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A BOTANICAL INVENTORY OF FOREST ON KARSTIC LIMESTONE AND METAMORPHIC SUBSTRATE IN THE CHIQUIBUL FOREST, BELIZE, WITH FOCUS ON WOODY TAXA

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The Chiquibul Forest Reserve and National Park in Belize is a priority conservation area within the 'Maya Forest' in Central America. Although taxonomic data are essential for the development of conservation plans in the region, there is limited knowledge of the existing species in the area. Here we present a botanical species list of mostly woody taxa based on voucher specimens, with particular focus on the Raspaculo watershed in the eastern part of the National Park. Within the Raspaculo watershed, a comparison is made between 0.1 ha of valley floor and 0.1 ha of hilltop vegetation, sampling trees, shrubs, palms and lianas ≥2.5 cm diameter at breast height. Additionally, a 1 ha plot was established in the Upper Raspaculo watershed. Our study shows 38 new species records for the region, and important additions to the flora of Belize. New records were recorded from forests on both metamorphic and karstic substrate, including previously overlooked hilltop forest elements. Quantitative assessment of vegetation across elevation zones shows distinct elements dominating on valley floors and hilltops. Our results show that the Chiquibul contains at least 58% of Belize's threatened plant species, and represent a source of information for the management and conservation of the area.

Keywords. Conservation, floristic affinity, karstic terrain, La Selva Maya, limestone forest, Maya Forest, Mesoamerica, threatened species.

Introduction

The Chiquibul Forest Reserve and National Park (CFRNP) in Belize is a priority conservation area within the 'Maya Forest' in Central America. The Maya Forest is

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the largest continuous tropical rain forest in Central America, a region that holds around 8% of the world's described vascular plant species, of which over 20% are endemic to the region (Myers *et al.*, 2000; Bridgewater *et al.*, 2006a). Due to its high biodiversity value and its high level of threat, it is the second most important of the 25 global hotspots (Conservation International, 2004). Located to the east of the Rio Chiquibul-Montañas Maya Biosphere Reserve in the Guatemalan Petén ecoregion, the CFRNP is situated within one of eight key conservation areas in the northern Mesoamerican ecosystem profile of the Critical Ecosystem Partnership Fund and forms part of the Mayan Forest corridor (Conservation International, 2004). At over 1744 km^2, the Chiquibul region comprises part of Belize's largest remaining forest, much of which occurs on karstic limestone terrain. Due to its remoteness, the eastern part of the Chiquibul remains botanically little explored (Bridgewater *et al.*, 2006a).

Karst is globally rare, but roughly half of the Caribbean and 25% of Central American landscapes are karstic, including the Greater Antilles, the Yucatan Peninsula and the Guatemalan Petén region (Kueny & Day, 1998, 2002). Belize, in particular the Chiquibul Forest, harbours significant areas of limestone forest. Studies of tropical forests over limestone are rare due to its restricted distribution, but also because the steep terrains are difficult to access (Kelly *et al.*, 1988).

The Chiquibul region is of high biological importance, providing key habitat for endangered and locally threatened species of vertebrates, including tapir (*Tapirus bairdii*), jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), spider monkey (*Ateles geoffroyi*) and the Central American scarlet macaw (*Ara macao cyanoptera*). While a provisional checklist of the vascular plants exists, this list is biased towards easily accessible sites (e.g. Guacamallo Bridge, Las Cuevas Research Station). Bridgewater *et al.* (2006a) show that of the total 7047 herbarium specimens known from the Chiquibul Forest, both the Upper and Lower Raspaculo area were extremely poorly represented, with only <50 and <200 collections, respectively. Several expeditions have been carried out in the area (Rogers & Sutton, 1991; Rogers *et al.*, 1994; Rogers, 2001) but, to our knowledge, no herbarium specimens were collected. Since most conservation prioritisation at global and local levels is based on species distributions and species threat status assessments (Myers *et al.*, 2000; Grenyer *et al.*, 2006; Joppa *et al.*, 2013), systematic collections are essential for local and site-specific biodiversity management. Complete species lists allow conservation managers to identify potentially restricted species distributions and compare and contrast forest types, ultimately establishing local biodiversity 'hotspots' of particular conservation concern (Kim & Byrne, 2006; Meerman, 2007). During recent decades, however, traditional taxonomy has been severely neglected (Boero, 2010) and the lack of site-specific knowledge is hampering applied conservation efforts.

The CFRNP consists of the Chiquibul Forest Reserve (CFR, 59,822 ha), the Chiquibul National Park (CNP, 106,838 ha), and the Caracol Archaeological Reserve (10,339 ha) (Conservation International, 2010; Friends for Conservation and Development, 2011). The CFR and CNP together comprise lowland to submontane broadleaved forest types ranging from semi-deciduous to evergreen, as well as riverine vegetation along the Macal and Raspaculo Rivers. The latter are important wildlife refuges, particularly during the dry season (Minty *et al.*, 2001).

The area occupied by riverine habitat in Belize is declining as a result of the construction of a series of hydroelectric dams (Chalillo, Mollejon and Vaca) on the Macal River. Much of the riverine forest in the Macal and Raspaculo watersheds was lost following the filling of the Chalillo Dam in 2006. The Raspaculo River is a large tributary to the Macal, and its lower reaches have now become part of the Chalillo reservoir. The riverine forest of the Upper Raspaculo region of the CNP thus comprises some of the last vestiges of this once more widely distributed vegetation type. Together, the Macal and Raspaculo watersheds hold 60% of Belize's broadleaved lowland riverine habitat, mostly on karstic but also on metamorphic rock (Minty *et al.*, 2001). However, the increased accessibility created by the Chalillo reservoir now also newly exposes the remaining habitat to regional threats such as deforestation, poaching, Xaté extraction and expansion of agriculture including cattle ranching (Conservation International, 2004; Bridgewater *et al.*, 2006b; Young, 2008; Briggs *et al.*, 2013).

Although there is a broad vegetation classification of Belize based on satellite data (Penn *et al.*, 2004), little is known about plant community composition within particular forest types. This is especially the case for the Upper Raspaculo region and the dry hilltop vegetation across the Chiquibul. Brewer *et al.* (2003) studied limestone vegetation across an elevation gradient, showing interesting phytosociological patterns and details of composition. Only a few studies of the Chiquibul Forest exist (Bird, 1998; Urban *et al.*, 2006; Cho *et al.*, 2013). Cho *et al.* (2013) focused on disturbed areas of the Western Chiquibul lowland forest based on data from Bird (1998), while Urban *et al.* (2006) studied phytosociology of seasonally inundated riverine vegetation. Quantitative vegetation studies are now needed to improve our understanding of the vegetation types within the Chiquibul Reserve across the elevation gradient within the context of Belize and the wider Petén region that hosts vast areas of tropical limestone broadleaved forest.

Here we present a floristic study of the eastern part of the Chiquibul Forest Reserve and National Park, focusing on the least collected areas identified in Bridgewater *et al.* (2006a). Our study aims to improve taxonomic documentation of the local biodiversity specifically in the Upper and Lower Raspaculo, and at Natural Arch, which lies further south. A comparison is made between 0.1 hectare datasets across elevation zones sampling trees, shrubs, palms and lianas. Additionally, we present data for one 1 ha plot from Upper Raspaculo. The results show clear differences between hilltop and valley floor vegetation communities, and include new species records for the area.

Study Site

The climate of Belize has a pronounced dry season (Dubbin *et al.*, 2006) and an average annual temperature of 26°C. The onset of the seasons is controlled by the position of the Intertropical Convergence Zone (ITCZ) which brings increased precipitation between late May and December (Gischler *et al.*, 2008; Bhattacharyaa *et al.*, 2011). Rainfall is particularly variable in the Maya mountains where precipitation decreases towards the northwestern flanks, with c.1000–2500 mm annual rainfall in the CFRNP (Pérez *et al.*, 2011).

Three major locations within CFRNP were sampled during this study with particular focus on the Raspaculo watershed in the east: (1) Natural Arch; (2) Lower Raspaculo; (3) Upper Raspaculo at Cuxta Bani (Fig. 1, Table 2). The Raspaculo River runs through the CNP from east to west before turning north and flowing into the Macal River. The watershed encompasses c.150 km^2 of mainly karstic limestone terrain with metamorphic substrates present at the upper reaches (Bateson & Hall, 1977). Water levels in the Raspaculo River fluctuate dramatically during the year depending on rainfall. The Lower Raspaculo was accessed from Chalillo Dam by canoe and flat-bottomed boat. Study sites in the Lower Raspaculo were reached by canoes and on foot, and Cuxta Bani was reached by canoe.

The different study sites (Table 2) mapped into two of Meerman & Sabido's (2001) broadleaved vegetation types, including the 'Tropical evergreen seasonal broadleaved lowland hill forest, Simarouba-Terminalia variant' [UNESCO classification code I.A.2.a.(1).(a).-ST] in the Lower Raspaculo and Cuxta Bani in the Upper Raspaculo. Natural Arch was classed as 'Tropical evergreen seasonal broadleaved submontane forest over rolling calcareous hills' [I.A.2.b.(1).K-r]. Penn *et al.* (2004) map all Lower Raspaculo and most Natural Arch transects as 'Deciduous forest' but distinguish Cuxta Bani as 'Semi-evergreen lowland forest' (Table 2). The substrate at the Lower Raspaculo is karstic with sedimentary deposits along the river channel whilst karstic limestone is absent from Cuxta Bani in the Upper Raspaculo where substrates are metamorphic and sedimentary (Bateson & Hall, 1977).

Methods

Floristic surveys across the study sites were done along 0.1 ha transects, on one 1 ha plot, and by general collecting (Fig. 1, Table 2). Woody vegetation was studied along transects in Natural Arch and Lower Raspaculo, while the 1 ha plot was established in Cuxta Bani. General collecting was done around Natural Arch on the Chiquibul River during May and around Lower Raspaculo in June and July, where additional fertile material, mainly of woody taxa, was collected along paths and around camp. The aim was to supplement infertile material from the transects so that more taxa could be determined; herbs and epiphytes were mostly ignored.

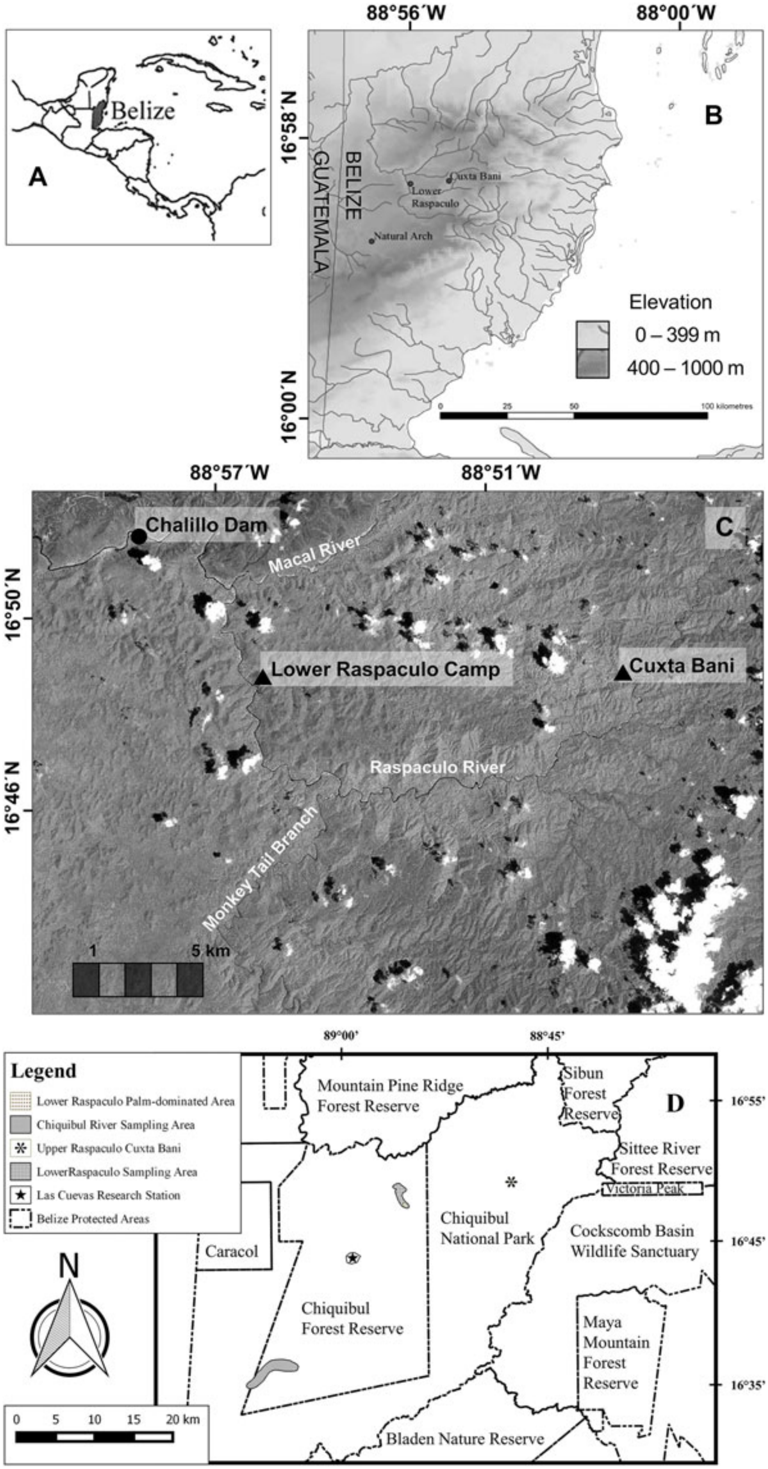
Quantitative 0.1 ha vegetation transects were done following the methodology of Gentry (Gentry, 1982b; Phillips & Miller, 2002) in which all individuals ≥2.5 cm DBH (diameter at breast height, i.e. 130 cm) within 10 lines of 2 × 50 m area were recorded. A total of forty 2 × 50 m transects were assessed across the study sites, totalling 0.4 ha. Eleven transects were placed near Natural Arch within an elevational range of 500–600 m, and the remaining 29 in the Lower Raspaculo. Of the 29 transects in the

Lower Raspaculo, 11 were placed on hilltops at 550–610 m elevation and 10 close to rivers on valley floors at c.410–470 m elevation in order to compare floristic composition in the visually distinct vegetation types along the elevational gradient in the karstic terrain. A further eight transects were placed in valley floors in areas with differing reflectance values as revealed by LANDSAT ETM 4-5-7 (RGB) satellite imagery. Species abundance data within equal areas of 0.1 ha were then compared between the Lower Raspaculo hilltops and the valley floors in terms of stem density, species importance value (Mori *et al.*, 1983) and species composition. At Natural Arch, only two size classes were recorded: above and below 10 cm DBH. All other transects recorded exact diameter measurements.

