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Original research article

A quantitative assessment of the vegetation types on the island of St. Eustatius, Dutch Caribbean

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ABSTRACT

Caribbean dry forests are among the most endangered tropical ecosystems on earth. Several studies exist on their floristic composition and their recovery after natural or man-made disturbances, but little is known on the small Dutch Caribbean islands. In this study, we present quantitative data on plant species richness and abundance on St. Eustatius, one of the smallest islands of the Lesser Antilles. We collected and identified trees, shrubs, lianas and herbs in 11 plots of 25 x 25 m in different vegetation types. We compared their floristic composition and structure to vegetation surveys from roughly the same locations in the 1990s and 1950s. We found substantial differences among our 11 plots: vegetation types varied from evergreen forests to deciduous shrubland and open woodland. The number of tree species $\geq$ 10 cm DBH ranged between one and 17, and their density between three and 82 per plot. In spite that all plots were subject to grazing by free roaming cattle, canopy height and floristic diversity have increased in the last decades. Invasive species are present in the open vegetation types, but not under (partly) closed canopy. Comparison with the earlier surveys showed that the decline of agriculture and conservation efforts resulted in the regeneration of dry forests between the 1950s and 2015. This process has also been reported from nearby islands and offers good opportunities for the future conservation of Caribbean dry forests.

1. Introduction

The Caribbean islands are hotspots of biodiversity, harbouring 2.3% of the world's endemic flora on a relatively small surface, with only 11% of the original primary vegetation remaining (Myers et al., 2000). Due to their small size and isolation, islands are particularly vulnerable to anthropogenic processes, resulting in habitat fragmentation, invasive species and extinction of endemic plants (MacArthur and Wilson, 1967; Stachowicz and Tilman, 2005). The climax vegetation on most Caribbean islands is dry forest, one of the most endangered tropical ecosystems on earth (Janzen, 1988). Several studies are available on the recovery of Caribbean dry forests after anthropogenic or natural disturbances, in Guadeloupe (Imbert and Portecop, 2008), Puerto Rico (Brandeis et al., 2009), the Bahamas (Franklin et al., 2015) and the Dominican Republic (Cano and Veloz, 2012; García-Fuentes et al., 2015). Little is known, however, on the composition of dry forests on the Dutch Caribbean islands. Such information is essential for adequate conservation and sustainable management plans. One

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Fig. 1A. Location of St. Eustatius.
Source: Dutch Caribbean Biodiversity Explorer (www.dcbiodata.net).

of the first steps is to produce accurate information on the spatial distribution of habitats and quantitative data on species abundance within different vegetation types (Helmer et al., 2008).

Here we provide quantitative data on plant species richness and abundance on St. Eustatius, with 21 km^2 one of the smallest islands of the Lesser Antilles (Fig. 1A). St. Eustatius is composed of two volcanic areas separated by lowlands that were once formed by volcanic debris. The northern hills (up to 289 m) are extinct volcanos formed around 500,000 years ago and now extinct. The southern Quill volcano is dormant, 600 m high, with an open, 750 m wide crater at ca. 273 m above sea level. This volcano is less than 50,000 years old, but has not erupted in the last 1600 years (Roobol and Smith, 2004). On the southern side of the Quill, a formation called the White Wall is found, a steep limestone slope that was uplifted due to submarine volcanism in the Holocene (Westermann and Kiel, 1961). Rainfall is quite variable, but averages at an annual 986 mm, with a wet season from August to November and a dry season from December to April. Rainfall is highest on the Quill volcano, while the northern hills receive less precipitation. The average daily temperature is over 30 °C in the warmer months (May to November) and 24 °C in the cooler months (December to April). Relative humidity ranges over the course of the year from a high of 94% to a low of 62% (NOAA, 2015). Due to the heterogenic landscape and climate, the island harbours diverse vegetation types: from xeric shrub land with cacti to seasonal deciduous and evergreen tropical forest (Roobol and Smith, 2004; Helmer et al., 2008; De Freitas et al., 2014).

In 1999, the St. Eustatius Government delegated the St. Eustatius National Parks Foundation (STENAPA) to protect the dry habitats in the northern hills in the Boven National Park and the southern, moister forests in the Quill National Park (Fig. 1B). The island has now 28% of the land under formal protection (Helmer et al., 2008). The lowlands in between the two mountainous protected areas, known locally as the Cultuurvlakte (agricultural plain) and occupying ca. 25% of the island surface, have been intensively used for agriculture, urban development and cattle grazing in the past three hundred years. In the heyday of the plantation economy, some 25,000 people lived on the island. Apart from the Cultuurvlakte, agricultural fields were established in the northern hills, almost up to the rim of the Quill and in the volcano crater itself. The population dropped to just 950 persons in the 1950s following the decline of agriculture and migration of people to Curaçao for paid labour (Palm, 1985). Following the construction of an oil terminal in 1982, now a major employer on the island, the population rose again. The latest figures (CBS, 2013) place the island's current population at to ca. 3900. Due to centuries of anthropogenic disturbance, none of the original lowland forests are left. The Cultuurvlakte suffers from the deleterious effects of invasive species and free roaming cattle, but most of the officially protected vegetation types on the island, also suffer from overgrazing, particularly by goats (Van der Burg et al., 2012).

