezing temperatures of páramo landscapes (3200–4500 m) where they may be creeping subshrubs or even cushion plants. On the opposite side of the spectrum, a few other taxa are found in much warmer habitats as epiphytes in the Pacific-coast mangrove or as lianoid scramblers in lowland rainforests (Smith 1946; Benzing 1987; Luteyn & Sylva 1994; Luteyn 1999, 2002; Cornejo 2014). As epiphytes, Ericaceae usually grow in the crotches of larger branches of medium-aged to older trees, not on young twigs or young trees. They have a mutualistic relationship with mycorrhizae. They are anchored to the substrate and are aided in climbing by roots that arise from lignotubers or adventitious roots from moss-covered nodes in very moist sites. These epiphytes receive nutrients and absorb water from host-plant bark runoff or through their roots that penetrate the organic matter and detritus that accumulate around their roots (i.e., non-terrestrial sources). Their relatively large and thick leaves with thick cuticles store water, provide ample surface area to photosynthesize, and slow transpiration during dry and/or windy periods (see Jeník 1971; Gotsch et al. 2015). In low-light or closed-canopy forest situations Ericaceae, whether terrestrial or as epiphytes, can be scandent, and some species are characteristically lianoid scramblers (Luteyn & Pedraza-Peñalosa 2021). Populations within mature, montane cloud forest, however, are usually epiphytic, often with a few inflorescences and sometimes with large lignotubers for

storage. Under these low light intensity situations it is difficult for Ericaceae to photosynthesize enough to produce flowers—some may never flower, there not being enough energy reserves for both vegetative growth and flowering (pers. observ.).

In the open subpáramo to páramo regions, Ericaceae tend to be terrestrial, larger in size (or sometimes cushion plants in highly exposed habitats), and often clonal (e.g., *Macleania rupestris*, *Pernettya prostrata*, *Gaultheria* spp., *Vaccinium floribundum*), frequently containing large numbers of inflorescences and flowers. In these areas, several species in the genera *Gaultheria* and *Pernettya* are frequently found as pioneers following volcanic activity or recent landslides, as part of the edge community around mature forests, or in disturbed areas such as clearings after logging or road building, where humans have had great influence. Pioneering populations, however, eventually become overgrown and shaded by other plants, then light is limited and after many years they become weak competitors and do not flower. A particularly abundant species in the páramo, *Pernettya prostrata*, is resistant to trampling by cattle and is a successional species in heavily grazed areas. This species is especially common in páramo where the vegetation is low and open and persists after the vegetation recovers—fire does not affect it directly, but actually helps spread it indirectly because it opens the vegetation (Pels & Verweij 1992). *Macleania salapa* (Loja-N Peru), on the other hand, is fire-resistant due to its large lignotuber that sprouts new growth after fire destroys the main stems (pers. observ.).

Distribution and Biogeography.—The family Ericaceae is clearly Andean-centered and the Ecuadorean species have a close relationship with those of Colombia and Peru. Several species that occur in Ecuador are geographically widespread, such as *Cavendishia bracteata* (S Mexico to N Bolivia), *Macleania rupestris* (Costa Rica to N Bolivia), and *Sphyrospermum buxifolium* (Caribbean and S Mexico to N Bolivia). However, about 57% of the Ecuadorean species are endemics (or nearly so) with a narrow altitudinal range (Luteyn 2002). Centers of species diversity in Ecuador (based on numbers of species) include: **1**) the general northwestern slopes of the Andes (1700–2500 m elevation); **2**) eastern Andean “Oriente”, extending from Sucumbíos Prov. south into Peru (900–2500 m elev.); **3**) the southern Ecuadorean scrub vegetation (mostly Loja Prov. and into Peru); **4**) the high-Andean páramo (3000–3500 m) extending from Colombia throughout the “volcanic belt” of Ecuador; and **5**) the low-elevation, Pacific-facing “Chocó biogeographic region” that extends from the Colombia/Ecuador border in Carchi Prov. south into Pichincha Prov. (0–1000 m) (see Luteyn 2002).

Breeding Systems and Dispersal

In the Ecuadorean species of Ericaceae there is still a scarcity of information about reproductive systems, pollination biology, and plant/animal interactions; many questions lack hard data and thus remain unanswered.

Asexual Reproduction.—Asexual or vegetative reproduction within Ericaceae in cloud forest, páramo, and boggy habitats, is often accomplished by means of rhizomes or stolons (see Laegaard 1992) and can form large clones and extensive colonies, especially in species such as *Pernettya prostrata*, *Disterigma empetrifolium*, and *Macleania rupestris*, among others. Some species of *Ceratostema* and *Macleania* have lignotubers within which there are meristematic zones—these taxa sprout easily after cutting or fire damage (Luteyn 2002). *Macleania rupestris* is also facultatively lignotuber-producing, probably depending on where the seeds initially land (Sierra & Mora-Osejo 1994).

