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BRYOPHYTES OF THE SANTA ELENA PENINSULA AND ISLAS MURCIÉLAGO, GUANACASTE, COSTA RICA, WITH SPECIAL ATTENTION TO NEOTROPICAL DRY FOREST HABITATS

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ABSTRACT. Fifty-five bryophyte species (21 hepatics, 34 mosses) are reported from the dry lowland forests and moist montane forests of the Santa Elena Peninsula and Islas Murciélago, Guanacaste Province, Costa Rica. Over 50% of the collected species are neotropical, 16% have a pantropical distribution and 12% are amphiatlantic (America-Africa). Nine percent of the species are of limited distribution in potentially dry forest areas of Mexico, Cuba and Costa Rica. *Brachymenium spirifolium, Fissidens juruensis var. juruensis, F. radicans, F. yucatanensis, Gymnostomiella vernicosa and Rhodobryum grandifolium* are reported as new to Costa Rica. *Uleobryum peruvianum and Cephaloziella subtilis* are new to Central America. By far the most diverse bryophyte vegetation type in the study area is found above 500 m, in the moist montane forest of the Cerros Santa Elena. These moist forests support many corticolous bryophytes; however, soil, logs and rocks are the most important bryophyte habitats in the dry forests.

RESUMEN. Se comunican cincuenta y cinco especies de briófitos (21 hepáticas, 34 musgos) de los bosques secos de bajura y húmedos de montaña en la Península de Santa Elena y las Islas Murciélago, Guanacaste, Costa Rica. Más del 50% de las especies recolectadas son de distribución neotropical, 16% son pantropicales y 12% anfiatlánticas (América-África). Nueve por ciento de las especies tiene una distribución limitada a áreas que potencialmente poseen bosque seco en México, Cuba y Costa Rica. *Brachymenium spirifolium, Fissidens juruensis var. juruensis, F. radicans, F. yucatanensis, Gymnostomiella vernicosa y Rhodobryum grandifolium* son nuevos registros de Costa Rica. *Uleobryum peruvianum y Cephaloziella subtilis* son nuevos registros de Centroamérica. La mayor diversidad de briófitos se encuentra por encima de 500 m de altitud, en el bosque húmedo de montaña de los Cerros Santa Elena, donde la mayor parte de las especies son cortícolas. En los bosques secos, suelo, troncos caídos y rocas son los hábitats briofíticos más importantes.

KEY WORDS / PALABRAS CLAVE: Bryophyta, Costa Rica, Santa Elena Peninsula, neotropical dry forest.

INTRODUCTION

Probably due to their low species diversity, bryophytes of tropical dry forest areas have generally been neglected. Bryological studies in the tropics have focused traditionally on moist evergreen forests and mountain areas with greater bryophyte diversity. Therefore, the bryological composition of tropical dry forest areas remains poorly known.

The New World tropical dry forest extends from the foothills west of Mazatlán, Mexico, and just south of Laredo, Texas, to near the Panama Canal (Janzen 1998: Fig. 1), thence deep into South America. Dry forests account for nearly 50% of the forested area of Central America, a higher proportion than for South America or the tropical and subtropical regions of the Earth in general (Murphy & Lugo 1986). The Santa Elena Peninsula harbors the only complete dry forest ecosystem left in Central America, and is not duplicated socio-economically or ecologically elsewhere in the New World Tropics (Janzen 1998). The Peninsula has remained above the sea throughout its 85 million years history, making it today the oldest continually exposed terrain in Central America (Janzen 1998). Due to its origin as an isolated oceanic island (see Geology), its extreme age, the underlying serpentine soils, its extremely seasonal tropical climate and its location in the driest area of Costa Rica, the Santa Elena Peninsula harbors a unique biological community which has also been invaded by species that, over time, have moved into Central America from the north and south (Janzen 1998).

With the assistance of a National Geographic Society Grant to the second author, vascular plant and bryophyte collecting was undertaken in the Santa Elena Peninsula and the Islas Murciélago, in the Gua-

nacaste Conservation Area (ACG), during the period 27 August–3 September, 2003. An account of the bryophyte species collected and reported from the area is presented, together with an analysis of their geographical affinities and descriptions of the different vegetation types where bryophytes occur. Special attention is paid to the bryophyte diversity of tropical dry forests.

Fig. 1. Location of Santa Elena in Central America. The shaded areas represent potential distribution of dry forest areas (according to Janzen 1974, cit. by Janzen 1998).

Description of the study area

Location. The Santa Elena Peninsula is located in Guanacaste Province, northwestern Costa Rica, between 10°8'-10°57'10"N, and 85°45'–85°59'W (Fig. 1). The elevation ranges from sea level to just over 700 m on the highest peaks.