The 1 ha plot was established according to RAINFOR methodology (Phillips & Baker, 2002). All woody stems of ≥10 cm DBH were recorded, including lianas. Due to lack of tree climbing equipment, 15% of the stems remained unvouchered. The plot data were used to measure the total stem basal area (BA), relative abundance, frequency, dominance, and the resulting importance value (IV) of all taxa following the methodology of Mori *et al.* (1983). Sterile vouchers of all species were collected in all vegetation transects and the 1 ha plot, including unidentified 'morphospecies'. Fertile specimens were collected with six duplicates, while non-fertile material was vouchered with two duplicates only. Duplicates of all vouchers have been deposited at Belmopan Forestry Department herbarium (BRH) and the Royal Botanic Garden Edinburgh (E). Further duplicates of specific families, where available, have been sent to BM (Solanaceae), MO (Rubiaceae), K (Leguminosae) and HBG (Lauraceae). Wood collections of lianas were made to aid species identification using stem anatomical characters, and are deposited at E.

Some of the determinations of voucher material by family experts include cf. qualifiers, given in the text and in Table 1. In cases where specimens both with cf. qualifier and without were identified, the cf. identifications are not listed in Table 1. 'Cf. cases' are treated as valid identifications that nonetheless do not hold the same level of confidence as those without the cf. qualifier. We refrain from downgrading these cf. determinations to generic rank, as the cf. determinations were given by experts in their group.

The authorities of species names follow Brummitt & Powell (1992) and are given in the text upon first mention and provided in Table 1. All species names were checked in TROPICOS, and new records were also checked in Flora Mesoamericana (2014). The species list was matched with the Catalogue of Life (CoL; Roskov *et al.*, 2014), and IUCN Red List status of each species was retrieved from the IUCN Red List official website, using the R package Taxize (Chamberlain & Szocs, 2013; Chamberlain *et al.*, 2014). The TROPICOS database was checked for further publications on species status assessments. Table 1 lists all species determined below genus rank, and functions as a preliminary species list for this study. All taxa listed in Table 1 have been collected, and a voucher specimen deposited at E, except most Arecaceae, *Pleradenophora tuerckheimiana* (Pax & K.Hoffm.) A.L.Melo & Esser, *Pimenta dioica* (L.) Merr. and *Ceiba pentandra* (L.) Gaertn., records of which stem from field



Belize
A
88°56´W
88°00´W
16°58´N
16°00´N
B
BELIZE
GUATEMALA
Cuxta Bani
Lower Raspaculo
Natural Arch
Elevation
0 – 399 m
400 – 1000 m
88°57´W
88°51´W
16°50´N
16°46´N
C
Chalillo Dam
Macal River
Lower Raspaculo Camp
Cuxta Bani
Raspaculo River
Monkey Tail Branch
1
5 km
89°00'
88°45'
16°55'
16°45'
16°35'
Legend
Lower Raspaculo Palm-dominated Area
Chiquibul River Sampling Area
Upper Raspaculo Cuxta Bani
LowerRaspaculo Sampling Area
Las Cuevas Research Station
Belize Protected Areas
D
Mountain Pine Ridge Forest Reserve
Sibun Forest Reserve
Sittee River Forest Reserve
Victoria Peak
Chiquibul National Park
Cockscomb Basin Wildlife Sanctuary
Caracol
Chiquibul Forest Reserve
Maya Mountain Forest Reserve
Bladen Nature Reserve
N
0 5 10 15 20 km

observations only. Taxa identified to genus level or above have not been included in Table 1, as they are not informative for the objective of this list. However, if these taxa constitute a significant quantitative element despite their low taxonomic resolution, they do appear in tables and figures. Family delimitations follow APG III (The Angiosperm Phylogeny Group, 2009).

Brewer *et al.*'s (2003) studies have revealed differences in phytogeographical affinities between high elevation karstic vegetation types and lower elevation valley floor forests in the Bladen Nature Reserve in southern Belize (Fig. 1D). To explore the effect of phytogeography in our study, we recorded the phytogeographical affinities of each species in our dataset using Wendt's (1993) coding method. Wendt's (1993) delimitation separates Central and South American species into four phytogeographical units based on the known southernmost extent of a species' distribution (Fig. 2): (1) northern Central America (N-MA), encompassing Mexico and the area north of the northern Nicaraguan border; (2) Mesoamerica (MA), including species assumed not to occur south of the southern Panamanian border; (3) northern South America (N-SA), with species occurring in the Guiana Shield and northwestern South America (including Colombia, Venezuela and Ecuador); and (4) South America (SA), with species reaching Brazil, Peru and further south. A fifth category was used following Wendt (1993) and Gentry (1982a) to test whether floristic affinities existed with the Greater Antilles, to which Belize has close ties (Brewer, pers. comm.). Species occurring on islands including Puerto Rico northwards were coded part of the Greater Antilles, whereas species occurring on the Lesser Antilles (e.g. Windward and Leeward Islands, Trinidad and Tobago) were classified as part of the Guiana Shield (Fig. 2). Species distributions were recorded based on occurrence records available through the TROPICOS database (www.tropicos.org, Missouri Botanical Garden, accessed 9 May 2009).

Results and Discussion

New species records for Belize and the Chiquibul

A total of 1359 voucher specimens were collected during the study, including 85 wood samples of lianas, 38 of which also have leaf material (Table 1). These collections represent 397 distinct taxa belonging to 87 families and 218 genera (Table 1). A total of 258 taxa (65%) were identified to species rank (including 'cf.' identifications), 56 (16%) taxa to genus, and 51 taxa (13%) to family only. Twenty-three (6%) taxa, including 10 lianas, remained unidentified even to family. Combining these figures

Fig. 1. Location of study sites in Belize. (A) Location of Belize within Central America. (B) The Greater Maya Mountains in southern Belize with three major collecting localities of the study. (C) Detailed location of study sites within the Raspaculo watershed (Landsat Enhanced Thematic Mapper image, 18 February 2002, pixel resolution 30 m, Global Land Cover Facility, www.landcover.org). (D) Overview of all collection localities in relation to the Belize Protected Areas from BERDS (Meerman & Clabaugh, 2015).

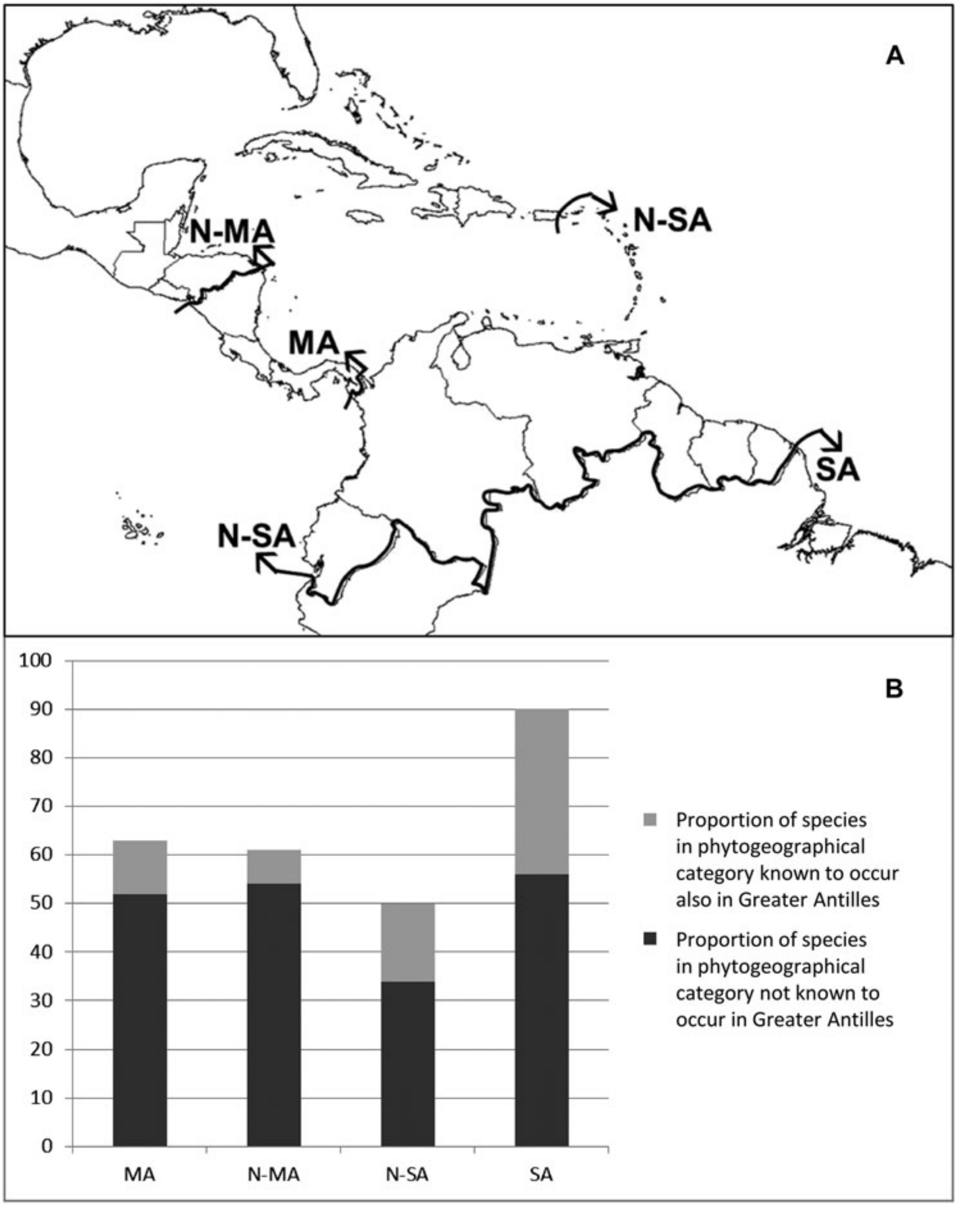


FIG. 2. (A) Map of Central and northern South America showing Wendt's (1993) four phytogeographical categories along political boundaries. N-MA = Northern Mesoamerica, extending as far south as the northern Nicaraguan border; MA = Mesoamerica until eastern Panamanian border; N-SA = Northern South America including the Lesser Antilles, i.e. south from Puerto Rico; SA = South America south from northern borders of Peru and Brazil. (B) Distribution of Wendt's phytogeographical categories across taxa from all study areas combined, i.e. a compilation of general collecting and quantitative surveys within the Chiquibul Forest. Known southernmost species distributions stem from TROPICOS accessed May 2009.

