

Seasonally dry tropical forests of the Greater Antilles yield a new species of the Caribbean clade of *Castela*, *Castela plenaensis* (Simaroubaceae), an endemic to the southern slopes of the Sierra de Bahoruco, Dominican Republic

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Abstract

Recent collections in the seasonally dry tropical forests of Hispaniola have uncovered a new species of the American clade *Castela*, described here as *Castela plenaensis*, endemic to the eastern side of the western extension of the Sierra de Bahoruco in the Dominican Republic just south of the geological formation, Hoyo del Pelempito. *Castela plenaensis* forms part of the diverse, Greater Antillean Caribbean clade, the most species-rich group among all *Castela*, and is sister to another recently described Hispaniolan endemic, *C. senticosa*. We provide a description and illustration of the new species and place it phylogenetically, using morphologic and molecular data. We also provide an identification key to the three species of *Castela* on Hispaniola and a distribution map of these species. Also, we lectotypify *Castela depressa*, the type species of the genus, as well as *C. erecta*. The description of yet another species of *Castela* from Hispaniola further highlights the importance of the understudied, but yet biodiverse, seasonally dry tropical forests of the Greater Antilles.

Keywords Biodiversity · dioecy · flora · Hispaniola · Sapindales

Introduction

The genus *Castela* comprises roughly 16 species that are restricted to dry zones across the Americas, from the southern South American Chaco of Argentina, Bolivia, Brazil, Paraguay and Uruguay, to the Chihuahuan and Sonoran deserts. It also occurs in seasonally dry tropical forests (SDTF) of the Greater and Lesser Antilles, Mexico, and northern South America, as far south as northern Peru (Cronquist, 1944; Majure et al., 2021a; Pirani et al., 2021). The Greater Antilles are a hotspot of diversity of the clade, with ca. 8–10 species from two subclades represented there, the Depressa and Caribbean clades (Majure et al., 2021a,

2021d). Cuba is the most species-rich part of the distribution of the genus in the Greater Antilles, with five species recognized (Noa-Monzón, 2022), while Jamaica and Puerto Rico house only one species each (Majure et al., 2021d). Cronquist (1944, 1945) and Liogier (1985) recognized only one species from the island of Hispaniola, *C. depressa* Turpin, the type species of the genus (Turpin, 1806). Majure et al. (2021a) recently described *C. senticosa* Majure & Clase from the Sierra Martín García, Dominican Republic and Môle St. Nicolas, Haiti, and showed that *C. depressa* and *C. senticosa* belonged to two different clades, the Caribbean and Depressa clades, respectively (Majure et al., 2021a, 2021d).

More recently, herbarium studies and fieldwork on the southern slopes of the Sierra de Bahoruco surrounding the Hoyo del Pelempito have revealed yet another species for the island from the Caribbean clade, *C. plenaensis* sp. nov., described here. We place this species phylogenetically using plastome data, provide an illustration and photographic plate, a distribution map, and an identification key to all three species of *Castela* on Hispaniola. *Castela depressa* and *C. erecta* are lectotypified.

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Materials & Methods

Specimens from the following herbaria were consulted for ongoing systematic studies in the genus *Castela* (ASU, FLAS, JBSD, NY, SRSU, US). Material of the new species was uncovered while revising the collection at the herbarium of the Jardín Botánico Nacional “Dr. Rafael M. Moscoso” (JBSD), and a subsequent field survey was undertaken in May 2021 to search for populations in the Sierra de Bahoruco at Loma la Plena, near the town of Maniel Viejo. Fieldwork revealed material in bud of the new species. However, one week later, W. Miniyeti discovered a larger population with fruiting material. Another survey of that population one year later in April 2022 by Miniyeti revealed flowering and fruiting (immature) material of the

new species (Figs. 1–2). Measurements of the new species of *Castela* followed the methods of Majure et al. (2021a), and material from the type specimen, as well as that of *Miniyeti* s.n. were used for illustration.

We extracted DNA from leaves of *Clase* 6245 using a modified CTAB extraction protocol as in Majure et al. (2021a). Whole genomic DNAs were sent to Rapid Genomics for library preparation and sequencing on the Illumina HiSeq X platform using pair-end reads (150 bp). Raw reads were then assembled using reference mapping based on the *Ailanthus altissima* (Mill.) Swingle chloroplast genome (Saina et al., 2018), following the methods of Majure et al. (2021a). Briefly, after reference mapping the entire chloroplast genome, one of the inverted repeats (IRb) was removed before alignment to the Majure et al.