Sexual Reproduction.—The flowers of the vast majority of Ericaceae have both staminate and pistillate parts (i.e., flowers perfect), although Sleumer (1952, 1985) reported dioecism for *Pernettya howellii* (endemic to the Galápagos Islands) and Middleton (1991) reported gynodioecism for *Pernettya prostrata* from Ecuador. Their pollen is already mature and sometimes shed within the bud. Slight tapping of the pendent or horizontally oriented flowers often produces a shower of pollen onto the stigma. The stigma appears receptive quite soon after flowers open, as evidenced by the appearance of a small viscid droplet on the stigma. Although most Ecuadorean Ericaceae pollination syndromes point toward cross-pollination, species such as *Bejaria resinosa*, *Pernettya prostrata*, and several *Gaultheria* are self-compatible

(Melampy 1987; Luteyn 1995; Kraemer 2001). The fact that several high-elevation species with high flower densities, such as *Pernettya prostrata*, *Gaultheria* spp., *Cavendishia bracteata*, *Macleania rupestris*, and *Thibaudia floribunda*, always produce abundant fruit leads me to hypothesize that some species are facultatively self-compatible (Luteyn 2002, but see also Baker 1974; Jacquemart 2003; Chamorro & Nates-Parra 2015). In fact, in environments where pollinators are more scarce (disturbed/regenerating areas) or in cold/wet páramos, species such as *Macleania rupestris* may benefit by having the option of multiple reproductive strategies (Navarro et al. 2007). In Ecuador I suspect that the small white flowers of *Vaccinium floribundum*, *Disterigma* spp., *Pernettya prostrata*, and *Gaultheria* spp., are self-compatible and most likely pollinated by European honeybees (*Apis mellifera*). However, the study of Navarro et al. (2007) showed that the Ecuadorean *Disterigma stereophyllum*, with small white flowers, has a mixed pollination syndrome, i.e., it prefers hummingbird pollination (outcrossing) and also profits from small bee visitors, but still maintains the option of autonomous self-pollination. Although no data are available concerning compatibility in the majority of Ecuadorean species of Ericaceae, Luteyn (2002) predicted and Navarro (1999, 2001) and Navarro et al. (2007, 2008) proved self-compatibility in *Macleania bullata*, *Macleania rupestris*, and *Disterigma stereophyllum*. Navarro (2001) stated that in *Macleania bullata* pollinator visits are required for reproduction.

In Ecuadorean Ericaceae, most plants depend on animals for pollination and seed dispersal with rewards of nectar, pollen and/or nutritious fruit. The long-tubular corollas of many Ecuadorean Ericaceae (tribe Vaccinieae) contain a large volume of high energy nectar that provides that reward and also helps to guard the nectar from non-pollinators. The red to orange colors of many Ericaceae flowers also provide a visual and/or contrasting display against the foliage for the birds and at the same time act again as a nectar guard since these floral colors are relatively invisible to insects (Raven 1972; Heinrich 1981). Ericaceae flowers obligately pollinated by hummingbirds may also support a variety of non-pollinating nectar-eating organisms including various “nectar robbers” such as birds, bees, ants, butterflies, mites, bats, bacteria, protozoans, and yeasts (see also Colwell 1973). However, organisms other than birds probably only rarely contact the reproductive parts of the flowers and although they may carry pollen between flowers, the quantities must be very small, so in effect, they do not add much as pollinators. Flowers of Ecuadorean species of Ericaceae are of major importance to birds in montane regions, not only as pollinators but as fruit dispersers. “If one considers numbers of flowers, ... the Ericaceae is easily the most important family...” (Stiles 1985). Parada-Quintero et al. (2012) stated that “Shrubs and species of Ericaceae were the most important elements ... throughout the year” [in central Colombia]. Ecuadorean species of Ericaceae display the floral traits commonly associated with plants adapted for pollination by hummingbirds, i.e., bird-pollination or “ornithophily” (Table 1).

Dispersal.— Nearly all Ecuadorean Ericaceae attract animal dispersers, especially birds, by means of certain fruit characters, i.e., a bird dispersal syndrome or strategy (see Table 2 and also Snow 1971; van der Pijl 1972; Denslow & Moermond 1985). Normally, Ecuadorean Ericaceae display large numbers of small, brightly-colored, fleshy, high carbohydrate/low lipid, accessible fruits with numerous, small seeds and a high pulp vs. seed ratio (i.e., nutrition). Vaccinieae especially are of great importance as sources of food for opportunists (herein defined as animals that take advantage of whatever food is available at any given time) with their brightly-colored flowers (pendant for hummingbird foraging and pollination) and many-seeded berry fruits (presented erect for foraging and dispersing frugivores), and they meet most of the fruit criteria for ornithochory listed in Table 2 [*Psammisia* fruits are the only exception known, having a green, tough outer pericarp and dry inner pulp (pers. observ.)].