TABLE 1. Species checklist resulting from collections (n = 1359) across all study sites. See table footnotes for details

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Actinidiaceae				
Saurauia yasicae Loes.	t	Bayly, D.W.R. 163	UR; LR-v	SA
Anacardiaceae				
Spondias mombin L.	t	Vandrot, H. 100	LR-v, -h, -p, -s; CR	N-SA
Annonaceae				
Annona reticulata L.	t	Pennil, C. 17	LR-h, -s; CR	SA†
***Annona scleroderma* Saff.**	**t**	**Särkinen, T. 528**	**UR**	**MA**
Cymbopetalum cf. *mayanum* Lundell	t	Vandrot, H. 54	LR-v, -s; UR; CR	N-MA
Mosannona depressa (Baill.) Chatrou	t	Vandrot, H. 12	LR-h; CR	N-MA
Apocynaceae				
Aspidosperma desmanthum Benth. ex Müll.Arg.	t	Baden, H.M. 136	LR-v, -h; CR	SA
Aspidosperma megalocarpon Müll.Arg.	t	Baden, H.M. 79	LR-v, -h, -p, -s; CR	N-SA
Forsteronia myriantha Donn.Sm.	l	Matthews, A.C. 70	LR-v, -s; CR	SA
***Marsdenia laxiflora* Donn.Sm.**	**l**	**Bayly, D.W.R. 164**	**CR; LR-v**	**MA**
***Odontadenia macrantha* (Roem. & Schult.) Markgr.**	**l**	**Matthews, A.C. 72**	**CR**	**SA†**
Tabernaemontana amygdalifolia Jacq.	t	Bayly, D.W.R. 104	LR-v; UR; CR	SA
Tabernaemontana donnell-smithii Rose	t	Pennil, C. 9	LR-v, -h, -s	MA
Thevetia ahouai (L.) A.DC.	s	Baden, H.M. 75	LR-p; CR	N-SA
Araliaceae				
Dendropanax arboreus (L.) Decne. & Planch.	t	Baden, H.M. 162	LR-v, -h; UR; CR	SA†
Oreopanax guatemalensis (Lem. ex Bosse) Decne. & Planch.	he/t	Bayly, D.W.R. 174	LR-v, -h	N-MA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Arecaceae				
Attalea cohune Mart.	pa		LR-v, -s; UR	N-SA
Bactris mexicana Mart.	pa		LR-s; CR	MA
Chamaedorea ernesti-augusti H.Wendl.	pa		UR	N-MA
Chamaedorea tepejilote Liebm.	pa		LR-v	N-SA
Cryosophila stauracantha (Heynh.) R.Evans	pa		LR-v, -h, -p, -s; CR	N-MA
Desmoncus orthacanthos Mart.	pa		CR	SA
Sabal mauritiiformis (H.Karst.) Griseb. & H.Wendl.	pa		LR-h, -p, -s; CR	N-SA
Balanophoraceae				
Helosis cayennensis (Sw.) Spreng. var. *mexicana* (Liebm.) B.Hansen	p	Särkinen, T. 348	LR-h	SA†
Bignoniaceae				
Adenocalymma cf. *inundatum* Mart. ex DC.	l	Särkinen, T. 244	LR-v	SA
Amphilophium crucigerum (L.) L.G.Lohmann	l	Särkinen, T. 184	LR-v	SA†
***Bignonia potosina* (K.Schum. & Loes.) L.G.Lohmann**	**l**	**Pennil, C. 1**	**LR-v, -s; CR**	**MA**
Fridericia chica (Bonpl.) L.G.Lohmann	l	Vandrot, H. 65	CR	SA
Martinella obovata (Kunth) Bureau & K.Schum.	l	Bayly, D.W.R. 119	LR-v	SA
Stizophyllum riparium (Kunth) Sandwith	l	Baden, H.M. 147	LR-h, -s, -v; CR	SA
Tabebuia rosea (Bertol.) A.DC.	t	Bayly, D.W.R. 180	LR-v	SA†
Tanaecium caudiculatum (Standl.) L.G.Lohmann	l	Matthews, A.C. 67	CR	N-MA
Tanaecium pyramidatum (Rich.) L.G.Lohmann	l	Särkinen, T. 248	LR-v; CR	SA
Tynanthus guatemalensis Donn.Sm.	l	Bayly, D.W.R. 173	LR-v	N-MA
Brassicaceae				
***Brassica juncea* (L.) Czern.**	**h**	**Särkinen, T. 16**	**CR**	**N-MA**
Burseraceae				
Bursera simaruba (L.) Sarg.	t	Särkinen, T. 74	CR	SA†
Protium copal (Schltdl. & Cham.) Engl.	t	Pennil, C. 3	LR-h; UR; CR	N-MA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Protium multiramiflorum Lundell	t	Vandrot, H. 137	LR-v, -h, -p, -s; CR	N-MA
Protium schippii Lundell	t	Särkinen, T. 523	UR	N-MA
Calophyllaceae				
Calophyllum brasiliense Cambess.	t	Matthews, A.C. 44	LR-v, -h; UR; CR	SA
Cannabaceae				
***Celtis schippii* Standl.**	**t**	**Särkinen, T. 514**	**UR**	**SA**
Capparaceae				
***Capparidastrum quiriguense* (Standl.) Cornejo & Iltis**	**t**	**Baden, H.M. 114**	**LR-v, -s**	**N-MA**
Forchhammeria trifoliata Radlk.	s	Baden, H.M. 11	LR-v; CR	MA†
Caprifoliaceae				
Valeriana scandens L.	l	Baden, H.M. 105	LR-s	SA†
Celastraceae				
Crossopetalum eucymosum (Loes. & Pittier) Lundell	t	Baden, H.M. 164	LR-h	MA
Hippocratea volubilis L.	l	Matthews, A.C. 69	CR	SA†
Salacia belizensis Standl.	l	Särkinen, T. 109	CR	SA
Wimmeria bartlettii Lundell	s/t	Vandrot, H. 67	CR	MA
Chrysobalanaceae				
Hirtella americana L.	t	Vandrot, H. 139	LR-h	SA
Clusiaceae				
Clusia massoniana Lundell	he/t	Vandrot, H. 98	LR-h	N-MA
Clusia minor L.	he/t	Bayly, D.W.R. 151	LR-h; UR	SA
***Garcinia intermedia* (Pittier) Hammel**	**t**	**Särkinen, T. 509**	**UR**	**N-SA**
Combretaceae				
Combretum fruticosum (Loefl.) Stuntz	l	Vandrot, H. 125	LR-v; CR	SA
Combretum laxum Jacq.	l	Bayly, D.W.R. 192	LR-v, -s; UR; CR	SA†
Terminalia amazonia (J.F.Gmel.) Exell	t	Matthews, A.C. 42	LR-v, -h, -p; UR; CR	SA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Commelinaceae				
Tripogandra grandiflora (Donn.Sm.) Woodson	h	Vandrot, H. 61	CR	N-MA
Convolvulaceae				
Ipomoea philomega (Vell.) House	l	Bayly, D.W.R. 171	LR-v	SA
Costaceae				
Costus pictus D.Don	h	Bayly, D.W.R. 196	LR-v	MA
Dichapetalaceae				
Dichapetalum donnell-smithii Engl.	l	Särkinen, T. 321	LR-h	N-SA
Dilleniaceae				
Doliocarpus dentatus (Aubl.) Standl.	l	Matthews, A.C. 68	CR	SA†
***Doliocarpus multiflorus* Standl.**	**l**	**Särkinen, T. 38**	**CR**	**N-SA†**
Tetracera volubilis L.	l	Baden, H.M. 92	CR	N-SA
Dioscoreaceae				
Dioscorea bartlettii C.V.Morton	l	Vandrot, H. 122	LR-v, -h	N-MA
Elaeocarpaceae				
Sloanea meianthera Donn.Sm.	t	Särkinen, T. 694	UR	N-SA
Euphorbiaceae				
Acalypha diversifolia Jacq.	t	Bayly, D.W.R. 166	LR-v	SA
Acalypha villosa Jacq.	s	Chicas, S. 1	CR; LR-v	SA
Adelia barbinervis Schltdl. & Cham.	s/t	Vandrot, H. 121	LR-v	MA
Alchornea latifolia Sw.	t	Pennil, C. 34	LR-v, -s; UR	SA†
Bernardia dodecandra (Sessé ex Cav.) Govaerts	t	Baden, H.M. 46	CR	N-MA
Cleidion castaneifolium Müll.Arg.	t	Vandrot, H. 32	CR	SA
Cnidoscolus multilobus (Pax) I.M.Johnst.	s	Vandrot, H. 101	LR-v	N-MA
Croton billbergianus Müll.Arg.	t	Chicas, S. 10	LR-v, -h; UR; CR	N-SA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
***Croton niveus* Jacq.**	**t**	**Särkinen, T. 343**	**LR-h**	**N-SA**
Croton schiedeanus Schltdl.	s	Matthews, A.C. 41	CR	N-SA
Pleradenophora tuerckheimiana (Pax & K.Hoffm.) A.L.Melo & Esser	t		LR-v, -h; CR	N-MA
Fabaceae (see Leguminosae)				
Gentianaceae				
Voyria parasitica (Schltdl. & Cham.) Ruyters & Maas	h/p	Särkinen, T. 198	LR	MA†
Labiatae (see Lamiaceae)				
Lacistemataceae				
Lacistema aggregatum (P.J.Bergius) Rusby	t	Särkinen, T. 612	UR	SA†
Lamiaceae				
Aegiphila monstrosa Moldenke	t	Pennil, C. 35	LR-v, -s	MA
Cornutia pyramidata L.	s	Särkinen, T. 992	UR; CR	SA
Vitex gaumeri Greenm.	t	Särkinen, T. 22	LR-v, -h; CR	MA
Lauraceae				
Licaria capitata (Schltdl. & Cham.) Kosterm.	t	Bayly, D.W.R. 189	CR; LR-v	N-MA
Licaria misantlae (Brandegee) Kosterm.	t	Baden, H.M. 166	LR-h	MA
Licaria peckii (I.M.Johnst.) Kosterm.	t	Särkinen, T. 119	LR-v, -h; CR	N-MA
Nectandra colorata Lundell	t	Baden, H.M. 40	CR	N-MA
Nectandra cf. *coriacea* (Sw.) Griseb.	t	Särkinen, T. 292	LR-h	N-SA†
***Nectandra martinicensis* Mez**	**t**	**Baden, H.M. 170**	**LR-v**	**N-SA**
Nectandra nitida Mez	t	Vandrot, H. 136	LR-s	MA
Nectandra salicifolia (Kunth) Nees	t	Baden, H.M. 169	LR-v, -h	MA
Ocotea cf. *cernua* (Nees) Mez	t	Särkinen, T. 623	UR	SA†

Table 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Leguminosae: Caesalpinioideae				
Bauhinia dipetala Hemsl.	s	Chicas, S. 5	LR-v	N-MA†
Dialium guianense (Aubl.) Sandwith	t	Baden, H.M. 119	LR-v, -p; UR	SA
Schizolobium parahyba (Vell.) S.F.Blake	t	Särkinen, T. 598	UR	SA
Schnella outimouta (Aubl.) Wunderlin *vel aff.*	l	Vandrot, H. 93	LR-s; CR	SA
Leguminosae: Mimosoideae				
Calliandra houstoniana (Mill.) Standl.	s	Särkinen, T. 189	Las Cuevas; LR-v	MA
Cojoba arborea (L.) Britton & Rose	t	Bayly, D.W.R. 162	LR-v	MA†
Cojoba graciliflora (S.F.Blake) Britton & Rose	s	Särkinen, T. 19	CR	N-MA
Inga nobilis* Willd.	**t**	**Särkinen, T. 664**	**UR**	**SA**
Inga sapindoides Willd.	t	Särkinen, T. 553	UR	SA
Inga vera Willd.	s/t	Baden, H.M. 95	LR-v; CR	SA†
Lysiloma auritum* (Schltdl.) Benth.	**t**	**Särkinen, T. 21**	**CR**	**MA**
Leguminosae: Papilionoideae				
Andira inermis (W.Wright) Kunth ex DC.	t	Baden, H.M. 161	LR-v; CR	SA†
Crotalaria cajanifolia Kunth	h	Matthews, A.C. 3	Las Cuevas	MA†
Dalbergia glabra (Mill.) Standl.	l	Baden, H.M. 51	LR-h	MA
Erythrina folkersii Krukoff & Moldenke	t	Bayly, D.W.R. 105	LR-v	N-MA
Lonchocarpus castilloi Standl. *vel aff.*	t	Baden, H.M. 59	CR	N-MA
Machaerium kegelii Meisn.	l	Särkinen, T. 169	LR-v	SA
Machaerium cf. *riparium* Brandegee	l	Chicas, S. 25	LR-h	MA
Machaerium seemannii Benth. ex Seem.	l	Särkinen, T. 351	LR-h	N-SA
Myroxylon balsamum (L.) Harms	t	Särkinen, T. 236	LR-v	SA
Platymiscium cf. *yucatanum* Standl.	t	Särkinen, T. 27	CR	N-MA
Loganiaceae				
Spigelia humboldtiana Cham. & Schltdl.	h	Särkinen, T. 45	CR	SA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Loranthaceae				
Psittacanthus pinicola Kuijt	p	Bayly, D.W.R. 193	LR-v	MA
Lythraceae				
Cuphea appendiculata Benth.	s	Matthews, A.C. 7	Las Cuevas	MA
Malpighiaceae				
Bunchosia lindeniana A.Juss.	s/t	Vandrot, H. 102	LR-v, -s	SA
Heteropterys obovata* (Small.) Cuatrec. & Croat	**l**	**Chicas, S. 17**	**LR-h, -v**	**MA**
Hiraea reclinata Jacq.	l	Vandrot, H. 94	CR; LR-s	N-SA
Stigmaphyllon lindenianum A.Juss.	l	Särkinen, T. 179	LR-v	N-SA
Tetrapterys schiedeana Schltdl. & Cham.	l	Baden, H.M. 165	LR-h	MA
Malvaceae				
Bernoullia flammea Oliv.	t	Chicas, S. 35	LR-h	MA
Ceiba pentandra (L.) Gaertn.	t		LR-v, -h	SA†
Guazuma ulmifolia Lam.	t	Matthews, A.C. 2	CR	SA†
Hampea stipitata S.Watson	t	Särkinen, T. 191	LR-v; UR; CR	MA
Hampea trilobata Standl.	s/t	Särkinen, T. 367	LR-h	N-MA
Malvaviscus arboreus Cav.	s	Baden, H.M. 25	CR; Las Cuevas	N-SA
Pseudobombax cf. *ellipticum* (Kunth) Dugand	t	Särkinen, T. 337	LR-h	N-MA†
Quararibea funebris (La Llave) Vischer	t	Pennil, C. 38	LR-v; UR	MA
Trichospermum grewiifolium (A.Rich.) Kosterm.	t	Pennil, C. 49	LR-v	MA†
Marcgraviaceae				
Ruyschia enervia Lundell	s/e	Vandrot, H. 99	LR-h	MA
Melastomataceae				
Clidemia petiolaris (Schltdl. & Cham.) Schltdl. ex Triana	s	Matthews, A.C. 8	Las Cuevas	MA
***Clidemia strigillosa* (Sw.) DC.**	**s**	**Vandrot, H. 66**	**CR**	**SA**