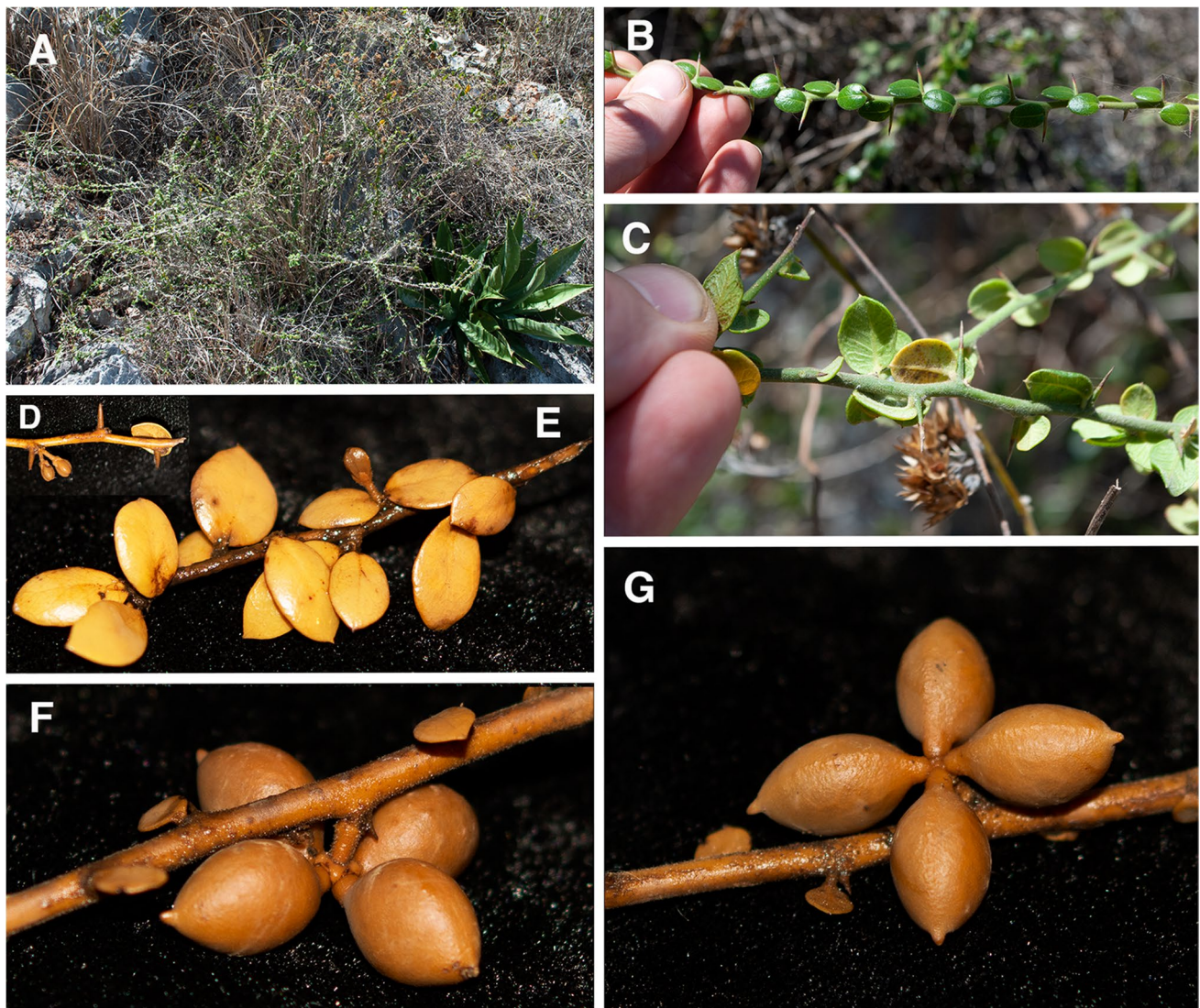


Fig. 1. *Castela plenaensis*. **A** erect, shrubby habit with pendent branches of *C. plenaensis* in seasonally dry tropical forest habitat over limestone, **B** shiny, adaxial leaf surfaces and simple thorns, **C**, abaxial leaf surfaces showing sparse indumentum leaving the epidermis visible and showing brachidodromous venation, **D–E** showing axillary inflorescences (buds of staminate flowers), **F–G** scythe-shaped fruit of *C. plenaensis* (dorsal vs. ventral surfaces). **A–C** from Majure 8716 and **D–G** from Miniyeti s.n. All photos taken by L.C. Majure.