Seed dispersal in Ecuadorean Vaccinieae is primarily of two types—autochory and zoochory. Autochory is the mechanism in which plants carry out dispersal of fruits and seeds by themselves, which occurs when, after falling to the ground, the sticky (viscous) mucilaginous sheath that encloses the seeds attaches them to the ground, where they cannot move any further—it is present in several species of *Macleania*. The second type of dispersal in Ericaceae is called zoochory of which dispersal via ingestion (endozoochory) followed by regurgitation or defecation is the most frequent type. In Ecuador, I have also observed ant-mediated seed

Table 1. Characters of ornithophily in Ericaceae seen as adaptations for hummingbird pollination (modified from Proctor & Yeo 1973; Faegri & van der Pijl 1979; Luteyn & Sylva 1999).

—cool, moist, montane habitats; sun-loving terrestrial and epiphytic lifestyles
—inflorescences with numerous hanging flowers exhibiting negative angles with respect to the horizontal, facing outward, often opening for a long time; held away from the rest of the plant to ease access by hoverers
—flowers odorless
—flowers often with presence of “parrot colors,” i.e., brightly colored, often in the red and orange range, often with contrasting colors in different parts of the inflorescence
—corolla thick in texture, long, narrow, tubular with a constricted throat and a slightly flaring mouth, but without a lip on which insects can land
—style usually equaling corolla length with receptive stigma and pollen load located at the mouth of the corolla tube so that the bird must come into contact with each when foraging
—anthers rigid, attached to the outside of the nectariferous disk, forming a tunnel leading to the nectar source; dehiscence introrse
—pollen located at bottom of long, tubular-adorned anthers, the theca of which are granular and need to be moved to effect pollen discharge; pollen dry, loose
—ovary inferior, the numerous ovules mechanically protected by and separated from the nectar source
—nectariferous disc located at base of corolla, fleshy
—nectar abundant, diluted, rich in sucrose with average sucrose equivalence 20.4% and highsucrose:hexose ratio

dispersal—myrmecochory—in *Cavendishia lebroniae*, where numerous small, black ants cleaned the seeds of their juicy pulp and then transported the seeds into the undergrowth—I presume to their nests. Ants do this to make “stores” or “caches” for feeding of the young, or possibly for their ant gardens; theoretically, any uneaten seeds would germinate some distance away from the parent plant. Within the superior-ovary genera such as *Gaultheria* and *Pernettya* seed dispersal is similar to the Vaccinieae (pers. observ.).

Interactions with Animals

In the following paragraphs I discuss avian and non-avian animal species that interact in some way with species of Ecuadorean Ericaceae.

Birds.—In Ecuador, hummingbirds are the most frequent pollinators of Ericaceae species with colorful (red to orange), long-tubular flowers, including tubular species of the superior-ovary genus *Bejaria* (Melampy 1987; Navarro 1999, 2001; Luteyn 2002 and pers. observ.; Navarro et al. 2007, 2008, but see also Kraemer 2001). Hummingbirds hover continuously while searching for food. They are guided to the nectar at the base of the flowers by the narrow, tubular corolla with constricted throats, where they drink nectar as a food source and in so doing touch the stamens dislodging pollen and causing it to fall downward onto the hummingbird’s body onto surfaces that brush against the stigmas as the bird probes for nectar. The pollen is then physically transported to the next flower to be visited effecting pollination (Table 2).

Birds are also the most common nectar-robbers of Ericaceae. Nectar-robbing birds or flowerpiercers (“pinchaflores,” “robamieles,” “robadores de néctar”) are not adapted to the elongated flower morphology of many Vaccinieae. Therefore, legitimate nectar-robbers pierce floral tissues near the base of the corolla to extract nectar. Illegitimate nectar-robbers, also called thieves (e.g., ants, mites), obtain nectar after entering the flower through prior-made holes or through the same natural openings used by legitimate pollinators. Thus, in so doing, both types of robbers generally circumvent the anthers and stigma, i.e., they remove floral resources without pollinating (Inouye 1980, 1983; Bronstein et al. 2006; Torres et al. 2008; Irwin et al. 2010). In Navarro et al.’s (2007, 2008) study of *Disterigma stereophyllum*, they found that “when the robber [*Diglossa albilatera*] forcefully shook the flower, this caused some release of pollen from the poricidal anthers, most of which fell to the ground, but some adhered to stigmas within the

Table 2. Adaptive ornithochorous characters seen in the plants and fruits of Ericaceae (including modifications from Snow 1971, van der Pijl 1972, and Denslow & Moermond 1985).