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Henriettella fascicularis (Sw.) C.Wright	t	Vandrot, H. 59	CR	N-SA†
Miconia impetiolaris (Sw.) D.Don ex DC.	s	Matthews, A.C. 47	LR-v; CR	SA†
Mouriri exilis Gleason	t	Särkinen, T. 611	UR	MA
Meliaceae				
Cedrela cf. *odorata* L.	t	Särkinen, T. 596	UR	SA†
Guarea glabra Vahl subsp. *rovirosae* (C.DC.) T.D.Penn.	t	Bayly, D.W.R. 159	LR-h, -v; UR; CR	N-MA
Guarea glabra Vahl subsp. *tuerckheimii* (C.DC.) T.D.Penn.	t	Baden, H.M. 202	LR-s; UR	N-MA
Guarea grandifolia DC.	t	Särkinen, T. 510	UR	SA
Swietenia macrophylla King	t	Särkinen, T. 501	UR; CR	SA†
Trichilia erythrocarpa Lundell	t	Bayly, D.W.R. 178	LR-v, -h, -p, -s; CR	N-MA
Trichilia havanensis Jacq.	t	Matthews, A.C. 61	CR	N-SA†
***Trichilia martiana* C.DC.**	**t**	**Baden, H.M. 160**	**LR-v**	**SA†**
Trichilia minutiflora Standl.	t	Särkinen, T. 154	LR-v, -h, -s; CR	N-MA
Trichilia moschata Sw.	t	Baden, H.M. 138	LR-h	N-SA
Trichilia pallida Sw.	t	Chicas, S. 7	LR-s, -v	SA†
Memecylaceae (see Melastomataceae)				
Moraceae				
Brosimum alicastrum Sw.	t	Baden, H.M. 36	LR-v, -h, -s; CR	SA†
***Brosimum guianense* (Aubl.) Huber**	**t**	**Särkinen, T. 973**	**UR**	**SA**
Castilla elastica Sessé	t	Vandrot, H. 111	UR; LR-s	N-SA†
Dorstenia lindeniana Bureau	h	Bayly, D.W.R. 165	LR-v	N-MA
Ficus americana Aubl.	t	Matthews, A.C. 60	CR	SA
Ficus apollinaris Dugand	t	Särkinen, T. 94	CR	N-SA
Ficus colubrinae Standl.	t	Chicas, S. 27	LR-h	N-SA
Ficus insipida Willd.	t	Bayly, D.W.R. 194	LR-v	SA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Ficus paraensis (Miq.) Miq.	t	Chicas, S. 12	LR-v	SA
Ficus cf. *tonduzii* Standl.	t	Särkinen, T. 907	UR	SA
***Pseudolmedia glabrata* (Liebm.) C.C.Berg**	**t**	**Särkinen, T. 640**	**UR**	**MA**
Pseudolmedia spuria (Sw.) Griseb.	t	Baden, H.M. 97	LR-v, -h, -p, -s; CR	N-SA†
Trophis mexicana (Liebm.) Bureau	t	Vandrot, H. 104	LR-v, -p, -s; CR	N-SA
Trophis racemosa (L.) Urb.	t	Särkinen, T. 282	LR-v; UR	N-SA
Myristicaceae				
***Compsoneura mexicana* (Hemsl.) Janovec**	**t**	**Baden, H.M. 203**	**UR**	**MA**
***Virola koschnyi* Warb.**	**t**	**Särkinen, T. 545**	**UR**	**N-SA**
Myrsinaceae (see Primulaceae)				
Myrtaceae				
Calyptranthes lindeniana O.Berg	s	Särkinen, T. 14	CR	N-MA
Pimenta dioica (L.) Merr.	t		LR-h, -p	N-SA†
Nyctaginaceae				
Neea psychotrioides Donn.Sm.	t	Särkinen, T. 174	LR-h, -s, -v; UR; CR	MA
Ochnaceae				
Ouratea lucens (Kunth) Engl.	t	Chicas, S. 6	LR-v, -h; CR	SA
Olacaceae				
Heisteria media S.F.Blake	t	Baden, H.M. 131	LR-v, -h, -s; CR	MA
Oleaceae				
Chionanthus oblanceolatus (B.L.Rob.) P.S.Green	s	Matthews, A.C. 40	CR	MA
Papaveraceae				
Bocconia frutescens L.	s	Baden, H.M. 9	CR	SA†

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Passifloraceae				
Erblichia odorata Seem.	t	Särkinen, T. 214	LR-p	MA
Turnera cf. *aromatica* Arbo	h/s	Baden, H.M. 167	LR-v	N-SA
Pentaphylacaceae				
Ternstroemia tepezapote Schltdl. & Cham.	t	Särkinen, T. 346	LR-h	MA
Phyllanthaceae				
Phyllanthus cf. *amarus* Schumach. & Thonn.	h	Baden, H.M. 74	CR	N-SA
Phyllanthus cf. *niruri* L.	h	Baden, H.M. 73	CR	SA†
Piperaceae				
***Peperomia hoffmannii* C.DC.**	**h/e**	**Matthews, A.C. 11**	**Las Cuevas**	**SA**
Peperomia obtusifolia (L.) A.Dietr.	h/e	Vandrot, H. 115	LR-h	SA†
Piper amalago L.	s	Bayly, D.W.R. 129	LR-v, -s	SA†
Piper jacquemontianum Kunth	s	Baden, H.M. 76	LR-v; CR	MA†
Piper psilorhachis C.DC.	s	Särkinen, T. 181	CR; LR-v	N-MA
***Piper sanctum* (Miq.) Schltdl. ex C.DC.**	**s**	**Särkinen, T. 155**	**LR-v**	**MA**
Piper yucatanense C.DC.	s/t	Bayly, D.W.R. 100	LR-v, -h, -p, -s; UR; CR	MA
Polygonaceae				
Coccoloba acapulcensis Standl.	t	Bayly, D.W.R. 156	LR-h, -s	MA
Coccoloba belizensis Standl.	t	Baden, H.M. 127	LR-v, -h, -p; CR	MA
***Coccoloba diversifolia* Jacq.**	**t**	**Chicas, S. 39**	**LR-h; CR**	**N-MA†**
***Gymnopodium floribundum* Rolfe**	**l**	**Vandrot, H. 96**	**LR-h**	**N-MA**
Primulaceae				
Ardisia nigrescens Oerst.	s	Pennil, C. 5	CR; LR-v	MA
Ardisia paschalis Donn.Sm.	s	Pennil, C. 2	LR-v	MA
Deherainia smaragdina (Planch. ex Linden) Decne.	s	Vandrot, H. 113	LR-v, -h	N-MA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Parathesis donnell-smithii Mez	s	Särkinen, T. 33	CR	N-MA
Parathesis cf. *rufa* Lundell	t	Baden, H.M. 107	LR-v	N-MA
Putranjivaceae				
Drypetes brownii Standl.	t	Matthews, A.C. 54	UR; CR	MA
Rhamnaceae				
Gouania cf. *polygama* (Jacq.) Urb.	l	Särkinen, T. 271	LR-v; CR	SA†
***Sageretia elegans* (Kunth) Brongn.**	**l**	**Bayly, D.W.R. 185**	**LR-v**	**SA**
Rhizophoraceae				
Cassipourea guianensis Aubl.	t	Vandrot, H. 140	CR; LR-h	SA
Rosaceae				
Photinia microcarpa Standl.	t	Chicas, S. 33	LR-h	MA
Rubiaceae				
Augusta rivalis (Benth.) J.H.Kirkbr.	s/t	Chicas, S. 13	CR; LR-v	N-SA
Chiococca alba (L.) Hitchc.	l	Baden, H.M. 28	CR	SA
Guettarda combsii Urb.	t	Bayly, D.W.R. 155	LR-h	MA†
Guettarda deamii Standl.	l	Baden, H.M. 88	CR	N-MA
Hamelia calycosa Donn.Sm.	t	Vandrot, H. 141	LR-v, -h	SA
Morinda panamensis Seem.	s/t	Bayly, D.W.R. 191	LR-v	N-SA
Palicourea domingensis (Jacq.) DC.	s	Bayly, D.W.R. 167	LR-v	N-SA†
Palicourea padifolia (Roem. & Schult.) C.M.Taylor & Lorence	t	Matthews, A.C. 50	CR	MA
Palicourea tetragona (Donn.Sm.) C.M.Taylor & Lorence	s/t	Baden, H.M. 103	UR; LR-v; CR	MA
Posoqueria latifolia (Rudge) Schult.	t	Särkinen, T. 537	UR	SA
Psychotria costivenia Griseb.	s/t	Chicas, S. 3	LR	N-MA†
Psychotria limonensis K.Krause	t	Särkinen, T. 151	LR-v	N-SA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Psychotria mexiae Standl.	t	Vandrot, H. 138	LR-v, -s; CR	N-MA
Psychotria poeppigiana Müll.Arg.	s	Vandrot, H. 71	CR; Las Cuevas	SA
Psychotria pubescens Sw.	s	Särkinen, T. 178	LR-v	MA†
Psychotria quinqueradiata Pol.	s	Särkinen, T. 42	CR	MA
Randia cf. *matudae* Lorence & Dwyer	t	Särkinen, T. 350	LR-h, -p, -s; CR	N-MA
Randia retroflexa Lorence & M.Nee	l	Vandrot, H. 133	LR-v, -s; CR	N-MA
Rogiera stenosiphon (Hemsl.) Borhidi	t	Bayly, D.W.R. 168	LR-v	N-MA
Simira salvadorensis (Standl.) Steyerm.	t	Baden, H.M. 108	LR-v, -s	N-MA
Rutaceae				
Amyris belizensis Lundell	t	Vandrot, H. 19	CR	N-MA
Zanthoxylum acuminatum (Sw.) Sw.	t	Chicas, S. 36	LR-h; CR	SA
Salicaceae				
Casearia commersoniana Cambess.	s/t	Särkinen, T. 504	UR	SA
Casearia corymbosa Kunth	s/t	Vandrot, H. 120	CR; LR-v	SA
Casearia tremula (Griseb.) Griseb. ex C.Wright	t	Baden, H.M. 71	LR-h; CR	N-SA†
Laetia thamnia L.	s	Vandrot, H. 58	UR; LR-h, -s; CR	N-SA†
Zuelania guidonia (Sw.) Britton & Millsp.	t	Vandrot, H. 37	CR	N-MA†
Sapindaceae				
Allophylus camptostachys Radlk.	t	Särkinen, T. 215	LR-v, -p; CR	N-MA
Allophylus cominia (L.) Sw.	t	Särkinen, T. 308	LR-h	N-MA†
Allophylus psilospermus Radlk.	t	Vandrot, H. 62	CR	N-SA†
Cupania belizensis Standl.	t	Matthews, A.C. 62	LR-v, -h; UR; CR	N-MA
Matayba apetala Radlk.	t	Baden, H.M. 133	LR-h; CR	MA
Paullinia costaricensis Radlk.	l	Pennil, C. 26	LR-v, -s	MA
Paullinia costata Schltdl. & Cham.	l	Baden, H.M. 78	LR-v; CR	MA
Paullinia pinnata L.	l	Särkinen, T. 223	LR-h, -v	SA†
Serjania atrolineata C.Wright	l	Baden, H.M. 65	LR-p; CR	N-SA†
Thinouia tomocarpa Standl.	l	Särkinen, T. 78	LR-s; CR	N-MA

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
***Thouinia paucidentata* Radlk.**	**t**	**Särkinen, T. 289**	**LR-h**	**N-MA**
Sapotaceae				
Manilkara zapota (L.) P.Royen	t	Särkinen, T. 108	LR-v, -h, -s; CR	MA†
Pouteria cf. *amygdalina* (Standl.) Baehni	t	Pennil, C. 23	LR-v, -h, -p, -s; CR	N-MA
Pouteria campechiana (Kunth) Baehni	t	Bayly, D.W.R. 113	LR-v; UR; CR	SA†
Pouteria durlandii (Standl.) Baehni	t	Chicas, S. 11	LR-v, -h, -p, -s; UR; CR	SA
Pouteria reticulata (Engl.) Eyma	t	Baden, H.M. 128	LR-v, -h, -s; CR	SA
***Pouteria sapota* (Jacq.) H.E.Moore & Stearn**	**t**	**Särkinen, T. 604**	**UR**	**N-SA†**
Sideroxylon foetidissimum Jacq. subsp. *gaumeri* (Pittier) T.D.Penn.	t	Bayly, D.W.R. 186	LR-p, -s, -v	N-MA
Sideroxylon salicifolium (L.) Lam.	s/t	Vandrot, H. 60	CR	N-MA†
Sideroxylon stevensonii (Standl.) Standl. & Steyerm.	t	Baden, H.M. 90	LR-h; CR	N-MA
Schoepfiaceae				
Schoepfia schreberi J.F.Gmel.	t	Särkinen, T. 335	LR-h	N-SA†
Simaroubaceae				
Picramnia antidesma Sw.	t	Bayly, D.W.R. 147	LR-h	N-SA†
Simarouba glauca DC.	t	Bayly, D.W.R. 145	LR-h, -p, -s	MA†
Siparunaceae				
Siparuna thecaphora (Poepp. & Endl.) A.DC.	t	Vandrot, H. 63	CR	SA
Solanaceae				
Capsicum annuum L.	s	Vandrot, H. 64	CR	SA†
Cestrum nocturnum L.	t	Chicas, S. 2	LR-v	SA†
Lycianthes hypoleuca Standl.	l	Särkinen, T. 170	LR-h, -v	N-MA
Solanum cordovense Sessé & Moc.	s	Matthews, A.C. 71	CR	N-SA
Witheringia solanacea L'Hér.	s	Vandrot, H. 20	CR	SA†