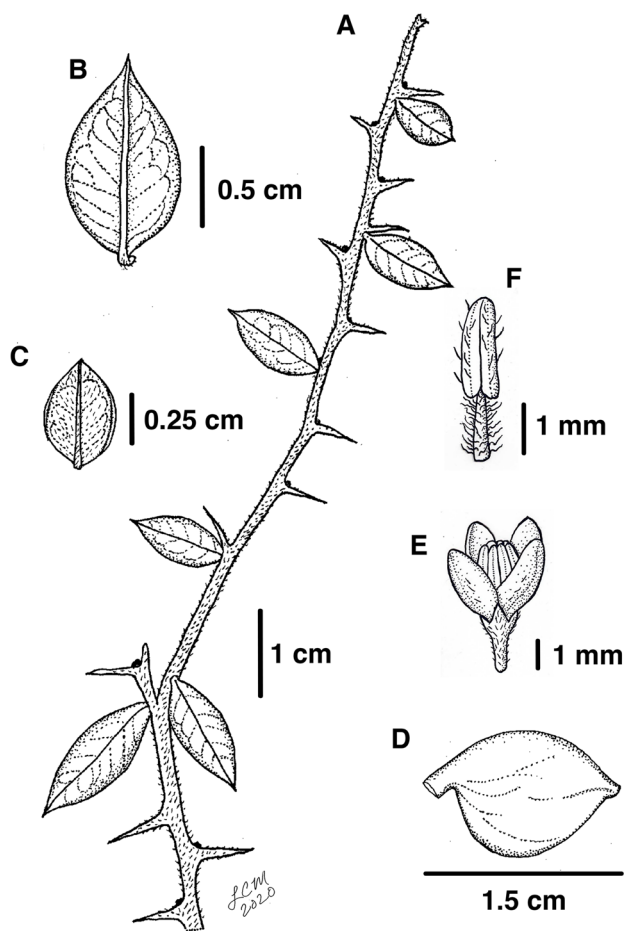


Fig. 2. Illustration of *Castela plenaensis*. **A** Habit showing simple thorns and pubescent stems, **B**, leaf adaxial surface showing brachidromous venation, **C** leaf abaxial surface showing indumentum and revolute leaf margins, **D** scythe-shaped fruit showing stipitate base, **E** staminate flower showing abaxially pubescent petals, and **F** stamen showing pubescent filaments and thecae. A–D from the type specimen (Clase et al. 6245), and E–F from *Miniyeti s.n.*

(2021a) dataset. We aligned the sequence of the new species using MAFFT (Kato & Standley, 2016) with sequences for all species of *Castela* so far generated based on a reduced

dataset (reduced from 30 to 16 terminals) derived from Majure et al. (2021a). We then carried out a maximum likelihood analysis with RAxML (Stamatakis, 2014) using the GTR + gamma model of molecular evolution in Geneious (Biomatters, Inc.), undertaking 1000 rapid bootstrap pseudoreplicates. Our plastome dataset and tree are available on Figshare (<https://doi.org/10.6084/m9.figshare.24843588>). The raw data for *Castela plenaensis* are deposited on GenBank (PRJNA750771) (Fig. 2).

Results

The new species, *Castela plenaensis*, was resolved as sister to the recently described *C. senticosa* (Fig. 3). Both species share the same hair type of unicellular, translucent hairs that although dense, do not completely cover the abaxial leaf and stem epidermis (a character differing from the more distantly related *Depressa* clade, which has appressed, dense gray to white hairs that completely obscure the abaxial leaf and stem epidermis; Majure et al., 2021d). Both *C. plenaensis* and *C. senticosa* also have large fruit, which is a common feature in the Caribbean clade, and which also differs from the members of the *Depressa* clade, which have smaller fruit (see description and key).