—“in secondary or open vegetation fruits with many small seeds are the rule, since a premium is set on efficient dispersal to take advantage of the many spaces available” (Snow 1971)
—plant with most abundant, accessible, and attractive fruits have selective advantage
—high visibility due to contrasting colors of fruit (often red, orange, white, blue/black) with accessory structures (red pedicels) and surrounding vegetation
—“ripeness signaled by change in color, carbohydrate content, and succulence” (Denslow & Moermond 1985)
—absence of a hard outer cover (i.e., no closed or hard rind)
—no smell (“birds have only a weak sense of smell, or none at all, and are purely visual animals” (van der Pijl 1972)
—fleshy, nutrient-rich, edible pulp
—small sizes of fruits and seeds
—outer protection against being eaten prematurely (acids or tannins present in the immature fruit)
—inner protection of the seed against damage in digestive tract (bitterness, hardness, presence of toxic compounds)
—semi-permanent attachment to pedicel until physical removal by frugivore
—occupy no special position on the plant (ex., not on long-pendent peduncles)

pierced flowers.” Nectar robbing is common in neotropical Ericaceae and Rojas-Nossa et al. (2016, in Colombia) also found nectar robbing in the Ecuadorean species *Bejaria resinosa*, *Cavendishia bracteata*, *Gaultheria erecta*, *G. lanigera*, *Gaylussacia buxifolia*, *Macleania rupestris*, *Pernettya prostrata*, *Thibaudia floribunda*, and *Vaccinium floribundum*.

Birds and to a much lesser extent mammals that eat fruits (i.e., frugivores) are the most important seed dispersers of Ericaceae. It is the pulp of the fruits that is normally eaten and digested by these frugivores. Seeds are generally regurgitated or defecated soon after being eaten, but remain viable and their germination rate may increase or decrease by passage through the digestive tract of the disperser (see for example, Traveset 1998; Herrera 2002; Ortiz & Umba 2010; Luteyn pers. observ.).

Bees.—In Ecuadorean Ericaceae, European honeybees (“abejas”) act as the primary pollinators of short-tubular or urceolate, white-flower species of the genera *Gaultheria*, *Pernettya*, *Agarista*, and *Vaccinium*; whereas, large bees (*Bombus*) are common pollinators of the long-tubular, red-flowered species of *Bejaria* (Clemants 1995; Melampy 1987; Navarro et al. 2007, 2008; Luteyn pers. observ., but see also Freitas et al. 2006). In the long-tubular flowers of the inferior-ovary Vaccinieae, bumblebees (*Bombus* spp.) along with carpenter bees, wasps, and ants commonly act as nectar-robbers; whether pollinators or nectar-robbers bees are usually foraging for nectar not pollen (Inouye 1983; Heinrich 1983; Irwin et al. 2010). Instead of hovering in front of a flower (as hummingbirds do), bees grasp the hanging flowers with their mandibles and shake the pollen out of the tubular anthers while probing for nectar (see Heinrich 1976).

Ants.—From field observations, ants do not appear to be pollinators, nor are they myrmecophilous, but rather are more likely nectar thieves, protectors from herbivores of young leaves or other plant parts that secrete nectar, secondary dispersers, or harvesters (see Blüthgen et al. 2000; Beattie and Hughes 2002; Bronstein et al. 2006). Interactions observed in Ecuadorean Ericaceae are seemingly based on resources provided by the plants, i.e., nectar, fruits, or seeds, three examples being: Luteyn (1979) observed ants that cleaned seeds from fruit pulp of *Cavendishia lebroniae* and then dispersed those seeds or possibly ate them; Luteyn (1981) also reported leaves and immature fruits of *Cavensishia colombiana* eaten by a black, fungus ant *Acromyrmex hystrix* in a fashion similar to leaf-cutter ants, and ants eating leaves of *C. palustris*; and Luteyn (1983) also observed aggressive red biting ants (genus unknown) present on badly damaged leaves of several species of Vaccinieae (*C. tenella*, *C. angustifolia*, *C. micayensis*, *C. palustris*, and *Macleania stricta*) growing together in a decaying tree trunk. Other interactions with ants

include nesting sites, for example: Luteyn and Wilbur (1977) reported that the root system of *Disterigma utleyorum* (Costa Rica-Ecuador) was associated with colonies of ants and in which the ants aggressively defended their home environment by painful bites. Pedraza-Peñalosa (2010 and pers. comm.) confirmed seeing plants of *D. utleyorum* in Ecuador defended by ants of the subfamilies Dolichoderinae and Formicinae, and also Luteyn (1979) noted that the pith region of mature stems of *Ceratostema megabracteatum* (endemic to Ecuador) became hollow with age and provided a home for tiny, black, non-biting ants.