Climate. The climate in Santa Elena is the driest in the country, with an estimated 100 to 300 mm less annual rainfall than that recorded for Santa Rosa (1528 mm/year, Janzen 1998). This portion of Costa Rica generally experiences a dry season of five to seven months, with a rainy season from May or June to November or December, with a shorter dry season ("veranillo de San Juan") of up to six weeks occurring in July or August (Janzen 1988a). The study period coincided with the latter half of this short, interstitial dry season. Temperatures in the Guanacaste region range from nocturnal lows of 16-23°C to diurnal highs of 26-38°C, with hotter temperatures (along with higher winds) prevailing during the dry season (Janzen 1988a).

Geology. The Santa Elena Peninsula represents a unique geological structure in Costa Rica. Together with the hills of the Nicoya Peninsula, this is one of the remnants of the Costa Rican external island arc, with an age of about 150 million years (inferior Jurassic and Paleocene, Castillo 1993, González 1998). According to Denyer *et al*. (2000), Santa Elena emerged in the inferior Jurassic (200-65 my), and is underlain by sedimentary rock (radiolarite) and basalts, the former including the oldest exposed rocks in Costa Rica (Tournon & Alvarado 1997). Most of the Santa Elena Peninsula is a massif of olivine altered in different degrees to serpentine (Kussmaul 2000), overlain by volcanic ignimbrites in the eastern portion.

Soil. The soils at the higher elevations of Santa Elena, on very steep sites, are shallow and not well developed (entisoles), and remain dry over 90 days a year (Gómez 1986). On the lowland areas, the soils (inceptisoles) remain dry for a similar period of time.

Vegetation. The vegetation of Guanacaste, and particularly that of the Santa Elena Peninsula, comprises seasonal forms of semi-deciduous or deciduous forest and tropical lowland semi-deciduous forest (Gómez 1986). According to Murphy & Lugo (1986), 60-75% of all trees in the Guanacaste region are deciduous, while Janzen (1988a: 157) reported that "at least 80%" of dry forest plant species in Guanacaste National Park "lose their leaves and may stand leafless for 3 to 5 months". In Santa Elena, the vegetation is mainly herbaceous to shrubby, with small, dispersed trees (larger in bottomlands and along watercourses); as in dry forests the world over, vascular epiphytes are exceedingly few. Following the Holdridge Life Zone System, the lowland areas of Santa Elena correspond to the Tropical Dry Forest zone, and the higher elevations to Tropical Moist Forest (Tosi 1969). However, this oversimplifies the case: the Guanacaste forests (and tropical dry forests in general) embody a complex mosaic of many habitats (16 were described by Janzen 1988a), a situation that is exaggerated during the dry season and complicated by human disturbance (Janzen 1988a, 1988b). The impact of human disturbance (especially through the agency of fire) has been particularly devastating for tropical dry forests. When the Spaniards arrived in the New World (1492), there was an estimated area of 550 000 km^2 of dry forest in the Mesoamerican region (Janzen 1988). Presently, only 2% of that total remains relatively undisturbed and just 0.08% is protected in reserves (in Costa Rica, mostly Guanacaste and Palo Verde National Parks). This atomization of what was already a mosaic of habitat types means that almost

all native dry forest species have become few and/or far between locally (Janzen 1988a), even if they may range widely throughout the Neotropics.

The phanerogam flora of the Guanacaste area is composed mainly of elements common to the Mexican and Guatemalan floras; some of these species have their southern distribution limits on the Panamanian Pacific coast (Zamora *et al*., in prep.), while others reach the northern coast of Colombia, Venezuela and the Guianas. A few species extend southward as far as the Brazilian caatingas (Pennington et al. 2000, Prado & Gibbs 1993), *e.g., Cordia alliodora* (Boraginaceae), *Coutarea hexandra* (Rubiaceae), *Crateva tapia* (Capparidaceae), *Hymenaea courbaril* (Fabaceae), *Ipomoea carnea* (Convolvulaceae), *Sideroxylon obtusifolium* (Sapotaceae), and *Tabebuia impetiginosa* (Bignoniaceae).

Fig. 2. The Santa Elena Peninsula and Islas Murciélago

RESULTS

The bryophyte species found in the study area are listed in Table 1, together with their substrates and geographical distributions. Distributional data for mosses were taken from Delgadillo et al. (1995), and for hepatics mostly from Gradstein & Costa (2003). To date, 21 hepatic species (17 genera, 6 families) and 32 moss species (21 genera, 14 families) have been identified from Santa Elena. *Brachymenium spirifolium, Fissidens juruensis var. juruensis, F. radicans, F. yucatanensis, Gymnostomiella vernicosa* and *Rhodobryum grandifolium* are reported as new to Costa Rica. *Uleobryum peruvianum* and *Cephaloziella subtilis* are new to Central America. An account of the new records is shown below, which includes species new to Costa Rica (*) and also to Central America (**).