In 2010, St. Eustatius, Bonaire and Saba became special municipalities of the Kingdom of the Netherlands. A new nature management plan was set up for the period 2013–2017 to create a framework for the protection and sustainable management of biodiversity in the Dutch Caribbean (Ministry of Economic Affairs, 2013). To facilitate scientific research in the region, the Caribbean Netherlands Science Institute (CNSI) was established on St. Eustatius (http://www.cnsi.nl). Early 2015, Naturalis Biodiversity Center started its Caribbean programme with a multi-taxon baseline assessment of the terrestrial and marine biodiversity of St. Eustatius. This allows us to reveal how patterns of richness and diversity co-vary within and between taxonomic groups, identify the drivers of these patterns and indicate terrestrial biodiversity hotspots on the island (Wesselingh et al., 2013). Occurrence data will include historic and recent collections, observations and DNA barcoding techniques to identify cryptic species. To serve as a basis for this multi-taxon approach, this paper focuses solely on vegetation and vascular plants.

The first vegetation map of the island was produced by Stoffers (1956) and based on botanical collections made between 1755 and 1953. Stoffers recorded 453 plant species and distinguished 18 different vegetation types, based on plots of different sizes (e.g., 20 × 10 m, 80 × 5 m) in which trees and shrubs over 5 m high were counted and smaller plants visually estimated. Helmer et al. (2008) published land cover and forest formation distributions for St. Kitts, Nevis, St. Eustatius, Grenada and Barbados. Their forest formations were based on cloud-cleared satellite images in stead of on-the-ground vegetation surveys or botanical collections, resulting on broad classifications in rather low resolution for St. Eustatius, as it is rather small compared to the other islands in this study. In 2014, De Freitas et al. (2014) published a landscape ecological vegetation map, based on areal photographs taken in 1991 and field observations from 1999. Based on 84 sample plots,

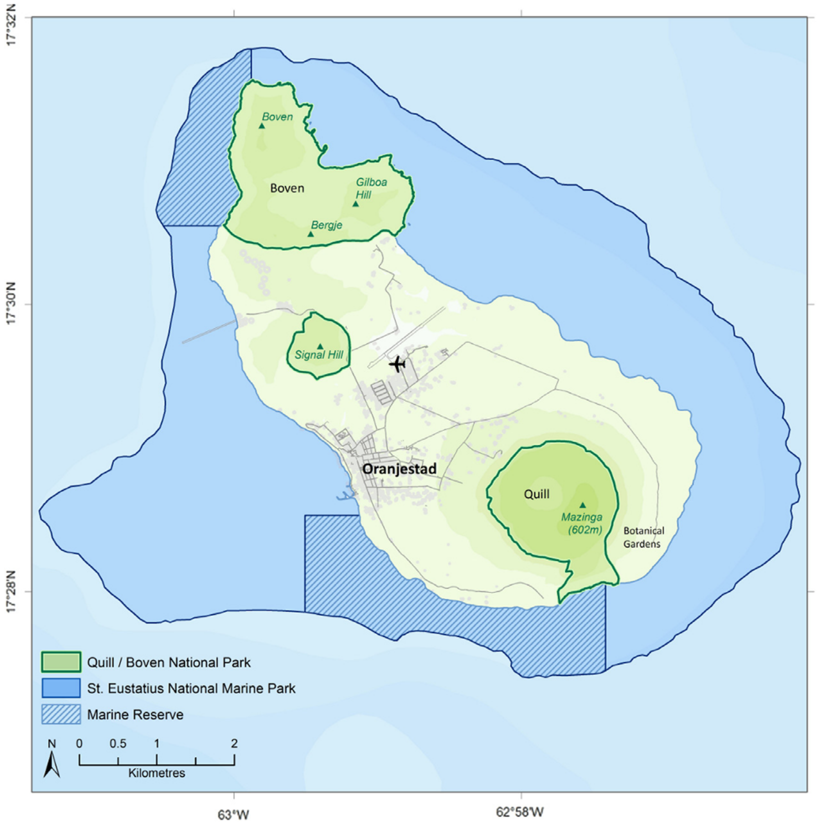

Fig. 1B. The island of St. Eustatius and its protected areas.
Source: Dutch Caribbean Nature Alliance (http://www.dcnanature.org/st-eustatius-national-marine-park/).

varying in size from 15 × 15 m (higher vegetation) to 3 × 3 m (grass vegetation), De Freitas et al. distinguished 13 (semi-) natural vegetation types, excluding the central lowlands around the urbanized parts of the island. Although De Freitas et al. considered their survey as a quantitative reference point for further studies, the exact locations and sizes of their 84 sample plots were never published. Their data on species dominance seemed to be based on visual estimations rather than on absolute counts, and no botanical collections were cited, although some vouchers were deposited at the Puerto Rico herbarium (UPRRP).

The most recent checklist of the vascular plants of St. Eustatius (Axelrod, in press), lists 617 different species of vascular plants, excluding strictly ornamental plants that rarely escape from cultivation and is based on the Flora of the Dutch West Indian Islands (Boldingh, 1909), the Flora of the Netherlands Antilles (Stoffers, 1962–1984), the Flora of the Lesser Antilles (Howard, 1974–1989), numerous historic and recent collections in the herbaria of Naturalis and Puerto Rico. The specific objective of this study was to obtain quantitative data on species diversity and abundance in the different vegetation types indicated on the map by (De Freitas et al., 2014), based on botanical collections, diameter measurements and absolute species counts in permanent sample plots. We sought to answer the following research questions:

(1) What are the dominant species in the tree, shrub and herb layers in the major vegetation types indicated on the map of De Freitas et al. (2014)?
(2) Does the floristic composition and species abundance in these plots coincide with the observations of Stoffers in the 1950s and De Freitas et al. in 1999?