Miscellaneous Insects.—In general, many insect larvae cause floral damage in Ericaceae and thereby interfere with seed production; they probably also drink nectar which reduces its reward to pollinators. Their presence is usually noted by debris within flowers including their own fecal material and exit holes in fruits and pedicels. Navarro's (2001) study of *Macleania bullata* noted that rotted flowers contained beetle larvae (Curculionidae). I have also observed maggot-like larvae feeding on flowers and ovaries of *Macleania rupestris* and leaving exit holes. Larval damage of the micromoth *Caloptilia camaroneae* (Gracillariidae) has been observed infecting *Macleania rupestris* in Colombia (Arévalo 2014). Wasps may act as nectar robbers in the corolla tubes of *Macleania rupestris* (G. Weber, pers. comm. 2019). Butterflies and moths have long enough tongues to forage in the long corollas of some Ecuadorean Vaccinieae and are probably mostly nectar-robbers. Navarro (1999, 2001, pers. comm.) noted the butterfly *Pronophila orcus* as a primary nectar robber on *Macleania bullata* along the Ecuador border with Colombia. The "Western Flower Thrip" (*Frankliniella occidentalis*), the "Treehopper" (*Ennya* sp.), "weevils" (Curculionidae), and "true bugs" (Hemiptera) have all been observed visiting *Macleania rupestris* in Colombia (J.-L. Combita, pers. comm. 2019). "Leaf miners" (Diptera, Lepidoptera, Coleoptera, and Hymenoptera) also visit *Macleania rupestris* in Colombia (Arévalo 2014).

Arachnids.—Mites of the family Ascidae depend upon Ericaceae flowers not only as their source of food (nectar and pollen), shelter, and a place for reproduction, but also upon the birds themselves, because their primary means of dispersal from flower to flower is on the bills and in the nasal cavities of hummingbirds (Colwell 1985; Colwell & Naeem 1994)—an ideal example of a three-way mutualistic relationship! Hummingbird-flower mites may also be classified as nectar thieves (Colwell et al. 1974)—they are not parasitic—, but given their abundance they are likely to be significant competitors with hummingbirds (Colwell 1995). Naskrecki and Colwell (1998) determined that *Rhinoesius* mites were quite conservative with regard to host plant genera and families, and that with but a single exception, "every species in the genus *Rhinoseius* for which host plant records exist has been collected from plants of the family Ericaceae. In contrast, none of the [mite] species of the genus *Tropicoseius* is known from ericads, except for a single specimen of *T. steini* collected from *Ceratostema peruvianum*." My own personal observations in the laboratory over nearly 50 years have demonstrated that mites of the genus *Rhinoseius* inhabit nearly every flower of Vaccinieae dissected and that their presence in the flowers of dried herbarium specimens, such as in *Macleania coccoloboides* (Ecuador, Luteyn 8474, NY), is indirect proof of hummingbird visitation and subsequent pollination.

Mammals.—The herbivorous rodent known as "guanta de páramo" in Ecuador (*Cuniculus taczanowskii* (the Mountain Paca, Colombia–Bolivia) eats mostly fruits and seeds. In Colombia its diet includes the fruits of Ericaceae such as *Gaultheria erecta*, *Thibaudia floribunda*, and *Macleania rupestris* (Osbaahr et al. 2007), species also represented in Ecuador. The Andean bear, better known as "oso de anteojos" (*Tremarctos ornatus*; spectacled bear), is an endangered forest and páramo dispersal agent (Panama–Bolivia) that eats primarily plant leaves, fruits and small animals (i.e., omnivore). It purportedly eats berries of *Gaultheria*, *Pernettya prostrata*, *Cavendishia bracteata*, *Macleania rupestris*, and *Vaccinium floribundum* (Hernani-Lineros et al. 2020).

Fungal Interactions

Fungal visitors with Ericaceae may be divided into two groups—phytopathogenic and mycorrhizal fungi.

Phytopathogens.— Studies of phytopathogens of Ericaceae are scarce, but studies from Colombia, which share many Ericaceae species with Ecuador, found necrotic lesions ("manchas")

on the leaves, flowers, and fruits of *Macleania rupestris* caused by the fungal pathogens *Pestalotia*, *Cladosporium*, *Alternaria*, *Stemphylium*, and *Gloeosporium*, as well as cotton-like (“algodonoso”) mycelia, brown lesions, and white pulverulent (“pulvurento”) mycelia of *Gloeosporium* and *Cladosporium* which covered flowers and fruits; these pathogens affected the normal growth, development, and fruit production of the plant (Gutiérrez 1991). Romero and Sánchez-Nieves (2004) found 12 genera of pathogenic and saprophytic fungi associated with *Macleania rupestris*, viz., *Absidia*, *Alternaria*, *Ascochyta*, *Aspergillus*, *Cladosporium*, *Fusarium*, *Mucor*, *Nigrospora*, *Pestalotia*, *Stemphylium*, *Thielaviopsis*, and *Trichoderma*. In Peru, Oblitas (2012) observed leaf lesions in cultivated *Macleania rupestris* that were produced by species of *Colletotrichum* and *Gloeosporium*.