Brachymenium spirifolium (C.Müll.) A.Jaeger
SANTA ELENA: Cerros Santa Elena, terrestrial among rocks in the shade, 10°53'24"N, 85°50'55"W, 650-700 m, *G. Dauphin, M. Grayum, F. Morales & R. Espinoza 3299* (INB, MO). **New to Costa Rica, this species was previously known from similar altitudes in Belize and Nicaragua (Allen 2002).**

****Cephaloziella subtilis*** (Lindenb. & Gottsche) Steph.
SANTA ELENA: Playa Respingue, dry forest area, on rotten wood, 10°53'22"N, 85°53'14"W, 0-50 m, *G. Dauphin & M. Grayum 3271, 3272* (INB, det. Dauphin). **This species was previously known from several localities in Sonora, Mexico (Fulford 1976). Its occurrence in Guanacaste suggests that it may be more widespread in the drier areas of northern Central America.**

****Fissidens juruensis*** Grout var. ***juruensis***
ISLAS MURCIÉLAGO: Isla Catalina, rocky canyon on slope with *Plumeria rubra, Stenocereus aragonii & Bursera graveolens*, 0-80 m, terrestrial on the base of *Stenocereus, G. Dauphin & F. Morales 3277* (INB, PAC, conf. det. R. Pursell.); Isla Pelada, terrestrial under grasses, next to an intermitent water course, *G. Dauphin, M. Grayum, F. Morales & R. Espinoza 3260* (INB, PAC, conf. det. R. Pursell). **New to Central America, this taxon was previously known only from Mexico and Cuba (Sharp *et al*. 1994). *Fissidens juruensis var. percurrens* (Grout) Pursell has been reported from Belize (Allen 1994).**

****Fissidens radicans*** Mont.
SANTA ELENA: Cerros Santa Elena, fila sobre Playa Respingue, at trunk base on ridge, *G. Dauphin, M. Grayum, F. Morales & R. Espinoza 3365* (INB, PAC, det. R.A. Pursell). **New to Costa Rica. This species was previously known from Belize, Nicaragua and Panama (Allen 1994).**

****Fissidens yucatanensis*** Steere
ISLAS MURCIÉLAGO: Isla San José, terrestrial on scrub, *G. Dauphin, M. Grayum, F. Morales & R.. Espinoza 3257* (INB, PAC, det. R.A. Pursell)_ Isla Catalina, on rotten log in the shade, *G. Dauphin & F. Morales 3282* (INB, PAC, det. R.A. Pursell). **New to Costa Rica, *Fissidens yucatanensis* is a widespread neotropical species. In Central America, it was previously reported only from Panama (Allen 1994).**

****Gymnostomiella vernicosa*** (Harv. in Hook.) Fleisch
ISLAS MURCIÉLAGO: Isla Catalina, on calcareous rock,

close to the intertidal zone, 0-10 m, *G. Dauphin & F. Morales 3273, 3276* (INB, MO). **Widespread in tropical America, Indochina, Malesia and Australia, this moss was previously reported in Central America only from Panama (Allen 2002).**

Rhodobryum grandifolium (Tayl.) Schimp.
Santa Elena: Cerros Santa Elena, fila sobre Playa Respingue, terrestrial in the shade among roots, 700 m, *G. Dauphin, M. Grayum, F. Morales & R. Espinoza 3307* (INB, MO). New to Costa Rica, this species was previously known from Guatemala, Honduras and Panama; therefore, its occurrence in Costa Rica was not unexpected, although here it is found at much lower elevation (*ca.* 700 m) than previously reported in Central America (2400-2640 m, Allen 2002). In Colombia, the species is known from 1500-3815 m (Churchill & Linares 1995).