2. Materials and methods

Fieldwork was carried out during two expeditions to St. Eustatius, using the field station of the Caribbean Netherlands Science Institute (CNSI) as a base. Permits for plant collection and DNA sampling were obtained from STENAPA. GIS layers indicating major vegetation types (De Freitas et al., 2014) were downloaded from the Dutch Caribbean Biodiversity Database (http://www.dcbd.nl/island/st-eustatius). We used QGIS (http://www.qgis.org/en/site/) to plot five random points within each major vegetation type, representing nearly the full range of habitats available on the island. Points were assigned a random order. During the exploratory expedition between 21 March and 2 April 2015, we attempted to reach each point in sequence until one from each vegetation type was determined to be sufficiently accessible and safe for sampling. Square

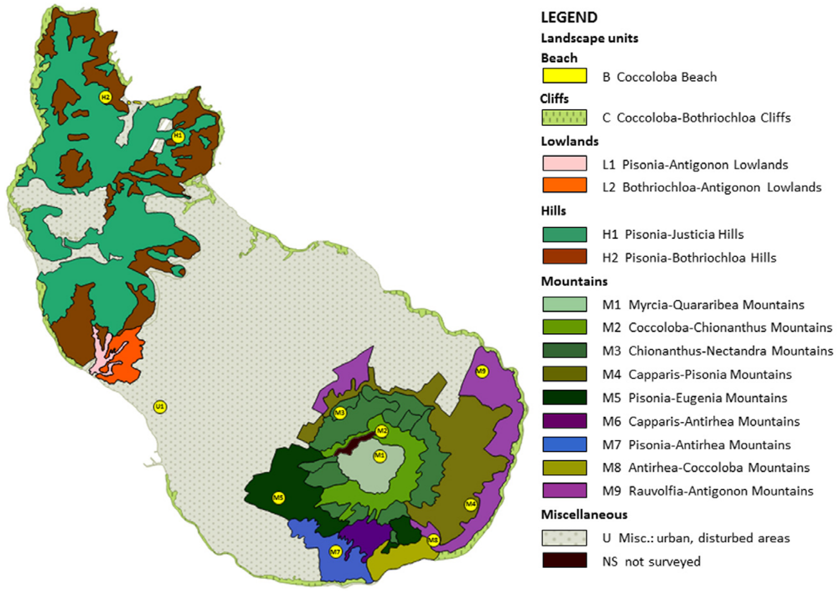

Fig. 2. Map of St. Eustatius showing the location of the 11 plots (yellow circles) and the vegetation types as defined by De Freitas et al. (2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

plots of 25 × 25 m were laid out in 11 different vegetation types, representing almost the full range of habitats present on the island (Fig. 2). Exact plot coordinates and explanations of the vegetation codes are listed in Table 1.

Our aim was to lay out one plot of 25 × 25 m in each of the 13 major vegetation types distinguished by De Freitas et al. (2014). However, two of these vegetation types, type M6 (*Capparis-Antirrhea* mountains) and C (*Coccoloba-Botriochloa* cliffs) were not covered because of safety issues and difficult access (see Table 1). Type B (*Coccoloba* Beach) was not included because this landscape unit only consisted of a few scattered *Coccoloba uvifera* shrubs on sandy beaches. Vegetation types L1 (*Pisonia-Antigonon* Lowlands) and L2 (*Botrichloa-Antigonon* Lowlands) could not clearly be told apart in the field, so they were both covered by our newly defined vegetation type U1 (urban vegetation with *Antigonon leptopus*). Details on all 11 plots are provided in Table 1.

From 2 to 18 October 2015, all plots were revisited with a group of students and surveyed in detail, using a multi-taxon approach. Data were collected in the framework of the Naturalis Caribbean programme and the related course Tropical Biodiversity and Field Methods, which contains a practical period in which students learn to use different sampling methods. In each plot, vascular plants, bryophytes, lichens, insects, snails, butterflies, reptiles and spiders were collected simultaneously, soil fungi samples were taken for lab analysis, while birds and bats were observed on separate mornings and evenings. Students actively participated in collecting specimens in the field and their processing and identification afterwards. All data collected during this course will be used in subsequent biodiversity analyses that will be published elsewhere. The current paper focuses on the results of the vascular plant surveys.

In each of the 11 plots of 25 × 25 m (0.0625 ha), we counted all trees and lianas $\geq$ 10 cm DBH (diameter at breast height), measured their diameter and estimated their height. In a subplot of 5 × 5 m, we counted lianas, tree saplings and shrubs $<$ 10 cm DBH and $\geq$ 1.5 m high. In a subplot of 1 × 1 m, we counted all seedlings and herbs. We made botanical collections of all plant species in the plots, except for CITES-listed species such as orchids, bromeliads, and cacti (see https://www.cites.org/eng/app/appendices.php). In case these species were encountered in the plot, they were identified by means of photographs. Extra flowering and fruiting specimens of non-CITES listed species were collected outside the plots to facilitate scientific identification of the sterile vouchers collected within the plots.

All collections were deposited at the Naturalis herbarium (L), while some duplicates were sent to Mr. Franklin Axelrod, botanist at the Puerto Rico herbarium (UPRRP) for identification. All specimens were identified between October and December 2015. Current scientific names were checked with The Plant List (www.theplantlist.org). Information on local names and plant uses provided by field assistants were documented and published elsewhere (Posthouwer, 2016; Verheijden, 2016). A list of all species encountered in the 11 plots, with their families and growth form is given in Supplementary Table 1 (see Appendix A).