Mycorrhizae.—Ericaceae depend strongly on mycorrhizal fungi for nutrient acquisition from soil organic matter and are viewed as a key adaptation that enables Ericaceae to survive and dominate in nutrient poor soils (Read et al. 2004; Vohník et al. 2012); however, mycorrhizae have rarely been studied in tropical regions. Early studies of Ecuadorean fungi by Bermudes and Benzing (1989) demonstrated “fungal associations” in epiphytic roots of *Macleania cordifolia*. It has also recently been shown that the tribe Vaccinieae is seemingly characterized by a group of ectendomycorrhizae, named “cavendishoid” mycorrhizae, because they were discovered in *Cavendishia nobilis* var. *capitata* from southern Ecuador (Setaro et al. 2006, 2013; Brundrett & Tedersoo 2018) and that the dominant mycobiont belongs to the Sebaciniales (Kottke et al. 2008, 2013; Selosse et al. 2007; Setaro & Kron 2011). Cavendishoid ectendomycorrhizae associations have been also reported in other *Cavendishia*, *Ceratostema*, *Diogenesia*, *Disterigma*, *Macleania*, *Orthaea*, *Psammisia*, *Semiramisia*, *Spherospermum* and *Thibaudia* (Brundrett 2008).

Hybridization

Hybridization in Ecuadorean Ericaceae under natural conditions is rare, although Middleton (1989, 1990, 1991) and Luteyn (1995 and pers. observ.) reported intergeneric hybridization events between *Pernettya* and *Gaultheria*, and infrageneric hybridization in *Gaultheria*. Several species of *Macleania*, such as *M. bullata*, *M. floribunda*, and *M. stricta*, do hybridize under greenhouse conditions (J.R. Ballington, pers. comm. 1993).

Ethnobotany

Naranjo (1994), stated he believed that at the time of the Spanish conquest in the 15th-Century, *Macleania floribunda* (“gualicón”, “joyapa”) was one of the species cultivated for its fruits within the interandean region. Currently, *Macleania rupestris* (“joyapa”, “zagalita”, amongst other names) may be purchased in some larger supermarkets, where they are found as fresh or dried fruits, jams or marmalades, or as nectar drinks or wine (Sælemyr 2004; Van den Eynden & Cueva 2008). *Vaccinium floribundum* (“mortiño”) is most commonly known in the traditional “colada morada” or “mazamorra morada” prepared with “guaguas de pan” (or “t’anta wawa” bread that has the shape of a doll) and consumed every year on November 2 “All Souls’ Day” or “Día de los Difuntos.”

Traditional Uses—Species of Ericaceae have a long history of use by indigenous Ecuadoreans and the large number of common names given to them give credence to the fact that numerous species have been and are currently used locally. Although understudied, ethnobotanical observations confirm culinary, cultural, and medicinal uses of several species. A comprehensive review of the useful species of Ericaceae are contained in the “Enciclopedia de las plantas útiles del Ecuador,” where the editors reported that 65 of the approx. 225 species of Ericaceae in Ecuador that they listed had a use (Torre et al. 2008: tabla 1 and pp. 311–316; see also Van den Eynden & Cueva 2008: table 1). A summary of which (with specific references, and where known species and common names) is given below:

Edible fruits: See Popenoe 1924 (*Ceratostema alatum* “pera silvestre”, “manzanilla”; *Disterigma alaternoides* “tira”; *Disterigma empetrifolium* “chirimote”; *Macleania rupestris* “hualicón”, “chaquilulii”, “joyapa”, “salapa”; *Vaccinium floribundum* “mortiño”); Cordero 1950 (*Ceratostema peruvianum* and other spp. “joyapa”, “hualicón”; *Macleania floribunda* “joyapa”; *Vaccinium floribundum* “mortiño”); CESA 1992 (*Macleania floribunda*, *M. rupestris*); Cerón 1993 (*Disterigma acuminatum* “gualicón”; *Macleania cordifolia*, *M. loeseneriana*, and *M. rupestris* all “gualicón”; *Psammisia*

graebneriana "gualicón de árbol"); Cerón 2002a (*Cavendishia bracteata* "zagalita"; *Disterigma acuminatum* "sarsal", *D. empetrifolium* "chirimote"; *Gaultheria glomerata* "chigunda"; *Macleania loeseneriana* "gualicón"; *Thibaudia floribunda* "gualicón"); Cerón 2002b (*Cavendishia tarapotana* "cuyac"; *Disterigma acuminatum* "mortiño", "tirag"; *Macleania* cf. *loeseneriana* "gualicón", *M. rupestris* "cuya"; *Psammisia sclerantha* "gualicón" all as "alimento").

Toxic fruits: See Cordero 1950 (*Pernettya prostrata* "taruga joyapa", "tirag"); Luteyn 1995 (*Pernettya prostrata*); Cerón 2002a (*Pernettya prostrata* "moridera"); Kvist & Alarcón S. 2008 (species not given).