Castela plenaensis differs dramatically from *C. senticosa* by the simple thorns and persistent leaves, as compared to the multibranched (compound) thorns and ephemeral leaves of *C. senticosa*. *Castela senticosa* also produces small, scale-like leaves on the highly modified, multibranched thorny stems, while these are absent in *C. plenaensis*. *Castela senticosa* has orange-red fruit. Based on the few specimens seen, *C. plenaensis* has pinkish-red fruit. Both species have white flowers, a likely synapomorphy for this clade of two known species (see Majure et al., 2021a, 2021d), and asymmetrical and slightly laterally flattened, scythe-shaped fruit with a moderately elongate stipe. Thus, both morphologic and phylogenetic data clearly place the new species in the Caribbean clade (Figs. 1–3) and provide evidence for its sister relationship with *C. senticosa*.

Key to the species of *Castela* on Hispaniola

1. Erect shrubs with highly ramified thorns.....*C. senticosa*.
1. Sprawling to erect shrubs, thorns unramified (simple).....2.
2. Leaves obscurely veined, abaxial surface covered in dense indumentum of appressed, white hairs obscuring epidermis; fruit small, 7–10 × 4.8–6 mm.....*C. depressa*.
2. Leaves clearly pinnately veined, abaxial surface covered in indumentum of erect to ascending, translucent hairs, not obscuring epidermis; fruit larger, 13–15 × 9–10 mm.....*C. plenaensis*.