To assess the dominance of tree species within the plots, we calculated for each tree species $>$ 10 cm DBH in a plot the basal area: $BA = \pi \times (DBH/2)^2$. We calculated total figures of basal area and tree density (number of individuals per plot) to compare differences in vegetation structure. We compared the floristic composition and tree species dominance of our plots with the vegetation descriptions of De Freitas et al. (2014) and Stoffers (1956) in the same area to see whether the vegetation had changed in the past decades. Apart from the qualitative descriptions provided in the previous studies,

Table 1
Location of the 11 plots and vegetation classifications from earlier surveys.

Code De Freita	Code This study	Location	Elevation (m)	Latitude[b] (degree)	Longitude (degree)	Date sampled	Stoffers (1956)	Helmer et al. (2008)	De Freitas et al. (2014) Vegetation type	De Freitas et al. (2014) Landscape ecological unit
M1[a]	M1	Crater bottom	293	17.4784	−62.9621	10-Oct-15	Evergreen seasonal forest [X]	Seasonal evergreen forest	*Myrcia splendens-Quararibea turbinata* type	*Myrcia-Quararibea* Mountains
M2	M2	Crater rim	541	17.4811	−62.9620	11-Oct-15	Dry evergreen forest [XVI]	Submontane semi-evergreen forest	*Coccoloba swartzii-Ardisia obovata* type	*Coccoloba-Ardisia* Mountains
M3	M3	Higher wet slope	276	17.4830	−62.9665	5-Oct-15	Semi-evergreen seasonal forest [X1]	Semi-evergreen forest	*Chionanthus compactus-Nectandra coriacea* type	*Chionanthes-Nectandra* Mountains
M4	M4	Lower dry slope	84	17.4733	−62.9521	3-Oct-15	Deciduous seasonal forest (XII)	Semi-deciduous forest	*Capparis cynophallophora-Gymnanthes lucida* type	*Capparis-Pisonia* Mountains
M5	M5	Halfway dry slope	141	17.4741	−62.9732	4-Oct-15	Deciduous seasonal forest (XII)	Deciduous mixed forest	*Pisonia subcordata-Eugenia axillaris* type	*Pisonia-Eugenia* Mountains
M6	–									*Capparis-Antirrhea* mountains
M7	M7	Foot of volcano	100	17.4684	−62.9669	9-Oct-15	Thorny woodland (XIX)	Deciduous mixed forest	*Pisonia subcordata-Ayenia insulaecola* type	*Pisonia-Antirrhea* Mountains
M8	M8	Limestone slope	109	17.4696	−62.9562	14-Oct-15	Dry evergreen bushland (XVIII)	Drought deciduous open woodland	*Antirhea acutata-Dodonaea elaeignoides type*	*Antirrhea-Coccoloba* Mountains
M9	M9	Recovering grassland	65	17.4874	−62.9509	8-Oct-15	Thorny woodland (XIX)	Deciduous mixed shrubland	*Rauwolfia viridis-Lantana involucrata* type.	*Rauvolfia-Antigonon* Mountains
C	–									*Coccoloba-Botriochloa* Cliffs
H1	H1	Northern hills forest	160	17.5121	−62.9843	6-Oct-15	Deciduous seasonal forest (XII)	Deciduous mixed forest with succulents	*Pisonia subcordata-Justicia sessilis* type	*Pisonia-Justicia* Hills
H2	H2	Northern hills shrubland	103	17.5163	−62.9923	7-Oct-15	Croton thickets (XX)	Drought deciduous shrubland	*Botriochloa pertusa-Boutelouaamericana* type	*Pisonia-Botriochloa* Hills
L1	U1[c]	Urban abandoned yard	61	17.4836	−62.9863	13-Oct-15	–	Semi-deciduous shrubland	*Antigonon leptopus* type	*Pisonia-Antigonon* Lowlands
B	–						Littoral woodland [XXI]			*Coccoloba* Beach

[a] M = mountains; H = hills, L = lowlands.
[b] Latitude and longitude measured in the centre of the square plot.
[c] Abbreviation of "urban".

Table 2
Vegetation analysis.

Plot nr.	H1	H2	U1	M1	M2	M3	M4	M5	M7	M8	M9
Nr. of tree species	9	1	1	6	17	17	7	8	7	5	1
Nr. of individual trees	59	3	5	24	57	56	33	82	77	16	2
Mean height (m)	5.2	3.3	6.5	16.5	8.6	8.2	5.1	6.6	5.2	3.7	3.3
Mean diameter (cm)	15.0	12.1	13.9	30.0	19.1	14.7	19.5	13.6	14.9	12.0	13.1
Total basal area ($m^2/25 \times 25$ m)	1.19	0.04	0.08	2.52	2.41	1.08	1.54	1.50	1.30	0.21	0.03
Total basal area (m^2/ha)	19.10	0.57	1.32	40.24	38.64	17.28	24.62	23.96	20.84	3.38	0.43
Nr. species shrub layer	7	1	4	4	3	4	3	3	3	2	4
Nr. species herb layer	1	6	5	4	4	1	3	5	5	4	6

we compared our most abundant species with the species previously mentioned as dominant, based on their abundance as expressed in the number of stems (Stoffers, 1956) or the percentages of individuals (De Freitas et al., 2014).

3. Results

3.1. General data on the different vegetation types

We found substantial differences in floristic diversity, composition and structure of the 11 different vegetation plots (Table 2). The number of tree species $\geq$ 10 cm DBH varied from 1 in the severely degraded vegetation types (H2, U1, M9) to 17 per plot on the heavily forested wet slope and crater rim of the Quill volcano (M2, M3). As expected, tree density varied from 1 tree per 25 $\times$ 25 m in the open vegetation types to 82 in the dense, thin-stemmed, dry forest on the lower parts of the Quill volcano. In total we recorded 75 species in the 11 plots, with the Leguminosae and Myrtaceae as most species-rich families (each 6 spp.), followed by the Capparaceae, Rubiaceae and Poaceae (each 4 spp.). Below we shortly describe the floristic composition in the 11 plots and compare these with the vegetation descriptions on the same location by Stoffers (1956) and De Freitas et al. (2014). All species encountered in the 11 plots are listed in the Supplementary Table 2 with their basal area values, mean height and diameter (for all trees $\geq$ 10 cm DBH). Abundance figures are given for all species in the plots. Photographs of several vegetation types and characteristic plant species are shown in Supplementary file 3 (see Appendix A).