TABLE 1. (*Cont'd*)

Taxon	Habit	Voucher specimen	Collection location(s) 2006	Floristic affinity
Staphyleaceae				
Staphylea occidentalis Sw.	l	Bayly, D.W.R. 170	LR-v; CR	SA
Urticaceae				
Coussapoa oligocephala Donn.Sm.	t	Baden, H.M. 104	CR	N-MA
Myriocarpa longipes Liebm.	t	Särkinen, T. 12	LR-v; CR	SA
Myriocarpa obovata Donn.Sm.	t	Pennil, C. 19	LR-v, -h, -s	MA
Pilea cf. *ecboliophylla* Donn.Sm.	h	Särkinen, T. 150	LR-v	MA
***Pourouma bicolor* Mart. subsp. *scobina* (Benoist) C.C.Berg & Heusden**	**t**	**Särkinen, T. 546**	**UR**	**SA**
Urera cf. *simplex* Wedd.	t	Baden, H.M. 106	LR-s, -v	N-SA
Violaceae				
Rinorea hummelii Sprague	t	Chicas, S. 9	LR-v, -h, -p, -s; CR	MA
Vitaceae				
Cissus biformifolia Standl.	l	Bayly, D.W.R. 190	LR-v; CR	N-SA
Vitis tiliifolia Humb. & Bonpl. ex Schult.	l	Vandrot, H. 108	CR	N-SA

– All species listed here, and/or in the text, have at least one voucher specimen, with the exceptions of *Ceiba pentandra*, *Pimenta dioica*, *Pleradenophora tuerckheimiana* and Arecaceae – these are listed from observation only. If a group of specimens were identified, some with and some without a cf. qualifier, then the taxon without the cf. has been listed in this species checklist as the voucher for this taxon. If recorded species were identified only with the cf. qualifier, these have been listed as such in the table, and quoted as such in the text throughout.

– Taxa identified to genus level only are not included in the species list, as their inclusion here would not contribute much of value for the overall species list, but they are nonetheless discussed in the text as plant records albeit insufficiently identified.

– List indicates habit (h = herb, s = shrub, t = tree, l = liana, e = epiphyte, he = hemiepiphyte, p = parasite, pa = palm), voucher, collection localities (LR = Lower Raspaculo, -h = hilltop, -v = valley, -s = slope, -p = palm-dominated area, UR = Upper Raspaculo, CR = Chiquibul River at Natural Arch), and floristic affinity after Wendt (1993) (N-MA = Northern Mesoamerica, MA = Mesoamerica, N-SA = Northern South America, SA = South America, † = Greater Antilles).

– Species records new to the Chiquibul vascular plant checklist by Bridgewater *et al.* (2006a) are highlighted in grey and bold, taxa that would be new if their 'cf.' identification were to be confirmed are highlighted in grey only (not bold), and species records new to the checklist of Belize (Balick *et al.*, 2000) are highlighted in grey, bold and marked with *.

TABLE 2. Sample sites, coordinates, sampling methods and corresponding vegetation classification based on previous classification schemes

			Vegetation classification	
Sampling site	Coordinates	Sampling technique	Meerman & Sabido (2001)	Penn *et al.* (2004)
Chiquibul River (Natural Arch)	16°31′49″N 89°01′52″W – 16°36′40″N 89°03′46″W, >500 m	11 transects and general collecting	Tropical evergreen seasonal broadleaf submontane forest over rolling calcareous hills [I.A.2.b.(1).K-r]	Deciduous forest
Lower Raspaculo (hilltops)	16°48′35″N 88°55′28″W – 16°48′44″N 88°56′01″W, >500 m	10 transects and general collecting	Tropical evergreen seasonal broadleaf lowland hill forest, Simarouba-Terminalia variant [I.A.2.a.(1).(a).-ST]	Deciduous forest
Lower Raspaculo (valley floor)	16°48′35″N 88°55′23″W – 16°49′00″N 88°55′52″W, <500 m	19 transects and general collecting	Tropical evergreen seasonal broadleaf lowland hill forest, Simarouba-Terminalia variant [I.A.2.a.(1).(a).-ST]	Deciduous forest
Upper Raspaculo (Cuxta Bani)	16°48′8″N 88°47′31″W	1 ha plot and general collecting	Tropical evergreen seasonal broadleaf lowland hill forest, Simarouba-Terminalia variant [I.A.2.a.(1).(a).-ST]	Semi-evergreen lowland forest

TABLE 3. New records to the preliminary checklist of the vascular plants of the Chiquibul Forest, Belize (Bridgewater *et al.*, 2006a) from this study, including 10 records that would be new to the Chiquibul, were their cf. qualifiers to be removed, shaded grey. See Methods and table footnotes for details

Taxon	Voucher specimen	Study site	Wendt affinity
Brassica juncea (Brassicaceae)	Särkinen, T. 16	CR	N-MA
Capparidastrum quiriguense (Capparaceae)	Baden, H.M. 114	LR-v, -s	
Gymnopodium floribundum (Polygonaceae)	Vandrot, H. 96	LR-h	
Parathesis cf. *rufa* (Primulaceae)	Baden, H.M. 107	LR-v	
Platymiscium cf. *yucatanum* (Leguminosae: Papilionoideae)	Särkinen, T. 27	CR	
Thouinia paucidentata (Sapindaceae)	Särkinen, T. 289	LR-h	
Coccoloba diversifolia (Polygonaceae)	Chicas, S. 39	LR-h; CR	N-MA†
Pseudobombax cf. *ellipticum* (Malvaceae)	Särkinen, T. 337	LR-h	
Annona scleroderma (Annonaceae)	Särkinen, T. 528	UR	MA
Bignonia potosina (K.Schum. & Loes.) L.G.Lohmann	Pennil, C. 1	LR-v, -s; CR	
Compsoneura mexicana (Myristicaceae)	Baden, H.M. 203	UR	
Heteropterys obovata (Small.) Cuatrec. & Croat (Malpighiaceae)	Chicas, S. 17	LR-h, -v	
Lysiloma auritum (Schltdl.) Benth. (Leguminosae: Mimosoideae)	Särkinen, T. 21	CR	
Machaerium cf. *riparium* Brandegee (Leguminosae: Papilionoideae)	Chicas, S. 25	LR-h	
Marsdenia laxiflora Donn.Sm. (Apocynaceae)	Bayly, D.W.R. 164	CR; LR-v	
Pilea cf. *ecboliophylla* Donn.Sm. (Urticaceae)	Särkinen, T. 150	LR-v	
Piper sanctum (Miq.) Schltdl. ex C.DC. (Piperaceae)	Särkinen, T. 155	LR-v	
Pseudolmedia glabrata (Liebm.) C.C.Berg (Moraceae)	Särkinen, T. 640	UR	
Croton niveus (Euphorbiaceae)	Särkinen, T. 343	LR-h	N-SA
Garcinia intermedia (Clusiaceae)	Särkinen, T. 509	UR	
Nectandra martinicensis (Lauraceae)	Baden, H.M. 170	LR-v	
Phyllanthus cf. *amarus* (Phyllanthaceae)	Baden, H.M. 74	CR	
Virola koschnyi (Myristicaceae)	Särkinen, T. 545	UR	

TABLE 3. (*Cont'd*)

Taxon	Voucher specimen	Study site	Wendt affinity
Doliocarpus multiflorus (Dilleniaceae)	Särkinen, T. 38	CR	N-SA†
Nectandra cf. *coriacea* (Lauraceae)	Särkinen, T. 292	LR-h	
Pouteria sapota (Sapotaceae)	Särkinen, T. 604	UR	
Adenocalymma cf. *inundatum* (Bignoniaceae)	Särkinen, T. 244	LR-v	SA
Brosimum guianense (Moraceae)	Särkinen, T. 973	UR	
Celtis schippii (Cannabaceae)	Särkinen, T. 514	UR	
Clidemia strigillosa (Melastomataceae)	Vandrot, H. 66	CR	
Inga nobilis (Leguminosae: Mimosoideae)	Särkinen, T. 664	UR	
Peperomia hoffmannii (Piperaceae)	Matthews, A.C. 11	Las Cuevas	
Pourouma bicolor subsp. *scobina* (Urticaceae)	Särkinen, T. 546	UR	
Sageretia elegans (Rhamnaceae)	Bayly, D.W.R. 185	LR-v	
Gouania cf. *polygama* (Rhamnaceae)	Särkinen, T. 271	LR-v; CR	SA†
Odontadenia macrantha (Apocynaceae)	Matthews, A.C. 72	CR	
Phyllanthus cf. *niruri* (Phyllanthaceae)	Baden, H.M. 73	CR	
Trichilia martiana (Meliaceae)	Baden, H.M. 160	LR-v	

Collection localities are indicated: CR = Chiquibul River at Natural Arch, LR = Lower Raspaculo with h = hilltop, v = valley, s = slope, UR = Upper Raspaculo. New records are grouped according to phytogeographical affinity after Wendt (1993; N-MA = Northern Mesoamerica, MA = Mesoamerica, N-SA = Northern South America, SA = South America; † also present in the Greater Antilles).

with those of Bridgewater *et al.* (2006a) brings the total numbers in the Chiquibul to 138 families, 688 genera, and 1344 species of angiosperms.

The collections revealed 28 new records compared to the CFRNP's preliminary vascular plant checklist (Bridgewater *et al.*, 2006a), plus a further 10 species with a cf. qualifier (Tables 1, 3). Three of these are new to Belize when compared to the latest national checklist (Balick *et al.*, 2000), namely *Heteropterys obovata* (Small.) Cuatrec. & Croat (Malpighiaceae), *Inga nobilis* Willd., and *Lysiloma auritum* (Schltdl.) Benth. (Leguminosae) (Tables 1, 3), though there are specimen records of *Lysiloma auritum* from Belize in Flora Mesoamericana (2014). Twenty of the 38 new records in the Chiquibul came from the karstic terrain above 500 m elevation.

Nine of the 38 new records in the CFRNP were from Cuxta Bani in the Upper Raspaculo (Table 3). They were found growing exclusively on the metamorphic substrate. This area hosted the only representatives of Myristicaceae, namely *Compsoneura mexicana* (Hemsl.) Janovec and *Virola koschnyi* Warb. A further new record, *Celtis schippii* Standl. (Cannabaceae), was strongly represented here with 12 individuals in the 1 ha plot (Table 4). Several abundant morphospecies still await identification and will probably represent further new records to this area. Due to the difficulty of access, the area has remained poorly collected, and the new records show that more species remain to be added to the local flora from this area.

Nineteen of the new records to the Chiquibul vascular plant checklist come from the Lower Raspaculo, some of which also occurred in the karstic limestone area around Natural Arch along the Chiquibul River (Table 3). New records from the karstic limestone area in the Lower Raspaculo include 11 species of trees and shrubs, and eight lianas of which one is new to Belize. Of the 19 new records, nine were restricted to valley floors, seven to the hilltop vegetation, and only one occurred in both habitats, the latter a new record for Belize. The new records from the valley floor vegetation of the Chiquibul were *Parathesis* cf. *rufa* Lundell (Primulaceae), *Pilea* cf. *ecboliophylla* Donn.Sm. (Urticaceae), *Piper sanctum* (Miq.) Schltdl. ex C.DC. (Piperaceae), *Trichilia martiana* C.DC. (Meliaceae) and the recently re-instated *Capparidastrum quiriguense* (Standl.) Cornejo & Iltis (Capparaceae) (Cornejo & Iltis, 2008) which have Mesoamerican distributions, but there are only a few previous records from Belize. *Nectandra martinicensis* Mez (Lauraceae) is documented from southern Mesoamerica and northern South America based on records available in TROPICOS (2014), with only one record from Belize, for which no collector is given and the geo-referencing is approximate, but we made three independent collections of it in the Lower Raspaculo valley floor vegetation. New records from the karstic hilltop vegetation included the tree species *Pseudobombax* cf. *ellipticum* (Kunth) Dugand (Malvaceae), *Croton niveus* Jacq. (Euphorbiaceae), *Coccoloba diversifolia* Jacq. (Polygonaceae), *Nectandra* cf. *coriacea* (Sw.) Griseb. (Lauraceae), and *Thouinia paucidentata* Radlk. (Sapindaceae) (Table 3). These species are all relatively widespread across Central America and, in some cases, in northern South America and the Caribbean but, in Belize, only a few records are currently available in TROPICOS (2014). The one exception is *Nectandra coriacea* with 17 records from Belize.