****Uleobryum peruvianum*** Broth.
Islas Murciélago: Isla Pelada, half exposed on rocky cliff, 0-80 m, *G. Dauphin, M. Grayum, F. Morales & R. Espinoza 3263* (INB, MO, det. B.H. Allen); Isla Golondrinas, on rocky cliff under grasses, *G. Dauphin & F. Morales 3374* (INB, MO, det. B.H. Allen). **New to Central America (B.H. Allen, pers. comm.)**

Murciélago Archipelago (basaltic islands)

The Islas Murciélago, off the south coast of the Santa Elena Peninsula, are all basaltic (Tournon & Alvarado 1997), except for the serpentinic Isla Colorada (not visited) and Isla Pelada (discussed separately). Bryophytes were inventoried on all the basaltic islands except Isla San Pedrito, the smallest and westernmost member of the chain. All of the islands visited (Isla Catalina, Isla Cocinera, Isla Golondrinas and Isla San José) have been more or less strongly impacted by burning, logging, fishing and camping (Janzen 1998). Therefore, the original vegetation has mostly disappeared, except for a few patches on the biggest islands; the most extensive forests occur on Isla San José, while neighboring Isla Cocinera (sometimes spelled "Cocinero" on maps) is almost completely barren. All of these basaltic islands are characterized by the presence (and sometimes dominance) of *Amphipterygium adstringens* (Anacardiaceae), a shrub or small tree that is otherwise known from Costa Rica by a few collections from scattered sites on the Santa Elena Peninsula. Other common elements include *Acanthocereus tetragonus* (Cactaceae), *Bursera glabra* (Burseraceae), *Esenbeckia berlandieri* (Rutaceae), *Exostema caribaeum* (Rubiaceae), *Plumeria rubra* (Apocynaceae), *Rehdera trinervis* (Verbenaceae), *Stenocereus aragonii* (Cactaceae), *Russelia sarmentosa* (Scrophulariaceae), *Senna skinneri* (Fabaceae), *Trigonia rugosa* (Trigoniaceae), and *Turnera pumilea* (Turneraceae).

Eight bryophyte species have been recorded from the basaltic Islas Murciélago, all adapted to extreme environments, and especially to long drought periods. These include the common, subcosmopolitan *Hyophila involuta*, but also rare species such as *Riccia vitalii*, known only from the Brazilian Planalto and these islands (Jovet-Ast 1991). *Riccia vitalii* grows abundantly in shaded places under grasses, rocks or at the base of *Stenocereus aragonii* (Cactaceae). Its sporophytes embodied in the thallus and very large spores (ca. 90 µm) are adaptations to long dry periods and enable it to withstand fires. The other bryophyte species present on the islands are *Fissidens flaccidus*, F. *goyazensis*, *F. juruensis var. juruensis, F. yucatanensis, Gymnostomiella vernicosa* (restricted to calcareous substrates at sea level, Allen 2002), and *Uleobryum peruvianum.*

Isla Pelada

This is a relatively barren serpentine block, with mainly herbaceous vegetation and scattered shrubs. Most of the woody elements listed above as characteristic of the basaltic islands are also present here, with the notable exception of *Amphipterygium adstringens.* On the other hand, several typical serpentine species occur on Isla Pelada that were not found on any of the basaltic islands, e.g., *Acacia villosa* (Fabaceae), *Krameria revoluta* (Krameriaceae) and *Turnera diffusa* (Turneraceae).

The bryophyte flora of Isla Pelada is extremely poor; only three mosses were found on this site: *Fissidens juruensis* var. *juruensis, Trichostomum sinaloensis,* and *Uleobryum peruvianum*. The species growing on these serpentine soils have probably developed the capacity to withstand high levels of magnesium, which would be deleterious to other bryophytes. A good example of this is *Riccia vitalii*, which grows abundantly on the neighboring basaltic islands, but seems completely absent from the serpentinic Isla Pelada.

Playa Gringos

This site, on the north side of the Santa Elena Peninsula, represents an old secondary-growth area on alluvial soils, within a dry forest zone. Among the woody phanerogams common in this vicinity are

Aphelandra scabra (Acanthaceae), *Bombacopsis* [*Pachira*] *quinata* (Bombacaceae), *Conocarpus erecta* (Combretaceae), *Garcinia intermedia* (Clusiaceae), *Hylocereus costaricensis* (Cactaceae), *Hymenaea courbaril* (Fabaceae), *Manihot aesculifolia* (Euphorbiaceae), *Ocotea veraguensis* (Lauraceae), *Phragmites australis* (Poaceae), *Plumeria rubra* (Apocynaceae), and *Turnera ulmifolia* (Turneraceae).

Eigth bryophyte species were found here: *Acrolejeunea emergens, Anoectangium aestivum, Calymperes palisotii, Entodontopsis leucostega, Fissidens pallidinervis, Frullania* cf. *cuencensis, Frullanoides corticalis*, and *Philonotis uncinata.* These are all widespread, typically xerophytic species, characteristic of old secondary-growth sites.