3.2. Forest in the northern hills

H1: This forest type is found on the less exposed slopes of the northern hills of the Boven National Park. The canopy is relatively low, and the forest is dense with relative thin stems, but tree diversity is slightly higher than in the dry forest on the lower slopes of the Quill (Table 2). Dominant tree species are *Pisonia subcordata*, *Acacia macracantha*, *Coccoloba swartzii* and *Bursera simaruba* (Supplementary Table 2, Appendix A). Typical tree species in this forest type are *Morisonia americana* and *Piscidia carthagenensis*, not found in other plots in this study, although the latter was also frequently observed along the dry creek bed leading to the nearby Venus bay. Large lianas, all belonging to the species *Stigmaphyllon emarginatum*, twist themselves through the canopy. In the shrub layer, the prickly *Randia aculeata* profits from gaps in the canopy. In open spaces at the edge of this forest, this shrub occurs massively. Other species occurring just outside the plot are *Comocladia dodonaea* and the columnar cactus *Pilosocereus royenii*. De Freitas et al. (2014) defined this forest type as the *Pisonia subcordata-Justicia sessilis* type and listed roughly the same species as we encountered, except that our forest plot did not have an open herb layer with grasses and herbs like *Justicia sessilis*. The latter herb, however, was frequently observed along cleared footpaths on the Quill and in Boven National Park. Possibly, this forest type has profited from its protected status, as its canopy (mean 6.3 m, max. 9 m) is now higher than in 1999 (mean 3.6 m, max 5 m). In the 1950s, this forest type did not seem to exist (yet). Although Stoffers (1956) mentions the majority of the tree species we encountered, he describes the vegetation as 'secondary woodland' with 'gnarled trees' hardly higher than 5 m high. Just like today, *P. subcordata* was the most abundant tree (up to 40% of the individuals), followed by *B. simaruba* (up to 24%). Stoffers also noted the presence of the domesticated fruit trees *Annona muricata, Crescentia cujete* and *Manilkara zapota*, now absent from the area and only found cultivated in gardens in Oranjestad (Verheijden, 2016).

3.3. Open shrubland in the northern hills

H2: The second vegetation type in the northern hills consists of open, grassy shrubland, with very few trees belonging to *Jacquinia armillaris* (in the plot), and *Cynophalla flexuosa* and *Ardisia obovata* (outside the plot). Young, flat crowned *Acacia tortuosa* trees are found in the shrub layer. The herb layer is dominated by the grass *Bouteloua americana*. A few juvenile cacti (*Opuntia* cf. *dillennii*) are encountered as well. De Freitas et al. (2014) defined this vegetation type as the *Botrichloa pertusa-Bouteloua americana* type, its two prominent grasses. The invasive Donna grass (*B. pertusa*), said to have arrived with hurricane Donna in 1960, apparently dominated this rocky shrubland in the 1990s, but we did not find it in the area designated on the map as H2. Although the area is heavily grazed, its present protected status probably allows for the return of some trees, like the ones we encountered in and around our plot. In the 1950s, there was still agricultural activity in the northern hills, combined with grazing and burning *Acacia* trees for charcoal (Stoffers, 1956). At that time, most of the non-cultivated vegetation in Boven consisted of *Croton* thickets, a sign of heavy grazing pressure, as goats do not eat from this shrub. We encountered these *Croton* thickets only around plot M9 on the intensively grazed foothills of the Quill volcano.

3.4. Abandoned agricultural land

U1: The archaeological site 'Deep Yard' was chosen as a representative example of the abandoned agricultural land of the Cultuurvlakte. Such "urban wasteland" is frequently found in empty lots in Oranjestad. This open vegetation, entirely covered by a blanket of the invasive corallita vine (*Antigonon leptopus*), contains a few scattered trees, like *Leucaena leucocephala* (also an invasive) and the cultivated fruit tree *Melicoccus bijuga*, whose broad crown shades out the corallita, allowing space for a few other herbs and grasses. De Freitas et al. (2014) defined this vegetation type as the *Antigonon leptopus* type, an adequate description. They mentioned *Jatropha gossypiifolia* as a characteristic species, which occurred just outside our plot. Neither *Pisonia subcordata* nor *Botriochloa pertusa* were encountered here, as were suggested in the vegetation types L1 and L2 respectively. We did an inventory of the vegetation in the areas depicted as L1 and L2 on the map of De Freitas et al. (2014), but they contained the same species as in our U1 plot. *Antigonon leptopus* was first collected in 1931 by Boldingh (Wesselingh et al., 2013). Stoffers (1956) also listed *A. leptopus* as an introduced species, but did not mention its invasive character. The Cultuurvlakte, now urbanized or covered by vegetation types L1, L2 or U1, was mostly still under cultivation in the 1950s.