TABLE 4. The 29 most important taxa in the Upper Raspaculo 1 ha plot at Cuxta Bani, representing two-thirds of the total taxa, in decreasing order of importance value (IV), based on absolute abundance, relative abundance, relative frequency and relative dominance

Taxon	Family	Absolute abundance	Relative abundance	Relative frequency	Relative dominance	IV
Dialium guianense	Leguminosae	29	6.76	4.87	9.15	20.78
Guarea glabra subsp. *tuerckheimii*	Meliaceae	28	6.53	5.52	6.53	18.57
Tabernaemontana sp.	Apocynaceae	25	5.83	3.90	4.53	14.25
Guarea grandifolia	Meliaceae	12	2.80	3.57	7.07	13.44
Celtis schippii	Cannabaceae	12	2.80	2.60	5.05	10.45
Dendropanax arboreus	Araliaceae	16	3.73	3.57	2.21	9.51
Leguminosae sp.1	Leguminosae	11	2.56	3.25	3.15	8.96
Compsoneura mexicana	Myristicaceae	11	2.56	2.92	3.41	8.90
Cymbopetalum cf. *mayanum*	Annonaceae	12	2.80	2.92	1.34	7.06
Unknown sp.		9	2.10	1.95	2.85	6.90
Zanthoxylum sp.	Rutaceae	7	1.63	1.95	2.63	6.21
Protium copal	Burseraceae	9	2.10	2.27	1.74	6.11
Terminalia amazonia	Combretaceae	6	1.40	1.30	3.25	5.94
Piper yucatanense	Piperaceae	8	1.86	2.27	1.77	5.91
Pouteria durlandii	Sapotaceae	8	1.86	2.60	1.21	5.67
Garcinia intermedia	Clusiaceae	11	2.56	2.27	0.76	5.60
Protium schippii	Burseraceae	10	2.33	2.27	0.60	5.20
Apocynaceae sp.	Apocynaceae	9	2.10	1.30	1.42	4.82
Ocotea cf. *cernua*	Lauraceae	7	1.63	1.95	0.99	4.57
Cecropia sp.1	Urticaceae	6	1.40	1.62	1.35	4.37
Quararibea funebris	Malvaceae	6	1.40	1.62	1.34	4.36
Schizolobium parahyba	Leguminosae	4	0.93	0.97	2.05	3.95
Inga sp.1	Leguminosae	5	1.17	1.30	0.57	3.04
Cedrela sp.1	Meliaceae	1	0.23	0.32	2.43	2.99
Protium sp.	Burseraceae	5	1.17	1.62	0.11	2.89
Lacistema aggregatum	Lacistemataceae	4	0.93	1.30	0.50	2.74
Annona scleroderma	Annonaceae	4	0.93	1.30	0.50	2.73
Swietenia macrophylla	Meliaceae	5	1.17	0.97	0.58	2.72
Mouriri exilis	Melastomataceae	5	1.17	0.97	0.57	2.71

Eight of the 19 new species in the Chiquibul recorded in the Lower Raspaculo are lianas. Lianas are generally under-represented in herbarium collections mainly because they are so difficult to collect. Our general collecting and vegetation transects included lianas and every effort was made to collect adequate material for identification, including wood, leaf and fertile material. The new records are *Heteropterys obovata* (Malpighiaceae), *Marsdenia laxiflora* Donn.Sm. (Apocynaceae), *Bignonia potosina* (K.Schum. & Loes.) L.G.Lohmann, *Adenocalymma* cf. *inundatum* Mart. ex DC. (Bignoniaceae), *Gymnopodium floribundum* Rolfe (Polygonaceae) and *Machaerium* cf. *riparium* Brandegee (Leguminosae). *Schnella outimouta* (Aubl.) Wunderlin *vel aff.* has not been marked as potentially new to the area. Two widespread species that extend their distributions from Central America to northern Argentina, *Gouania* cf. *polygama* (Jacq.) Urb. and *Sageretia elegans* (Kunth) Brongn. (Rhamnaceae), are here recorded in the Chiquibul for the first time.

Twelve of the new taxa occurred in the Chiquibul River area in Natural Arch but, as mentioned above, some overlapped in their distribution with the Lower Raspaculo study sites which are also on karstic limestone. They represented four trees and shrubs, five lianas and three herbs. The Chiquibul River area has not yet been exhaustively collected, although many more collections exist than in the remote Raspaculo valley. Our results suggest that between the three areas studied, there seems to be no geographical trend in the number of new records encountered, proving that many areas within the Chiquibul Forest are insufficiently studied. However, given that only one week was spent at Cuxta Bani (compared to three weeks at Natural Arch and seven around our Lower Raspaculo base), strictly collecting trees >10 cm DBH within one hectare, the rate at which new records were encountered at Cuxta Bani was clearly highest.

Upper Raspaculo at Cuxta Bani

Forest structure and species composition

The 1 ha plot in the Upper Raspaculo (Cuxta Bani) had a basal area (BA) for stems above 10 cm DBH of 78.2 m^2 with more than 7% of stems reaching diameters >1 m DBH. Compared to the other study sites it was a much higher stature forest. While Meerman & Sabido (2001) lump this area into the same class as our Lower Raspaculo sampling sites, we have to agree with Penn *et al.* (2004) that this vegetation type is different from areas sampled by us before and we can confirm their estimate of around 80 spp./ha (>10 cm DBH). The forest undergrowth was open with large tree ferns, fishtail palms (Xaté; *Chamaedorea ernesti-augusti* H.Wendl.) and less abundant liana cover. No signs of cutting of the Xaté palms were observed (see Bridgewater *et al.*, 2006b), highlighting the remoteness of the area. The 10 most important taxa (based on abundance, frequency and BA) were *Dialium guianense* (Aubl.) Sandwith (Leguminosae), *Guarea glabra* Vahl subsp. *tuerckheimii* (C.DC.) T.D.Penn. (Meliaceae), *Tabernaemontana* sp. (morphospecies 'Yellow IB Apocynaceae'), *Guarea* *grandifolia* DC. (Meliaceae), *Celtis schippii* (Cannabaceae), *Dendropanax arboreus* (L.) Decne. & Planch. (Araliaceae), Leguminosae sp.1, *Compsoneura mexicana* (Myristicaceae), *Cymbopetalum* cf. *mayanum* Lundell (Annonaceae), and one unknown species (Table 4). Species that were abundant but smaller in basal area included *Garcinia intermedia* (Pittier) Hammel (Clusiaceae) and *Protium schippii* Lundell (Burseraceae) (Table 4). *Terminalia amazonia* (J.F.Gmel.) Exell (Combretaceae) and *Zanthoxylum* sp. (Rutaceae) had high relative dominance but low relative abundance (Table 4). At least 41% of Penn *et al.*'s (2004; Table 2) species found at Cuxta Bani – and 64% including the 'genus sp.' identifications – overlap with our records but we did find both *Protium copal* (Schltdl. & Cham.) Engl. and *Protium schippii* in this area. It should be stated that a 26–30% overlap also existed with Penn *et al.*'s 'Class 1'.

Chiquibul and Lower Raspaculo

Overview of vegetation transects

The four 0.1 ha vegetation transects (40 transects of 10 m × 2) established along the Chiquibul River and the Lower Raspaculo consisted of 1892 stems ≥2.5 cm DBH, yielding an average of 4730 stems ≥2.5 cm/ha. The 11 Chiquibul River transects at Natural Arch consisted of 539 stems, the 10 Lower Raspaculo valley floor transects had 501 stems, and the 11 Lower Raspaculo hilltop transects had 577 individuals. A further eight transects placed along slopes in the Lower Raspaculo included a total of 274 individuals. The vegetation structure was relatively homogeneous across most Lower Raspaculo and Chiquibul River sample sites, compared to the Upper Raspaculo site at Cuxta Bani. However, a stark difference in canopy height and forest structure was observed on the karstic hilltops above the Lower Raspaculo River. Chiquibul River and Lower Raspaculo sites had generally smaller trees with more stems, and relatively high abundance of lianas, except for hilltops, where liana abundance was low.

Table 2 shows the categorisation of the study areas according to previous vegetation classifications (Meerman & Sabido, 2001; Penn *et al.*, 2004). All transects mapped into lowland type forests, although hilltop sites were above 500 m elevation and would hence be considered by Meerman & Sabido in the 'submontane' category. Meerman & Sabido (2001) used Iremonger & Brokaw's (1995) species list to hypothesise frequent species for the UNESCO class 'I.A.2.a.(1).(a).ST' (Table 2). From their list, excluding those taxa we would not have sampled due to our >2.5 cm DBH size threshold, 39% did not occur in either of the three sampling locations, and 11% occurred in all three locations (namely *Calophyllum brasiliense* Cambess., *Dendropanax arboreus* and *Terminalia amazonia*). Hilltops only overlapped with 20–22% of the list, valley floors overlapped with 30–33% and Cuxta Bani with 41%.

Penn *et al.* (2004) group all areas (except Cuxta Bani, Table 2) into the same category (Class 1, Deciduous forest), and our respective lists of taxa matched their species list by 33–48% (valley floors), 44–48% (hilltops) and 52% (Natural Arch). It is worth mentioning that species commonly found throughout otherwise heterogeneous vegetation types make up most of the matching taxa within our area (i.e. *Dendropanax arboreus*, *Pouteria durlandii* (Standl.) Baehni and *Terminalia amazonia* occurred throughout all four sample sites (Table 2), and *Brosimum alicastrum* Sw., *Manilkara zapota* (L.) P.Royen, *Pleradenophora tuerckheimiana*, *Pseudolmedia spuria* (Sw.) Griseb., *Spondias mombin* L. and *Vitex gaumeri* Greenm. were represented in all sampled areas except Cuxta Bani). High percentages of matching names therefore do not equal adequate description of the heterogeneity of the vegetation type itself. Penn *et al.* (2004) do raise awareness of considerable local variation due to the dramatic topography of the area. Kelly *et al.* (1988) ascribe structural differences in plant community composition measured across elevation gradients on Jamaican karst to locally differing water regimes but potentially also to differing degrees of historical disturbance. Local variation in plant community structure on karstic substrate is therefore to be expected (Trejo-Torres & Ackerman, 2002). Our results confirm this, and prove that ground-truthing is absolutely necessary to account for the fine-scale differences in species composition and environmental gradients in the heterogenic landscape.

Forest structure

Transect data were used to compare forest structure, species composition, abundance, dominance, and importance value (IV) across the c.200 m elevation gradient from the valley floors at 400 m to the hilltops at 600 m in the Lower Raspaculo study area. Equal areas of 0.1 ha, respectively, were taken into account (Table 5; see below). The 0.1 ha on hilltops in the Lower Raspaculo showed slightly higher stem density with a total of 532 (52%) recorded stems (i.e. stem density of 5320 stems >2.5 cm DBH/ha), compared to an equal area of 0.1 ha on the Lower Raspaculo valley floors with 501 (48%) stems (i.e. stem density of 5010 stems >2.5 cm DBH/ha; Table 6). Similarly, 0.1 ha of Natural Arch transects near the Chiquibul River had a total of 494 stems (i.e. stem density of 4940 stems >2.5 cm DBH/ha). Within the Lower Raspaculo, total basal area (BA) was inversely proportional to stem density, with the hilltops having more stems but smaller basal area (BA; 8 m^2) compared to valley floors with fewer stems but larger basal area (BA; 9.5 m^2) (Fig. 3, Table 6). More than two-thirds of the valley vegetation fell into the small size category of <7.5 cm DBH compared to 52% in the hilltop vegetation (Fig. 3). Accordingly, a large proportion of hilltop vegetation fell into higher size categories, with nearly half of stems ≥7.5 cm DBH (Fig. 3). Lianas were found to be more diverse in terms of species numbers in the valley floor vegetation, with 32 recorded species compared to 12 species in the hilltop vegetation. These results are congruent with those of Brewer *et al.* (2003) who also found a significant increase in stem density with elevation above valley floors and observed a higher density and frequency of lianas in valley forests compared with ridge forests in the Bladen Nature Reserve. Bladen, at 350 km^2 in area (Brewer *et al.*, 2003), borders the southeast of the Chiquibul and forms part of Belize's contiguous rain forest block within the Maya Mountains. At Natural Arch, 78.3% of all stems were between 2.5 and 10 cm DBH, and 25.7% of all stems were lianas. Only six liana individuals at Natural Arch

TABLE 5. Taxa in order of highest importance from the Lower Raspaculo transects. Absolute and relative abundance, relative dominance, relative frequency and importance value (IV) indices are given, calculated per Gentry transect summing up to an area of 0.1 ha at each location. The taxa listed cumulatively explain two-thirds of the total transects' importance values within a 0.1 ha area of hilltop and valley floor transects, respectively. Only a few taxa are listed as important on both the hilltops (h) and valleys floors (v), e.g. *Cryosophila stauracantha* and *Pleradenophora tuerckheimiana*