Playa Respingue

On the slopes behind Playa Respingue, on the south coast of the Santa Elena Peninsula, stands an apparently old growth lowland dry forest. Prominent elements of the woody vegetation include *Caesalpinia coriaria* (Fabaceae), *Capparis indica* (Capparaceae), *Gliricidia sepium, Haematoxylum brasiletto* and *Lysiloma divaricatum* (Fabaceae), *Melanthera nivea* (Asteraceae), *Simarouba glauca* (Simaroubaceae), and *Thouinidium decandrum* (Sapindaceae). Bryophytes are absent from the tree trunks, but grow on logs. Five bryophyte species were found in this habitat type and the neighboring disturbed vegetation, growing along the intermittent ravines, *e.g., Calymperes palisotii, Entodontopsis leucostega, Fissidens neglectus,* and *Octoblepharum albidum*. A single hepatic species, *Cephaloziella subtilis*, was found; this species seems restricted to this kind of habitat and was not found at other sites in Santa Elena. A rare species, it was previously known only from some localities in Sonora, Mexico (Fulford 1976). It is probable that this species represents an endemic element of the disappearing Central American dry forest areas.

Cerros Santa Elena

The higher, frequently cloud-capped peaks of the axial Cerros Santa Elena, harbor a tropical moist forest island between dry forest areas. The forests here (above *ca.* 500 m) are dense and unbroken, without clearings caused by fire or other human disturbance. Some common woody elements of this diverse assemblage are *Arrabidaea costaricensis* (Bignoniaceae), *Bursera permollis* (Burseraceae), *Calliandra tergemina* (Fabaceae), *Coursetia elliptica* (Fabaceae), *Croton niveus* and *C. yucatanensis* (Euphorbiaceae), *Diospyros salicifolia* (Ebenaceae), *Diphysa humilis* (Fabaceae), *Erythroxylum rotundifolium* (Erythroxylaceae), *Euphorbia schlechtendalii* (Euphorbiaceae), *Exostema caribaeum* (Rubiaceae), *Guettarda macrosperma* (Rubiaceae), *Lonchocarpus phlebophyllus* (Fabaceae), *Pedilanthus nodiflorus* (Euphorbiaceae), and *Roupala montana* (Proteaceae). Also conspicuously diverse are terrestrial or epilithic herbs not or seldom seen in adjacent dry forests, including ferns (*Adiantum, Dryopteris, Selaginella*), Gesneriaceae (*Koellikeria, Kohleria, Sinningia*), grasses (*Olyra, Streptochaeta, Tripsacum*) and orchids (*Habenaria, Malaxis*). However, perhaps the most striking aspect of these upland moist forests is their relatively heavy epiphyte load, with ferns (*Pecluma*), bromeliads (*Werauhia*) and orchids (*Encyclia, Epidendrum, Maxillaria, Pleurothallis, Polystachya, Scaphyglottis*) all well represented, at least in terms of numbers of individuals. Thus it should come as no surprise that the higher portions of the Cerros Santa Elena also support by far the most diverse bryophyte vegetation type in the study area. About 72% (33 spp.) of the bryophytes collected in the Santa Elena region were found on the cloudy, relatively wet slopes of the upper ridges and summits of these hills. Hanging mats of the unusually abundant *Orthostichopsis tetragona* are at once evident. The twigs on the ridges at the highest elevations are covered with *Frullania intumescens*. On the branches below, *Cheilolejeunea rigidula* is the most frequent corticolous species. *Marchesinia brachiata* is another dominant species, growing on bark and occasionally on rocks. The rocky outcrops on the ridges harbor a series of different taxa, including *Brachymenium spirifolium, Frullania* spp. and *Rhodobryum grandifolium*.

All Lejeuneaceae (see Table 1) are exclusive to this upper belt, excepting Frullanoides corticalis, which also occur in the secondary lowland forest of Playa Gringos, and the transition areas in between. Other bryophytes exclusive to the Cerros Santa Elena are *Brachymenium spirifolium, Campylopus pilifer, C. savannarum, Fissidens radicans, Groutiella mucronifolia, Mittenothamnium reptans, Orthostichopsis tetragona, Plagiochila patula, Racopilum tomentosum, Rhodobryum beyrichianum, R. grandifolium, Sematophyllum* sp.*, Syrrhopodon incompletus,* and *S. parasiticus.*

The unusual dominance of species such as *Cheilolejeunea rigidula* and *Marchesinia brachiata* in the isolated upper hills of the Cerros Santa Elena suggests a disharmonic flora, typical of an island.

Substrate use of the bryophyte species in Santa Elena

Table 1 shows the occurrence of bryophyte species on the different substrate types. The bryophyte flora of most tropical forests is dominated by corticolous species (*e.g*. Dauphin 1999). This pattern is clear in the Santa Elena region only at the higher elevations (Cerros Santa Elena). When higher elevation species are left out of the analysis, the substrate use of bryophytes in Santa Elena is strikingly different than in other forest types: saxicolous species, terrestrial species and species growing on logs are equally abundant (33% each).