3.5. Forest in the crater

M1: Protected from the strong winds by the vertical crater walls, the humid, evergreen forest on the bottom of the Quill volcano is the highest forest with the largest trees on the island. Tree diversity is lower than on the crater rim and wet slopes, because a few large giants (*Spondias mombin* and the 40 m high strangler fig *Ficus nymphaeifolia*) occupy the space and light needed by other trees. Just a few smaller species make up the subcanopy (*Pouteria multiflora* and *Casearia decandra*), while several large individuals of *Cecropia schreberiana* have occupied previous gaps. The shrub and herb layer is occupied by large numbers of the climbing hemi-epiphyte *Philodendron lingulatum*. A characteristic shrub occurring only in this forest is *Piper reticulatum*. Ferns (e.g., *Lomariopsis sorbifolia*, *Pecluma pectinata*) are abundant on the forest floor, although we collected them just out of our 1 × 1 m herb plot. Another characteristic element in this vegetation is the large herb *Heliconia caribea*, which occurred just outside our plot. Relics of plantations on the crater bottom (established in the early 1900s) were also observed outside our plot, such as coffee shrubs (*Coffea arabica*), fruiting cacao (*Theobroma cacao*) and mamee trees (*Mammea americana*).

De Freitas et al. (2014) defined this forest type as the *Myrcia splendens-Quararibea turbinata* type. While *Q. turbinata* was encountered outside our plot, *M. splendens* was only observed on the crater rim. The only large tree they identified was *Ficus trigonata*, but this species has never been collected on the island (Axelrod, in press). Stoffers (1956) also mentioned a high forest in the crater, with similar large tree species as today (*Spondias mombin*, *Ceiba pentandra*), but also some typical species from dryer, exposed forest (*Pisonia subcordata* and *P. fragrans*), which are not present in this forest type today.

3.6. Forest on the crater rim

M2: The forest on the crater rim (541 m) is lower and denser than that in the crater bottom, with smaller trees growing on and between large boulders. It contains almost three times as many tree species, of which *Ficus americana*, *Byrsonima spicata*, *Chionanthus compactus*, *Inga laurina* and *Coccoloba swartzii* are the most abundant. Tree species found only in this forest type are *Pimenta racemosa*, *Chrysophyllum argenteum* and *Clusia major* and, outside the plot, *Ternstroemia seemannii*. Vegetation on the forest floor is characterized by the large hemi-epiphyte *Philodendron giganteum*. Orchids are common epiphytes and fleshy herbs (e.g., *Peperomia* spp., *Talinum paniculatum*) grow on the rocks. Our data largely coincide with the description of De Freitas et al. (2014), who defined this forest type as the *Coccoloba swartzii-Ardisia obovata* type, with a canopy of max. 4 m high. Both species occurred in our plot, but the latter one only in the lower strata. Tree diversity on the crater rim documented by Stoffers (1956) was much lower, with *Tabebuia heterophylla* as the dominant species. In the 1950s, trees were still felled for timber here and no individuals over 5 cm diameter were found. With a mean height of 8.6 m and a mean diameter of 19.1 cm, this forest has recovered substantially since then.

3.7. Forest on the higher, moist slopes

M3: The plot on the higher, moist slopes (276 m) on the northern part of the Quill has a similar floristic diversity, tree density and height as the forest on the crater rim, but the species composition differs. There are no obviously dominant trees, but *Tabebuia heterophylla*, *Chionanthus compactus*, *Citharexylum spinosum* and *Bursera simaruba* are most abundant. Typical species are *Daphnopsis americana* subsp. *caribea* and *Zanthoxylum martinicense*. The shrub and herb layer consists entirely of saplings and seedlings of canopy trees. De Freitas et al. (2014) defined this forest type as the *Chionanthus compactus-Nectandra coriacea* type. Although the first species was frequently found in our plot, we encountered only one sapling of *N. coriacea* just outside of our plot. Although De Freitas et al. (2014) distinguished no differentiating species in this forest type, we did not encounter *D. americana* subsp. *caribea* and *Z. martinicense* anywhere else than here. According to Stoffers (1956), forest started only above 275 m altitude, although trees were still felled for timber at this altitude. In the 1950s, *Ceiba pentandra* and *Hymenaea courbaril* were dominant species in this forest type, but we only found a few individuals of *H. courbaril* somewhat lower down the mountain. According to local people, this tree was planted along the roads to the Quill in the past, but nowadays less people eat the powdery seed coat and the species has become rare. *C. pentandra* is found both in the crater as in the urban area of Oranjestad. Stoffers also noted high numbers of *N. coriacea* in the forest understorey in this forest type.

3.8. Forest on the lower, dry slopes

M4: The forest on the lower, dry slopes on the south side of the Quill near the Miriam C. Schmidt Botanical Garden is heavily dominated by *Quadrella cynophallophora*, representing 41% of the total basal area, followed by *Ficus citrifolia*, and to a lesser extent *Citharexylum spinosum*. The shrub and herb layer are characterized by *Randia aculeata* and *Rauvolfia viridis*. This forest has a much lower diversity, density and canopy height than the forest on the wetter slope. De Freitas et al. (2014) defined this forest type as the *Capparis cynophallophora-Gymnanthes lucida* type. The first species is a synonym of the dominant tree (*Q. cynophallophora*), but the latter species we only found on the limestone slope of M8. The rest of their description matches our plot data, although some of their typical dry forest species (*Samyda dodecandra* and *Heteropteris purpurea*) were only found outside our plot. In the 1950s, this area was likely still under cultivation or used as grazing lands, as Stoffers (1956) does not mention it.