	Absolute abundance		Relative abundance		Relative dominance		Relative frequency		IV		
Hilltops (h)	h	v	h	v	h	v	h	v	h	v	Valleys floors (v)
Manilkara zapota	17	11	3.2	2.2	29.7	34.8	2.7	3.0	35.6	40.0	*Brosimum alicastrum*
Pseudolmedia spuria	66	59	12.4	11.8	3.2	0.9	3.5	4.2	19.1	16.9	*Combretum laxum*
Pleradenophora tuerckheimiana	18	61	3.4	12.2	8.6	0.7	2.7	3.4	14.7	16.3	*Piper amalago*
Cryosophila stauracantha	42	1	7.9	0.2	2.6	14.0	3.9	0.4	14.4	14.6	*Coccoloba belizensis*
Leguminosae sp.2	16	43	3.0	8.6	2.3	0.9	3.9	3.0	9.2	12.4	*Rinorea hummelii*
Nectandra cf. *coriacea*	17	24	3.2	4.8	3.0	2.4	2.3	3.8	8.5	11.0	*Cryosophila stauracantha*
Sapindaceae sp.	18	15	3.4	3.0	2.1	3.2	2.7	3.0	8.2	9.2	*Tabernaemontana donnell-smithii*
Zanthoxylum acuminatum	14	9	2.6	1.8	2.1	4.4	2.7	3.0	7.5	9.1	*Spondias mombin*
Coccoloba diversifolia	9	4	1.7	0.8	2.6	6.9	2.3	1.3	6.6	9.0	Unknown sp.
Heisteria media	16	21	3.0	4.2	1.3	0.8	2.3	2.5	6.6	7.6	*Aegiphila monstrosa*
Protium multiramiflorum	17	14	3.2	2.8	1.0	2.2	1.9	2.5	6.2	7.5	*Protium* sp.
Pouteria reticulata	9	21	1.7	4.2	1.8	0.3	2.3	2.5	5.8	7.0	*Paullinia costaricensis*
Guettarda combsii	10	4	1.9	0.8	1.0	4.0	2.7	1.7	5.5	6.5	Malvaceae sp.2
Celastraceae sp.2	13	17	2.4	3.4	0.8	1.3	2.3	1.3	5.5	6.0	*Myriocarpa obovata*
Aspidosperma megalocarpon	13	1	2.4	0.2	0.8	5.3	2.3	0.4	5.5	5.9	*Terminalia amazonia*
Neea psychotrioides	6	6	1.1	1.2	2.4	1.8	1.9	1.7	5.5	4.7	*Pleradenophora tuerckheimiana*
Photinia microcarpa	10	7	1.9	1.4	1.3	1.6	1.9	1.3	5.1	4.3	*Dendropanax arboreus*
Trichilia erythrocarpa	14	6	2.6	1.2	0.2	1.3	1.9	1.7	4.8	4.2	*Alchornea latifolia*
Cedrela sp.	2	8	0.4	1.6	3.5	0.1	0.8	2.1	4.7	3.8	*Tynanthus* cf. *guatemalensis*
Protium sp.	10	6	1.9	1.2	0.8	1.1	1.9	1.3	4.7	3.6	*Trichilia minutiflora*
Ternstroemia tepezapote	6		1.1		2.3		1.2		4.6		
Simarouba glauca	7		1.3		1.3		1.9		4.6		
Schoepfia schreberi	7		1.3		1.4		1.5		4.2		
Sideroxylon stevensonii	6		1.1		1.8		1.2		4.0		

TABLE 6. Comparison between the compositions of species and stems from the four phytogeographical categories (following Wendt, 1993)

Wendt's category*	Valley floor		Hilltop	
	Species	Stems	Species	Stems
N-MA (%)	27.5	17.9	30.0	33.4
MA (%)	25.0	32.4	25.7	23.4
N-SA (%)	13.8	6.8	21.4	30.2
SA (%)	33.8	43.0	22.9	12.9
No. of spp. ID < spp. level	24	59	31	122
Total no. of spp. and stems	104	501	101	532
Total basal area (m^2)	9.49		7.99	
Stem density per hectare (extrapolated)	5010		5320	

*N-MA = Northern Mesoamerica, MA = Mesoamerica, N-SA = Northern South America, SA = South America, from 0.1 ha of valley floor and 0.1 ha of hilltop flora >2.5 cm DBH; 100% equals the total number of species and stems identified to species level, on valley floors and hilltops, respectively.

reached a diameter of >10 cm; therefore, lianas explained over 30% of all stems in the smallest size class, but only 5% of stems in the larger class.

Species composition

A considerable overlap at the species level exists between the limestone forests of the Raspaculo and Chiquibul River valley with limestone assemblages of the Greater Antilles, for example Cuba, Hispaniola and Puerto Rico (Areces-Mallea *et al.*, 1999) and, at least at generic rank, with Jamaica (Kelly *et al.*, 1988). This is not surprising, given their geographical proximity. The 10 most important species in the Lower Raspaculo valley floors, according to the importance value (IV), were *Brosimum alicastrum* (Moraceae), *Combretum laxum* Jacq. (Combretaceae), *Piper amalago* L. (Piperaceae), *Coccoloba belizensis* Standl. (Polygonaceae), *Rinorea hummelii* Sprague (Violaceae), *Cryosophila stauracantha* (Heynh.) R.Evans (Arecaceae), *Tabernaemontana donnell-smithii* Rose (Apocynaceae), *Spondias mombin* (Anacardiaceae), Unknown sp.1, and *Aegiphila monstrosa* Moldenke (Lamiaceae) (Table 5). Species that were amongst the most abundant but which did not score highly in importance value due to their low basal area (BA) included *Protium* sp. (Burseraceae), *Paullinia costaricensis* Radlk. (Sapindaceae) and *Myriocarpa obovata* Donn.Sm. (Urticaceae) (Table 5). *Terminalia amazonia* (Combretaceae), *Pleradenophora tuerckheimiana* (Euphorbiaceae) and Malvaceae sp.2 had high relative dominance but low relative abundance (Table 5).

On hilltops, the most important taxa, based on the importance value (IV), included *Manilkara zapota* (Sapotaceae), *Pseudolmedia spuria* (Moraceae), *Pleradenophora tuerckheimiana* (Euphorbiaceae), *Cryosophila stauracantha* (Arecaceae), Leguminosae sp., *Nectandra* cf. *coriacea* (Lauraceae), Sapindaceae sp. (liana), *Zanthoxylum acuminatum* (Sw.) Sw. (Rutaceae; see also Brewer, 2013), *Coccoloba diversifolia* (Polygonaceae) and *Heisteria media* S.F.Blake (Olacaceae) (Table 5). Species that

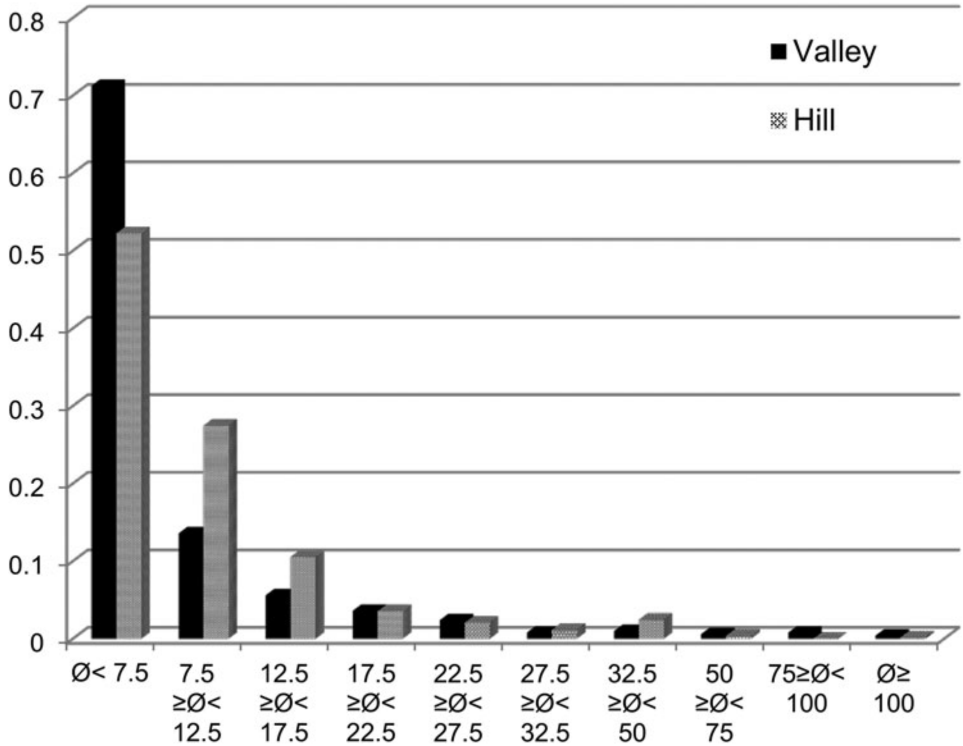


FIG. 3. Fractions of individuals (*y*-axis) occupying the indicated size classes (in cm DBH, here expressed with diameter symbol Ø on *x*-axis). Fractions from the valley and from the hill-top sample each add up to 1.

were amongst the most abundant but which did not score highly in importance value (IV) due to lower basal area (BA) included *Protium multiramiflorum* Lundell (Burseraceae), *Trichilia erythrocarpa* Lundell (Meliaceae), Celastraceae sp.2 and *Aspidosperma megalocarpon* Müll.Arg. (Apocynaceae) (Table 5). *Neea psychotrioides* Donn.Sm. (Nyctaginaceae) and *Cedrela* sp. (Meliaceae) scored highly in relative dominance due to the presence of a few large individuals (Table 5).

At Natural Arch, only abundance and frequency but not basal areas were recorded. Therefore, the following list of species from here is not commensurate with the lists above. However, noteworthy occurrences at Natural Arch (Table 7) were the most frequently recorded trees and shrubs *Chionanthus oblanceolatus* (B.L.Rob.) P.S.Green (Oleaceae), *Spondias mombin* (Anacardiaceae), *Heisteria media* (Olacaceae), the palm *Cryosophila stauracantha* and the lianas *Dalbergia glabra* (Mill.) Standl. (Leguminosae) and *Combretum laxum* (Combretaceae). Abundant but not as frequent as the above were *Cleidion castaneifolium* Müll.Arg. and *Pleradenophora tuerckheimiana* (Euphorbiaceae), *Pouteria durlandii* (Sapotaceae), *Protium copal* (Burseraceae), *Piper psilorhachis* C.DC. (Piperaceae), a palm *Bactris* sp. and the liana *Bignonia potosina* (Bignoniaceae).

TABLE 7. The 29 most abundant taxa recorded at Natural Arch on the Chiquibul River, with absolute and relative abundances and frequencies. Total number of stems ≥2.5 cm was 494 within 10 transects of 0.1 ha (10 × 2 × 50 m)

Taxon	Absolute abundance	Relative abundance	Absolute frequency	Relative frequency
Chionanthus oblanceolatus	25	5.06	8	2.88
Cryosophila stauracantha	20	4.05	5	1.80
Dalbergia glabra	19	3.85	6	2.16
Piper psilorhachis	17	3.44	5	1.80
Combretum laxum	16	3.24	5	1.80
Cleidion castaneifolium	15	3.04	3	1.08
Pleradenophora tuerckheimiana	14	2.83	3	1.08
Bactris sp.	13	2.63	3	1.08
Protium copal	13	2.63	4	1.44
Bignonia potosina	12	2.43	1	0.36
Heisteria media	10	2.02	5	1.80
Spondias mombin	10	2.02	6	2.16
Tynanthus cf. *guatemalensis*	10	2.02	4	1.44
Pouteria durlandii	9	1.82	5	1.80
Pseudolmedia spuria	9	1.82	4	1.44
Tabernaemontana sp.	8	1.62	5	1.80
Calophyllum brasiliense	7	1.42	4	1.44
Casearia corymbosa	7	1.42	3	1.08
Staphylea occidentalis	7	1.42	2	0.72
Celastraceae sp.2	6	1.21	4	1.44
Hippocratea volubilis	6	1.21	1	0.36
Moraceae sp.	6	1.21	1	0.36
Rinorea hummelii	6	1.21	2	0.72
Sabal mauritiiformis	6	1.21	4	1.44
Schnella outimouta vel aff.	6	1.21	4	1.44
Dendropanax arboreus	5	1.01	4	1.44
Protium multiramiflorum	5	1.01	4	1.44
Protium sp.	5	1.01	2	0.72
Hiraea reclinata	4	0.81	4	1.44

Species overlap across Lower Raspaculo vegetation types

Only a few species recorded as important in the Lower Raspaculo valleys and hilltops were present in both vegetation types, for example the palm *Cryosophila stauracantha* and *Pleradenophora tuerckheimiana* (Euphorbiaceae) (Fig. 4, Table 5). *Brosimum alicastrum* (Moraceae), *Rinorea hummelii* (Violaceae), *Spondias mombin* (Anacardiaceae), *Coccoloba belizensis* (Polygonaceae), *Myriocarpa obovata* (Urticaceae) and *Dendropanax arboreus* (Araliaceae) were found to be characteristic of the valley floors but with low occurrence on the hilltops (Table 5). Species that show the opposite pattern of being characteristic elements of the hilltop vegetation but found in low numbers on the valley floors include *Manilkara zapota*, *Pouteria reticulata* (Engl.) Eyma (Sapotaceae),