Wood as firewood and for woodworking: See Cerón 1993 (*Cavendishia bracteata* "zagalita"); Cerón 2002a (*Thibaudia floribunda* "gualicón"); CESA 1992 (*Macleania floribunda*, *M. rupestris*); Clemants 1995 (*Bejaria*). Ellemann (1991) listed useful woods, but did not give more specific uses, for the following species: *Bejaria aestuans* "payama", *Gaultheria erecta* "mote pelado", *Macleania rupestris* "joyapa", and *Pernettya prostrata* "payanchillo de cerro."

Medicinals: Cordero (1950) mentioned that from *Bejaria resinosa* (and other spp. of *Bejaria*) a decoction was made from "aserraduras of polvo del tronco o de la raíz" for people suffering from liver or intestinal diseases. For *Macleania rupestris* the leaves were made into a drink that accelerated labor ("parto") and reduced labor pains (CESA 1992; Abril 2015). Cerón et al. (2004) found that in *Macleania pentaptera* the entire plant was macerated and applied on the forehead as a plaster, then in steam baths and as a drink to eliminate cholesterol, fainting attacks, and severe headaches. The Cayapa Indians use *Macleania smithiana* medicinally as a cure for poisonous and non-poisonous snake bites (see Luteyn 1996; Cornejo 2014). Tene et al. (2007) found that an aqueous infusion of the fresh, mature leaves of *Macleania rupestris* was drunk as a tonic, while Rios et al. (2007) stated that *Macleania rupestris* was drunk in a decoction of the flowers to treat nerves.

For other, more general but less specific, cultural and medicinal uses of Ecuadorean Ericaceae, including cooking, see Muñoz (2004), Bussmann and Sharon (2006), Rios et al. (2007), Reyna Achi (2012), Moncayo (2014), Abril (2015), and Gallardo de la Puente (2015).

Horticultural and Ornamental Uses.—Many species of *Cavendishia*, *Ceratostema*, *Disterigma*, *Macleania*, *Psammisia*, and *Vaccinium* have potential as new floricultural crop plants, some being highly ornamental with large, dark green, evergreen leaves and large, brightly colored flowers (Ballington et al. 1993; photos in Luteyn 1996). Although Torre et al. (2008) reported that in Ecuador no native species were known to be used as ornamentals, Cerón (2002a,b) reported that both *Cavendishia tarapotana* ("orquidea", "cuyac") and *Macleania loeseneriana* ("gualicón") were used as both "ornamento" and "alimento."

Medicinal Uses.—A few Ecuadorean species of Ericaceae have been investigated for their antioxidant compounds, including *Anthopterus wardii*, *Cavendishia grandifolia*, *Cav. isernii*, *Ceratostema silvicola*, *Disterigma rimbachii*, *Macleania coccoloboides*, *M. cordifolia*, *M. rupestris*, and *Sphyrospermum buxifolium*—they are high in natural antioxidants and have been called "superfruits" because of their bioactive properties and high levels of antioxidant compounds (NRC 1989; Ballington et al. 1990; Cardozo et al. 2009; Dastmalchi et al. 2011; Flores et al. 2012). These antioxidant compounds, such as phenolics (polyphenols, flavonoids, and tannins), fruit colorants (anthocyanins and carotenoids), vitamins (ascorbic acid), and minerals play a fundamental role in preventing chronic and degenerative diseases. Some of these neotropical blueberries, demonstrated significantly stronger antioxidant activities than North American highbush blueberry *Vaccinium corymbosum* (Flores et al. 2012; Ma et al. 2013; Debnath & Goyal 2020). For other recent articles about the chemical composition and antioxidant activity of the Andean *Vaccinium floribundum*, see Vasco et al. (2009), Schreckinger et al. (2010), Ortiz et al. (2013), Prencipe et al. (2014), Alarcón-Barrera et al. (2018), and Llivisaca et al. (2018).

Nutritional Uses.—Within the last two decades major efforts are underway in Colombia and Ecuador to produce new, small-fruit crops from native (wild) species from the Andean regions,

namely *Cavendishia bracteata* ("uva de anís"), *Macleania rupestris* ("joyapa", "gualicón"), and *Vaccinium floribundum* ("mortiño"), all three also native to Ecuador (see Ligaretto 2009). In all propagation studies of *Macleania rupestris* and *Vaccinium floribundum*, propagation by cuttings is recommended (Brand-Prada 1994; Acero & Bernal 2003; Boni Duchitanga 2016). Although the plants are readily accessible to small producers and the cost is low, the absence of an adequate propagation protocol is still one of the difficulties in their introduction for commercial cultivation (Durán-Casas et al. 2013; Veloza-Suan et al. 2014). For further discussion of the cultivation of wild Andean species, see Torres et al. (2009) and Debnath and Goyali (2020).