Corticolous species are absent from both the basaltic and serpentinic islands. In these drier habitats, most bryophytes (*ca*. 80%) grow on soil, and the rest may grow on rocks. This may be explained by the absence of water during the long dry seasons, and the fire history. All bryophytes on the islands are acrocarpous mosses, excepting the thallose liverwort *Riccia vitalii*. The acrocarpous mosses found on the Islas Murciélago present one or more adaptations to dryness similar to those described from desertic areas by Frye (1990, cit. per Frahm 2001), such as contorted, thick leaves with costal lamellae and water-storing cells, papillose leaf cells, and inrolled leaf margins. Logs are important habitat in the primary lowland forests, with 80% (4) of the species. Tree trunks are almost not colonized by bryophytes in this forest type. Corticolous bryophytes become more dominant with increasing moisture and altitude.

This means that in neotropical dry forest habitats, soil and logs play a special role in water retention for several bryophyte species which otherwise would be absent, and exposed rocks also provide a habitat suitable for bryophyte colonization.

Most species seem to occur in a single ecosystem type, and only about 9% of the species were found on more than one site. This suggests that the turnover of bryophyte species is particularly marked in Santa Elena; 97% of the bryophyte species occurring on the moist hilltops are exclusive to that forest type. Trejo & Dirzo (2002) also reported very high turnover rates (of phanerogam species) in Mexican dry forests, with just 28% of a total of 917 species present at more than one site, and not a single species common to all 20 sites sampled.

It is expected that, due to their niche specificity, and high substrate and atmospheric water dependence, some bryophyte species can constitute a valuable indicator of the conservation and regeneration status of tropical dry forest areas.

Biogeography of the bryophytes of the Santa Elena Peninsula

The distribution patterns of the bryophyte flora of the Santa Elena Península and the Islas Murciélago are documented in Table 2. Distributional data for hepatics were taken mainly from Gradstein & Costa (2003), and for the mosses from Sharp *et al.* (1994), Allen (1994, 2002), and Delgadillo (1995).

As usual for inventories in tropical America (e.g. Dauphin 1999, Dauphin & Ilkiu-Borges 2002), bryophyte species with exclusively neotropical distributions outnumber the rest (51%), followed by the pantropical (18.2%) and amphiatlantic (10.9%) elements. In these three groups, common widespread species are included. The Mexican-Cuban-Central American element is about equally dominant as the amphiatlantic element. This percentage is high and includes rare species known from scattered localities in Mexico, Cuba and Costa Rica and probably restricted to undisturbed tropical dry forest areas, e.g., *Brachymenium spirifolium*, *Cephaloziella subtilis,* and *Fissidens juruensis* var. *juruensis*. It is likely that *C. subtilis*, restricted in the Santa Elena region to the shaded understory of the evergreen tropical forest behind Playa Respingue, is now absent from its former potential distribution area in Central America (Fig. 1). Another interesting component in this flora is the "Costa Rican-Brazilian" element, represented on the basaltic islands by *Riccia vitalii* and in secondary growth areas by *Frullania* cf. *cuencensis*, accounting for 4.5% of the flora. Inventories of dry areas in Panama would probably reveal these species.

The dominance of the amphiatlantic *Cheilolejeunea rigidula* and *Marchesinia brachiata* at higher elevations suggests an early colonization of the Santa Elena rocky outcrops by archaic, miocenic species, followed by the accrual of widespread neotropical, pantropical, and dry forest species during 85 million years, to produce this particular array of bryophyte species.

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Table 1. Santa Elena's bryophyte species: localities, substrates, distributions, and voucher citations.