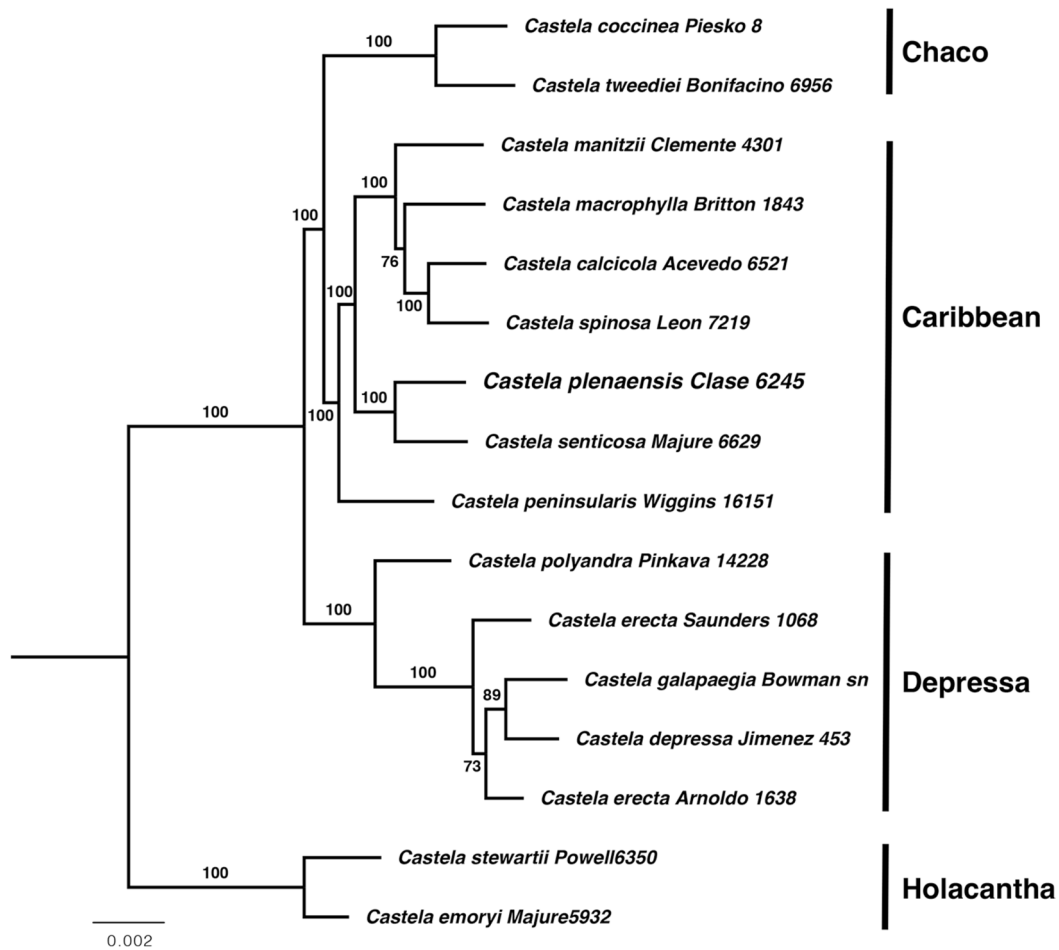


Fig. 3. Phylogeny including the new species, *C. plenaensis*, showing sister relationship to the Hispaniolan endemic *C. senticosa*, both of which are part of the Greater Antillean Caribbean clade. Note that material previously referred to as *C. jacquiniifolia* Ekman ex Urb. in Majure et al. (2021a) based on Clemente 4301 is referable to the recently described species, *C. manitzii* A.Noa (Noa-Monzón, 2022). Bootstrap values are given above branches, and collector names and numbers are given after species names.

Taxonomic Treatment

***Castela plenaensis* Majure & Clase, sp. nov.** TYPE: La Española. República Dominicana. Prov. Bahoruco. Loma la Plena, en el firme, yendo hacía El Sabinal, zona limítrofe entre las Provincias de Barahona y Pedernales, UTM 240054 E, 1995693 N (18.03418°N, -71.45536°W), 1038 m, 4 ago 2010, T. Clase et al. 6245 (holotype: JBSD!, isotype: FLAS!).

Diagnosis. Differing from the sister and phenetically similar species, *Castela senticosa*, by the simple vs. ramified thorns, persistent vs. ephemeral leaves, and the absence of scale-like leaves in *C. plenaensis* (vs. present in *C. senticosa*).

Description. Erect shrub to 0.6 m tall, with pendent branches; stems with simple (unramified) thorns 3.5–9 mm long, stems pubescent with ascending to spreading, uniseriate, translucent hairs; leaves nearly sessile, petioles 0.6–1 mm long, blades 7–17 × 4–7 mm, ovate to elliptic, bases rounded, apices acute, broadly acute to rarely emarginate, with a mucronate apex and conspicuous, brochidodromous secondary veins, adaxial surface lustrous, sparsely pubescent with uniseriate, ascending to spreading translucent hairs, abaxial surface densely pubescent with uniseriate, ascending to spreading, translucent hairs, leaves mostly appressed to the upper surface of the stem and apparently maintained on the plant for long durations (i.e., not ephemeral), scale-like leaves absent; flowers (staminate) in axillary, cymose clusters; staminate flowers: pedicels 1.5–2.6 mm, sepals 4–5, 1.1–1.2 × 0.8–1 mm, ovate, green, covered with erect to ascending, translucent,

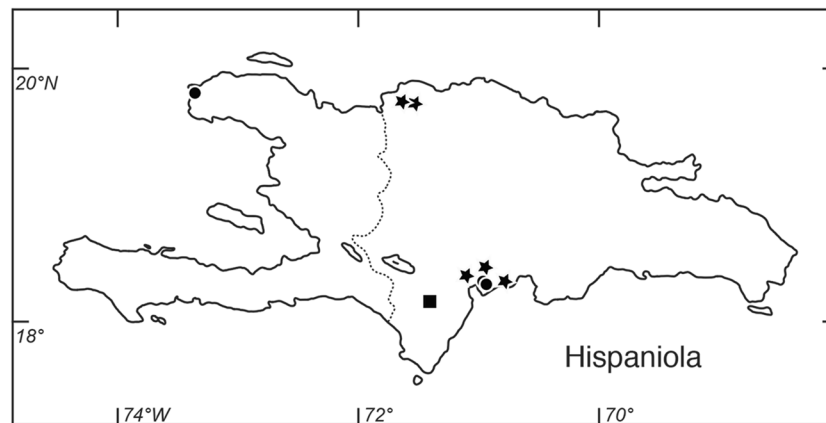


Fig. 4. Map of the distribution of *Castela plenaensis* (square), *C. senticosa* (circles) and *C. depressa* (stars) on Hispaniola. Points for *C. depressa* and *C. senticosa* are based on Majure et al. (2021d).

uniseriate hairs, hair apices with a black gland; petals 4–5, white, ovate to elliptic, slightly keeled or rounded abaxially $2.5\text{--}5.3 \times 1.4\text{--}3$ mm, bases unguiculate or merely acute, apices rounded, often hooded, glabrous or with a few uniseriate, erect, translucent hairs along abaxial surface; stamens 8–10, filaments densely, long pubescent, 1.3–2.1 mm long, anthers $1.9\text{--}2.3 \times 0.8\text{--}0.9$ mm, sagittate at the base, apices acute to slightly rounded, with occasional translucent, uniseriate hairs on the thecae; carpellate flowers unknown; fruit drupes, $13\text{--}15 \times 9\text{--}10$ mm, scythe-shaped, pinkish-red, with a stipe-like base, endocarp surface smooth.