3.9. Forest halfway the dry slopes

M5: The forest halfway on the dryer, southwestern slopes (141 m) has similar levels of floristic diversity, but much more, thinner-stemmed trees that are slightly higher than in M4. The canopy is dominated by *Bourreria baccata*, *Pisonia subcordata*, *Guettarda scabra* and to a lesser extent *Bursera simaruba*. The shrub *Eugenia axillaris* is a typical species in the understorey, next to the prickly *Randia aculeata* and saplings of the invasive tree *Leucaena leucocephala*. De Freitas et al. (2014) defined this forest type as the *Pisonia subcordata-Eugenia axillaris* type, in which *Pisonia subcordata* reached a higher frequency than in all other forest types. This may have been the case in the 1990s, but today the species seems to have lost some of its dominance with only 22 individuals per plot, much less than the 49 in the hurricane-affected plot (M7). The rest of the species in our plots corresponded with those found in the 1990s. These forests were formerly used as farmlands, still visible by some stonewalls and remnant graves, but have recovered to forests. In the 1950s, this area was described as secondary vegetation, consisting of thorny *Acacia* thickets not higher than 4 m.

3.10. Forest on the mountain foot

M7: This forest on the foot of the volcano grew on the windy southwest side of the island. The canopy was quite open and heavily dominated by *Pisonia subcordata*, taking up 62% of the basal area, followed from a distance by *Quadrella cynophallophora* and *Krugiodendron ferreum*, a tree only found in this type of vegetation. The low canopy and low mean diameter were caused by a previous hurricane: many of the *Pisonia* and *Acacia* trees had broken their branches or fell down, so most of the stems at breast height were in fact new sprouts growing from old stems. *Pisonia subcordata* has very light wood that breaks easily: living branches can be broken by hand. This seems an adaptation to strong winds: *P. subcordata* looses its branches but does not die, and quickly sprouts again after the hurricane. Ants frequently inhabit the gnarled stems and hollow branches of *P. subcordata*. They probably function as a protection against insects and provide an extra source of nutrients for the tree. *Acacia macracantha* tumbles over entirely in a storm, but regenerates by producing strong, vertical sprouts from its fallen trunk. The open canopy allows grasses to invade the herb layer (*Paspalidium utowanaeum*), although tree seedlings (*Krugiodendron ferreum*) are still abundant. During heavy rains, large amounts of soil are washed away from this vegetation. De Freitas et al. (2014) defined this forest type as the *Pisonia subcordata-Ayenia insulaecola* type. They found *P. subcordata* to be dominant, but did not mention tree species like *Krugiodendron ferreum*. The differentiating species (*A. insulaecola*) was not encountered by us, nor did we find the cacti *Opuntia triacanthos* or *Pilosocereus royenii* in our plot. Stoffers (1956) referred to this vegetation as 'thorny woodland', dominated by *Acacia* spp., overtopped mostly by *P. subcordata*, *Bursera simarouba* (present near our plot, but only in gullies) and *Delonix regia*, an exotic ornamental tree, originally from Madagascar, grown for its red flowers. Several parts of this slope were still used for agriculture or as grazing land.

3.11. Vegetation on the limestone cliff

M8: The White Wall, a steep limestone slope on the south side of the volcano, was sparsely vegetated and heavily affected by erosion. In the open spaces, the sharp, white rock came to the surface, only allowing some grass (*Aristida cognata*) to grow. Only under the few trees, some litter and soil could be found. The most abundant trees were *Pisonia subcordata* and *Leucaena leucocephala*, while two trees characteristic for this vegetation type, but less common in the plot, were *Sideroxylon salicifolium* and *Gymnanthes lucida*. In the shrub layer, *Dodonaea elaeagnoides* was present, a typical shrub for limestone cliffs. Other specific species for this vegetation type (*Stenostomum acutatum* and *Erithalis fruticosa*) were found just outside the plot.

De Freitas et al. (2014) defined this vegetation type as the *Antirhea acutata-Dodonaea elaeignoides* type, but do not list any tree species. Shrubs and herb species coincided with our plot, but we did not find the shrub *Crossopetalum rhacoma*. Neither did we find the grass *Botriochloa pertusa*, which apparently dominated the herb layer in 1999. Stoffers (1956) described this 'vegetation of the rock pavement' as xerophytic, with 4-m high, shrubby trees, in which some of our typical species figure (*Dodonaea*, *Sideroxylon*, *Pisonia*) but also species that occur now in lower forest with less degraded soils (*Bursera simaruba*, *Guettarda scabra*, *Myrcia citrifolia*). It seems that the White Wall has further eroded since the 1950s and lost several of its species.

3.12. Regenerating grasslands

M9: This shrubland has been heavily grazed, open grassland before and is now regenerating, although still frequently visited by goats. Only two trees with diameters $\geq$ 10 cm were present in our plot in this low diversity vegetation type, both *Acacia macracantha*. The invasive vine *Antigonon leptopus* covers large parts of this vegetation, except for the patches of shade formed by *Acacia* crowns. *Volkameria aculeata* and *Lantana involucrata* are also common in the shrub layer. *Paspalum laxum* is the main grass in the herb layer, while *Rauwolfia viridis*, *Pentalinon luteum*, *Jatropha gossypiifolia* and *Croton flavens* are common just outside the plot.

De Freitas et al. (2014) defined this disturbed vegetation type as the *Rauwolfia viridis-Lantana involucrata* type. Most species they listed also occurred in or around our plot, except from the invasive Donna grass (*Botriochloa pertusa*), which we did not encounter at all. This vegetation type coincides mostly with the heavily grazed *Croton* tickets described by Stoffers (1956). The location of M9 is indicated on his map as 'cultivated or semi-cultivated area'.