Class	Family	Species	SJO	COC	CAT	GOL	PEL	PG	PR	CSE	dist	subs	ref.	notes
h	Cephaloziellaceae	*Cephaloziella subtilis* (Lindenb. & Gottsche) Steph.							1		na-ca	l	Dauphin 3272, INB	**
h	Fossombroniaceae	*Fossombronia porphyrorhiza* (Nees) Prosk.								1	neo	s	Dauphin 3300 INB	
h	Jubulaceae	*Frullania* cf. *cuencensis* Taylor						1			neo	c	Dauphin 3289, INB, F	**
h	Jubulaceae	*Frullania intumescens* (Lehm. & Lindenb.) Lehm. & Lindenb								1	neo	c, r	Dauphin 3306, INB, GOET	
h	Jubulaceae	*Frullania riojaneinerensis* (Raddi) Aongstr.								1	pan	c	Dauphin 3304, INB	
h	Lejeuneaceae	*Acrolejeunea emergens* (Mitt.) Steph.						1			pan	c	Dauphin 3291, INB	
h	Lejeuneaceae	*Bryopteris filicina* (Sw.) Nees								1	neo	c	Dauphin 3308, INB	
h	Lejeuneaceae	*Cheilolejeunea* cf. *adnata* (Kunze) Grolle								1	neo	c	Dauphin 3310, INB	
h	Lejeuneaceae	*Cheilolejeunea* cf. *fragrantissima* (Spruce) R. M. Schust.								1	nsa-cr	r	Dauphin 3356, INB	
h	Lejeuneaceae	*Cheilolejeunea holostipa* (Spruce) Grolle & R. –L. Zhu								1	neo	c	Dauphin 3322 INB	
h	Lejeuneaceae	*Cheilolejeunea rigidula* (Nees ex Mont.) R. M. Schust.								1	neo-afr	c	Dauphin 3319, INB	
h	Lejeuneaceae	*Colura tortifolia* (Mont. ex Nees) Trevis.								1	neo	c	Dauphin 3346 INB	
h	Lejeuneaceae	*Diplasiolejeunea rudolphiana* Steph.								1	pan	c	Dauphin 3346.3, INB	
h	Lejeuneaceae	*Drepanolejeunea bidens* Steph.								1	neo	c	Dauphin 3317, INB	
h	Lejeuneaceae	*Drepanolejeunea fragilis* Bischl.								1	neo	c	Dauphin 3323, INB	
h	Lejeuneaceae	*Frullanoides corticalis* (Lehm. & Lindenb.) van Slageren						1		1	neo	c	Dauphin 3292, 3338 INB	
h	Lejeuneaceae	*Harpalejeunea uncinata* Steph.								1	neo	c	Dauphin 3311, INB	
h	Lejeuneaceae	*Marchesinia brachiata* (Sw.) Schiffn.								1	neo-afr	c	Dauphin 3353, INB	
h	Lejeuneaceae	*Microlejeunea bullata* (Tayl.) Steph.								1	neo	c	Dauphin 3309, INB	
h	Lejeuneaceae	*Symbiezidium transversale* (Sw.) Trevis.								1	neo	c	Dauphin 3341, INB	
h	Plagiochilaceae	*Plagiochila patula* (Sw.) Lindenb.								1	neo	c	Dauphin 3345 INB, GOET	
h	Ricciaceae	*Riccia breutelii* Hampe ex Steph.	1								na-ca	s	Jovet-Ast 1991	
h	Ricciaceae	*Riccia vitalii* Ast	1	1	1	1					cr-bra	s	Dauphin 3371 INB	
m	Bartramiaceae	*Philonotis uncinata* (Schwägr.) Brid.						1			pan	r	Dauphin 3296, INB, MO	
m	Bryaceae	*Brachymenium mexicanum* Mont.				1					na-ca	s	Dauphin 3378, INB, MO	
m	Bryaceae	*Brachymenium spirifolium* (C. Müll.) A. Jaeger								1	na-ca	s	Dauphin 3299, INB, MO	*
m	Bryaceae	*Rhodobryum beyrichianum* (Hornsch.) C. Müll.								1	neo	s	Dauphin 3350, INB, MO	
m	Bryaceae	*Rhodobryum grandifolium* (Tayl.) Schimp.								1	neo	s	Dauphin 3307, INB, MO	*
m	Calymperaceae	*Calymperes palisotii* Schwaegr.						1	1		pan	c	Dauphin 3296, 3288, INB, MO	
m	Calymperaceae	*Syrrhopodon incompletus* Schwaegr. var. *incompletus*								1	neo-afr	c	Dauphin 3340, INB	
m	Calymperaceae	*Syrrhopodon parasiticus* (Brid.) Besch.								1	pan	c	Dauphin 3325, INB	
m	Dicranaceae	*Campylopus pilifer* Brid.								1	cos	s	Dauphin 3369, INB, MO	
m	Dicranaceae	*Campylopus savannarum* (C. Müll.) Mitt.								1	neo	l	Dauphin 3328, INB, MO	
m	Entodontaceae	*Entodontopsis leucostega* (Brid.) W. R. Buck & Irel.						1	1		pan	l	Dauphin 3287, INB, MO	
m	Fissidentaceae	*Fissidens elegans* Brid.								1	neo	s	Dauphin 3334, INB, PAC	
m	Fissidentaceae	*Fissidens flaccidus* Mitt.				1					neo-afr	s	Dauphin 3375, INB, PAC	
m	Fissidentaceae	*Fissidens goyazensis* Broth.	1			1					neo	s	Dauphin 3259, 3376, INB, PAC	
m	Fissidentaceae	*Fissidens guianensis* Mont. var. *guianensis*								1	neo	s	Dauphin 3329, INB, PAC	
m	Fissidentaceae	*Fissidens juruensis* Grout var. *juruensis*			1		1				na-ca-cu	s	Dauphin 3277, 3260, INB, PAC	*
m	Fissidentaceae	*Fissidens pallidinervis* Mitt.						1	1		neo-asi	c, l	Dauphin 3266, 3295, INB, PAC	
m	Fissidentaceae	*Fissidens radicans* Mont.								1	neo	c	Dauphin 3365, INB, PAC	*
m	Fissidentaceae	*Fissidens yucatanensis* Steere	1		1						neo	s, l	Dauphin 3257, 3282, INB, PAC	*
m	Fissidentaceae	*Fissidens zollingerii* Mont.			1						pan	l	Dauphin 3280, INB, PAC	
m	Hypnaceae	*Mittenothamnium reptans* (Hedw.) Cardot								1	neo	r, l	Dauphin 3364, INB	
m	Leucobryaceae	*Ochrobryum gardneri* (C. Müll.) Mitt.								1	neo-afr	l	Dauphin 3337, INB, MO	
m	Leucobryaceae	*Octoblepharum albidum* Hedw.							1	1	pan	l	Dauphin 3268, 3327, INB	
m	Meteoriaceae	*Papillaria nigrescens* (Hedw.) A. Jaeger								1	neo-asi	c	Dauphin 3359, INB	
m	Orthotrichaceae	*Groutiella mucronifolia* (Hook. & Grev.) H. A. Crum & Steere								1	neo	c	Dauphin 3361, INB	
m	Pottiaceae	*Anoectangium aestivum* (Hedw.) Mitt.						1			cos	s	Dauphin 3337, INB, MO	
m	Pottiaceae	*Gymnostomiella vernicosa* (Harv. in Hook.) Fleisch			1						pan	r	Dauphin 3276, INB, MO	*
m	Pottiaceae	*Hyophila involuta* (Hook.) A. Jaeger			1						cos	r	Dauphin 3274, INB, MO	
m	Pottiaceae	*Trichostomum sinaloensis* (E. B. Bartram) Zander					1				neo	r	Dauphin 3262, INB, MO	
m	Pottiaceae	*Uleobryum peruvianum* Broth.				1	1				neo	s	Dauphin 3263, 3374, INB, MO	**
m	Pterobryaceae	*Orthostichopsis tetragona* (Sw. ex Hedw.) Broth.								1	neo	c	Dauphin 3301, INB, MO	
m	Racopilaceae	*Racopilum tomentosum* (Hedw.) Brid.								1	neo-afr	r	Dauphin 3354, INB	
m	Sematophyllaceae	*Sematophyllum* sp.								1		c	Dauphin 3339, INB, MO	
		total	4	1	6	5	3	8	5	36				
Class	Family	Species	SJO	COC	CAT	GOL	PEL	PG	PR	CSE	dist	subs	ref.	notes