Additional Specimens Examined. DOMINICAN REPUBLIC. Prov. Bahoruco Loma la Plena, en el firme, en ruta hacia El Sabinal, ca. 14 km al noroeste de Maniel Viejo (Jorgillo), 18.03588°N , -71.45277°O , 975 m, 24 mayo 2021, *Majure 8716* (FLAS, HAJB, JBSD, NY). Loma la Plena, en el firme, en ruta hacia El Sabinal, ca. 14 km al noroeste de Maniel Viejo (Jorgillo), 13 abril 2022, *Miniyeti s.n.* (FLAS, JBSD). Note: *Miniyeti s.n.* possesses both carpellate (fruit) and staminate (flowers) reproductive organs.

Etymology. The specific epithet “*plenaensis*” refers to the type locality, Loma la Plena of the eastern flank of the western portion of the Sierra de Bahoruco, just south of Hoyo del Pelempito.

Phenology. This species is known from only three collections. It was collected in fruit August 2010 (type cited above) and in bud in May 2021 (*Majure 8716*, cited in Additional Specimens Examined), then fertile once again with both flowers and immature fruits in April 2022 (*Miniyeti s.n.*). Mature fruit were also seen and photographed by W. Miniyeti in the latter part of May 2021 from a nearby population with dozens of individuals.

Distribution & Habitat. *Castela plenaensis* is endemic to the SDTF between the western and eastern

high elevation forests of the Sierra de Bahoruco in the Dominican Republic, just south of the Hoyo del Pelempito (Fig. 4). It is the only species of *Castela* known from the “South Island” of Hispaniola, which represents a biogeographic region frequently differing in species composition from the “North Island” of Hispaniola (Schwartz, 1980; Judd, 2007; Majure et al., 2016, 2021b; Landestoy et al., 2018; Nieto-Blázquez et al., 2021; Viñola-López & Almonte, 2022).

Castela plenaensis occurs in SDTF over dogtooth limestone and has been collected with the following associates: *Agave antillarum* Descourt., *Amyris elemifera* L., *Arcoa gonavensis* Urb., *Bursera simaruba* (L.) Sarg., *Celtis trinervia* Lam., *Chrysophyllum oliviforme* L., *Clusia rosea* Jacq., *Colubrina elliptica* (Sw.) Brizicky, *Eugenia foetida* Pers., *E. linearis* (Rich. Ex O.Berg, *Ficus trigonata* L., *Gouania lupuloides* Urb., *Hybanthus havanensis* Jacq., *Krugiodendron ferreum* (Vahl) Urb., *Melinis repens* (Willd.) Zizka, *Opuntia taylorii* Britton & Rose, *Pilosocereus polygonus* (Lam.) Byles & G.D.Rowley, *Senna atomaria* (L.) H.S.Irwin & Barneby, *Sideroxylon foetidissimum* Jacq., *Tillandsia usneoides* (L.) L., and *Zanthoxylum nashii* P.Wilson.

Species Concept

Populations of *Castela plenaensis* are disjunct from those of *C. senticosa*, and thus, could be considered reproductively isolated from that species, therefore upholding a biological species concept (Mayr, 2000). Morphologically *C. plenaensis* is divergent from its sister taxon, *C. senticosa*, thus conforming to phenetic and diagnosable species concepts (Wheeler & Platnick, 2000; Judd, 2007).

Lectotypifications

Castela depressa Turpin, Annales du Muséum d'histoire Naturelle 7: 79. 1806. TYPE: L'île de Saint-Domingue, entre Mont-Christ et Saint-Yague, 1805, *M. Turpin s.n.* (**Lectotype designated here:** P, P00679098, online image!).

Turpin did not expressly state the repository for the type of *C. depressa*. The specimen donated to Jussieu's herbarium by Turpin in 1805, which was then donated to P by Jussieu's children in 1857 (according to labels on the type specimen), clearly was intended to be the type of the species.