4. Discussion and conclusions

4.1. Changes in vegetation since the 1950s

Although exact plot locations of Stoffers (1956) and De Freitas et al. (2014) could not be retrieved, and their plot sizes and field methods differed from ours, these past vegetation studies offered valuable comparison material to the present study. The Montane thicket and Elfin forest described by Stoffers (1956) on crater rim have been lost, either by hurricanes, fire or erosion by rain or goats (De Freitas et al., 2014). The vegetation on the White Wall also seemed to have deteriorated since the 1950s. Forest on the lower crater rim, in the crater itself, the slopes of the Quill volcano and in Boven National Park, however, seemed to have developed and now has a higher canopy and a greater floristic diversity than in the past decades. Long-lived pioneers like *Pisonia subcordata* and *Guapira fragrans*, still present on higher altitudes on the volcano in the 1950s, made space to late successional species like *Casearia decandra* (in the crater) and *Krugiodendron ferreum* on the mountain foot (Atkinson and Marín-Spiotta, 2015).

4.2. Grazers and invasives

Although grazing still occurs within the two National Parks – we observed goats in or near all our plots –, the prohibition of fire by the Nu Star oil company and their protected status clearly benefits the conservation of the forests on St. Eustatius. Exclusion of grazers from the National Parks will allow the forests to recover even more towards their original composition, especially the dryer types on the mountain foot and the steep slopes of the White Wall. The grazers' preference for tree saplings and seedlings favour the spread of invasive species, spiny plants (e.g., *Acacia* spp., *Randia aculeata*), toxic plants (e.g., *Jatropha gossypiifolia*, *Lantana involucrata*) or even plants that are both prickly and poisonous (*Comocladia dodonaea*).

Invasive species were encountered in four of the 11 plots: *Antigonon leptopus* in the urban plot and the heavily grazed M9, but *Leucaena leucocephala* occurred also on the limestone cliff (M8) and in the lower slope forest (M5). In areas with a more or less closed canopy, however, invasive species were no longer present. Although considered highly invasive, *L. leucocephala* has the potential to restore ecosystem function and structure by creating a moderately shaded understory, fixing nitrogen, and producing readily decomposing, N-rich leaf litter that supports natural regeneration (Atkinson and Marín-Spiotta, 2015).

4.3. From agriculture to pasture to forest

The economic shift from agriculture to industry and (tourist) services that St. Eustatius has undergone is strikingly similar to the situation in St. Kitts, St. Croix, Barbados, St. Lucia and Puerto Rico. Here, land cover changed from the 1950s to 2000 from agriculture (sugarcane and banana fields) to pasture, and then transformed into urban area or was allowed to regenerate into so-called 'emerging forests' (Lugo and Helmer, 2004; Atkinson and Marín-Spiotta, 2015; Walters, 2016). While in Puerto Rico such forests are characterized by alien species, formerly introduced to shade coffee, on St. Eustatius they are typified by high densities of *Leucaena leucocephala*. As land under cultivation has declined and forest has increased over the second half of the 20th century, there is now more land available for conservation at lower elevations. Development and construction, however, have also increased at lower elevations. Protection and restoration of drier forests on abandoned cultivated lands are probably among the most important conservation priorities for these islands (Helmer et al., 2008).

4.4. Comparison with dry forests in the wider Caribbean region

Moist forests of Puerto Rico have several elements in common with those of St. Eustatius (e.g., *Bourreria baccata*, *Guettarda scabra* and *Chionanthus compactus*), while *Pisonia subcordata* and *Quadrella cynophallophora* are also dominant in dry forests (Brandeis et al., 2009). The composition of the forests in general, however, differs substantially. The dry forests of the Dominican Republic (Cano and Veloz, 2012; García-Fuentes et al., 2015) and the Bahamas (Franklin et al., 2015) share very few species with those of St. Eustatius, apart from a few widely distributed Caribbean trees like *Bursera simaruba*, *Pisonia subcordata* and *Krugiodendron ferreum*. On genus level, however, the compositional similarity is much higher. Common genera on St. Eustatius (*Erythroxylum*, *Guettarda*, *Sideroxylon*, *Coccoloba*) were also present on the Bahamas, but with different species. The nearby islands of Saba and St. Kitts probably share much more species and vegetation types with St. Eustatius, although they have a higher altitude and rainfall. Detailed vegetation descriptions, however, are not yet available for these islands, although vegetation surveys have recently been carried out on Saba (A. Debrot, pers. comm.). Comparisons with Saba and duplicating this study on St. Kitts are needed to assess the uniqueness of the vegetation of St. Eustatius.

4.5. Suggestions for future research

The plot size (25 × 25 m) used in this study was much smaller than the hectare plots commonly used in vegetation studies in mainland South America (ter Steege et al., 2013), but is adequate for landscapes with a small mosaic pattern of forest types like the Caribbean islands (Imbert and Portecop, 2008; Brandeis et al., 2009). Although our plots seemed representative for each forest type, we may have missed some typical elements in the vegetation types. Especially the vegetation in lesser accessible areas in the Boven National Park was not covered by this study. Future research could focus on different plots in the same vegetation types on St. Eustatius to capture possible variation in floristic diversity in the same landscape unit.

Small islands with steep environmental gradients (altitude, moisture, exposure, wind) and clear differences in human-induced disturbance (from tropical rainforest to degraded pasture) offer great opportunities to combine field research with teaching. The relatively low floristic diversity, covered by recent botanical checklists (Axelrod, in press), and well illustrated regional floras (Hawthorne et al., 2004; Van Proosdij, 2012), allowed students to identify nearly all plant specimens they have collected in the field. This makes St. Eustatius not only a suitable location for field courses but also for the long-term monitoring of changes in the vegetation composition and structure as a result of hurricanes, grazing pressure and/or protective measures.

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Appendix A. Supplementary data

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