Localities:
CAT=Isla Catalina;
COC=Isla Cocinera;
CSE=Cerros Santa Elena;
GOL=Isla Golondrinas;
PEL=Isla Pelada;
PG=Playa Gringos;
PR=Playa Respingue;
SJO=Isla San José.

Substrates:
c=corticolous;
l=logs;
r=rock;
s=soil.

Distributions:
cos=cosmopolitan or subcosmopolitan;
cr-bra=Costa Rica-Brazil;
na-ca=north and Central America, mostly Mexico (na-ca-cu=also occurring in Cuba);
neo=neotropical;
neo-afr=amphiatlantic;
neo-asi=neotropical and Asian;
nsa-cr=northern South America and Costa Rica;
pan=pantropical.
*=New to Costa Rica;
**=New to Central America.

Table 2. Substrate use of the bryophytes on the Santa Elena Peninsula.

Substrate	Species number (%)
Corticolous	25 (47.2%)
On soil	15 (28.3%)
On rocks	7 (13.2%)
On logs	6 (11.3%)

Table 3. Geographical distribution of bryophyte species on the Santa Elena Peninsula.

Geographic element	Species number (%) n = 55
Neotropical	**28 (51.0%)**
Pantropical	**10 (18.2%)**
Amphiatlantic (Neotropical - African)	**6 (10.9%)**
North and Central America	**4 (7.3%)**
Subcosmopolitan	**3 (5.4%)**
Neotropical - Asian	**2 (3.6%)**
Costa Rica - Brazil	**1 (1.8%)**
Northern South America - Central America	**1 (1.8%)**