Land Use, Restoration Ecology, and Conservation

Hofstede et al. (2002) and Quiroz Dahik et al. (2019) have demonstrated in Ecuadorean subpáramo and páramo areas where species of Ericaceae are represented, that pine plantations (*Pinus patula*), intensity of grazing by cattle, and the frequency of burning were all factors in lowering species richness when compared with natural grassland vegetation, thus highlighting the importance of controlling these activities so commonly practiced in the Ecuadorean Andes. Therefore, the several native species of Ericaceae that act as pioneers are increasingly seen as beneficial species for land use, restoration ecology, and vegetation regeneration purposes, especially in areas of anthropogenic disturbance, where biodiversity loss is creating serious problems (see Rodríguez & Peña 1984; DAMA 2000; Zuluaga & Espinosa 2005; Montenegro & Vargas 2008; Torre et al. 2008; Cardozo et al. 2009; Álvarez & Contreras 2012). Añazco (2008), for example, mentioned six species of Ericaceae, native to Ecuador, that are of major importance in regeneration after forest fires—*Bejaria aestuans* ("joyapa") and *B. resinosa* ("payana"), *Gaultheria erecta* and *G. reticulata* ("mote pelado"), *Macleania salapa* ("joyapa blanca"), and *Vaccinium floribundum* ("mortiño"). Fadaei (2019) also pointed to the importance of reclamation with ericaceous shrubs, because they add beneficial mycorrhizal fungi to the soils. Studies that have also shown the importance of Ericaceae in the overall maintenance of avian biodiversity include the following. In the Andes of eastern Ecuador, Nieto and Silva (2012) studied the influence of timber extraction, grazing, burning, and alien plant species in Ericaceae-dominated, shrubby vegetation areas, where only a few remnants of original vegetation remained and how that habitat alteration affected hummingbird usage of floristic resources (i.e., nectar). There, six species of Ericaceae proved to be the most visited species during their flowering periods and the most important plant resources for the hummingbirds in the secondary forest. In another study in the Colombian Andes, Ortiz and Umba (2010) have shown that Ericaceae are the principal plant family in the diet of frugivorous birds throughout the year and that they are responsible for Ericaceae dispersal.

As seen throughout this paper, several species of Ecuadorean Ericaceae are among the most widespread and ubiquitous neotropical Ericaceae and some may even act as pioneers in areas of natural or man-made disturbance. However, others are rare in nature and poorly known or scarcely collected. Approximately 57% of Ecuadorean Ericaceae are endemic (occur only in Ecuador) or nearly so (i.e., in close proximity in two adjacent countries). Many of these species have restricted distributional ranges and are known from very few specimens, about 51% are known from fewer than 10 collections (Luteyn 1996 and unpubl. data). These and others often grow in areas with deteriorating environmental conditions and increasing human pressure. Therefore, it is imperative that better land-use practices and conservation efforts are undertaken to protect these and other species.

The Tropical Andes biogeographic region is the most species rich and ecologically threatened region on Earth and montane ecosystems like the cloud forests, where Ericaceae abound, are today reduced to 10% of their original extent, mostly due to destructive human activities such as burning, deforestation, road-building, and introduction of domestic livestock (Henderson et al. 1991; Chaves & Arango 1998; Mast et al. 1999; Hamilton 2001; Orme et al. 2005; United States Agency for International Development 2009). According to Pedraza-Peñalosa et al. (2011) and Luteyn and Pedraza-Peñalosa (2013) "89% of the Ericaceae endemic to Ecuador have some level of threat." Therefore, many of the Ecuadorean Ericaceae are endangered.

In summary, Andean montane ecosystems are home to about 80% of the different neotropical Ericaceae species. For this reason, reforestation programs are needed, taking into account that some native Ericaceae are successful colonizers of natural or anthropogenically disturbed areas,

while others are threatened by habitat loss and are on the verge of extinction (see Durán-Casas et al. 2013). Thus, conservation of native vegetation, including ericaceous-rich habitats especially in montane elevations, must be undertaken in order to sustain species diversity of both plants and animals. Valencia et al. (2000), León-Yáñez et al. (2011), and Luteyn and Pedraza (2013) have made critical evaluations of the endemic Ecuadorean species of Ericaceae in which they followed the *IUCN Red List* guidelines—it is hoped that formal conservation assessments might soon be carried out for the entire family.

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Author's Request: As stated several times in the text, there are few actual studies of many of the biological aspects of Ecuadorean Ericaceae—pollination and dispersal systems, chemistry, cytology, mycorrhizae, conservation—and this author would very much appreciate receiving general information of ongoing research in these areas, as well as references to and pdf copies of published papers, or contact information from current researchers (i.e., email addresses). It is also hoped that this review of Ecuadorean Ericaceae will stimulate others to collect more field data and make more observations on pollination and dispersal interactions, as well as other biological phenomena in neotropical Ericaceae.

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