Castela erecta Turpin, Annales du Muséum d'histoire Naturelle 7: 80. 1806. TYPE: Antigua, *Richard s.n.* (not found). **Lectotype** designated here: Illustration of the type specimen in Turpin (1806), plate 5, figure B, b, 1–4 (in Figure 5 of this present paper), as no specimens of *C. erecta* collected by Richard from Antigua have been found. The illustration clearly shows the vegetative and floral features of this species, which reliably distinguish it from close relatives.

Discussion

The discovery of yet another species of the genus *Castela* on the island of Hispaniola suggests that the SDTF communities on the island are still in need of floristic and systematic work to fully understand the biodiversity of the region (Majure et al., 2021b, 2021c, 2021d). Ongoing threats from charcoal production, overharvesting of selected tree and shrub species, and deforestation for agriculture in the SDTF of Hispaniola make it all the more important for concerted efforts to better understand the biodiversity of these diverse forests in a biodiversity hotspot (Myers et al., 2000; Acevedo-Rodríguez & Strong, 2008). Forests near the type locality of *C. plenaensis* are currently being cut for small-scale agriculture, and this activity could pose a threat to the apparently small populations of the species in the area.

The disjunct distributions of both *C. depressa* and *C. senticosa* are intriguing. *Castela senticosa* occurs in the Sierra Martín García and northwestern Haiti near Mole St. Nicolas.

Castela depressa occurs in northern Dominican Republic in the Monte Cristi region, as well as around the Sierra Martín García and south of Azua along the southern coast of the North Island (Fig. 4). Both of these species are “North Island” endemics in contrast to *C. plenaensis*, which is restricted to the “South Island”, based on the few collections known for the species. The more widespread, but disjunct, distributions of *C. depressa* and *C. senticosa* may be real, or they could also represent a lack of collections across SDTF over the island. This is especially concerning for Haiti, where precious few modern plant collections have been made, and collections are most notably lacking in SDTF. However, presumed bird dispersal of *Castela* could account for the disjunct distributions of these species. Regardless, species of *Castela* on Hispaniola are overall greatly restricted in population sizes and distributions, a similar pattern to that seen across Cuba (Noa-Monzón, 2022).

The Hoyo del Pelempito, a large geological depression, and adjacent areas may act as a significant barrier to vegetation between the eastern and western cloud forests of the range, as well as to the north and south of the Sierra de Bahoruco. In *Miconia* (Melastomataceae), sister species or close relatives are often found on either side of the depression in higher elevation cloud forest of western and eastern ranges of the Sierra de Bahoruco (e.g., Majure et al., 2018), potentially providing evidence for the influence of this geological structure acting as a barrier to gene flow. Phylogeographic analyses within species or close relatives would greatly inform this biogeographic hypothesis. The genus *Leptocereus* (Cactaceae) shows a pattern between the northern and southern slopes of the Sierra de Bahoruco, where the closely related species *L. demissus* Areces to the south and *L. velozianus* Clase, Encarnación, Peguero & Majure to the north are found on either side of the sierra (Majure et al., 2021c; Encarnación et al., 2023), thus showing the potential for influence of the Hoyo del Pelempito as a disrupting barrier among these populations in SDTF.

Yet another species of *Castela* described from SDTF on Hispaniola underscores the current incomplete understanding of the biodiversity of these forests, especially in the Greater Antilles (see also Acevedo-Rodríguez & Strong, 2008). Further exploration and continued fieldwork are an absolute imperative to fully appreciate the role these forests have played in the evolution of the Antillean flora. With the global destruction of SDTF an ever-increasing problem (Banda et al., 2016), we must vigorously work to understand and protect these unique communities.



Fig. 5. Illustration of *Castela depressa* (A, 5–14) and *C. erecta* (B, b, 1–4) taken from Turpin (1806). We lectotipify *C. erecta* using the illustration of the habit, vegetative and floral features (B, b, 1–4).

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Data Availability

Our plastome dataset and tree are available on Figshare (<https://doi.org/10.6084/m9.figshare.24843588>). The raw data for *Castela plenaensis* are deposited on GenBank (PRJNA750771).

Declarations

Conflict of interest

The authors have no competing or conflicting interests.

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