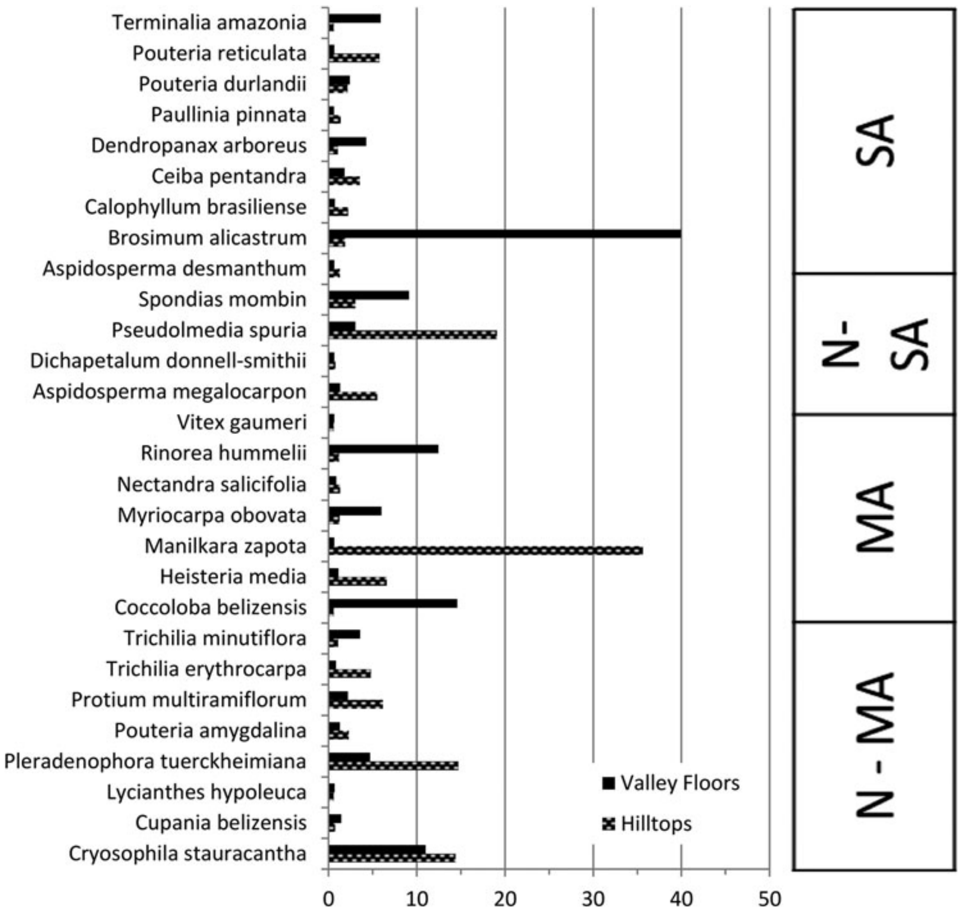


FIG. 4. Comparison of the importance values (IV) of those species occurring in both vegetation types, i.e. the Lower Raspaculo valley floor and hilltop areas, as sampled from equal areas of 0.1 ha respectively, listed alphabetically within Wendt's (1993) phytogeographical categories Northern Mesoamerican (N-MA), Mesoamerican (MA), Northern South American (N-SA) and South American (SA).

Heisteria media (Olacaceae), *Pseudolmedia spuria* (Moraceae), *Aspidosperma megalocarpon* (Apocynaceae) and *Protium multiramiflorum* (Burseraceae) (Table 5).

Pearson's Chi-squared test indicated a statistically significant difference (χ-squared = 158.4537, df = 3, p-value $<2.2 \times 10^{-16}$) between valley floors and hilltops in respect to the distribution of stems from the four different phytogeographical categories. Of those species identified to species level, hilltops contained a significantly higher proportion of stems (33.4%) of species restricted to northern Mesoamerica (N-MA) than did the valley floors, where only 17.9% were made up of this category (Table 6). Similarly, the Northern South America category (N-SA) was more strongly represented on hilltops (30.2%) than on valley floors (6.8%). Of species commonly referred to as 'generalists', i.e. the South American (SA) category, stems were significantly more strongly represented on valley floors (43%) than on hilltops (12.9%). These results are congruent with Brewer *et al.*'s (2003) findings in the Bladen Nature Reserve in southern Belize, where valley floors were also found to be much more likely to be populated by generalist (SA) taxa.

Characteristic species

Characteristic species common and abundant in the valley floor vegetation included *Brosimum alicastrum* (Moraceae), *Combretum laxum* (Combretaceae), *Piper amalago* (Piperaceae), *Coccoloba belizensis* (Polygonaceae), *Rinorea hummelii* (Violaceae), *Tabernaemontana donnell-smithii* (Apocynaceae), *Spondias mombin* (Anacardiaceae), *Paullinia costaricensis* (Sapindaceae) and *Aegiphila monstrosa* (Lamiaceae). These species did not occur in high abundance in the hilltop vegetation nor the Upper Raspaculo forest on metamorphic substrates. In our hilltop vegetation sample, characteristic species were *Manilkara zapota* (Sapotaceae), *Pseudolmedia spuria* (Moraceae), Leguminosae sp.6, *Nectandra* cf. *coriacea* (Lauraceae), *Zanthoxylum acuminatum* (Rutaceae), *Coccoloba diversifolia* (Polygonaceae), *Protium multiramiflorum* (Burseraceae), *Trichilia erythrocarpa* (Meliaceae), *Neea psychotrioides* (Nyctaginaceae) and *Heisteria media* (Olacaceae). On the metamorphic rather than karstic substrate at Cuxta Bani, the list of characteristic taxa included *Dialium guianense* (Leguminosae), *Guarea glabra* subsp. *tuerckheimii* (Meliaceae), *Tabernaemontana* sp. (Apocynaceae), *Guarea grandifolia* (Meliaceae), *Celtis schippii* (Cannabaceae), Leguminosae sp.1, *Compsoneura mexicana* (Myristicaceae), *Cymbopetalum* cf. *mayanum* (Annonaceae), *Garcinia intermedia* (Clusiaceae) and *Protium schippii* (Burseraceae). *Terminalia amazonia* (Combretaceae) was common but also present in the riparian vegetation along the Lower Raspaculo downriver.

Several congeneric species pairs were found to occur in different vegetation types. One of these was *Coccoloba*, in which *Coccoloba belizensis* was an important component of the Lower Raspaculo valleys, whilst *Coccoloba diversifolia* and, to a lesser extent, *Coccoloba acapulcensis* Standl. occurred on the hilltops. *Allophylus cominia* (L.) Sw., *Trichilia erythrocarpa* (also *T. minutiflora* Standl. and *T. moschata* Sw.), *Hampea trilobata* Standl. and *Randia* cf. *matudae* Lorence & Dwyer occurred on hilltops – also reported in Brewer (2013) from Oak Ridge, Bladen Nature Reserve – whilst *Allophylus camptostachys* Radlk., *Trichilia minutiflora* (also *T. erythrocarpa*), *Hampea stipitata* S.Watson and *Randia retroflexa* Lorence & M.Nee occurred on valley floors. *Piper amalago* was dominant in Lower Raspaculo valleys, whilst *Piper yucatanense* C.DC. was found, to a lesser degree, dominant in Upper Raspaculo (Tables 4, 5). *Zanthoxylum acuminatum* and *Pouteria reticulata* dominated in Lower Raspaculo hilltops whilst *Zanthoxylum* sp. and *Pouteria durlandii* dominated in Upper Raspaculo. Care should be taken when comparing the presence and abundance of these species between Lower and Upper Raspaculo because only stems ≥10 cm were recorded in the Upper Raspaculo and stems ≥2.5 cm were recorded in the Lower Raspaculo. It would be interesting to test the environmental niche width of these species pairs, as their respective occurrences suggest specialised adaptations to the different habitat types.

Implications for conservation

The Red List of the International Union for Conservation of Nature (IUCN) considers 33 plants to be threatened in Belize (one Critically Endangered, 13 Endangered and 19 Vulnerable) and a further 130 to be of lesser concern (four Near Threatened, two Data Deficient and 124 of Least Concern; IUCN, 2014). Both of our study sites – the Chiquibul River (CR) and Raspaculo River (LR; UR) – hosted nine species that have been assessed in the Red List (IUCN), and seven of these are threatened (Tables 8, 9). However, we found that 96% (257/267) of the species are not yet assessed by the IUCN Red List. This percentage persists when checking the combined list of Bridgewater *et al.* (2006a) with our additional taxa (Table 9). Therefore, we checked the name entries in TROPICOS, which occasionally supplies more up-to-date and additional information on conservation status of some groups of taxa, even if often at national level (Charlotte Taylor, pers. comm. 2014) (Table 8). Considering our finds and those taxa reported in Bridgewater *et al.* (2006a), at least 58% of all threatened vascular plant taxa of Belize are represented in the Chiquibul Forest alone. Frequently recorded in valley floor vegetation was the Vulnerable *Aegiphila monstrosa*; Near Threatened *Aspidosperma megalocarpon* was recorded several times on the Lower Raspaculo hilltops; and the Endangered *Cymbopetalum* [cf.] *mayanum* and the Vulnerable *Swietenia macrophylla* were recorded many times from the Upper Raspaculo Cuxta Bani plot. The Vulnerable taxa *Pouteria* [cf.] *amygdalina* and *Sideroxylon stevensonii* (Standl.) Standl. & Steyerm. were recorded a few times in the higher elevation forest types both in the Lower Raspaculo and at Natural Arch. The Endangered *Vitex gaumeri* was recorded four times in total at Natural Arch and Lower Raspaculo. Bridgewater *et al.* (2006a) state that, in the Chiquibul Forest, several of the IUCN assessed plant species are locally fairly abundant compared to their entire Mesoamerican distribution. Therefore, the Chiquibul is a key area within the

TABLE 8. IUCN Status for assessed species from the present study (not including Bridgewater *et al.*, 2006a); from the Red List itself and, if applicable, from the TROPICOS main database, with respective reference of publication*

Taxon	Red List Status†
Aegiphila monstrosa	VU A1c, C2a
Aspidosperma megalocarpon	NT
Cedrela odorata	VU A1cd+2cd‡
Cymbopetalum mayanum	EN C2a
Inga sapindoides	LC
Pouteria amygdalina	VU B1+2c
Sideroxylon stevensonii	VU B1+2c
Swietenia macrophylla	VU A1cd+2cd
Vitex gaumeri	EN C2a

*Note that TROPICOS does not usually duplicate the conservation status information from the Red List, but it does sometimes refer to taxon assessments published elsewhere that are not yet available in the Red List, or done on a national scale.

†LC = Least Concern, NT = Near Threatened (Lower Risk), EN = Endangered, VU = Vulnerable (Threatened); for 'hierarchical alphanumeric numbering system of criteria and subcriteria', please refer to IUCN (2014).

‡Pennington & Muellner (2010) indicate LC status.

Maya Forest for biodiversity conservation. Although the Chiquibul is legally protected, there has been an increase of illegal activities including poaching and illegal logging (Briggs *et al.*, 2013). Furthermore, the Chiquibul Forest is located within Cayo District; of the total deforestation that occurred in Belize between 2010 and 2012, some 35% occurred in Cayo (Cherrington *et al.*, 2012). This is not surprising since there has been a steady decline in the Mayan Forests' cover in Belize averaging ~10,000 ha/year (0.6%) over the last three decades, where ~15.2% has occurred within protected areas (Cherrington *et al.*, 2010). The total deforestation in the Maya Forests is a major concern due to its high biodiversity value (Myers *et al.*, 2000; Conservation International, 2004; Young, 2008; Briggs *et al.*, 2013). The data gathered from this

TABLE 9. Percentages of species in IUCN Red List categories from both the present study and Bridgewater *et al.*'s (2006a) angiosperm species list combined; less than 5% of species reported from the Chiquibul have been assessed by IUCN

IUCN	No. of species	Percentage
Not assessed	1288	95.8
EN	4	0.3
VU	10	0.7
NT	1	0.01
LR/nt	1	0.01
LR/lc	3	0.2
LC	37	2.8
Total	1344	100

study will serve to emphasise the importance of the Chiquibul, and can be used for the development of conservation and management plans in the region.

Conclusion

The data from this expedition constitute a first step to filling knowledge gaps in plant diversity in the remote eastern Chiquibul National Park. The number of new records found in the Upper Raspaculo confirms our relatively poor knowledge of the Chiquibul flora in areas of metamorphic rather than karstic substrate. Since our survey in the Upper Raspaculo was relatively short and covered only trees above 10 cm DBH, further expeditions in this area will be important to gather missing data for the Chiquibul plant inventory. Based on our results, we expect that many more species not yet recorded will be found. Our study supports Bridgewater *et al.*'s (2006a) conclusions that the higher altitudes within the Chiquibul Forest are the most poorly collected and are expected to deliver many more new records to the local flora. We found 38 new records in the Chiquibul, 20 of which came from the karstic terrain above 500 m elevation. Additionally, our list reveals that, within our study area in the CFRNP, there are at least 58% of the threatened plant species listed for Belize (IUCN, 2014). However, 96% of the species in our inventory have not yet been globally assessed in the IUCN Red List. Given the biodiversity value of the Chiquibul Forest, our results stress the pressing need for further botanical inventories and the urgency required in producing threat assessments of its plant species.

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